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General Palaeontology

Fossiliferous amber deposits from the Cretaceous (Albian) of Spain

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Abstract

Amber-bearing deposits are a specific kind of fossil bioaccumulation that preserves exceptionally well palaeobiological information from the past. The present article discusses the 'state of the art' of the knowledge of certain Spanish amber-bearing deposits from the Cretaceous (Albian-Cenomanian). A bibliographic compilation of previous studies, together with new discoveries, shows the existence of over 100 amber localities; nevertheless, only in seven of these have arthropod inclusions been found. The sites are Albian in age, associated with coal deposited on deltaic environments. These outcrops are distributed in a strip curve through the North to the East of the Iberian Peninsula and which corresponds to the coastal line during the Early Cretaceous. It includes (from the northwest to the east): the Central Asturian Depression, the Basque-Cantabrian Basin, and the Maestrat Basin, respectively. Infrared spectroscopy (IRTF) analyses show close similarities between all these amber localities. Gas chromatography–mass spectrometry (GC–MS) of the Álava amber suggests that *Agathis* (Coniferales: Araucariaceae) or another closely related group of conifers was one of the resin producer trees of Spanish ambers. Numerous new records and taxa occur in the botanical source for Spanish Cretaceous amber; additional material has been newly excavated in the Moraza-Peñacerrada, Arroyo de la Pascueta, La Hoya, and San Just outcrops. More than two thousand inclusions are found in the Moraza-Peñacerrada sites (Burgos and Álava Provinces). In all the amber outcrops, the dominant group is composed by arthropods, and among them hexapods, with 17 orders being recognized to date. The most abundant and diverse insect groups are dipterans, hymenopterans and coleopterans, mainly parasitoid, saproxylic or herbivorous forms. ***To cite this article: X. Delclòs et al., C. R. Palevol 6 (2007).***

Résumé

Dépôts d'ambre fossilifère du Crétacé (Albien) d'Espagne. Les dépôts d'ambre sont des bioaccummulations à fossiles particulières, préservant de manière exceptionnelle l'information paléobiologique du passé. Dans ce travail, nous exposons les dernières

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connaissances sur les dépôts à ambre du Crétacé d'Espagne (Albien–Cénomanien). Une compilation bibliographique et de nouvelles découvertes montrent l'existence d'une centaine de localités contenant de l'ambre. Jusqu'à présent, seules sept d'entre elles, d'âge Albien, ont livré des inclusions d'arthropodes. Dans ces gisements, correspondant à des paléoenvironnements deltaïques, l'ambre est associé à d'importants dépôts de lignite. Les gisements sont distribués le long d'une courbe allant du Nord jusqu'à l'Est de la péninsule Ibérique, qui correspond à la ligne de côte pendant le Crétacé inférieur et inclut, du nord-ouest jusqu'à l'est, la dépression centrale Asturienne, le bassin Basque-Cantabrique et le bassin du Maestrat. L'analyse des ambres en spectroscopie infrarouge (IRTF) montre de grandes similitudes entre toutes les localités. L'analyse en spectroscopie de masse par chromatographie gazeuse (GC–MS) de l'ambre Álava suggère que *Agathis* (Coniférales : Araucariaceae), ou un autre groupe de conifères étroitement apparenté, ait pu être l'arbre producteur des ambres crétacés en Espagne. Le nouveau matériel excavé dans les gisements de Moraza–Peñacerrada, Arroyo de la Pascueta, La Hoya et San Just a livré de nombreuses inclusions ; plus de 2 miliers d'inclusions ont été trouvées dans les gisements de Moraza–Peñacerrada (provinces de Burgos et d'Álava). Dans tous les gisements d'ambre, les arthropodes constituent le groupe dominant, avec 17 ordres reconnus, les insectes les plus abondants et diversifiés étant les diptères, les hyménoptères et les coléoptères, principalement des formes parasites, saproxyliques ou herbivores. ***Pour citer cet article : X. Delclòs et al., C. R. Palevol 6 (2007).***

Keywords: Amber; Lower Cretaceous; Sedimentary environments; Geochemistry; Palaeobiology; Spain

