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Cretaceous Spanish amber: History, research and checklist of taxa

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Abstract

The present work is a checklist of taxa described or cited from bioinclusions preserved in Spanish amber outcrops (nine type localities). All these bioinclusions are Albian in age (*ca.* 110–102 Ma), except for a few from a Cenomanian outcrop. All the listed taxa are arthropods (mostly insects), with the exception of some plant parataxa and plant palynomorphs. The present checklist of taxa has been elaborated 30 years after the first bioinclusion was discovered in Spain, thus virtually it spans over 30 years of study by a Spanish team (AMBERIA) thanks to a series of national projects funded by the Spanish Ministry of Science and other public institutions as the Natural Science Museum of Álava (Provincial Council of Álava), and the Government of Cantabria together with the semi-public enterprise EL SOPLAO S.L. The list comprises 7 classes (or similar rank), 24 orders (or similar rank), 101 families, 169 genera and 186 species (including the plant parataxa). Eight families, 104 genera (implicating a total of 104 type species) and 184 species were described based on 184 holotypes from Spanish amber. We provide all the relevant data for each taxon, focusing on new families, genera and species described based on Spanish bioinclusions, pretending to be as useful and readable as possible.

Keywords: bioinclusions, described taxa, holotypes, type localities, Mesozoic

This work is in memory of the renowned acarologist Luis S. Subías Esteban (1948–2024).

Introduction

Amber is a fossilized resin of different tree sources. A huge variety of organisms can be trapped in resin when it is still fresh and sticky, and eventually become fossilized. Plant and animal fossils preserved in amber (bioinclusions) are usually exquisitely three dimensionally preserved. In the trap that the sticky resin originally was, a huge biodiversity of the hyperdiverse insects of the forested palaeoenvironments has been recorded, but also abundant arachnids, myriapods, *etc*. (Solórzano-Kraemer *et al*., 2018).

Spanish Cretaceous amber was known since the 1700s (Casal, 1762), but the first amber with bioinclusions was not discovered until 1994. Since then, several outcrops have been discovered in Spain, five of them are very rich in bioinclusions and nine are type localities (Figs 1–3). The first paper describing species from Spanish amber was Szadziewski & Arillo (1998), four years after the first bioinclusion was discovered, based on two fossil Ceratopogonidae (Diptera) from Peñacerrada I (Moraza) outcrop.

Spanish amber has a conifer origin, and probably the sources of the resin were Araucariaceae or †Cheirolepidiaceae trees (Dal Corso *et al*., 2013; Menor-Salván *et al*., 2016; Kvaček *et al*., 2018; Álvarez-Parra *et al*., 2021b). The age of the Spanish amber with palaeontological content is middle Cretaceous, ranging between the lower Albian (Ariño outcrop, Teruel Province) and the lower Cenomanian (La Hoya, Castellón Province), based on stratigraphic and palynological studies (Barrón *et al*., 2015, 2023).

The vast majority of the diverse organismal bioinclusions identified in Spanish amber are arthropods (*e.g*., Peñalver & Delclòs, 2010), and a small number correspond to vertebrate integumentary remains (*e.g*., Álvarez-Parra *et al*., 2020), plant remains (*e.g*., Kvaček

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et al., 2018) and microorganisms (*e.g*., Speranza *et al*., 2015). The vertebrate integumentary remains and microorganisms preserved in Spanish amber are not treated in this work, because no new taxa have been described within these groups, and existing identifications are limited to the suprafamilial level. The abundant fungal mycelia in the form of cortices in the amber lumps, virtually present in all the Spanish amber outcrops, are the only clear fossils of microorganisms (Speranza *et al*., 2015; Peñalver *et al*., 2025b). Putative microorganisms could be considered pseudo-protists, also termed protist-like inclusions, and many of these actually correspond to resin-in-sap-in-resin double emulsions (Lozano *et al*., 2020).

Several papers providing general information about the different amber outcrops were also published: El Caleyu (Arbizu *et al*., 1999), Peñacerrada I and Peñacerrada II (Alonso *et al*., 2000), San Just (Peñalver *et al*., 2007; Peñalver, 2011), El Soplao (Najarro *et al*., 2009, 2010), La Rodada (Peñalver *et al*., 2018) and Ariño (Álvarez-Parra *et al*., 2021b). Three extensive works were published about Spanish amber as a whole focusing on diverse topics (Delclòs *et al*., 2007; Peñalver & Delclòs, 2010; Rodrigo *et al*., 2018).

This work reviews the history of Cretaceous Spanish amber, its discovery and the subsequent research, focusing on palaeontological aspects and with some notes on the geology of the deposits. It provides a checklist of taxa, including relevant data for each, with an emphasis on new families, genera, and species described from Spanish bioinclusions in the 30 years since the first discovery of bioinclusions.

Geological setting

Amber deposits in the Iberian Peninsula span a wide range of Mesozoic deposits, from the Carnian (late Triassic) to the Maastrichtian (late Cretaceous) (Peñalver & Delclòs, 2010), excluding rare occurrences of Caenozoic ambers. Despite this extensive temporal range, the most significant amber deposits—those yielding thousands of bioinclusions—are primarily found in rocks of Albian age (early Cretaceous). This section focuses on the geology of this specific period.

Approximately 140 amber deposits have been documented in the Iberian Peninsula, though bioinclusions have only been identified in 12 (Peñalver & Delclòs, 2010; Peñalver *et al*., 2018; Álvarez-Parra, 2023; Álvarez-Parra *et al*., 2023). Three main sedimentary basins containing Lower Cretaceous amber, namely from the Albian, are recognized: the Central Asturian Depression (CAD), the Basque-Cantabrian Basin (BCB), and the Maestrazgo Basin (MB). Part of these areas correspond to ancient continental margins of the Iberian Plate during the Cretaceous.

The formation of amber-bearing basins in Iberia began in the late Palaeozoic and is one of the consequences of the broader Mesozoic Iberian Rift system. This system experienced two distinct rifting phases, followed by two post-rifting phases, which concluded during the Late Cretaceous (Mas *et al*., 2004). Cretaceous amber deposits, in particular, were formed during the second rifting phase (Oxfordian to middle Albian), which saw the development of large depressions, and the subsequent post-rifting stage (middle Albian to Maastrichtian), when these depressions were filled.

During the early Cretaceous, the northward propagation of the North Atlantic Ocean caused the Iberian, North American, and European Plates to diverge. By the Albian, the Iberian Plate was bordered by major strike-slip fault zones along its northern margin, contributing to the formation of the Bay of Biscay (Ábalos, 2016), and along its southern boundary with the African Plate. The eastern margin bordered the Tethys Sea, while the western side faced the proto-Atlantic, forming the Iberia Island within the European archipelago (Antolín-Tomás *et al*., 2007; Salas *et al*., 2019).

The counterclockwise rotation of the Iberian Plate not only opened the Bay of Biscay but also triggered the closure of the Tethys Sea (Ábalos, 2016). This movement initiated an extensional phase (the second rifting phase), creating or reactivating highly subsident basins. Large deltaic systems, supporting diverse flora and fauna, formed on the margins of Iberia (Najarro *et al*., 2009; Barrón *et al*., 2023). These ecosystems fostered extensive resin production which, when buried, eventually became amber.

Central Asturian Depression

The Central Asturian Depression (CAD) developed significantly at the end of the Jurassic, coinciding with the initial formation of the Bay of Biscay. This tectonic event led to the formation of large sedimentary basins along a Pyrenean-Cantabrian trough.

Since the Barremian to the early Aptian, the CAD was filled with a range of continental and shallow marine sediments, deposited on a basement of varying ages (Bernárdez, 1994, 2005; González-Fernández *et al*., 2004, 2005). Cretaceous amber has been found in three areas of this basin, from west to east: (1) the surroundings of Oviedo, (2) the Pola de Siero area, and (3) the Infiesto area (Arbizu *et al*., 1999).

The oldest amber-bearing levels belong to the Ullaga Formation, which was deposited unconformably over Palaeozoic rocks in the Oviedo area (González-Fernández *et al*., 2004). This formation consists of grey or yellowish

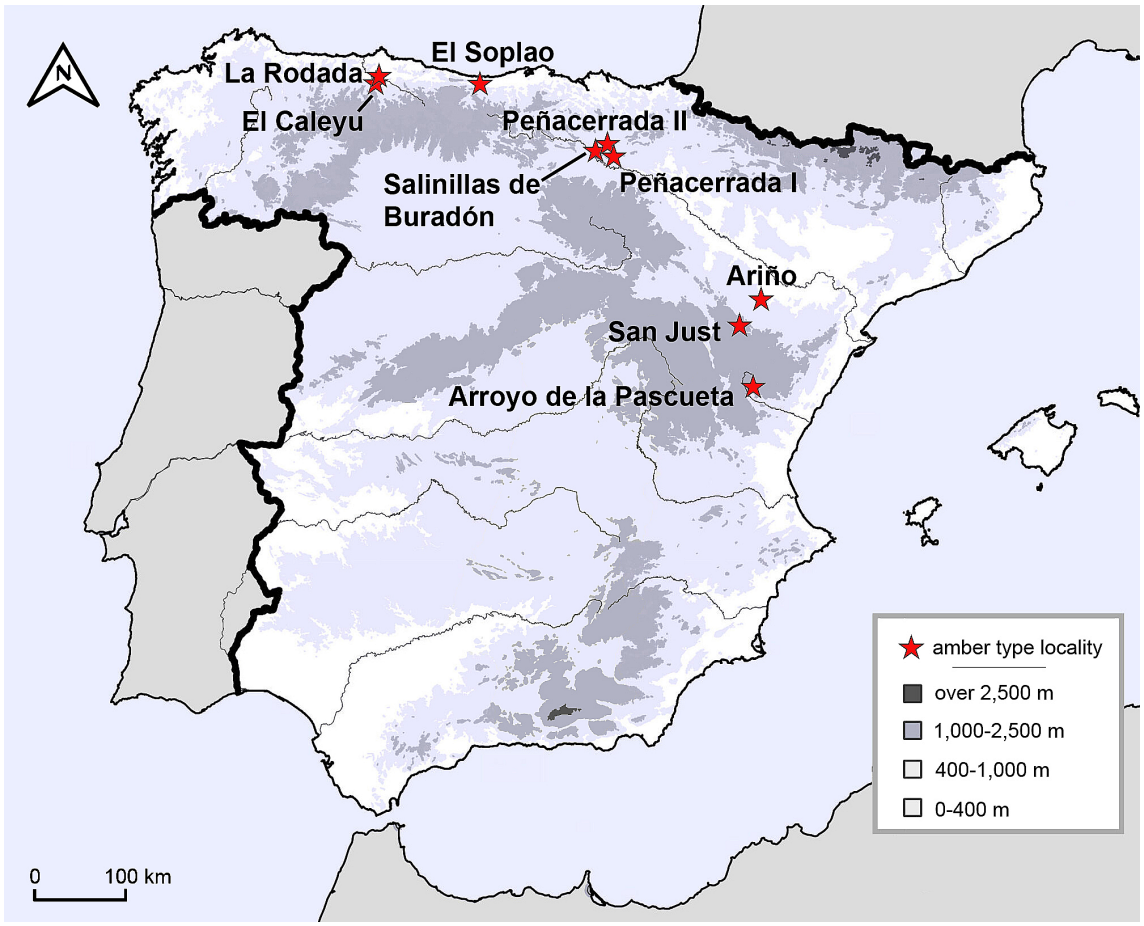

FIGURE 1. Map showing Spanish amber sites that are type localities (the La Hoya outcrop in Cortes de Arenoso and Pola de Siero in Siero are excluded as they are not type localities); the map in Álvarez-Parra *et al*. (2023) shows more Spanish amber localities.

bioclastic limestones, with interbedded grey or black clay layers, siltstones, and fine- to medium-grained sandstones. These sediments were formed in a muddy-clayey tidal flat, a lagoon influenced by river inputs, where amber is associated with plant remains (Arbizu *et al*., 1999). Bioinclusions have been found in amber from El Caleyu, dating to the late Albian (Arbizu *et al*., 1999).

Above the Ullaga Formation lie the deposits of the El Caleyu Formation, consisting of weakly cemented fine- to medium-grained sandstones with some clayey and silty layers (González-Fernández *et al*., 2004). Amber from these levels, dated to the late Albian to early Cenomanian, has also yielded a few bioinclusions, particularly in some areas like La Rodada (Peñalver *et al*., 2018; Arillo *et al*., 2020). These deposits are interpreted as having formed in a sandy intertidal flat (Bahamonde, 1984).

The youngest amber-bearing deposits are found at the La Manjoya Formation, dating to the early-middle Cenomanian. This formation comprises limestone, siltstone, and, in some locations, claystone, with significant lateral facies variations. These deposits are thought to have formed in an intertidal or shallow subtidal environment. To date, no bioinclusions have been discovered in the amber from this formation.

The Central Asturian Depression is rich in amber outcrops, but poor in bioinclusions, whereas the Basque-Cantabrian and Maestrazgo basins are richer in both amber outcrops and bioinclusions.

Basque-Cantabrian Basin

The Basque-Cantabrian Basin (BCB) evolved in a distensive rift setting along the northern Iberian margin. This process involved the counterclockwise rotation of the Iberian Plate relative to the European Plate, initiating the opening of the Bay of Biscay (Ábalos, 2016). The resulting extensional forces led to the creation of depositional basins with varying rates of subsidence, which generated diverse sedimentary environments. The BCB is characterized by a thick sequence of Cretaceous sediments, highlighting intense subsidence in certain sub-basins during this period (Martín-Chivelet *et al*., 2002; Barnolas & Pujalte, 2004; Robles *et al*., 2014).

On the western margin of the BCB lies the El Soplao outcrop in Cantabria. This outcrop is part of a siliciclastic unit that transitions between continental and marine environments (Las Peñosas Formation) of Albian age, positioned within a regressive-transgressive marine carbonate sequence from the early Aptian to the Albian. The amber deposits are found in the maximum regressive phase, within interdistributary bays between meandering channels, in a deltaic-estuarine environment with marine influence, as evidenced by the association with marine invertebrates (Najarro *et al*., 2009, 2010).

On the eastern margin of the BCB, amber-bearing outcrops include Peñacerrada I (Condado de Treviño, Burgos Province) and Peñacerrada II and Salinillas de Buradón (Álava Province). The Peñacerrada outcrops were originally dated to the Aptian-Albian and assigned to the Nograro Formation (Alonso *et al*., 2000), later considered part of the Escucha Formation (Martínez-Torres *et al*., 2003). Currently, they are included in the base of the "Utrillas Group" (Barrón *et al.*, 2015). The majority of the bioinclusions in amber from Iberia have been found at the Peñacerrada I outcrop (also known as Moraza), while Peñacerrada II (slightly younger than Peñacerrada I) has yielded a few hundreds of bioinclusions and Salinillas de Buradón has been especially poor in bioinclusions (Arillo *et al*., 2008b). These three outcrops are currently dated to the upper Albian (Barrón *et al*., 2015).

Maestrazgo Basin

The Maestrazgo Basin (MB), also referred to as the Maestrat Basin, formed during the rifting process between the Oxfordian and Albian stages. Oriented east-west, it connected to the Tethys Sea on its eastern side. During this time, the MB formed a large gulf in the eastern part of Iberia. In the eastern regions, sedimentation consisted mostly of sandy and fine detrital materials rich in organic matter, deposited in a shallow marine shelf. In contrast, the western part of the basin was characterized by fluvial and swampy deposits (Querol *et al*., 1992).

Towards the end of the rifting period, significant depocenters developed, which filled the MB with fluviodeltaic and estuarine sediments, now part of the Escucha Formation (Querol *et al*., 1992; Peyrot *et al*., 2007; Bover-Arnal *et al*., 2016). Some researchers (Rodríguez-López *et al*., 2009; Barrón *et al*., 2023) suggested that these sediments were deposited on a delta plain, in lagoons and marshes, adjacent to a desert environment (fore-erg).

Amber in the MB is found within the upper member of the Escucha Formation (Peñalver & Delclòs, 2010) or at the base of the "Utrillas Group", which encompasses the upper member of the Escucha Formation and the Utrillas Formation (Rodríguez-López *et al*., 2009). These formations were once interpreted as fluvial-alluvial deposits (Pardo *et al*., 1991), but reinterpreted as part of a desert environment (Rodríguez-López *et al*., 2009). Several amber deposits in the MB have together yielded hundreds of bioinclusions, including Ariño (early Albian), San Just, and Arroyo de la Pascueta (late Albian), and La Hoya (early Cenomanian; see Barrón *et al*., 2023). The richest sites in terms of bioinclusions are San Just and Ariño (Peñalver & Delclòs, 2010; Álvarez-Parra *et al*., 2021b; Álvarez-Parra, 2023; Barrón *et al*., 2023). In contrast, only a few specimens have been found in Arroyo de la Pascueta (Álvarez-Parra, 2023; Barrón *et al*., 2023) and La Hoya (Solórzano-Kraemer *et al*., 2023).

Results

History of the discoveries and research

The main amber outcrops

Outcrops are listed from northwest to southeast, rather than by their age or date of discovery. All the listed outcrops are type localities (Figs 2, 3) except La Hoya. Table 1 contains the most important data on these localities.

EL CALEYU (Ribera de Arriba municipality) (late Albian) (11 bioinclusions recorded)

During the 1990s, the amber outcrop was discovered due to works of road improvement, amber was extracted and the first bioinclusions were detected (Fig. 2A). The people involved were Miguel Ángel Prieto Canseco (gemmologist), Enrique Bernárdez and Miguel Arbizu Senosiáin; the last two are geologists of the Oviedo University. During the 1998 World Congress on Amber Inclusions in Álava, Spain, this amber outcrop, and its bioinclusions, were presented to the international scientific community. In 1999, the first paper about Asturias amber (and its bioinclusions) was published by Arbizu *et al*. (1999). In 2007, the first and only described species of this outcrop was published (Peñalver & Arillo, 2007): *Alavesia prietoi* (Diptera: Atelestidae). The holotype of *Alavesia prietoi*, lost from 2007, reappeared in 2016 and it is finally stored in the lithotheque collection of the University of Oviedo. No excavation has been carried out at this outcrop. Several trees have grown on the outcrop and the amber is not easily accessible (observation in July 2013) (Fig. 2B).

POLA DE SIERO (Siero municipality) (late Albian) (1 bioinclusion recorded)

This outcrop was discovered during the 1990s by Enrique Bernárdez during his doctoral research. The amber-bearing level consists of 10–40 cm of clays rich in organic matter

FIGURE 2. Spanish amber type localities. **A**, **B**, El Caleyu in March 2003 during a visit of Dr. Miguel Arbizu Senosiáin and one of the authors (E.P.), and in July 2013, ten years later, covered by several trees, respectively. **C**, **D**, La Rodada during a palaeontological excavation in August 2017 using a power shovel and sieves, respectively. **E**, **F**, El Soplao in June 2008, one year after its discovery, and in June 2016 during a visit with Drs. Eduardo Barrón and Jiří Kvaček, respectively. **G**, **H**, Panoramic view of the area where Salinillas de Buradón is located in April 2007 and detail of the outcrop in 2009 during a visit with the Dr. Ricardo Pérez-de la Fuente, respectively; this outcrop has not been previously figured in photographs (arrow in (**G**) indicates the amber outcrop).

TABLE 1. Most important data of the main Spanish amber outcrops. The outcrops are listed from northwest to southeast, rather than by their age or date of discovery. The "Discovery" column indicates the outcrop's discovery; if the first bioinclusion was found significantly later, the year of that discovery is given in parentheses. (*) For some authors these outcrops are included in the "Utrillas Group" (Barrón *et al*., 2015, 2023).

Name	Discovery	Province	Municipality	Basin	Formation	Age	Number described species	Total number bioinclusions	Main reference
El Caleyu	the 1990s	Asturias	Ribera de Arriba	Central Asturian Depression	Ullaga Fm.	late Albian	1	11	Arbizu *et al*. (1999)
La Rodada	2012	Asturias	Oviedo	Central Asturian Depression	El Caleyu Fm.	late Albian	1	4	Peñalver *et al*. (2018)
Pola de Siero	the 1990s	Asturias	Siero	Central Asturian Depression	Ullaga Fm.	late Albian	no type locality	1	Arbizu *et al*. (1999)
El Soplao	2007	Cantabria	Herrerías	Basque-Cantabrian Basin	Las Peñosas Fm.	middle Albian	30	1,554	Najarro *et al*. (2009)
Salinillas de Buradón	2005	Álava	Labastida	Basque-Cantabrian Basin	Escucha Fm.*	late Albian	1	3	Arillo *et al*. (2008)
Peñacerrada I/Moraza	the 1970s (1994)	Burgos	Condado de Treviño	Basque-Cantabrian Basin	Escucha Fm.*	late Albian	106	*ca*. 2,455	Alonso *et al*. (2000)
Peñacerrada II	*ca*. 1996	Álava	Peñacerrada	Basque-Cantabrian Basin	Escucha Fm.*	late Albian	13	*ca*. 385	Alonso *et al*. (2000)
San Just	the mid 1990s (1999)	Teruel	Utrillas	Maestrazgo Basin	Escucha Fm.*	late Albian	28	*ca*. 370	Peñalver *et al*. (2007)
Arroyo de la Pascueta	the early 1960s (1998)	Teruel	Rubielos de Mora	Maestrazgo Basin	Escucha Fm.*	late Albian	1	12	Peñalver *et al*. (2010)
Ariño	2010 (2019)	Teruel	Ariño	Maestrazgo Basin	Escucha Fm.	early Albian	3	*ca*. 165	Álvarez-Parra *et al*. (2021)
La Hoya	2000 (2003)	Castellón	Cortes de Arenoso	Maestrazgo Basin	Escucha Fm.*	early Cenomanian	no type locality	7	Solórzano-Kraemer *et al*. (2023)
						TOTAL	**184**	***ca*. 4,967**	

and contains amber lumps most likely reworked. Enrique Bernárdez discovered an impression of an "orthopteroid" wing in an amber lump, which is the only insect remain found to date. No excavation has been carried out at this outcrop. Two studies mentioning this outcrop are Arbizu *et al*. (1999) and Peñalver & Delclòs (2010).

LA RODADA (Oviedo municipality) (late Albian) (4 bioinclusions recorded)

The outcrop was discovered in 2012 by Iñaki Irisarri Oroz, a gemmologist from Pamplona, Navarra. He gave the information to Rafael López Del Valle. In July 2013, the outcrop was visited during an extensive expedition in search of Asturian amber. Between 28 August and 1 September 2017 an excavation was carried out in La Manjoya/Vistasol residential area by the researchers of the Geological and Mining Institute of Spain (IGME) (Fig. 2C, D). This excavation was funded with a Project of the National Plan of de Spanish Ministry of Sciences. The first paper about La Rodada amber was published by Peñalver *et al.* (2018). The first and only species was described two years later (Arillo *et al*., 2020): *Epieremulus sidorchukae* (Oribatida: Caleremaeidae).

EL SOPLAO (Herrerías municipality) (middle Albian) (1,554 bioinclusions recorded)

During the road improvement to access to El Soplao Cave in 2005, the amber layers of El Soplao outcrop were cut and the amber concentration was exposed. Two geologists from the IGME, Idoia Rosales Franco and María Najarro de la Parra, who recently had discovered the outcrop, brought some samples of amber to Enrique Peñalver at the Geominer Museum in Madrid in May 2007. They soon realized that the amber had fossil insects inside. They visited the outcrop some weeks later to evaluate its importance (Fig. 2E). The first excavation of the El

Soplao outcrop was carried out on 20 October 2008, followed by more excavations in March 2009, July 2009 and May 2010. The first preparations of bioinclusions for suitable study were available in 2007–2008. They showed the abundance of amber in the outcrop, the richest in Spain and, perhaps the richest among the European Cretaceous amber outcrops. These excavations were funded by the Government of Cantabria/El Soplao S.L., the IGME and the UB. The El Soplao institutional collection was started in 2009, and the first paper about El Soplao amber was published (Najarro *et al*., 2009). The first described species of this outcrop was published (Pérez-de la Fuente *et al*., 2010): *Cantabroraphidia marcanoi* (Raphidioptera: Mesoraphidiidae). Ricardo Pérez-de la Fuente received his doctoral certificate on 21 December 2012 following his PhD thesis defence at the University of Barcelona, the institution that funded the PhD thesis on the amber from El Soplao. Currently, the outcrop is protected by a fence (Fig. 2F).

SALINILLAS DE BURADÓN (Labastida municipality) (late Albian) (3 bioinclusions recorded)

Rafael López Del Valle discovered the outcrop in 2005. The first excavation of the outcrop was carried out in 2006 by the Álava Museum of Natural Sciences (MCNA). The first and only paper about Salinillas de Buradón amber was published together with the description of its first species (Arillo *et al*., 2008b): *Ommatocepheus nortoni* (Oribatida: Cepheidae). The outcrop is accessible (Fig. 2G, H), but no further excavations have been done.

PEÑACERRADA I/MORAZA (Condado de Treviño municipality) (late Albian) (*ca*. 2,455 bioinclusions recorded)

The amber of this outcrop was known to collectors since the 1970s, but details of its early discovery are unknown. Several people began visiting the outcrop in the early 1990s, such as Carmelo Corral and Andoni Tarriño. At that time, Rafael López Del Valle also started visiting the outcrop. Rafael López Del Valle discovered the first bioinclusion in Spanish amber in this outcrop in March 1994 while polishing a cabochon. It was later published by Grimaldi *et al*. (2011) as a Diptera, ?Xylomyidae (MCNA-8833). At the beginning of 1995, for the first time a huge quantity of uncemented rock samples was removed with a bulldozer for later separation of the amber content. The first excavation of the outcrop was carried out from July to August 1995, and a second one in 1997, by the MCNA. An old slagheap was also processed as the area was mined in the past to extract quartziferous sands and shales were discarded. Peñacerrada amber was mentioned for the first time in a scientific paper in 1996 (Arillo, 1996). The first described species of this outcrop, and of the whole Spanish amber, were published by Szadziewski & Arillo (1998): *Protoculicoides skalskii* (now *Gerontodacus skalskii*) and *Archiaustroconops alavensis* (Diptera: Ceratopogonidae). Between 20 and 23 October 1998, the First World Congress on Amber Inclusions was held in Vitoria-Gasteiz, organized by the MCNA and the Provincial Council of Álava. Spanish amber was there introduced to the international scientific community. The first extensive paper about this outcrop was published by Alonso *et al*. (2000). The amber-bearing levels (Fig. 3A), outcropped in a small area of the municipality of Condado de Treviño (Fig. 3B), are now buried and are no longer available.

PEÑACERRADA II (Peñacerrada municipality) (late Albian) (*ca*. 385 bioinclusions recorded)

José Ramón Subijana and Luis Miguel Martínez-Torres discovered a layer of black shales on a side of the road A-2124 (Fig. 3C) and informed the MCNA in 1996. Jesús Alonso, Carmelo Corral and Rafael López Del Valle went back with them to the outcrop and took some samples. They soon realized that the amber had bioinclusions. The first excavation of the outcrop was carried out from July to August 1997, and another during the summer of 2006, by the MCNA. The outcrop was protected in 1998 under the name "Yacimiento Paleontológico de Peñacerrada/Urizaharra (Álava)" as a "Qualified Cultural Asset" (Bien Cultural Calificado) by the Basque Government. During the First World Congress on Amber Inclusions in 1998, the outcrop was visited by the delegates of the Congress (Barbara Kosmowska-Ceranowicz, Curt Beck, André Nel, and Vladimir V. Zherikhin, among others). The first paper about this outcrop was published by Alonso *et al*. (2000). The first described species of this outcrop was published by Penney & Ortuño (2006): *Mesozygiella dunlopi* (Araneae: Araneidae). The Peñacerrada II outcrop was declared as a "Place of Geological Interest number 129" by the Basque Government in 2011 and it is also currently protected with a fence (Fig. 3D).

SAN JUST (Utrillas municipality) (late Albian) (*ca*. 370 bioinclusions recorded)

In a construction work to improve the road N-420 to avoid a tunnel, the layers containing amber were cut in the mid 1990s, being discovered by Marcial Marco Saura. During the First Heritage Journeys of the Province of Teruel, held between 24 and 26 September 1998 in Rubielos de Mora (Teruel), Marcial Marco informed Enrique Peñalver, at that time at the University of Valencia, about the discovery. On 15 June 1999, Marcial Marco and Enrique Peñalver visited the outcrop and found many amber

FIGURE 3. Spanish amber type localities (cont.) **A**, **B**, Detail of an amber-bearing level of the Peñacerrada I outcrop, also named Moraza, shortly after its discovery by the scientific community, and view of the outcrop during a visit with French palaeontologists in April–May 2006; this outcrop has not been previously figured in photographs. **C**, **D**, Peñacerrada II in 2006 and with the protection of a fence photographed in November 2013, respectively. **E**, **F**, San Just in July 2012 and June 2021 during two palaeontological excavations, respectively. **G**, **H**, Arroyo de la Pascueta in 2007 (arrow in (**G**) indicates the amber-bearing level) and amber-bearing level in June 2010, respectively; this outcrop has not been previously figured in photographs. **I**, Ariño in July 2019 during a palaeontological excavation.

pieces on the surface. The first samples with biological inclusions were recovered from the outcrop in 2003. A paper describing a spider web with its prey was published in the journal *Science* (Peñalver *et al*., 2006). The first extensive paper about this outcrop was published by Peñalver *et al*. (2007). From 2 to 11 July 2007, the first excavation of the outcrop was carried out, followed by more excavations on October 2010, July 2012 (Fig. 3E) and June to July 2021 (Fig. 3F) by the IGME, UB, and Fundación Conjunto Paleontológico de Teruel-Dinópolis. These excavations were funded at times by the Projects of the National Plan of de Spanish Ministry of Sciences and sometimes also by the General Council of Aragón (DGA) and with the help of the Fundación Conjunto Paleontológico de Teruel-Dinópolis. During the IV World Congress of Paleoentomology in 2007, the outcrop was visited by some of the delegates of the Congress (Sarah Martin, Jörg Ansorge, Haichun Zhang, and Bo Wang). The first described species of this outcrop was published by Arillo *et al*. (2008a): *Microphorites utrillensis* (Diptera: Dolichopodidae).

ARROYO DE LA PASCUETA (Rubielos de Mora municipality) (late Albian) (12 bioinclusions recorded)

The first record of amber in Teruel Province was mentioned by Vilanova y Piera (1860). Rubielos de Mora municipality, where the amber outcrop is located, was indicated as yielding amber but without specifying an exact location. During the early 1960s, José Górriz Monleón "Chime" noticed in a miner reporting the presence of amber around the area of "Arroyo de la Pascueta" and informed Vicente Arnau Górriz. Later, together with Federico Górriz Martín, the three neighbours of Rubielos de Mora, visited the outcrop (Fig. 3G, H) and found amber. The first published indication of the presence of amber in the area named Mas del Paso, where the Arroyo de la Pascueta is located, is present in the text that complements the 1971 geological map (# 591 Mora de Rubielos; scale 1:50.000). During the mid 1990s, Federico Górriz Martín and Federico Alegre Catalán, also neighbours of Rubielos de Mora, showed the location of the outcrop to Enrique Peñalver, at that time in the University of Valencia. Between 4 and 9 October 1998, an excavation was carried out in the outcrop of Arroyo de la Pascueta by the University of Valencia and funded by the "Instituto de Estudios Turolenses". The first and only described species of this outcrop was published by Peñalver *et al*. (2010): *Cretevania rubusensis* (Hymenoptera: Evaniidae).