Mots clés : Ambre ; Crétacé inférieur ; Environnements sédimentaires ; Géochimie ; Paléobiologie ; Espagne

1. Introduction

The fossilization processes imply, in almost all cases, an important loss of palaeobiological information; nevertheless, it is possible to gain sedimentological and palaeoenvironmental information with respect to other deposits [57]. In amber, the fossilization processes imply an excellent preservation of the palaeobiological content. Inclusions in amber show the best palaeobiological and palaeoenvironmental information of organism remains in the fossil record, and in the deposits where amber is placed, their sedimentological, palaeoenvironmental and diagenetic history is recorded as well. The amber deposits should be interpreted as Konservatt-Lagerstätten, not as Koncentrat-Lagerstätten [48], and should be considered as a particular type of fossil concentration with excellent preserved organism remains.

A concentration of organism remains, fossil or not, may be defined as a relatively dense accumulation of biological remains or fossils, independent of the composition in organism remains (one or several different species), their state of preservation, size, or taphonomic degree of modification [24]. The concentration processes may have a very different time range of formation depending on the cases. Amber inclusions can be geologically instantaneous.

Concentrations may be defined descriptively or genetically. Descriptive classification of concentrations includes the taxonomic composition, the internal structure of the deposit, the spatial distribution and disposition of remains, etc. Genetically, the palaeobiological concentrations are usually defined as biogenical, sedimentological or diagenetical, depending on the formation process. Amber inclusions may be classified into biogenical concentrations (a unique piece of amber may contain hundred of insect remains), as well as sedimentological concentrations (many pieces of amber, originally resin, can be found in the same stratigraphic level) [39]. Genetically, concentrations may also be divided into (1) episodic: where concentrations took place in a single layer, and in registered moments of usually unique and brief concentrations, as is the case of insect swarm inclusions, and termite or ant mass mortality due to a copious resin production [3,34]; (2) multiepisodic or composed: where concentration is characterized by an outflow or stalactite resin formation with several episodic sets of resin microlayers; and (3) condensed: with fine multilayers distributed over several centimetres, such as the litter fauna preserved in the Early Cretaceous amber of southwestern France [40].

Amber usually includes remains of organisms that lived close to the resinous trees, inside the forests, and this allows the interpretation of palaeoecological relationships between organisms better than any other fossil deposits. Nevertheless, amber is not usually found at its place of production, but transported by water flows to the final sedimentological deposits [34]. During transport the mixing of resins produced by different trees at different altitudes can occur. For this reason, palaeoecological reconstructions of forests ecosystems based on amber inclusions need to be especially accurate [42].

2. Geological settings of the Early Cretaceous amber-bearing deposits of Spain

The first reference to Spanish Early Cretaceous amber dates from 1762 [18], when the presence of amber

(termed *succino*) was cited in Asturias, including the localities, origin, composition, etc. In the last decade, several other Cretaceous amber localities have been found in Spain. A bibliographic compilation, together with new unpublished discoveries, shows the existence of more than 100 Lower Cretaceous amber localities. Nevertheless, only some of these have as yet been confirmed, and others previously mentioned in old coal mines no longer exist. Furthermore, in some, the fossiliferous content is low. Only in seven outcrops are bioinclusions found: La Hoya in Cortes de Arenós (Castellón Province), Arroyo de la Pascueta in Rubielos de Mora and San Just in Escucha (Teruel Province), Peñacerrada (Álava Province), Moraza (Burgos Province), and El Caleyu and Pola de Siero (Asturias Province). Most of these seven localities are distributed in a strip curve from the North to the East of the Iberian Peninsula, a curve that corresponds to the coastal line during the Early Cretaceous [52]. These locations are usually associated with coal deposited on deltaic environments [22].

In the last six years, the sedimentology, geochemistry, taphonomy and palaeobiology of Spanish amber sites have been widely studied (see references below).

2.1. Age of the amber-bearing deposits

The Spanish Cretaceous amber-bearing deposits range from the Barremian (La Huérguina Fm.) to the Maastrichtian (Tremp Fm.). Up to now, amber with palaeobiological inclusions has only been found in a few localities that are Albian in age and are included in the widely extended Escucha Fm.