ARIÑO (Ariño municipality) (early Albian) (*ca*. 165 bioinclusions recorded)

During the first months of 2010, Dr Luis Alcalá, director of the Fundación Conjunto Paleontológico de Teruel-Dinópolis at that time, contacted the directive staff of the Santa María de Ariño Mine, of the enterprise Grupo SAMCA, because some clues indicated the possibility of discovering dinosaur bones in this mine of lignite. Thanks to Mr. Ángel Luengo, president of SAMCA, an agreement was established to carry out potential palaeontological excavations in that unstable relief establishing safety protocols for the excavation team. On 24 May 2010, an abandoned slope, rich in well-preserved dinosaur bones and amber pieces, was discovered. In 2013, Luis Alcalá sent samples of this amber to Enrique Peñalver at the Geominer Museum of the IGME to assess its relevance, but no bioinclusions were found, because the amber was of root type. On 25 July 2018, the mine "Santa María de Ariño" was visited to prepare an excavation in search of amber. Between 1 and 4 July 2019, a palaeontological excavation was carried out in this outcrop (Fig. 3I) by the UB, IGME and Fundación Conjunto Paleontológico de Teruel-Dinópolis. The first "aerial amber" pieces (from resin that flowed from the branches and trunks in aerial conditions and generally trapped flying insects) were found. This excavation was funded with the Fundación Conjunto Paleontológico de Teruel-Dinópolis and a Project of the National Plan of the Spanish Ministry of Sciences. The first special preparations of bioinclusions started in 2020. A paper describing hairs preserved in Ariño amber was published in the journal *Scientific Reports* (Álvarez-Parra *et al*., 2020). A new expedition in search of amber was carried out in May 2021. The first extensive paper about this outcrop was published in the journal *eLife* (Álvarez-Parra *et al*., 2021b). The first described species of this outcrop was published by Arillo *et al*. (2022): *Liacarus* (*Procorynetes*) *shtanchaevae* (Oribatida: Liacaridae). Sergio Álvarez Parra received his doctoral certificate in February 2023 following his PhD thesis defence at the University of Barcelona on the amber from Ariño and the Maestrazgo Basin. For the first time, in 2024, a member of the Spanish amber team, Sergio Álvarez Parra, joined the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). The outcrop is now buried and is currently no longer available.

LA HOYA (Cortes de Arenoso municipality) (early Cenomanian) (7 bioinclusions recorded)

Vicente Arnau Górriz, from Rubielos de Mora, showed the location of the outcrop to Enrique Peñalver in 2000. Between 11 and 19 October 2003, an excavation was carried out in the outcrop La Hoya, Castellón Province, by the University of Valencia and funded by the "Generalitat Valenciana". Although the amber finds were not abundant and were extremely fragile, a few bioinclusions were detected some years later. The first described species (not named) was published by Solórzano-Kraemer *et al*.

(2023): *Grimaldipeza* sp. (Diptera: Hybotidae). No further taxa have been described based on specimens from this outcrop. This outcrop is not a type locality.

The research projects and PhD theses

Although the rediscovery of Spanish amber occurred in the early 1990s, with the first scientific studies emerging at that time, it was not until 2004 that funding was requested and granted by the Spanish Ministry of Culture to study amber deposits across Spain. Since then, several research projects have consistently focused on a multidisciplinary approach to amber, emphasizing not only the study of its bioinclusions but also its scientific context. These projects have involved teams from diverse fields, including palaeontology, mainly palaeoentomology and palaeobotany, geology, taphonomy, geochemistry, biostatistics, and science communication, in order to conduct a holistic investigation of the amber deposits.

- The first major project to consolidate the Spanish amber research group began in 2004, when the Spanish Ministry of Education and Science awarded an Integrated Action grant with France named *Palaeobiological and Palaeoenvironmental Evolution of the Cretaceous Amber Deposits of Spain and France* (HF2004-0053). The Spanish team, led by Xavier Delclòs from the University of Barcelona (UB), collaborated with Didier Néraudeau from the University of Rennes 1 (France). This project allowed for the mutual exchange of knowledge about amber deposits in both countries and established lasting scientific collaborations.
- In December 2005, the Directorate General of Research from the Spanish Ministry of Education and Science awarded the first national amber project: *Cretaceous Amber from Spain: Palaeobiology, Taphonomy, and Biogeochemistry* (CGL2005-00046/BTE) for a period of three years. The project was led by Xavier Delclòs, with contributions from Antonio Arillo, Eduardo Barrón, Enrique Peñalver, Vicente Manuel Ortuño, and Carmen Soriano, along with three international collaborators: André Nel and Bernard Gomez (France), and Guido Roghi (Italy).
- Following the completion of the previous project in 2008, the Directorate General for Research and the National I+D+I Plan of the Ministry of Economy and Competitiveness in Spain awarded a new amber-focused project: *Cretaceous Amber from Spain: A Multidisciplinary Study* (CGL2008-00550), also led by Xavier Delclòs and for a three-year period. This project involved 13 researchers, including five international collaborators from France, Italy, and the UK, as well as three PhD students in training.
- In 2012, the Spanish Ministry of Economy and Competitiveness, through the General Secretariat for Science, Technology and Innovation, renewed the research project with the title *Cretaceous Amber from Spain: A Multidisciplinary Study II* (CGL2011-23948), extending it for three years and also led by Xavier Delclòs. This phase involved 16 researchers, five of whom were international, alongside three PhD students. It was also during this period that the AMBARES research group was founded (acronym for "Ambers from Spain").
- In 2015, the Spanish State Secretariat for Research, Development, and Innovation awarded a new project of excellence: *Amber from Iberia: An Exceptional Record of Cretaceous Forests at the Dawn of Modern Terrestrial Ecosystems* (CGL2014-52163). This marked a shift in leadership, with two Principal Investigators (PIs): Xavier Delclòs from the UB and Eduardo Barrón from the IGME. The project, which expanded the research to include both Spanish and Portuguese ambers, involved 21 researchers and two students in training, with international participation from Germany, Poland, France, Lebanon, the USA, Italy, Portugal, the Czech Republic, and the Netherlands. The team was renamed AMBERIA, an acronym for "Ambers from Iberia".
- In 2018, a new four-year project, *Cretaceous Resin Event: A Global Bioevent of Mass Production of Resin at the Dawn of Modern Terrestrial Ecosystems*, was awarded by the Spanish State Research Agency of the Ministry of Economy, Industry, and Competitiveness as another project of excellence. Directed by the same PIs as the previous project, this one involved 31 researchers, 17 of whom were international, from countries including Germany, Poland, France, Lebanon, the USA, the UK, Brazil, Colombia, Portugal, the Czech Republic, and Australia, as well as two students in training.
- In 2022, a new research agreement was established between the UB and the IGME, funded by the Ministry of Industry, Tourism, Innovation, Transport, and Commerce of the Spanish Government of Cantabria, to study the amber from El Soplao (Cantabria). This agreement, alongside a research contract with IGME, will run for four years under the semi-public enterprise EL SOPLAO S.L. [Research Agreement #20963 with UB, and Research Contract Ref. VAPC 20225428 to IGME, CSIC].
- A current project, *Cretaceous Resinous Interval: Abiotic and Biotic Causes and Their Paleoecological Implications* (PID2022-137316NB), began in September 2023. Awarded by the Spanish State Research Agency of the Ministry of Science, Innovation, and Universities, this coordinated project will be co-led by Xavier Delclòs (UB) and Enrique Peñalver (IGME, CSIC), with additional co-PIs: Antonio Monleón (UB) and Eduardo Barrón (IGME, CSIC). The project involves 44 researchers, including 21 international collaborators from Germany, Poland,

France, Lebanon, the USA, the UK, Colombia, Portugal, the Czech Republic, Argentina, Chile, Ecuador, and Australia, as well as three students in training.

Several scientists from the amber Spanish team received their doctoral certificate following their PhD thesis defences:

2010 Jaime Ortega Blanco
"Diversidad de himenópteros del ámbar cretácico inferior de España"
Supervised by Xavier Delclòs (UB October 2010)

2012 Ricardo Pérez-de la Fuente
"Paleobiología de los artrópodos del ámbar cretácico de El Soplao: (Cantabria, España)"
Supervised by Xavier Delclòs and Enrique Peñalver (UB October 2012)

2015 David Peris Cerdán
"Paleobiología de los escarabajos (Insecta: Coleoptera) de los ámbares cretácicos del oeste europeo"
Supervised by Xavier Delclòs (UB November 2015)

2017 Alba Sánchez García
"Paleobiología de los artrópodos edáficos y acuáticos del ámbar del Cretácico Inferior de España"
Supervised by Xavier Delclòs and Enrique Peñalver (UB September 2017)

2023 Sergio Álvarez Parra
"Yacimientos de ámbar del Cretácico de la Cuenca del Maestrazgo: tafonomía, bioinclusiones y paleoecología"
Supervised by Xavier Delclòs and Enrique Peñalver (UB February 2023)

2025 Constanza Peña Kairath
"Inferencias paleoecológicas de la relación de polinización insecto-planta en el ámbar del Cretácico"
Supervised by Xavier Delclòs and David Peris (UB March 2025)

Checklist of taxa

The checklist focuses only on taxa having a description in the papers on Spanish amber bioinclusions, discarding citations of taxa without any discussion, in order to avoid possible erroneous, preliminary identifications. The checklist contains information of all the holotypes from Spanish amber and a selection of holotypes of the diverse groups that have been found are in Figs 4–6. It contains each described family, genus and species (and recorded genus), the outcrop where the holotype comes from, the paper where it was published, the repository place of the holotype specimens, and their definite collection number. Several taxa, found as bioinclusions, but not described as new, are indicated by the collection number of the non-holotype specimen. The data presentation partially follows the format typical of synonymy lists, with inclusion of the studies that revised the classification of the taxon or included anatomical remarks of it.

The following eight families (6 insect families, 1 mite family and 1 crustacean family) were described based on Spanish amber bioinclusions; therefore, these families have their authors and description dates indicated. With the exception of Archaeorchestidae, which is also recorded from the Cretaceous to the Eocene, the remaining families are only known from the Cretaceous.

†Alavarommatidae Ortega-Blanco, Peñalver, Delclòs & Engel, 2011
†Alavatanaidae Vonk & Schram, 2007
†Archaeorchestidae Arillo & Subías, 2000 (the type genus was a junior synonym of a genus described from Baltic amber)
†Cantabridae Soszyńska-Maj, Pérez-de la Fuente, Krzemiński & Wang, 2022
†Hispanocaderidae Golub, Popov & Arillo, 2012
†Proterosceliopsidae Talamas, Johnson, Shih & Ren, 2019 (the current type genus was originally ascribed to Scelionidae)
†Radiophronidae Ortega-Blanco, Rasnitsyn & Delclòs, 2010
†Spathiopterygidae Engel & Ortega-Blanco, 2013

The following two families were described based on Peñacerrada I material, but any specimen of the Spanish amber is in the type series of these families and type genera:

†Chimeromyiidae Grimaldi & Cumming, 2009
†Tethepomyiidae Grimaldi & Arillo, 2008

The family †Archaeatropidae Baz & Ortuño, 2000 was described based on bioinclusions in Spanish amber, but was later considered a junior synonym of Empheriidae Kolbe, 1884 by Li *et al*. (2022).

For several holotypes from Álava amber, the type localities in the original publications were indicated incorrectly, with Peñacerrada I (PEÑ) and Peñacerrada II (PII) being interchanged. Additionally, some holotype specimens were referred to with inaccurate collection numbers in their original descriptions. These errors have been indicated and corrected in the checklist.

In all the genera described from Spanish amber holotypes (104 genera to date) the type species are indicated.

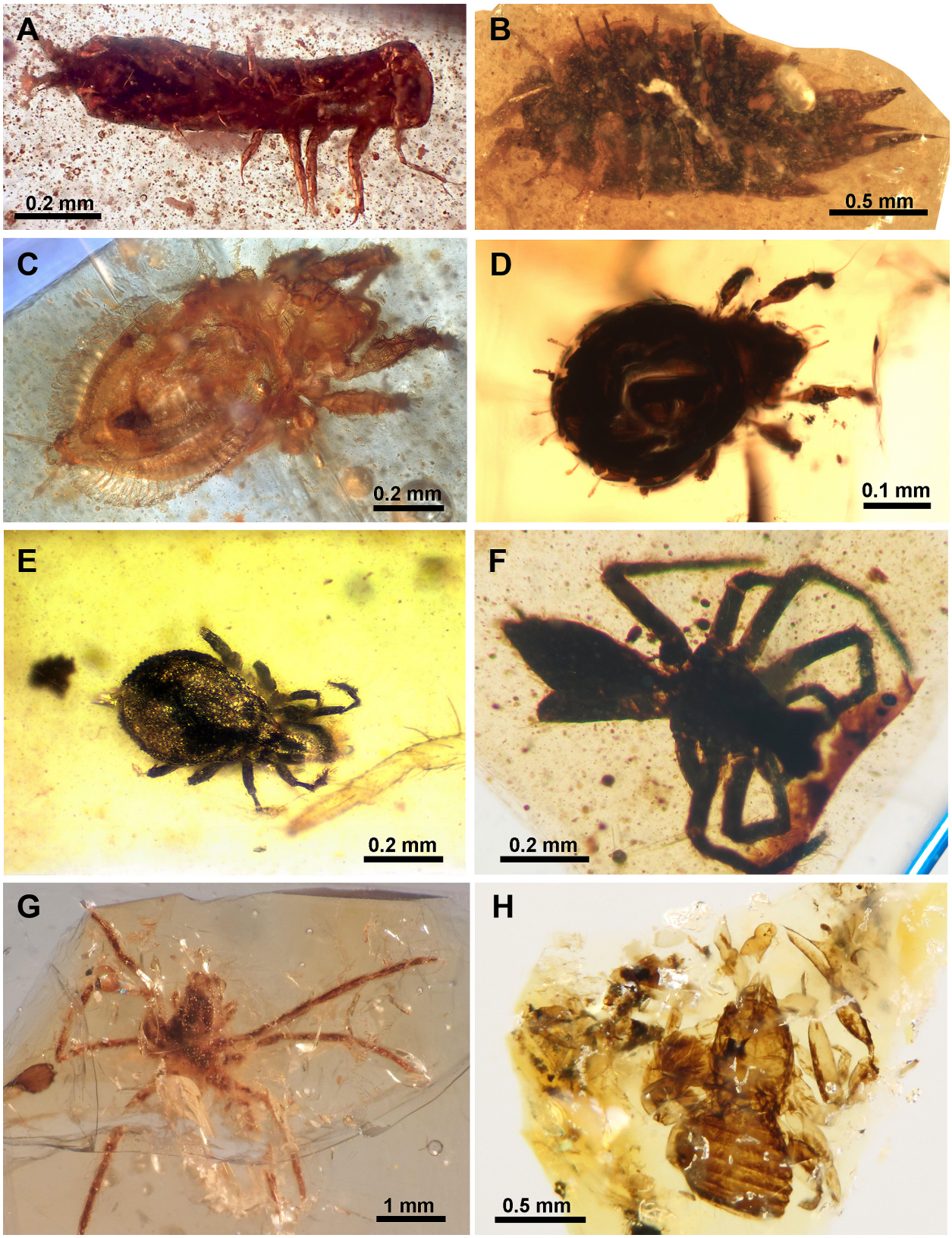

FIGURE 4. Selection of holotypes of crustaceans and arachnids from Spanish amber. **A**, *Electrotanais monolithus* Sánchez-García, Peñalver & Delclòs, 2014 from Peñacerrada I. **B**, *Autrigoniscus resinicola* Sánchez-García, Peñalver, Delclòs & Engel, 2021 from Peñacerrada I. **C**, *Platyliodes sellnicki* Arillo & Subías, 2016 from El Soplao. **D**, *Epieremulus sidorchukae* Arillo & Subías, 2020 from La Rodada. **E**, *Eupterotegaeus bitranslamellatus* Arillo & Subías, 2002 from Peñacerrada I; this holotype resulted damaged during further studies on the amber fragment. **F**, *Soplaogonomegops unzuei* Pérez-de la Fuente, Saupe & Selden, 2013 from El Soplao. **G**, *Burlagonomegops alavensis* Penney, 2006 from Peñacerrada I. **H**, *Cretogarypinus zaragozai* Sánchez-García, Palencia, Delclòs & Peñalver, 2024 from Peñacerrada II.

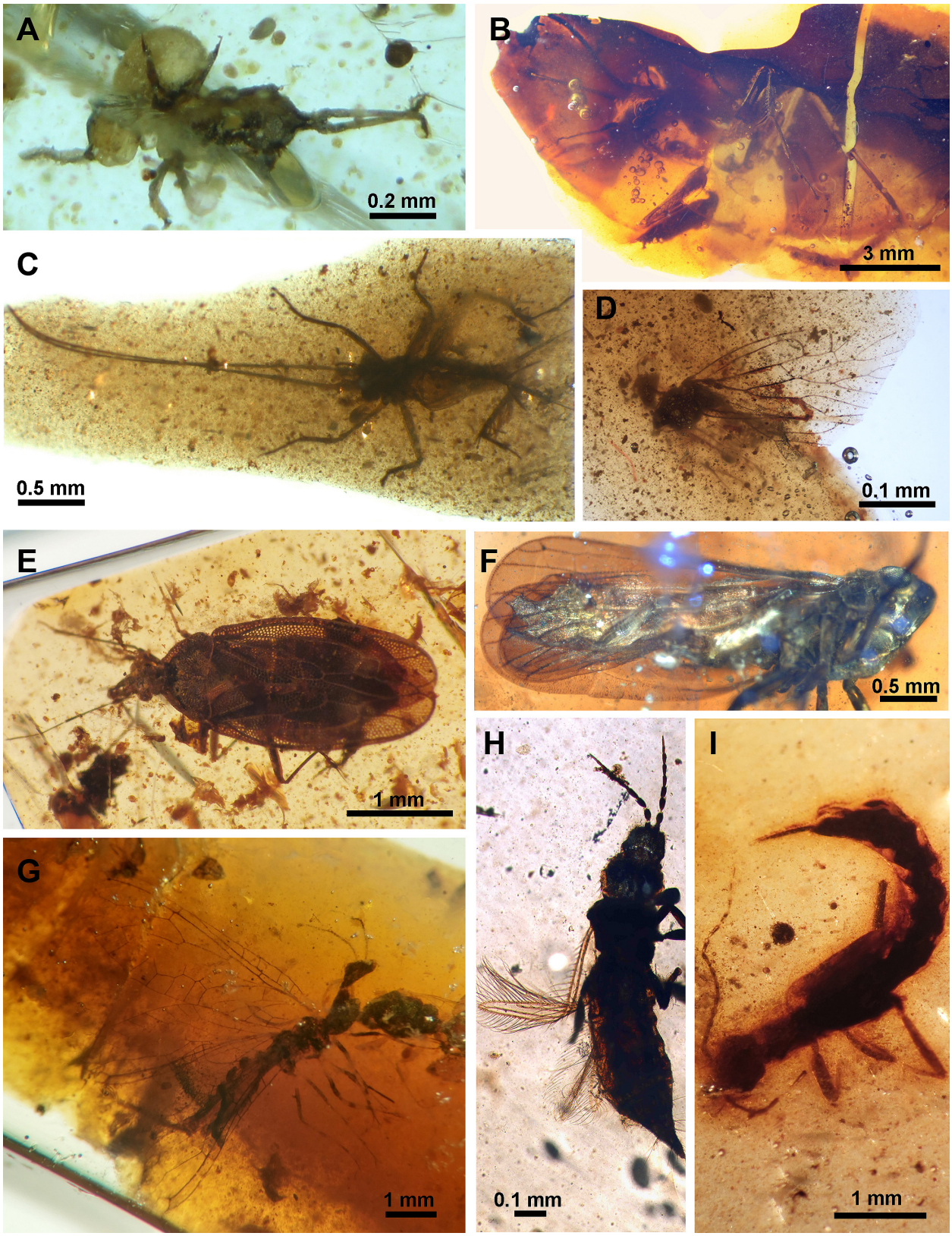

FIGURE 5. Selection of holotypes of hexapods. **A**, *Pseudosminthurides stoechus* Sánchez-García & Engel, 2016 from Peñacerrada II. **B**, *Aragonimantis aenigma* Delclòs, Peñalver, Arillo, Engel, Nel, Azar & Ross, 2016 from San Just. **C**, *Hispanelcana arilloi* Peñalver & Grimaldi, 2010 from Peñacerrada I. **D**, *Libanoglaris hespericus* Álvarez-Parra, Peñalver, Nel & Delclòs, 2022 from Ariño. **E**, *Hispanocader lisae* Golub, Popov & Arillo, 2012 from Peñacerrada I. **F,** *Iberofoveopsis miguelesi* Peñalver & Szwedo, 2010 from San Just. **G**, *Amarantoraphidia ventolina* Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 from El Soplao. **H**, *Tethysthrips hispanicus* Nel, Peñalver, Azar, Hodebert & Nel, 2010 from El Soplao. **I**, *Autrigonoforceps iberica* Engel & Peris, 2015 from Peñacerrada I.

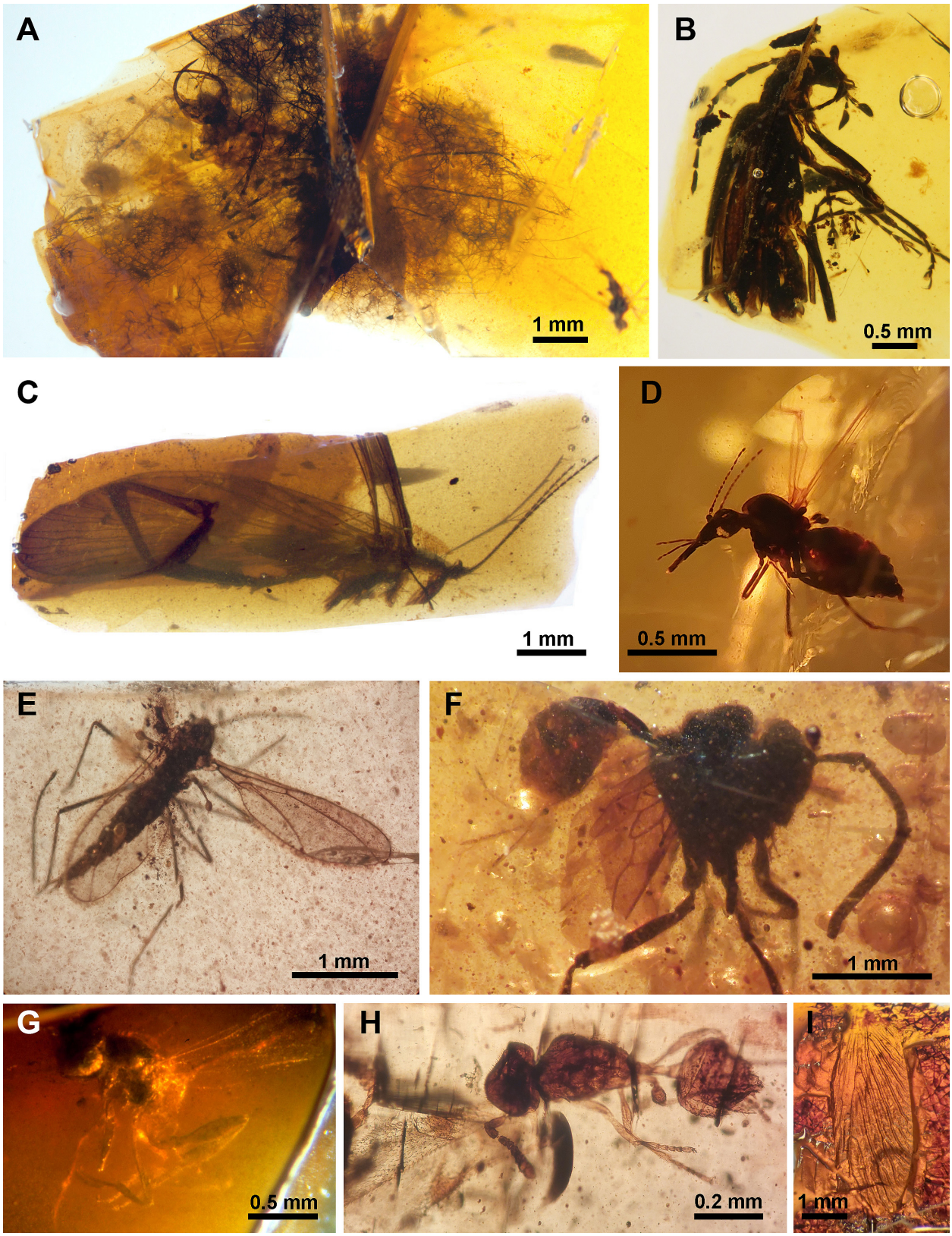

FIGURE 6. Selection of holotypes of insects. **A**, *Hallucinochrysa diogenesi* Pérez-de la Fuente, Delclòs, Peñalver & Engel, 2012 from El Soplao. **B**, *Molliberus albae* Peris & Fanti, 2018 from El Soplao. **C**, *Cantabra soplao* Soszyńska-Maj, Pérez-de la Fuente, Krzemiński & Wang, 2022 from El Soplao. **D**, *Gerontodacus skalskii* (Szadziewski & Arillo, 1998) from Peñacerrada I; this was the first holotype established from Spanish amber. **E**, *Cretohaplusia ortunoi* Arillo & Nel, 2000 from Peñacerrada I. **F**, *Iberoevania roblesi* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 from Peñacerrada I. **G**, *Cretevania rubusensis* Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 from Arroyo de la Pascueta. **H**, *Microserphites soplaensis* Ortega-Blanco, Delclòs, Peñalver & Engel, 2011 from El Soplao. **I**, *Cantabritermes simplex* Engel & Delclòs, 2010 from Peñacerrada I.

Acronyms of repositories

MCNA = Museum of Natural Science of Álava(Vitoria-Gasteiz, Álava Province, Spain)

CES = El Soplao Institutional Collection in El Soplao Cave (Celis, Cantabria Province, Spain); some specimens retain the first field catalogue number (*e.g.*, ES-07-40), but they also have a CES number in the Collection even not indicated in the checklist

CPT = Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel Province, Spain); the specimens from San Just retain the initial field catalogue number (*e.g.*, SJ-07-05) as indicated in parentheses. Recently the Museum changed its name to Museo Aragonés de Paleontología and started cataloging pieces using the acronym MAP

MGM = Geominer Museum, Geological and Mining Institute of Spain (Madrid, Spain)

DGO = Department of Geology in Oviedo University (Oviedo, Asturias Province, Spain)

MGUV = Museum of Natural History of the University of Valencia (Burjassot, Valencia Province, Spain)

Acronyms of outcrops

Álava Province (Basque-Cantabrian Basin)
(PEÑ) Peñacerrada I-Moraza / Condado de Treviño
(PII) Peñacerrada II / Peñacerrada
(SAL) Salinillas de Buradón / Labastida
Asturias Province (Asturian Depression)
(LRO) La Rodada / Oviedo
(CAL) El Caleyu / Ribera de Arriba
Cantabria Province (Basque-Cantabrian Basin)
(SOP) El Soplao / Herrerías
Castellón Province (Maestrazgo Basin)
(LHO) La Hoya / Cortes de Arenoso
Teruel Province (Maestrazgo Basin)
(SJU) San Just / Utrillas
(ARI) Ariño / Ariño
(APA) Arroyo de la Pascueta/ Rubielos de Mora

† denotes extinct families (not applied in the checklist to genera and species)

ANIMALIA
CRUSTACEA
Malacostraca, Tanaidacea

†Alavatanaidae Vonk & Schram, 2007

Alavatanais Vonk & Schram, 2007
Type genus

Alavatanais carabe Vonk & Schram, 2007 **(PEÑ)***
Type species
Holotype: MCNA-9537 (erroneously as AMNS 9537 in the original description)
2007 Vonk & Schram, 1502.
(= *Proleptochelia euskadiensis* Vonk & Schram, 2007)
2014 Sánchez-García *et al*., 649.
This species was also recorded in:
(SOP) Sánchez-García *et al*. (2014)
* This taxon has only been found in PEÑ, and the indication by Vonk & Schram recording this species in PII was a mistake.

Alavatanais margulisae Sánchez-García, Peñalver & Delclòs, 2014 **(PEÑ)**
Holotype: MCNA-9583a
2014 Sánchez-García *et al.,* 655.
This species was also recorded in:
Sánchez-García *et al*., 2014, who recorded two specimens (MCNA-12703 and MCNA-12749) as belonging to this species. Although they assigned them to PEÑ they are actually from **(PII)**

Eurotanais Sánchez-García, Peñalver & Delclòs, 2014

Eurotanais terminator Sánchez-García, Peñalver & Delclòs, 2014 **(PII)** (erroneously as PEÑ in the original publication)
Type species
Holotype: MCNA-13285
2014 Sánchez-García *et al*., 658.

Electrotanais Sánchez-García, Peñalver & Delclòs, 2014

Electrotanais monolithus Sánchez-García, Peñalver & Delclòs, 2014 **(PEÑ)**
Type species
Holotype: MCNA-12530
2014 Sánchez-García *et al*., 660.

Family indet.

Proleptochelia Vonk & Schram, 2007

Proleptochelia tenuissima Vonk & Schram, 2007 **(PEÑ)***
Type species
Holotype: MCNA-9846a (erroneously as 9846 A AMNS in the original description)
2007 *Proleptochelia tenuissima* (Alavatanaidae) Vonk & Schram, 1505.
2014 *Proleptochelia tenuissima* (Fam. indet.): Sánchez-García *et al*., 664.
* This taxon has only been found in PEÑ, and the indication by Vonk & Schram recording this species in PII was a mistake.

Malacostraca, Isopoda

Ligiidae

Eoligiiscus Sánchez-García, Peñalver, Delclòs & Engel, 2021
Eoligiiscus tarraconensis Sánchez-García, Peñalver, Delclòs & Engel, 2021 **(PEÑ)**
Type species
Holotype: MCNA-9751
2021 Sánchez-García *et al*., 5.

Trichoniscidae
Autrigoniscus Sánchez-García, Peñalver, Delclòs & Engel, 2021
Autrigoniscus resinicola Sánchez-García, Peñalver, Delclòs & Engel, 2021 **(PEÑ)**
Type species
Holotype: MCNA-12522
2021 Sánchez-García *et al*., 13.

Detonidae?
Heraclitus Sánchez-García, Peñalver, Delclòs & Engel, 2021
Heraclitus helenae Sánchez-García, Peñalver, Delclòs & Engel, 2021 **(PEÑ)**
Type species
Holotype: MCNA-12546
2021 Sánchez-García *et al*., 21.

CHELICERATA
Acariformes, Oribatida
Trhypochthoniidae
Afronothrus Wallwork, 1961
Afronothrus ornosae Arillo & Subías, 2016 **(SOP)**
Holotype: CES-412
2016 Arillo *et al*., 71.
Trhypochthonius Berlese, 1904
Trhypochthonius lopezvallei Arillo, Subías & Shtanchaeva, 2012 **(SJU)**
Holotype: CPT-4161 (SJ-07-108)
2012 Arillo *et al*., 108.

Nothridae
Nothrus Koch, 1836
Nothrus vazquezae Arillo & Subías, 2016 **(SOP)**
Holotype: CES-505
2016 Arillo *et al*., 70.

Cepheidae
Ommatocepheus Berlese, 1913
Ommatocepheus nortoni Arillo, Subías & Shtanchaeva, 2008 **(SAL)**
Holotype: MCNA-13348
2008 Arillo *et al*., 253. (See Arillo *et al*., 2008b)

Eupterotegaeus Berlese, 1916
Eupterotegaeus bitranslamellatus Arillo & Subías, 2002 **(PEÑ)**
Holotype: MCNA-9943 (this holotype resulted damaged during further research on the amber fragment)
2002 Arillo & Subías, 404.

Neoliodidae
Platyliodes Berlese, 1916
Platyliodes sellnicki Arillo & Subías, 2016 **(SOP)**
Holotype: CES-582
2016 Arillo *et al*., 72.

†Archaeorchestidae Arillo & Subías, 2000
Strieremaeus Sellnick, 1918
(= *Archaeorchestes* Arillo & Subías, 2000)
2011 Sidorchuk & Norton, 51.
Strieremaeus minguezae (Arillo & Subías, 2000) **(PEÑ)**
Holotype: MCNA-8866
2000 *Archaeorchestes minguezae* Arillo & Subías, 234.
2011 *Strieremaeus minguezae*: Sidorchuk & Norton, 51.