2.1.1. Maestrat Basin

To date, incipient palynological studies have been carried out in the Lower Cretaceous amber-bearing deposits from this basin (Fig. 1). The biostratigraphical data are based on the inferred age from other nearby non-amberiferous outcrops of the Escucha Fm. with similar geological context and facies. A Lower–Middle Albian age for Escucha Fm. is stipulated on the basis

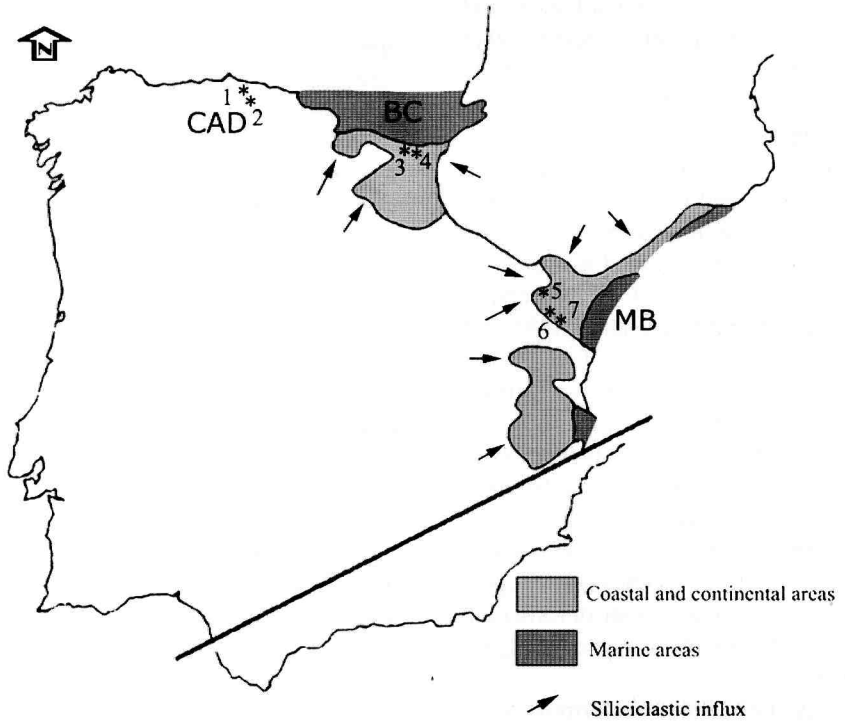


Fig. 1. Map of Spain showing the location of the Albian–Cenomanian basins and the Albian amber-bearing localities where palaeobiological inclusions are found. **MB**: Maestrat Basin, **BCB**: Basque Cantabrian Basin, **CAD**: Central Asturian Depression. **1**. Pola de Siero, **2**. El Caleyu, **3**. Peñacerrada (= Peñacerrada II), **4**. Moraza (= Peñacerrada I), **5**. San Just, **6**. Arroyo de la Pascueta, **7**. La Hoya. Early–Middle Albian Iberian Plate reconstruction after [45].

Fig. 1. Carte d'Espagne montrant la localisation des bassins de l'Albien–Cénomanien et les localités à ambre de l'Albien où ont été trouvées les inclusions paléobiologiques. **MB** : Bassin du Maestrat, **BCB** : bassin basque Cantabrique, **CAD** : dépression centrale Asturienne. **1**. Pola de Siero, **2**. El Caleyu, **3**. Peñacerrada (= Peñacerrada II), **4**. Moraza (= Peñacerrada I), **5**. San Just, **6**. Arroyo de la Pascueta, **7**. La Hoya. Reconstitution de la plaque Ibérique dans l'Albien Inférieur–Moyen, d'après [45].

of assemblages integrated by a predominance of spores (mainly *Cicatricosisporites* and *Cyathidites*) over bisaccate pollen grains [51]. This age is corroborated by the presence of the ammonite *Douvilleiceras monile* (Zone with *Mammillatum*) in the Traigera area [31].