Caleremaeidae
Epieremulus Berlese, 1916
Epieremulus sidorchukae Arillo & Subías, 2020 **(LRO)**
Holotype: MGM-10889C
2020 Arillo *et al*., 3.

Otocepheidae
Cretaceobodes Arillo, Subías & Shtanchaeva, 2010
Cretaceobodes martinezae Arillo, Subías & Shtanchaeva, 2010 **(SJU)**
Type species
Holotype: MAP-4062 (SJ-07-05) (erroneously as CPT-SJ07-05 in the original description)
2010 Arillo *et al*., 288.

Liacaridae
Liacarus Michael, 1898
***Liacarus* (*Procorynetes*)** Woolley, 1969
Liacarus (*Procorynetes*) *shtanchaevae* Arillo & Subías, 2022 **(ARI)**
Holotype: MAP-8661 (AR-1-A-2019.45)
2022 Arillo *et al*., 4.

Ametroproctidae

Ametroproctus Higgins & Woolley, 1968

Ametroproctus valeriae Arillo, Subías & Shtanchaeva, 2009 **(SJU)**

Holotype: CPT-3341 (SJ-07-04)

2009 Arillo *et al*., 323. (See Arillo *et al*., 2009b)

Lamellareidae

Tenuelamellarea Subías & Iturrondobeitia, 1978

Tenuelamellarea estefaniae Arillo & Subías, 2016 **(SJU)**

Holotype: CPT-4165 (SJ-07-122)

2016 Arillo *et al*., 73.

Scutoverticidae

Hypovertex Krivolutsky, 1969

Hypovertex hispanicus Arillo & Subías, 2016 **(SJU)**

Holotype: CPT-4068 (SJ-07-12)

2016 Arillo *et al*., 74.

Acariformes, Trombidiformes

Erythraeidae

Leptus Latreille, 1796

Leptus sp. **(SJU)**

Specimen: CPT-4167 (SJ-07-114)

2018 Arillo *et al*., 29.

Araneae, Araneomorphae

†Lagonomegopidae

Burlagonomegops Penney, 2005

Burlagonomegops alavensis Penney, 2006 **(PEÑ)** (erroneously as PII in the original publication)

Holotype: MCNA-8635

2006 *Burlagonomegops alavensis* Penney, 379.

2013 *Burlagonomegops alavensis*: Pérez-de la Fuente *et al*., 547.

2015 *Archaelagonops alavensis*: Wunderlich, 236.

2023 *Burlagonomegops alavensis*: Dunlop *et al*., 153.

Lagonomegops Eskov & Wunderlich 1995

Lagonomegops? *cor* Pérez-de la Fuente, Saupe & Selden, 2013 **(PII)** (erroneously as PEÑ in the original publication)

Holotype: MCNA-13295

2013 Pérez-de la Fuente *et al*., 534.

Spinomegops Pérez-de la Fuente, Saupe & Selden, 2013

Spinomegops arcanus Pérez-de la Fuente, Saupe & Selden, 2013 **(PII)** (erroneously as PEÑ in the original publication)

Type species

Holotype: MCNA-13307

2013 Pérez-de la Fuente *et al*., 537.

Spinomegops aragonensis Pérez-de la Fuente, Saupe & Selden, 2013 **(SJU)**

Holotype: CPT-4155 (SJ-07-102)

2013 Pérez-de la Fuente *et al*., 540.

Soplaogonomegops Pérez-de la Fuente, Saupe & Selden, 2013

Soplaogonomegops unzuei Pérez-de la Fuente, Saupe & Selden, 2013 **(SOP)**

Type species

Holotype: CES-362

2013 Pérez-de la Fuente *et al*., 543.

Araneidae

Mesozygiella Penney & Ortuño, 2006

Mesozygiella dunlopi Penney & Ortuño, 2006 **(PEÑ)** (erroneously as PII in the original publication)

Type species

Holotype: MCNA-8938a

2006 Penney & Ortuño, 448.

Oonopidae

Orchestina Simon, 1882

Orchestina rabagensis Saupe, Pérez-de la Fuente, Selden, Delclòs, Tafforeau & Soriano, 2012 **(SOP)**

Holotype: CES-013

2012 Saupe *et al*., 132.

Orchestina sp.1 **(SJU)**

Specimen: CPT-4100

2012 Saupe *et al*., 134.

Orchestina sp.2 **(PEÑ)**

Specimen: MCNA-12593

2012 Saupe *et al*., 138.

Pseudoscorpiones

Garypinidae

Cretogarypinus Sánchez-García, Palencia, Delclòs & Peñalver, 2024

Cretogarypinus zaragozai Sánchez-García, Palencia, Delclòs & Peñalver, 2024 **(PII)**

Type species

Holotype: MCNA-13271

2024 Sánchez-García *et al*., 3.

Ithioreolpium Sánchez-García, Palencia, Delclòs & Peñalver, 2024

Ithioreolpium alavensis Sánchez-García, Palencia, Delclòs & Peñalver, 2024 **(PII)**

Type species

Holotype: MCNA-12774
2024 Sánchez-García *et al*., 9.

Pseudogarypidae

Pseudogarypus Ellingsen, 1909

Pseudogarypus sp. **(SJU)**

Specimen: MAP-9106 (SJNB-2012-44)
2024 Sánchez-García *et al*., 12.

HEXAPODA

Collembola, Entomobryomorpha

Isotomidae

Burmisotoma Christiansen & Nascimbene, 2006

Burmisotoma spinulifera Sánchez-García & Engel, 2016 **(PEÑ)**

Holotype: MCNA-12583
2016 Sánchez-García & Engel, 5. (See Sánchez-García & Engel, 2016a)

Protoisotoma Christiansen & Pike, 2002

Protoisotoma autrigoniensis Sánchez-García & Engel, 2016 **(PII)** (erroneously as PEÑ in the original publication)

Holotype: MCNA-12788.2
2016 Sánchez-García & Engel, 8. (See Sánchez-García & Engel, 2016a)

Proisotoma Börner, 1901

Proisotoma communis Sánchez-García & Engel, 2016 **(PEÑ)**

Holotype: MCNA-9273.1
2002 *Micranurida*? sp. Simón-Benito *et al*., 86.
2002 *Onychiurus*? sp. Simón-Benito *et al*., 86.
2002 *Anurophorus*? sp. Simón-Benito *et al*., 86.
2002 *Proisotoma (Ballistura)*? sp. Simón-Benito *et al*., 86.
2002 *Cryptopygus*? sp. Simón-Benito *et al*., 87.
2016 *Proisotoma communis* Sánchez-García & Engel, 10. (See Sánchez-García & Engel, 2016a)

Collembola, Symphypleona

Sminthurididae

Pseudosminthurides Sánchez-García & Engel, 2016

Pseudosminthurides stoechus Sánchez-García & Engel, 2016 **(PII)** (erroneously as PEÑ in the original publication)

Type species
Holotype: MCNA-12788.1
2016 Sánchez-García & Engel, 516. (See Sánchez-García & Engel, 2016b)

Sminthuridae

Sphyrotheciscus Sánchez-García & Engel, 2016

Sphyrotheciscus senectus Sánchez-García & Engel, 2016 **(PEÑ)**

Type species
Holotype: MCNA-9311
2002 *Arrhopalites* sp. Simón-Benito *et al*., 87.
2016 *Sphyrotheciscus senectus* Sánchez-García & Engel, 521. (See Sánchez-García & Engel, 2016b)

Archeallacma Sánchez-García & Engel, 2016

Archeallacma dolichopoda Sánchez-García & Engel, 2016 **(PEÑ)**

Type species
Holotype: MCNA-13850.4
2016 Sánchez-García & Engel, 524. (See Sánchez-García & Engel, 2016b)

Katiannidae

Cretokatianna Sánchez-García & Engel, 2016

Cretokatianna bucculenta Sánchez-García & Engel, 2016 **(PEÑ)**

Type species
Holotype: MCNA-10047
2002 *Fasciosminthurus*? sp. Simón-Benito *et al*., 87.
2016 *Cretokatianna bucculenta* Sánchez-García & Engel, 519. (See Sánchez-García & Engel, 2016b)

Family indet.

Katiannasminthurus Sánchez-García & Engel, 2016

Katiannasminthurus xenopygus Sánchez-García & Engel, 2016 **(PEÑ)**

Type species
Holotype: MCNA-10048
2002 *Sminthurus*? sp. Simón-Benito *et al*., 87.
2016 *Katiannasminthurus xenopygus* Sánchez-García & Engel, 528. (See Sánchez-García & Engel, 2016b)

Blattodea, Isoptera

Family indet.

Morazatermes Engel & Delclòs, 2010

Morazatermes krishnai Engel & Delclòs, 2010 **(PEÑ)**

Type species

Holotype: MCNA-12621
2010 Engel & Delclòs, 116.

Cantabritermes Engel & Delclòs, 2010
Cantabritermes simplex Engel & Delclòs, 2010 **(PEÑ)**
Type species
Holotype: MCNA-12803
2010 Engel & Delclòs, 120.

Ithytermes Sánchez-García, Peñalver, Delclòs & Engel, 2020
Ithytermes montoyai Sánchez-García, Peñalver, Delclòs & Engel, 2020 **(PEÑ)**
Type species
Holotype: MCNA-14936.1
2020 Sánchez-García *et al*., 4.

Aragonitermes Engel & Delclòs, 2010
Aragonitermes teruelensis Engel & Delclòs, 2010 **(SJU)**
Type species
Holotype: CPT-4065
2010 Engel & Delclòs, 121.

Mantodea
Family indet.

Aragonimantis Delclòs, Peñalver, Arillo, Engel, Nel, Azar & Ross, 2016
Aragonimantis aenigma Delclòs, Peñalver, Arillo, Engel, Nel, Azar & Ross, 2016 **(SJU)**
Type species
Holotype: MAP-7022 (SJ-10-17)
2016 Delclòs *et al*., 96.

Dermaptera
Family indet.

Autrigonoforceps Engel & Peris, 2015
Autrigonoforceps iberica Engel & Peris, 2015 **(PEÑ)**
Type species
Holotype: MCNA-13964
2015 Engel *et al*., 294.

Orthoptera
†Elcanidae

Hispanelcana Peñalver & Grimaldi, 2010
Hispanelcana arilloi Peñalver & Grimaldi, 2010 **(PEÑ)**
Type species
Holotype: MCNA-9588
2010 Peñalver & Grimaldi, 92.

Hispanelcana alavensis Peñalver & Grimaldi, 2010 **(PEÑ)**
Holotype: MCNA-9569
2010 Peñalver & Grimaldi, 94.

Hispanelcana lopezvallei Peñalver & Grimaldi, 2010 **(PEÑ)**
Holotype: MCNA-9898
2010 Peñalver & Grimaldi, 96.

Psocodea
Empheriidae (= Archaeatropidae Baz & Ortuño, 2000)
2022 Li *et al*., 3.

Archaeatropos Baz & Ortuño, 2000
Archaeatropos alavensis Baz & Ortuño, 2000 **(PEÑ)**
Type species
Holotype: MCNA-8834
2000 Baz & Ortuño, 369.
This species was also recorded in: **(SOP) (SJU) (APA)** Álvarez-Parra *et al*. (2022b)

Empheropsocus Baz & Ortuño, 2001
Empheropsocus arilloi Baz & Ortuño, 2001 **(PEÑ)**
Type species
Holotype: MCNA-8677
2001 Baz & Ortuño, 577. (See Baz & Ortuño, 2001a)

Empheropsocus margineglabrus Baz & Ortuño, 2001 **(PEÑ)**
Holotype: MCNA-9755
2001 Baz & Ortuño, 578. (See Baz & Ortuño, 2001a)

Libanoglaris Azar, Perrichot, Néraudeau & Nel, 2003
Libanoglaris hespericus Álvarez-Parra, Peñalver, Nel & Delclòs, 2022 **(ARI)**
Holotype: MAP-8650 (AR-1-A-2019.35)
2022 Álvarez-Parra *et al*., 12. (See Álvarez-Parra *et al*., 2022b)
This species was also recorded in: **(SOP)** Álvarez-Parra *et al*. (2022b)

Preempheria Baz & Ortuño, 2001
Preempheria antiqua Baz & Ortuño, 2001 **(PEÑ)**
Type species
Holotype: MCNA-8888
2001 Baz & Ortuño, 581. (See Baz & Ortuño, 2001a)
This species was also recorded in: **(SJU)** Álvarez-Parra *et al*. (2022b)

Manicapsocidae

Manicapsocidus Baz & Ortuño, 2001
Manicapsocidus enigmaticus Baz & Ortuño, 2001 **(PEÑ)**
Type species
Holotype: MCNA-8867

2001 Baz & Ortuño, 29. (See Baz & Ortuño, 2001b)

Azarpsocus Maheu & Nel, 2020

Azarpsocus anjana Álvarez-Parra & Nel, 2023 **(SOP)**

Holotype: CES-057.3

2023 Álvarez-Parra *et al*., 2.

This species was also recorded in: (**ARI**) Álvarez-Parra *et al*. (2023)

Compsocidae

Burmacompsocus Nel & Waller, 2007

Burmacompsocus ojancano Álvarez-Parra & Nel, 2023 **(SOP)**

Holotype: CES-315.8

2023 Álvarez-Parra *et al*., 6.

Hemiptera, Sternorrhyncha

†Burmitaphididae

Alavesiaphis Peñalver & Wegierek 2008

2008 *Alavesiaphis* (Tajmyraphididae) Peñalver & Wegierek, 187.

2019 *Alavesiaphis* (Burmitaphididae): Wegierek *et al*., 321.

Alavesiaphis margaritae Peñalver & Wegierek, 2008 **(PEÑ)**

Type species

Holotype: MCNA-10021

2008 Peñalver & Wegierek, 189.

†Perforissidae

Iberofoveopsis Peñalver & Szwedo, 2010

Iberofoveopsis miguelesi Peñalver & Szwedo, 2010 **(SJU)**

Type species

Holotype: CPT-4132 (SJ-07-79)

2010 Peñalver & Szwedo, 98.

Hemiptera, Heteroptera

†Hispanocaderidae Golub, Popov & Arillo, 2012

Hispanocader Golub, Popov & Arillo, 2012

Type genus

Hispanocader lisae Golub, Popov & Arillo, 2012 **(PEÑ)**

Type species

Holotype: MCNA-10656

2012 Golub *et al*., 43.

Hydrometridae

Alavametra Sánchez-García & Nel, 2016

Alavametra popovi Sánchez-García & Nel, 2016 **(PEÑ)**

Type species

Holotype: MCNA-12686

2016 Sánchez-García *et al*., 115.

Mesoveliidae

Iberovelia Sánchez-García & Nel, 2017

Iberovelia quisquilia Sánchez-García & Nel, 2017 **(PEÑ)**

Type species

Holotype: MCNA-12804

2017 Sánchez-García *et al*., 5.

Glaesivelia Sánchez-García & Solórzano-Kraemer, 2017

Glaesivelia pulcherrima Sánchez-García & Solórzano-Kraemer, 2017 **(PEÑ)**

Type species

Holotype: MCNA-12806

2017 Sánchez-García *et al*., 13.

Family indet.