The amber localities of La Hoya, Arroyo de la Pascueta, and San Just (Fig. 1) are included in the Escucha Fm. site in the Maestrat Basin [43,44]. This basin, along with other Mesozoic basins of the Iberian Peninsula, is characterized by listric faults that occurred during a significant rift stage of the Oxfordian–Albian interval, associated with the opening of the northern part of the Atlantic [45,46].

During the Early Cretaceous, the sedimentation in the Maestrat Basin was dominated by sandstones, limestones and marls, deposited in shallow marine and freshwater environments (tide-influenced deltas); even so, during the Lower–Middle Albian, at the end of the rift stage, deltaic and estuarine systems developed and evolved vertically into a deltaic system dominated by a fluvial environment with siliciclastic sedimentation, represented by the Escucha Fm. This formation has traditionally been subdivided into three members that appear in sedimentological continuity, denominated as follows: (a) the lower or Barriada Member, (b) the middle or Regachuelo Member, and (c) the upper or La Orden Member. These members are differentiated into two groups of facies [43]: the lower delta plains (that comprise the tide plain and the belt of salt marshes), and the upper delta plains with the flood and fluvial plains. Up to now, amber deposits have only been found in the upper part of the Barriada Member and in the El Regachuelo Member (they are more abundant in the latter), which consist of brackish water swamp belt and freshwater swamp plain deposits, respectively [44].

2.1.2. *Basco-Cantabrian Basin*

The Moraza and Peñacerrada palynological assemblages suggest an Upper Aptian–Lower Albian age due to the presence of *Distaltriangulatisporites costatus*, *Gregussisporites orientalis*, and *Phlebopteris globosus*, as well as pollen grains of ancient angiosperms related to the top of Zone I of the Potomac Group [11]. This Zone is characterised by the presence of monosulcate pollen grains of the genera *Liliacidites*, *Stellatopollis*, *Retimonocolpites*, the species *Clavatipollenites hugessii* and small, scarce reticulate tricolpate pollen grains of the genus *Tricolpites*.

The amber sites at Moraza and Peñacerrada (Peñacerrada I and II respectively in previous references) (Fig. 1) are also included in the Escucha Fm. (previously cited as Nograro Fm.), and in the Lower Albian in the Basco-Cantabrian Basin. In this basin, the Escucha Fms. are divided into three subunits (not correlated with the three members established for this formation in the Maestrat Basin). It is represented in this area by a deltaic succession that shows a vertical tendency to a depositional regression of this deltaic system in the lower–middle subunits, and a vertical transgression in the upper one. Amber deposits are always associated with coal layers that are more abundant in the middle member of the formation [35], coinciding with the period of maximum regression and the deltaic progradation [35,46]. The major amber accumulations took place at the top of the filling sequences of the interdistributaries deltaic bays. Sometimes, thin levels rich in coal with amber are found at the top of channels or on crevasse splay facies, and also possibly in the abandoned channels. The lower subunit is predominantly composed of grey clays or heterolytic deposits with sparse intercalations of carbonate sandstones with orbitolinids; the middle subunit is characterized by sandstones and siliceous microconglomerates from channel filling, and abundant coal levels. The upper subunit is predominantly composed of grey lutitic with intercalation of carbonate sandstones with orbitolinids, bivalves, etc. [35].

2.1.3. *Central Asturian Depression*

The amber from Asturias is found in several localities, mainly situated in the central Asturian Depression (Fig. 1), an east–west-elongated depression extending along 90 km between Oviedo and Cangas de Onis. Cretaceous sediments in the central Asturian Depression range in age from Late Albian to Santonian, although Coniacian and Santonian outcrops have not yielded amber. The main localities with amberiferous outcrops are located near the cities and villages of Oviedo, Pola de Siero, Infiesto, Nava, and Corao. Amber has been found in the Ullaga Fm. (Upper Albian), Corao Fm. (Lower Cenomanian), El Caleyu Fm. (Lower Cenomanian), La Manjoya Fm. (Lower-Middle Cenomanian), and Las Tercias Fm. (Upper Cenomanian–Middle or Upper Turonian) [16,29]. Other amber-bearing outcrops are located in the coastal area (Llanes town) in Aptian sediments.

Insects are only found in El Caleyu and Pola de Siero localities in the Ullaga Formation [2]. The amber-bearing levels of the Ullaga Fm. are mainly composed by grey siltstones and silty marls with abundant oysters, ostracodes, foraminifers, selachian remains, and different leaf remains [2,15]. In the amber-bearing locality of the stratotypic El Caleyu Fm. the amber is rich in bioinclusions, although the insects have not been studied yet.

Amberiferous levels in this locality are found in lenticular layers of black limes that correspond to lag deposits of intertidal channels, associated with abundant plant remains. The amber has frequent plant inclusions, mainly roots, suggesting that this material was included in the soil before its transport to the intertidal area [2].

3. Material and methods

Only in Peñacerrada-Moraza have intensive extractions of amber been performed [20]. In La Hoya (Cortes de Arenós) and Arroyo de la Pascueta (Rubielos de Mora), more minor palaeontological excavations have been done. In the other fossil localities of Spain, all the material collected was picked over by hand, and left unselected by size.

4. Collections

4.1. Teruel outcrops

The fossiliferous amber outcrops in the Maestrat Basin are San Just, Arroyo de la Pascueta and La Hoya. The richest site is San Just, which contains the best-preserved bioinclusions. Up to now, the bioinclusions' collections from these deposits have been poor, but an extensive excavation in San Just outcrop is planned. The material is housed in the 'Fundación Conjunto Paleontológico de Teruel-Dinópolis' (CPT collection) and in the 'Museu de Geologia de la Universitat de València' (MGUV collection). Some of the specimens recorded are especially interesting, such as several Evaniidae, one thrip, and specimens of Araneae (body fossils and spider web remains).

4.2. Álava outcrops

The Moraza and Peñacerrada ambers (also called the Álava ambers) show an impressive diversity, abundance and state of preservation of the included organisms. The 10% of the material from excavations performed over the past two years have alone revealed approximately 2300 arthropod inclusions, constituting one of the most diverse Mesozoic terrestrial microbiota, together with New Jersey, French, Lebanese, Burmese, Siberian, and Canadian ambers. The preliminary study of the organisms trapped in Álava amber allowed us to establish a faunistic profile at the ordinal level (Fig. 2). Insects are the dominant class of this amber fauna, among which Diptera and Hymenoptera are predominant as in the San Just amber, and in all Cenozoic and other Cretaceous ambers as well. All the material from these outcrops is housed in the 'Museo de Ciencias Naturales de Álava' (MCNA collection).

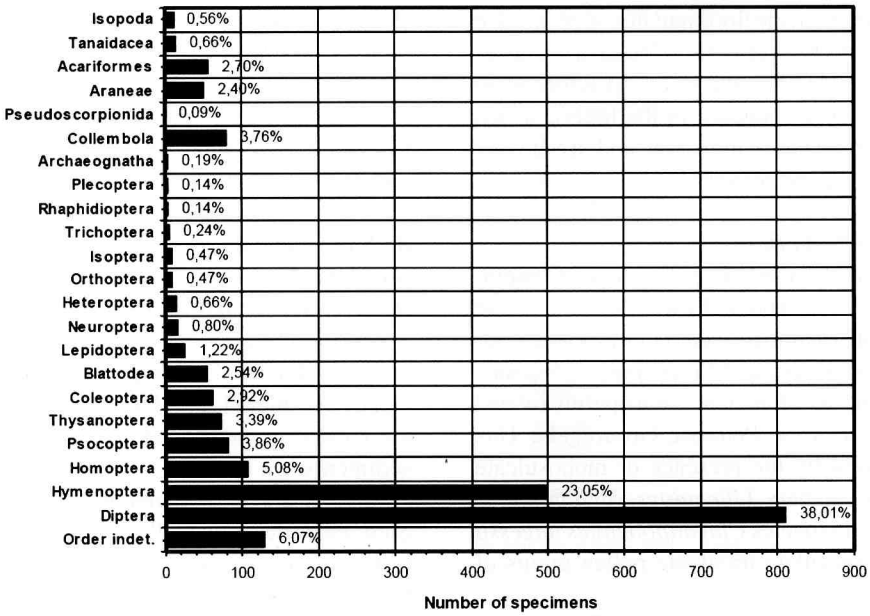


Fig. 2. Frequency distribution of arthropods found in Álava amber. The total number of arthropods found in the other localities is extremely low in comparison.