Enicocephalinus Azar, Fleck, Nel & Solignac, 1999

Enicocephalinus ibericus Davranoglou, Pérez-de la Fuente, Bañař & Peñalver, 2024 **(ARI)**

Holotype: AR-1-A-2019.55

2024 Davranoglou *et al*., 3.

Thysanoptera

Melanthripidae

Gymnopollisthrips Peñalver, Nel & Nel, 2012

Gymnopollisthrips minor Peñalver, Nel & Nel, 2012 **(PEÑ)**

Type species

Holotype: MCNA-10731

2012 Peñalver *et al*., 8624.

2017 Peris *et al*., 900. (See Peris *et al*., 2017b)

2025 Peñalver *et al*., 6. (See Peñalver *et al*., 2025a)

Gymnopollisthrips maior Peñalver, Nel & Nel, 2012 **(PEÑ)**

Holotype: MCNA-9283

2012 Peñalver *et al*., 8624.

2017 Peris *et al*., 900. (See Peris *et al*., 2017b)

2025 Peñalver *et al*., 6. (See Peñalver *et al*., 2025a)

Thripidae

Tethysthrips Nel, Peñalver, Azar, Hodebert & Nel, 2010

Tethysthrips hispanicus Nel, Peñalver, Azar, Hodebert & Nel, 2010 **(SOP)**

Type species

Holotype: CES 451 (ES-07-11)

2010 Nel *et al*., 158.

2025 Peñalver *et al*., 2. (See Peñalver *et al*., 2025a)

Tethysthrips attenboroughi Peñalver, Peña-Kairath, P. Nel & A. Nel, 2025 **(PEÑ)**

Holotype: MCNA 12629a

2025 Peñalver *et al*., 2. (See Peñalver *et al*., 2025a)

Stenurothripidae

Hispanothrips Peñalver & Nel, 2010

Hispanothrips utrillensis Peñalver & Nel, 2010 **(SJU)**

Type species

Holotype: MAP-4099 (SJ-07-45)

2010 Peñalver & Nel, 141.

Phlaeothripidae (stem group)*

Alavathrips Peñalver, Nel & Nel, 2022

Alavathrips moralesi Peñalver, Nel & Nel, 2022 **(PII)**

Type species

Holotype: MCNA-13362

2022 female *Alavathrips moralesi* (Phlaeothripidae, stem group) Peñalver *et al*., 3. (See Peñalver *et al*., 2022b)

2022 male *Alavathrips moralesi* (Rohrthripidae): Ulitzka, 2.*,**

* We consider this taxon as stem group Phlaeothripidae, since the monophyly of Rohrthripidae is questionable and there is no apomorphy to support the group as a clade, following Peñalver *et al*. (2022b, 2025a).

** The specimen has been confirmed as female, consistent with the original description. Ulitzka (2022) incorrectly identified it as male based solely on the published photographs in the original description. A direct microscopic examination, employing varying illumination and focus adjustments, is required for proper identification.

Lophioneurida

†Lophioneuridae

Jantardachus Vishnyakova, 1981

Jantardachus sp. **(SJU)**

Specimen: MAP-7751 (SJNB2012-10)

2021 Álvarez-Parra *et al*., 187. (See Álvarez-Parra *et al*., 2021a)

Hymenoptera

Anaxyelidae

Eosyntexis Rasnitsyn, 1990

Eosyntexis parva Ortega-Blanco, Rasnitsyn & Delclòs, 2008 **(PEÑ)**

Holotype: MCNA-8756

2008 Ortega-Blanco *et al*., 43.

Diapriidae

Iberopria Engel, Ortega-Blanco & Delclòs, 2013

Iberopria perialla Engel, Ortega-Blanco & Delclòs, 2013 **(PEÑ)**

Type species

Holotype: MCNA-9896

2013 Engel *et al*., 17. (See Engel *et al*., 2013b)

†Spathiopterygidae Engel & Ortega-Blanco, 2013

Spathiopteryx Engel & Ortega-Blanco, 2013

Type genus

Spathiopteryx alavarommopsis Engel & Ortega-Blanco, 2013 **(PEÑ)**

Type species

Holotype: MCNA-12603

2013 Engel *et al*., 6. (See Engel *et al*., 2013b)

Diameneura Santer &Álvarez-Parra, 2022

Diameneura marveni Santer & Álvarez-Parra, 2022 **(SJU)**

Type species

Holotype: CPT-4095 (SJ-07-41)

2022 Santer *et al*., 3.

Mymaropsis Engel & Ortega-Blanco, 2013

Mymaropsis turolensis Engel & Ortega-Blanco, 2013 **(SJU)**

Type species

Holotype: CPT-4077 (SJ-07-22)

2013 Engel *et al*., 7. (See Engel *et al*., 2013b)

Evaniidae

Cretevania Rasnitsyn, 1975

Cretevania alcalai Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 **(SJU)**

Holotype: CPT-960 (SJ-11)

2010 Peñalver *et al*., 817.

Cretevania alonsoi Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 **(PEÑ)**

Holotype: MCNA-9601

2010 Peñalver *et al*., 814.

Cretevania montoyai Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 **(SJU)**

Holotype: CPT-957 (SJ-8)

2010 Peñalver *et al*., 815.

Cretevania rubusensis Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 **(APA)**

Holotype: CPT-3335 (erroneously as CPT-2260 in the original description)

2010 Peñalver *et al*., 818.

Cretevania soplaensis Pérez-de la Fuente, Peñalver & Ortega-Blanco, 2012 **(SOP)**
Holotype: CES-364.2
2012 Pérez-de la Fuente *et al*., 72. (See Pérez-de la Fuente *et al*., 2012c)

Iberoevania Peñalver, Ortega-Blanco, Nel & Delclòs, 2010
Iberoevania roblesi Peñalver, Ortega-Blanco, Nel & Delclòs, 2010 **(PEÑ)**
Type species
Holotype: MCNA-8759
2010 Peñalver *et al*., 820.

Braconidae

Archephedrus Ortega-Blanco, Bennett, Delclòs & Engel, 2009
Archephedrus stolamissus Ortega-Blanco, Bennett, Delclòs & Engel, 2009 **(PEÑ)**
Type species
Holotype: MCNA-8785
2009 Ortega-Blanco *et al*., 278.

Cantabriazyx Álvarez-Parra & Jouault, 2024
Cantabriazyx perezdelafuentei Álvarez-Parra & Jouault, 2024 **(SOP)**
Type species
Holotype: CES-430
2024 Álvarez-Parra *et al*., 481. (See Álvarez-Parra *et al*., 2024b)

Protorhyssalopsis Ortega-Blanco, Delclòs & Engel, 2011
Protorhyssalopsis perrichoti Ortega-Blanco, Delclòs & Engel, 2011 **(PEÑ)**
Type species
Holotype: MCNA-9796
2011 Ortega-Blanco *et al*., 53. (See Ortega-Blanco *et al*., 2011a)

Utrillabracon Álvarez-Parra & Engel, 2022
Utrillabracon electropteron Álvarez-Parra & Engel, 2022 **(SJU)**
Type species
Holotype: MAP-7819 (SJE2012 49-04)
2022 Álvarez-Parra & Engel, 70. (See Álvarez-Parra *et al*., 2022a)

Megalyridae

Megalava Perrichot, 2009
Megalava truncata Perrichot, 2009 **(PEÑ)**
Type species
Holotype: MCNA-9416
2009 Perrichot, 25.

Valaa Perrichot, 2009
Valaa delclosi Perrichot, 2009 **(PEÑ)**
Type species
Holotype: MCNA-12578a
2009 Perrichot, 27.

†Alavarommatidae Ortega-Blanco, Peñalver, Delclòs & Engel, 2011

Alavaromma Ortega-Blanco, Peñalver, Delclòs & Engel, 2011
Type genus
Alavaromma orchamum Ortega-Blanco, Peñalver, Delclòs & Engel, 2011 **(PEÑ)**
Type species
Holotype: MCNA-9127
2011 Ortega-Blanco *et al*., 514. (See Ortega-Blanco *et al*., 2011e)
This species was also recorded in:
(SJU) Ortega-Blanco *et al*. (2011e)

†Gallorommatidae

Cretaceomma Rasnitsyn & Azar, 2022
Cretaceomma turolensis (Ortega-Blanco, Peñalver, Delclòs & Engel, 2011) **(SJU)**
Holotype: CPT-4139 (SJ-07-86)
2011 *Galloromma turolensis* Ortega-Blanco *et al*., 519. (See Ortega-Blanco *et al*., 2011e)
2022 *Cretaceomma turolensis* Rasnitsyn *et al*., 120.

Galloromma Schlüter, 1978
Galloromma alavaensis Ortega-Blanco, Peñalver, Delclòs & Engel, 2011 **(PEÑ)**
Holotype: MCNA-12630
2011 Ortega-Blanco *et al*., 518. (See Ortega-Blanco *et al*., 2011e)

Mymarommatidae

Archaeromma Yoshimoto, 1975
Archaeromma hispanicum Ortega-Blanco, Peñalver, Delclòs & Engel, 2011 **(PEÑ)**
Holotype: MCNA-9482
2011 Ortega-Blanco *et al*., 514. (See Ortega-Blanco *et al*., 2011e)
This species was also recorded in:
(SOP) Ortega-Blanco *et al*. (2011e)

†Proterosceliopsidae Talamas, Johnson, Shih & Ren, 2019

Proterosceliopsis Ortega-Blanco, McKellar & Engel, 2014
Type genus
Proterosceliopsis masneri Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**
Type species
Holotype: MCNA-13631
2014 *Proterosceliopsis masneri* (Scelionidae) Ortega-Blanco *et al*., 555.
2019 *Proterosceliopsis masneri*

(Proterosceliopsidae): Talamas *et al*., 3.

Scelionidae

Alavascelio Ortega-Blanco, McKellar & Engel, 2014

Alavascelio delvallei Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**

Type species

Holotype: MCNA-9912.1

2014 Ortega-Blanco *et al*., 562.

Amissascelio Ortega-Blanco, McKellar & Engel, 2014

Amissascelio temporarius Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**

Type species

Holotype: MCNA-13643

2014 Ortega-Blanco *et al*., 558.

Bruescelio Ortega-Blanco, McKellar & Engel, 2014

Bruescelio platycephalus Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**

Type species

Holotype: MCNA-9536

2014 Ortega-Blanco *et al*., 556.

Electroteleiopsis Ortega-Blanco, McKellar & Engel, 2014

Electroteleiopsis hebdomas Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**

Type species

Holotype: MCNA 8909.1

2014 Ortega-Blanco *et al*., 563.

Juxtascelio Ortega-Blanco, McKellar & Engel, 2014

Juxtascelio interitus Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**

Type species

Holotype: MCNA-12600

2014 Ortega-Blanco *et al*., 559.

Perimoscelio Ortega-Blanco, McKellar & Engel, 2014

Perimoscelio tyrbastes Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**

Type species

Holotype: MCNA-9844

2014 Ortega-Blanco *et al*., 565.

Perimoscelio confector Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**

Holotype: MCNA-9806

2014 Ortega-Blanco *et al*., 566.

Tithonoscelio Ortega-Blanco, McKellar & Engel, 2014

Tithonoscelio resinalis Ortega-Blanco, McKellar & Engel, 2014 **(PEÑ)**

Type species

Holotype: MCNA-8633.3

2014 Ortega-Blanco *et al*., 557.

†Serphitidae

Aposerphites Kozlov & Rasnitsyn, 1979

Aposerphites angustus Ortega-Blanco, Delclòs, Peñalver & Engel, 2011 **(PEÑ)**

Holotype: MCNA-8651

2011 Ortega-Blanco *et al*., 148. (See Ortega-Blanco *et al*., 2011d)

Microserphites Kozlov & Rasnitsyn, 1979

Microserphites soplaensis Ortega-Blanco, Delclòs, Peñalver & Engel, 2011 **(SOP)**

Holotype: CES-566 (ES-07-1)

2011 Ortega-Blanco *et al*., 144. (See Ortega-Blanco *et al*., 2011d)

Serphites Brues, 1937

Serphites lamiak Ortega-Blanco, Delclòs, Peñalver & Engel, 2011 **(PEÑ)**

Holotype: MCNA-8753

2011 Ortega-Blanco *et al*., 151. (See Ortega-Blanco *et al*., 2011d)

Serphites silban Ortega-Blanco, Delclòs, Peñalver & Engel, 2011 **(SJU)**

Holotype: CPT-4059 (SJ-07-01)

2011 Ortega-Blanco *et al*., 153. (See Ortega-Blanco *et al*., 2011d)

†Maimetshidae

Iberomaimetsha Ortega-Blanco, Perrichot & Engel, 2011

Iberomaimetsha rasnitsyni Ortega-Blanco, Perrichot & Engel, 2011 **(PEÑ)**

Type species

Holotype: MCNA-9928

2011 Perrichot *et al*., 433.

Afrapia Rasnitsyn & Brothers, 2009

Afrapia nihtmara (Ortega-Blanco, Delclòs & Engel, 2011) **(PII)** (erroneously as PEÑ in the original publication)

Holotype: MCNA-13049

2011 *Iberomaimetsha nihtmara* Perrichot *et al*., 437.

2025 *Afrapia nihtmara*: Li *et al*., 6.

†Radiophronidae Ortega-Blanco, Rasnitsyn & Delclòs, 2010

Radiophron Ortega-Blanco, Rasnitsyn & Delclòs, 2010

Type genus

Radiophron ibericus Ortega-Blanco, Rasnitsyn & Delclòs, 2010 **(PEÑ)**

Type species

Holotype: MCNA-8754

2010 Ortega-Blanco *et al*., 267.

Microcostaphron Ortega-Blanco, Rasnitsyn & Delclòs, 2010

Microcostaphron parvus Ortega-Blanco, Rasnitsyn & Delclòs, 2010 **(PEÑ)**

Type species
Holotype: MCNA-8769
2010 Ortega-Blanco *et al*., 272.

Stigmaphronidae

Burmaphron Engel & Grimaldi, 2009

Burmaphron jentilak Ortega-Blanco, Delclòs & Engel, 2011 **(PEÑ)**

Holotype: MCNA-8981
2011 Ortega-Blanco *et al*., 768. (See Ortega-Blanco *et al*., 2011b)

Burmaphron iratxoak Ortega-Blanco, Delclòs & Engel, 2011 **(PEÑ)**

Holotype: MCNA-9346.2
2011 Ortega-Blanco *et al*., 770. (See Ortega-Blanco *et al*., 2011b)

Burmaphron sorginak Ortega-Blanco, Delclòs & Engel, 2011 **(PEÑ)**

Holotype: MCNA-12618
2011 Ortega-Blanco *et al*., 768. (See Ortega-Blanco *et al*., 2011b)

Elasmophron Engel & Grimaldi, 2009

Elasmophron mari Ortega-Blanco, Delclòs & Engel, 2011 **(PEÑ)**

Holotype: MCNA-9502
2011 Ortega-Blanco *et al*., 763. (See Ortega-Blanco *et al*., 2011b)

Hippocoon Kozlov, 1975

Hippocoon basajauni Ortega-Blanco, Delclòs & Engel, 2011 **(PEÑ)**

Holotype: MCNA-9765
2011 Ortega-Blanco *et al*., 766. (See Ortega-Blanco *et al*., 2011b)

Libanophron Engel & Grimaldi, 2009

Libanophron sugaar Ortega-Blanco, Delclòs & Engel, 2011 **(PEÑ)**

Holotype: MCNA-8983
2011 Ortega-Blanco *et al*., 766. (See Ortega-Blanco *et al*., 2011b)

Tagsmiphron Engel & Grimaldi, 2009

Tagsmiphron olentzero Ortega-Blanco, Delclòs & Engel, 2011 **(PII)** (erroneously as PEÑ in the original publication)

Holotype: MCNA-12733
2011 Ortega-Blanco *et al*., 770. (See Ortega-Blanco *et al*., 2011b)

Bethylidae

Cretepyris Ortega-Blanco & Engel, 2013

Cretepyris martini Ortega-Blanco & Engel, 2013 **(PEÑ)**

Type species
Holotype: MCNA-8782
2013 Ortega-Blanco & Engel, 271.

Liztor Ortega-Blanco & Engel, 2013

Liztor pilosus Ortega-Blanco & Engel, 2013 **(PEÑ)**

Type species
Holotype: MCNA-9200
2013 Ortega-Blanco & Engel, 269.

Zophepyris Engel, Ortega-Blanco & Acevedo, 2016

Zophepyris alavaensis (Ortega-Blanco & Engel, 2013) **(PEÑ)**

Type species
Holotype: MCNA-9759
2013 *Lancepyris alavaensis* Ortega-Blanco & Engel, 266.
2016 *Zophepyris alavaensis* Engel *et al*., 1.

Embolemidae

Ampulicomorpha Ashmead, 1893

Ampulicomorpha perialla (Ortega-Blanco, Delclòs & Engel, 2011) **(PII)** (erroneously as PEÑ in the original publication)

Holotype: MCNA-12709
2011 *Embolemus periallus* Ortega-Blanco *et al*., 37. (See Ortega-Blanco *et al*., 2011c)
2014 *Ampulicomorpha perialla* Olmi *et al*., 623.