Fig. 2. Distribution de fréquences des arthropodes trouvés dans l'ambre d'Álava. Le nombre total des arthropodes trouvés dans des autres localités à ambre est, en comparaison, très bas.

4.3. Asturias outcrops

The fossiliferous amber deposits from the Central Asturian Depression are El Caleyu and Pola de Siero. El Caleyu contains very clear amber with abundant bioinclusions, but this has not been excavated yet. But even if the Cenomanian amber has not yet yielded bioinclusions, it would be of great interest because it enables future comparisons between different Mesozoic terrestrial microbiotas in the Iberian and European plates. The specimens recorded up to now are housed in the 'Museo de la Universidad de Oviedo' (MUO Collection).

5. Geochemistry of the amber

Ambers have been widely studied by solid-state spectroscopic techniques such as IRTF, cross-polarization of ^{13}C nuclear magnetic resonance spectroscopy, etc., but the majority of fossil resins show similar patterns that do not allow their clear classification. Gas chromatography–mass spectrometry (GC–MS) makes it possible to determine the individual non-volatile components of the fossil resin and their molecular structure, and this technique can provide evidences of their resin producer [30].

IRTF analyses have been made in pieces from all the amber-bearing deposits with palaeobiological inclusions. All the IR spectra correspond with the previous results obtained from the Peñacerrada–Moraza samples [1]: spectra dominated by C–H stretching bands near 2950 cm^{-1}, C–H bending between 1470 and 1380 cm^{-1} and the carbonyl bands close to 1700 cm^{-1}. Also, the lack of exocyclic methylenic bands at 880, 1640 and 3070 cm^{-1} are consistent with the high degree of maturity of these Cretaceous ambers.

GC–MS studies of the Spanish ambers have only been performed on the Peñacerrada–Moraza ambers [1,19]. The analysis of their residual compounds suggests a possible plant affinity of the amber. The amber is rich in kauranes that are abundant in the araucariaceans, especially in the genus *Agathis* (Coniferales: Araucariaceae), and the absence of tetracyclic diterpenoids and amyrins and other triterpanes discards their origin in podocarpaceans and burseraceans, respectively. The lack of α-cedrene and cuparene also suggests the unreliability with the cupressaceans, and the absence of bicadinanes and tricadinanes also eliminates the dipterocarpaceans as a producer. Pimaric acid and related compounds are distinctive of resins from *Agathis* genus. Derivative specific compounds found in these ambers that may originate from agathic acid suggest that *Agathis,* or another close relationship group of Coniferales, was one of the tree resin producers of Spanish ambers.

6. Plants and palynomorphs related to amber-bearing deposits

The Lower Cretaceous amber-bearing deposits of Spain are always associated with coal and are rich in plant megaremains that appear as coalified compressions. Therefore, branchlets of Cheirolepidiaceae and leaflets of Bennettitales have been recorded in both the Rubielos de Mora (Barranco de la Pascueta) and the Peñacerrada-Moraza outcrops [1,25]. In addition, pinna fragments of *Weichselia reticulata*, male cones of Cheirolepidiaceae, ovuliferous scales of Bennettitales, wood of *Agathoxylon* sp., and leaves of Ginkgoales and *Pseudotorellia* sp. were only found in the Barranco de la Pascueta outcrop [25,26], which includes (at the top of the stratigraphic section) the amber locality with insects named Arroyo de la Pascueta. In this outcrop, plant cuticles of diverse Cretaceous gymnosperms such as *Nehvizdya penalveri*, *Frenelopsis turolensis*, and *Classostrobus turolensis* are also found [27,28]. In the Valle del Río Martín, some plant-bearing levels in the Regachuelo and La Orden members have been located [49], and these enclose ferns, Ginkgoales, Bennettitales, Caytoniales, Cycadales, cheirolepidacean conifers, and angiosperms. In the same stratigraphic levels, the tree fern *Weichselia reticulata* has been recognized [23].