Chrysididae

Ectenobythus Engel, Ortega-Blanco & McKellar, 2013

Ectenobythus iberiensis Engel, Ortega-Blanco & McKellar, 2013 **(PEÑ)**

Type species
Holotype: MCNA-9815
2013 *Ectenobythus iberiensis* (Scolebythidae) Engel *et al*., 33. (See Engel *et al*., 2013a)
2024 *Ectenobythus iberiensis* (Chrysididae): Lepeco & Melo, 83.

Sierolomorphidae

Orisolemorpha Álvarez-Parra & Engel, 2024

Orisolemorpha dyscheres Álvarez-Parra & Engel, 2024 **(SJU)**

Type species
Holotype: CPT-4076 (SJ-07-21)

2024 Álvarez-Parra *et al*., 3. (See Álvarez-Parra *et al*., 2024a)

Raphidioptera

†Baissopteridae

Baissoptera Martynova, 1961

Baissoptera? *cretaceoelectra* Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 **(PEÑ)**

Holotype: MCNA-12068.4

2012 Pérez-de la Fuente *et al*., 7. (See Pérez-de la Fuente *et al*., 2012b)

†Mesoraphidiidae

Alavaraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012

Alavaraphidia imperterrita Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 **(PEÑ)**

Type species

Holotype: MCNA-13608

2012 Pérez-de la Fuente *et al*., 23. (See Pérez-de la Fuente *et al*., 2012b)

Amarantoraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012

Amarantoraphidia ventolina Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 **(SOP)**

Type species

Holotype: CES-364.1

2012 Pérez-de la Fuente *et al*., 18. (See Pérez-de la Fuente *et al*., 2012b)

Cantabroraphidia Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010

Cantabroraphidia marcanoi Pérez-de la Fuente, Nel, Peñalver & Delclòs, 2010 **(SOP)**

Type species

Holotype: CES-479.1 (ES-07-6)

2010 Pérez-de la Fuente *et al*., 110.

Necroraphidia Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012

Necroraphidia arcuata Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 **(SOP)**

Type species

Holotype: CES-391.1

2012 Pérez-de la Fuente *et al*., 12. (See Pérez-de la Fuente *et al*., 2012b)

Styporaphidia Engel & Ren, 2008

Styporaphidia? *hispanica* Pérez-de la Fuente, Peñalver, Delclòs & Engel, 2012 **(PEÑ)**

Holotype: MCNA-9343

2012 Pérez-de la Fuente *et al*., 15. (See Pérez-de la Fuente *et al*., 2012b)

Neuroptera

Coniopterygidae

Soplaoconis Pérez-de la Fuente, Delclòs, Peñalver & Engel, 2019

Soplaoconis ortegablancoi Pérez-de la Fuente, Delclòs, Peñalver & Engel, 2019 **(SOP)**

Type species

Holotype: CES-348

2019 Pérez-de la Fuente *et al*., 281.

Mantispidae

Aragomantispa Pérez-de la Fuente & Peñalver, 2019

Aragomantispa lacerata Pérez-de la Fuente & Peñalver, 2019 **(SJU)**

Type species

Holotype: MAP-7848 (SJ-10-22)

2019 Pérez-de la Fuente & Peñalver, 2.

Berothidae

Cantabroberotha Pérez-de la Fuente, Peñalver & Engel, 2021

Cantabroberotha soplaensis Pérez-de la Fuente, Peñalver & Engel, 2021 **(SOP)**

Type species

Holotype: CES-004

2021 Pérez-de la Fuente *et al*., 3.

Family indet. (Chrysopoidea)

Hallucinochrysa Pérez-de la Fuente, Delclòs, Peñalver & Engel, 2012

Hallucinochrysa diogenesi Pérez-de la Fuente, Delclòs, Peñalver & Engel, 2012 **(SOP)**

Type species

Holotype: CES-418.1

2012 Pérez-de la Fuente *et al*., 1. (See Pérez-de la Fuente *et al*., 2012a)

Coleoptera

Staphylinidae

Cretasonoma Peris, Chatzimanolis & Delclòs, 2014

Cretasonoma corinformibus Peris, Chatzimanolis & Delclòs, 2014 **(PEÑ)**

Type species

Holotype: MCNA-8654

2014 Peris *et al*., 88. (See Peris *et al*., 2014a)

This species was also recorded in:

(SOP) Peris *et al*. (2014a)

Penarhytus Peris, Chatzimanolis & Delclòs, 2014

Penarhytus tenebris Peris, Chatzimanolis & Delclòs, 2014 **(PEÑ)**

Type species

Holotype: MCNA-12683

2014 Peris *et al*., 89. (See Peris *et al*., 2014a)

Prosolierius Thayer, Newton & Chatzimanolis, 2012

Prosolierius parvus Peris, Chatzimanolis & Delclòs, 2014 **(PEÑ)**

Holotype: MCNA-14190

2014 Peris *et al*., 89. (See Peris *et al*., 2014a)

Archeutheia Jałoszyński & Peris, 2016

Archeutheia magnifica (Peris, Chatzimanolis & Delclòs, 2014) **(SOP)**

Type species

Holotype: CES-463

2014 *Kachinus magnificus* Peris *et al*., 91. (See Peris *et al*., 2014a)

2016 *Archeutheia magnifica*: Jałoszyński & Peris, 194.

Leiodidae

Cretaciella Perreau, 2019

Cretaciella sorianoae Perreau, 2019 **(PEÑ)**

Type species

Holotype: MCNA-9423

2019 Perreau, 2.

Mordellidae

Mediumiuga Peris & Ruzzier, 2013

Mediumiuga sinespinis Peris & Ruzzier, 2013 **(PEÑ)**

Type species

Holotype: MCNA-8839

2013 Peris & Ruzzier, 3.

Monotomidae

Cretakarenni Peris & Delclòs, 2015

Cretakarenni hispanicus Peris & Delclòs, 2015 **(PEÑ)**

Type species

Holotype: MCNA-8655

2015 Peris & Delclòs, 4,

Rhizophtoma Kirejtshuk & Azar, 2009

Rhizophtoma longus Peris & Delclòs, 2015 **(PEÑ)**

Holotype: MCNA-9184

2015 Peris & Delclòs, 5.

Oedemeridae

Darwinylus Peris, 2017

Darwinylus marcosi Peris, 2017 **(PEÑ)**

Type species

Holotype: MCNA-11229

2017 Peris, 270.

2017 Peris *et al*., 900. (See Peris *et al*., 2017b)

Ptinidae

Actenobius Fall, 1905

Actenobius magneoculus Peris, Philips & Delclòs, 2015 **(SJU)**

Holotype: MAP-7727 (SJ-10-18)

2015 Peris *et al*., 445. (See Peris *et al*., 2015b)

Nemonychidae

Arra Peris, Davis & Delclòs, 2014

Arra legalovi Peris, Davis & Delclòs, 2014 (**SJU**)

Type species

Holotype: CPT-4106 (SJ-07-52)

2014 Peris *et al*., 537. (See Peris *et al*., 2014b)

This species was also recorded in: **(SOP)** Peris *et al*. (2014b)

Caridae

Albicar Peris, Davis, Engel & Delclòs, 2014

Albicar contriti Peris, Davis, Engel & Delclòs, 2014 **(SOP)**

Type species

Holotype: CES-432

2014 Peris *et al*., 541. (See Peris *et al*., 2014b)

Cryptophagidae

Albocryptophagus Peris, Lyubarsky & Perkovsky, 2017

Albocryptophagus cantabricus Peris, Lyubarsky & Perkovsky, 2017 **(SOP)**

Type species

Holotype: CES-571

2017 Peris *et al*., 192. (See Peris *et al*., 2017a)

Elmidae

Elmadulescens Peris, Maier & Sánchez-García, 2015

Elmadulescens rugosus Peris, Maier & Sánchez-García, 2015 **(SOP)**

Type species

Holotype: CES-567

2015 Peris *et al*., 183. (See Peris *et al*., 2015a)

Cantharidae

Molliberus Peris & Fanti, 2018

Molliberus albae Peris & Fanti, 2018 **(SOP)**

Type species

Holotype: CES-522

2018 Peris & Fanti, 264.

Mecoptera

†Cantabridae Soszyńska-Maj, Pérez-de la Fuente, Krzemiński & Wang, 2022

Cantabra Soszyńska-Maj, Pérez-de la Fuente, Krzemiński & Wang, 2022

Type genus

Cantabra soplao Soszyńska-Maj, Pérez-de la Fuente, Krzemiński & Wang, 2022 **(SOP)**

Type species

Holotype: CES-437

2022 Soszyńska-Maj *et al*., 7.

Diptera

Limoniidae

Alavia Krzemiński & Arillo, 2007

Alavia neli Krzemiński & Arillo, 2007 **(PEÑ)**

Type species

Holotype: MCNA-8816

2007 Krzemiński & Arillo, 11.

Chilelimnophila Alexander, 1968

***Chilelimnophila* (*Ribeironia*)** Krzemiński, Kania-Kłosok & Arillo, 2024

Chilelimnophila (*Ribeironia*) *amorimi* Krzemiński, Kania-Kłosok & Arillo, 2024 **(PEÑ)**

Type species

Holotype: MCNA-9845

2024 Krzemiński *et al*., 3.

Gonomyia Meigen, 1818

***Gonomyia* (*Iberiana*)** Kania-Kłosok, Arillo, Tuchowski, Zhang & Krzemiński, 2022

Gonomyia (*Iberiana*) *penalveri* Kania-Kłosok, Arillo, Tuchowski, Zhang & Krzemiński, 2022 **(PEÑ)**

Type species

Holotype: MCNA-8818

2022 Kania-Kłosok *et al*., 3.

Helius Lepeletier & Serville, 1828

Helius alavensis Kania, Krzemiński & Arillo, 2016 **(PEÑ)**

Holotype: MCNA-9112

2016 Kania *et al*., 34.

Helius hispanicus Kania-Kłosok, Krzemiński & Arillo, 2021 **(PEÑ)**

Holotype: MCNA-9946

2021 Kania-Kłosok *et al*., 5. (See Kania-Kłosok *et al*., 2021a)

Helius spiralensis Kania, Krzemiński & Arillo, 2017 **(PEÑ)**

Holotype: MCNA-15078

2017 Kania *et al*., 4.

Helius turolensis Kania-Kłosok, Krzemiński & Arillo, 2021 **(SJU)**

Holotype: SJ-10-54 (not yet a final collection number)

2021 Kania-Kłosok *et al*., 4. (See Kania-Kłosok *et al*., 2021a)

Trichoneura Loew, 1850

***Trichoneura* (*Cretalinea*)** Kania-Kłosok, Krzemiński, Kopeć & Arillo, 2021

Trichoneura (*Cretalinea*) *xavieri* Kania-Kłosok, Krzeminski, Kopeć & Arillo, 2021 **(PEÑ)**

Type species

Holotype: MCNA-9735

2021 Kania-Kłosok *et al*., 6. (See Kania-Kłosok *et al*., 2021b)

Ceratopogonidae

Archiaustroconops Szadziewski, 1996

Archiaustroconops alavensis Szadziewski & Arillo, 1998 **(PEÑ)**

Holotype: MCNA-8836.1

1998 Szadziewski & Arillo, 294.

Archiaustroconops borkenti Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 **(SOP)**

Holotype: CES-606 (ES-07-17)

2011 Pérez-de la Fuente *et al*., 755.

Atriculicoides Remm, 1976

Atriculicoides szadziewskii Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 **(SOP)**

Holotype: CES-363 (ES-07-12)

2011 Pérez-de la Fuente *et al*., 758.

Austroconops Wirth & Lee, 1959

Austroconops sp. **(PEÑ) (SOP)**

2003 Szadziewski & Arillo, 271.

2011 Pérez-de la Fuente *et al*., 757.

Gerontodacus Borkent, 2019

Gerontodacus skalskii (Szadziewski & Arillo, 1998) **(PEÑ)**

Holotype: MCNA-8645 (erroneously as MCNA-8648 in the original description)

1998 *Protoculicoides skalskii* Szadziewski & Arillo, 292.

2016 *Archiculicoides skalskii*: Szadziewski *et al*., 2.

2019 *Gerontodacus skalskii*: Borkent, 8.

This species was also recorded in:

(SJU) Arillo *et al*. (2008a)

(SOP) Pérez-de la Fuente *et al*. (2011)

Lebanoculicoides Szadziewski, 1996

Lebanoculicoides excantabris Pérez-de la Fuente, Delclòs, Peñalver & Arillo, 2011 **(SOP)**

Holotype: CES-607 (ES-07-9)

2011 Pérez-de la Fuente *et al*., 752.

Leptoconops Skuse, 1889

Leptoconops zherikhini Szadziewski & Arillo, 2003 **(PEÑ)**

Holotype: MCNA-9176.
2003 Szadziewski & Arillo, 273.
This species was also recorded in:
(SJU) Arillo *et al*. (2008a)

Protoculicoides Boesel, 1937
Protoculicoides hispanicus Szadziewski & Arillo, 2016 **(SJU)**

Holotype: SJNB2012 12-32 (erroneously as NBSJ 09/12, A,c in the original description; not yet a final collection number)
2016 Szadziewski *et al*., 5.

Protoculicodes sanjusti Szadziewski & Arillo, 2016 **(SJU)**

Holotype: SJNB2012 12-31 (erroneously as NBSJ 09/12, A,a in the original description; not yet a final collection number)
2016 Szadziewski *et al*., 6.

Keroplatidae

Hegalari Blagoderov & Arillo, 2002
Hegalari antzinako Blagoderov & Arillo, 2002 **(PEÑ)**

Type species
Holotype: MCNA-8820
2002 Blagoderov & Arillo, 32.

Hegalari minor Blagoderov & Arillo, 2002 **(PEÑ)**

Holotype: MCNA-9292
2002 Blagoderov & Arillo, 34.

Mycetophilidae

Alavamanota Blagoderov & Arillo, 2002
Alavamanota hispanica Blagoderov & Arillo, 2002 **(PEÑ)**

Type species
Holotype: MCNA-8819
2002 Blagoderov & Arillo, 34.

Allocotocera Mik, 1886
Allocotocera xavieri Blagoderov & Arillo, 2002 **(PEÑ)**

Holotype: MCNA-9941.1
2002 Blagoderov & Arillo, 36.

†Archizelmiridae

Burmazelmira Grimaldi, Amorim & Blagoderov, 2003
Burmazelmira grimaldii Arillo, Blagoderov & Peñalver, 2018 **(SJU)**

Holotype: CPT-3342 (SJ-07-9)
2018 Arillo *et al*., 25.

Cecidomyiidae

Eltxo Arillo & Nel, 2000
Eltxo cretaceus Arillo & Nel, 2000 **(PEÑ)**

Type species
Holotype: MCNA-8824
2000 Arillo & Nel, 285.

Eltxo grimaldii Peñalver, Arillo & Nel, 2022 **(SOP)**

Holotype: CES-485 (ES-07-40)
2022 Peñalver *et al*., 462. (See Peñalver *et al*., 2022a)

Cretohaplusia Arillo & Nel, 2000
Cretohaplusia ortunoi Arillo & Nel, 2000 **(PEÑ)**

Type species
Holotype: MCNA-9076
2000 Arillo & Nel, 287.

Ptychopteridae

Eoptychoptera Handlirsch, 1906
Eoptychoptera cantabrica Lukashevich & Arillo, 2016 **(SOP)**

Holotype: CES-059
2016 Lukashevich & Arillo, 257.

Tanyderidae

Espanoderus Skibińska, Krzemiński & Arillo, 2017
Espanoderus barbarae Skibińska, Krzemiński & Arillo, 2017 **(PII)** (erroneously as PEÑ in the original publication; the holotype was erroneously assigned, but the paratypes are actually from PEÑ)

Type species
Holotype: MCNA-13034
2017 Skibińska *et al*., 2.

Stratiomyidae

Lysistrata Grimaldi & Arillo, 2011
Lysistrata emerita Grimaldi & Arillo, 2011 **(PII)** (erroneously as PEÑ in the original publication)

Type species
Holotype: MCNA-12698
2011 Grimaldi *et al*., 298.

†Tethepomyiidae

Tethepomyia Grimaldi & Cumming, 1999
Tethepomyia buruhandi Grimaldi & Arillo, 2008 **(PEÑ)**

Holotype: MCNA-8821
2008 Grimaldi & Arillo, 259.

Tethepomima Grimaldi & Arillo, 2008
Tethepomima holomma Grimaldi & Arillo, 2008 **(PEÑ)**

Type species
Holotype: MCNA-9915
2008 Grimaldi & Arillo, 261.

†Zhangsolvidae
Buccinatormyia Arillo, Peñalver & Pérez-de la Fuente, 2015
Buccinatormyia magnifica Arillo, Peñalver & Pérez-de la Fuente, 2015 **(SOP)**
Type species
Holotype: CES-349.1
2015 Arillo *et al*., 245.
2015 Peñalver *et al*., 1917.
2017 Peris *et al*., 900. (See Peris *et al*., 2017b)
Buccinatormyia soplaensis Arillo, Peñalver & Pérez-de la Fuente, 2015 **(SOP)**
Holotype: CES-015.2 (+CES-392.2) (in two parts)
2015 Arillo *et al*., 249.
2015 Peñalver *et al*., 1917.

Rhagionidae
Litoleptis Chillcott, 1963
Litoleptis fossilis Arillo, Peñalver & García-Gimeno, 2009 **(SJU)**
Holotype: CPT-3344 (SJ-07-26)
2009 Arillo *et al*., 34. (See Arillo *et al*., 2009a)

Atelestidae
Alavesia Waters & Arillo, 1999
Alavesia subiasi Waters & Arillo, 1999 **(PEÑ)**
Type species
Holotype: MCNA-8837
1999 *Alavesia subiasi* (Hybotidae) Waters & Arillo, 60.
2010 *Alavesia subiasi* (Atelestidae): Sinclair & Kirk-Spriggs, 268.
Alavesia prietoi Peñalver & Arillo, 2007 **(CAL)**
Holotype: DGO-3502
2007 *Alavesia prietoi* (Hybotidae) Peñalver & Arillo, 63.
2010 *Alavesia prietoi* (Atelestidae): Sinclair & Kirk-Spriggs, 268.

Hybotidae
Grimaldipeza Solórzano-Kraemer, Sinclair, Arillo &Álvarez-Parra, 2023
Grimaldipeza coelica Solórzano-Kraemer, Sinclair, Arillo &Álvarez-Parra, 2023 **(SOP)**
Type species
Holotype: CES-404.1
2023 Solórzano-Kraemer *et al*., 7.
Grimaldipeza sp. 1 **(SOP)**
Specimen: CES.372
2023 Solórzano-Kraemer *et al*., 11.
Grimaldipeza sp. 2 **(LHO)**
Specimens: MGUV-16348 and MGUV-16349
2023 Solórzano-Kraemer *et al*., 13.

Dolichopodidae
Microphorites Hennig, 1971
Microphorites utrillensis Peñalver, 2008 **(SJU)**
Holotype: CPT-963 (SJ-14)
2008 Arillo *et al*., 31. (See Arillo *et al*., 2008a)
Microphorites sp. **(PEÑ)**
2008 Arillo *et al*., 35. (See Arillo *et al*., 2008a)

†Chimeromyiidae
Chimeromyia Grimaldi & Cumming 1999
Chimeromyia alava Grimaldi & Arillo, 2009 **(PEÑ)**
Holotype: MCNA-9238
2009 Grimaldi *et al*., 48.
Chimeromyina Grimaldi & Arillo, 2009
Chimeromyina concilia Grimaldi & Arillo, 2009 **(PEÑ)**
Type species
Holotype: MCNA-8882
2009 Grimaldi *et al*., 50.

Phoridae
Euliphora Arillo & Mostovski, 1999
Euliphora grimaldii Arillo & Mostovski, 1999 **(PEÑ)**
Type species
Holotype: MCNA-8648
1999 Arillo & Mostovski, 252.

PLANTAE
SPERMATOPHYTA
Gymnospermae, Araucariales
Araucariaceae
Brachyphyllum Brongniart, 1828*
Brachyphyllum obesum Heer, 1881 **(PEÑ)**
Specimens: MCNA 12736 and MCNA 13926
2018 Kvaček *et al*., 645.
Rabagostrobus Kvaček, Barrón, Heřmanová, Mendes, Karch, Žemlička & Dudák, 2018*
Rabagostrobus hispanicus Kvaček, Barrón, Heřmanová, Mendes, Karch, Žemlička & Dudák, 2018 **(PEÑ)**

Specimen: MCNA-13684 (paratype)
2018 Kvaček *et al*., 647.

* The parataxa *Brachyphyllum obesum* and *Rabagostrobus hispanicus* are different parts of the same plant (twigs and pollen cones). They are found as bioinclusions in the amber from Peñacerrada I, but they are also present in El Soplao outcrop outside the amber, in the amber-bearing rock.

Palynomorphs*

* The palynomorphs listed below can be related to Ginkgoales, Cycadales and/or Bennettitales, but a specific assignment to one of these groups or at family level is not possible. They have been found inside amber on the body of pollinating insects, but all the listed palynomorphs are also present in the respective outcrops in the amber-bearing rock (Eduardo Barrón, pers. comm., 2025).

Cycadopites Wodehouse, 1933**
Cycadopites sp. (**PEÑ**)
Specimens: without number and present on thrips of three species
2012 Peñalver *et al*., 8625.
2017 Peris *et al*., 900. (See Peris *et al*., 2017b)
2025 Peñalver *et al*., 3. (See Peñalver *et al*., 2025a)

** This palynomorph has been found inside the amber on the body of thrips and also as isolated spots.

Monosulcites Cookson and Couper, 1953***
Monosulcites sp. (**PEÑ**)
Specimens: without number and present on the beetle *Darwinylus marcosi* (MCNA-11229)
2017 Peris *et al*., 897. (See Peris *et al*., 2017b)

*** This palynomorph has been found inside the amber on the body of a beetle.

Exesipollenites Balme, 1957****
Exesipollenites sp. **(SOP)**
Specimens: without number and present on the fly *Buccinatormyia magnifica* (CES-349.1)
2015 Peñalver *et al*., 1917.
2017 Peris *et al*., 900. (See Peris *et al*., 2017b)

**** This palynomorph has been found inside the amber on the body of a fly, but it is also present in El Soplao outcrop outside the amber as *Exesipollenites tumulus* and *Exesipollenites* sp., in the amber-bearing rock.

General results

Up to date, more than 100 taxonomic papers have been published, with a rapid increase since 2005 (Fig. 7). The number of described species based on bioinclusions to date is 184, with a rapid increase since 2007, from 9 amber type localities. Based on the holotypes, the most prolific amber is Peñacerada I and the best represented arthropod group is Hymenoptera, followed by Diptera and then by Coleoptera (Fig. 9; Table 2). Hymenoptera and Diptera are the most diverse in families represented, followed by Coleoptera and Acariformes/Oribatida (Table 2). Hymenoptera and Diptera contain the most

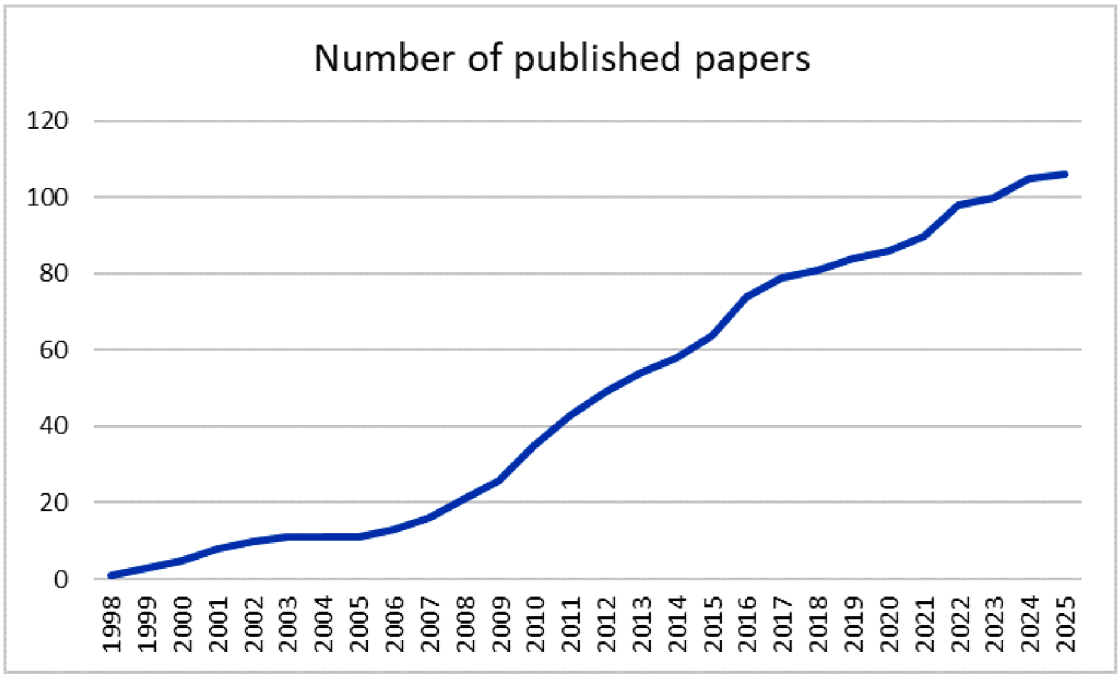

FIGURE 7. Cumulative graph of published taxonomic papers on Spanish amber.

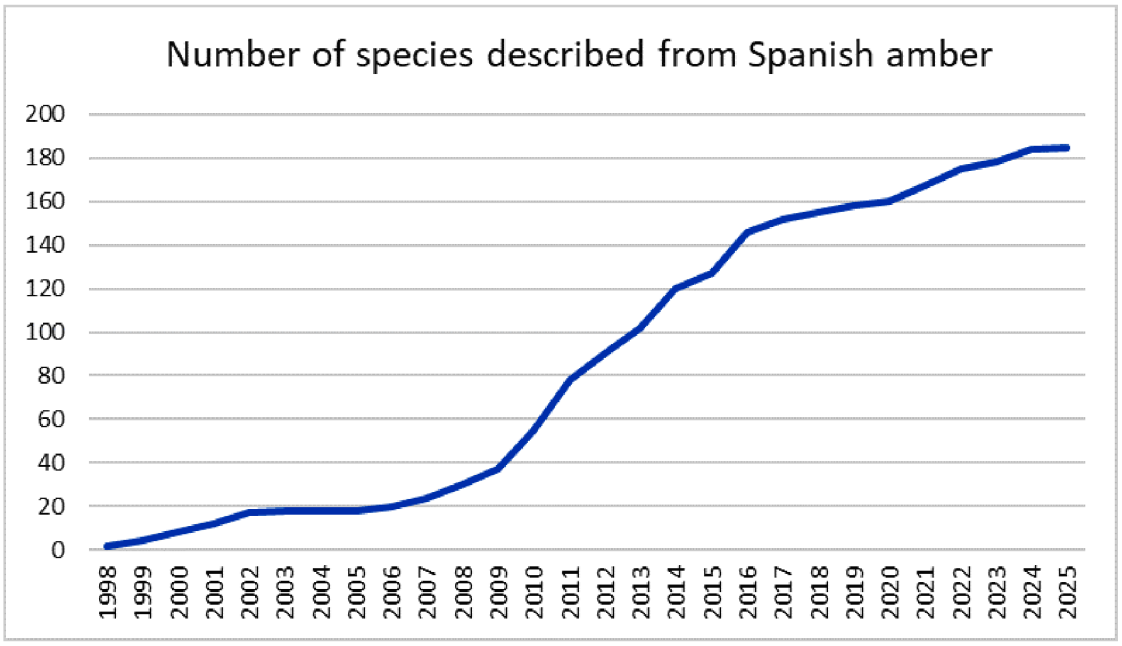

FIGURE 8. Cumulative graph of described species based on bioinclusions in Spanish amber.

TABLE 2. Number of Spanish amber holotypes and number of families represented for each arthropod order. * = one of the families is indet., ** = one of the families has been identified with doubt.

Arthropod order	**Spanish amber holotypes**	**Families represented**
Hymenoptera	51	19
Diptera	39	17
Coleoptera	15	11
Acariformes, Oribatida	13	11
Psocodea	8	3
Araneae, Araneomorphae	7	3
Thysanoptera	6	4
Raphidioptera	6	2
Malacostraca, Tanaidacea	5	2
Collembola, Symphypleona	5	4*
Hemiptera, Heteroptera	5	4*
Blattodea, Isoptera	4	1*
Neuroptera	4	4*
Malacostraca, Isopoda	3	3**
Collembola, Entomobryomorpha	3	1
Orthoptera	3	1
Pseudoscorpiones	2	2
Hemiptera, Sternorrhyncha	2	2
Mantodea	1	1*
Dermaptera	1	1*
Mecoptera	1	1
Acariformes, Trombidiformes	0	1
Lophioneurida	0	1
TOTAL	**184**	**101**

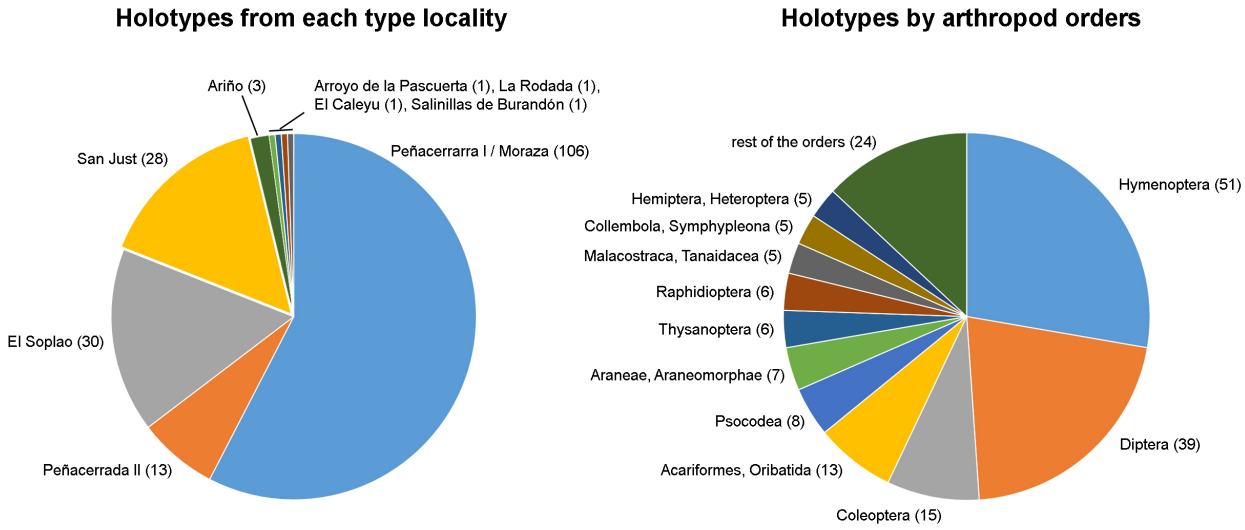

FIGURE 9. Distribution of the 184 Spanish amber holotypes by type localities and by the diverse arthropod groups.

diverse families in genera represented (Scelionidae and Ceratopogonidae, 7 genera each) and the most diverse genera in species represented (*Cretevania* with 5 species and *Helius* with 4 species). Interestingly, all the families of one of the best represented orders, Coleoptera, are living families. Comparing the taxonomic record of Spanish amber with other Cretaceous ambers, notably the richest known, Burmese (Kachin) amber, reveals that Spanish amber boasts the most extensive taxonomic lists of Tanaidacea (Malacostraca) and Acari. Spanish amber mites are three quarters of all mites described in Cretaceous ambers and this distinction is attributable to the Spanish team's emphasis on the study of this arachnid group, a field where the contribution of Dr Luis Subías was paramount.

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