The amberiferous sediments of the Basque–Cantabrian Basin have yielded rich and diverse palynological assemblages integrated by vascular cryptogam spores, gymnosperm and angiosperm pollen grains, dinoflagellate cysts, acritarchs and phycomas of prasinophycean algae [1,11]. Their study revealed high percentages of pollen grains related to Araucariaceae, which agrees with the chemical data on amber [1,19]. Coniferous forests formed by Araucariaceae, Cupressaceae/Taxodiaceae and Cheirolepidiaceae with a rich undergrowth constituted by Lycophyta, Pteridophyta (mainly Schizaeaceae and Cyatheaceae/Dicksoniaceae), and other gymnosperms such as cycads, Bennettitales, and Gnetales, as well as ancient angiosperms, developed in the Basque–Cantabrian Basin during the Lower Cretaceous. Coastal cheirolepidiacean and lowland fern forests lived on a delta plain and grew under warm and wet climatic conditions.

The amberiferous outcrops from the Maestrat Basin also yielded rich and diverse palynofloras, but their study is still fragmentary and incomplete. The assemblages from the Oliete Subbasin present conspicuous percentages of pteridophytic spores of

Cyatheaceae/Dicksoniaceae and Schizaeaceae, inaperturate pollen grains (mainly *Inaperturopollenites dubius* and *Classopollis*). The pollen grains of ancient angiosperms are very scarce at this locality [41,51]. The Barranco de la Pascueta outcrop also exhibits high percentages of pollen grains of Cheirolepidiaceae and Cupressaceae/Taxodiaceae [26,41]. However, the spores present lower diversity than in the Oliete Subbasin, those of Cyatheaceae/Dicksoniaceae being predominant. The ancient angiosperms are well represented by several genera of monosulcate and tricolpate pollen grains such as *Clavatipollenites*, *Brenneripollis*, and *Tricolpites* [41].

The scarce plant remains that occur in the amberiferous outcrops of the Central Asturian Depression have not been studied yet [2].

7. Amber fossil inclusions

7.1. Plant inclusions

The plant-related inclusions in Spanish amber are scarce. They have been recorded in ambers from the Maestrat, Basque–Cantabrian and Asturian basins; however, to date, no study of these inclusions has been carried out. Particularly, the amber from Peñacerrada and Moraza has yielded a relatively high number of undetermined fragments of leaves possibly related to gymnosperms, flattened and prostrate sheet-like bodies similar to those found in lichens and liverworts, herbaceous leafy branches possibly related to gametophytes of mosses, and very scarce cupressaceous-like shoots of conifers. Sometimes amber pieces with inaperturate pollen grains similar to those of Araucariaceae occur.

7.2. Other non-Animalia inclusions

In the Peñacerrada and Moraza ambers, the application of different light and SEM techniques has allowed the characterization of different microstructures with ultrastructural details that have been interpreted as protozoa and fungal hyphae [9,10]; however, the structures interpreted as fungal hyphae are fossil bacteria for other authors [47]. Clear fungal hyphae have been found in El Caleyu, San Just [39] and La Hoya ambers (Fig. 3A). Likewise, the presence of mummified bacteria trapped in the fossil gas bubbles has been recorded.

7.3. Arthropods

Specimens of Crustacea, Arachnida and mainly Hexapoda have been found in Spanish amber (Fig. 2). The majority of specimens originate from the Peñacerrada-Moraza amber, but a few of them are found in almost five other fossil localities.

7.3.1. Crustacea

This group is represented in Peñacerrada-Moraza amber by the orders Isopoda (Fig. 3B) and Tanaidacea (Fig. 3C). Around 14 inclusions found in this amber belong to Tanaidacea, although they were first assigned to Amphipoda [1]. A similar number of specimens (12) are assigned to Isopoda. Neither of these two orders has been studied yet.

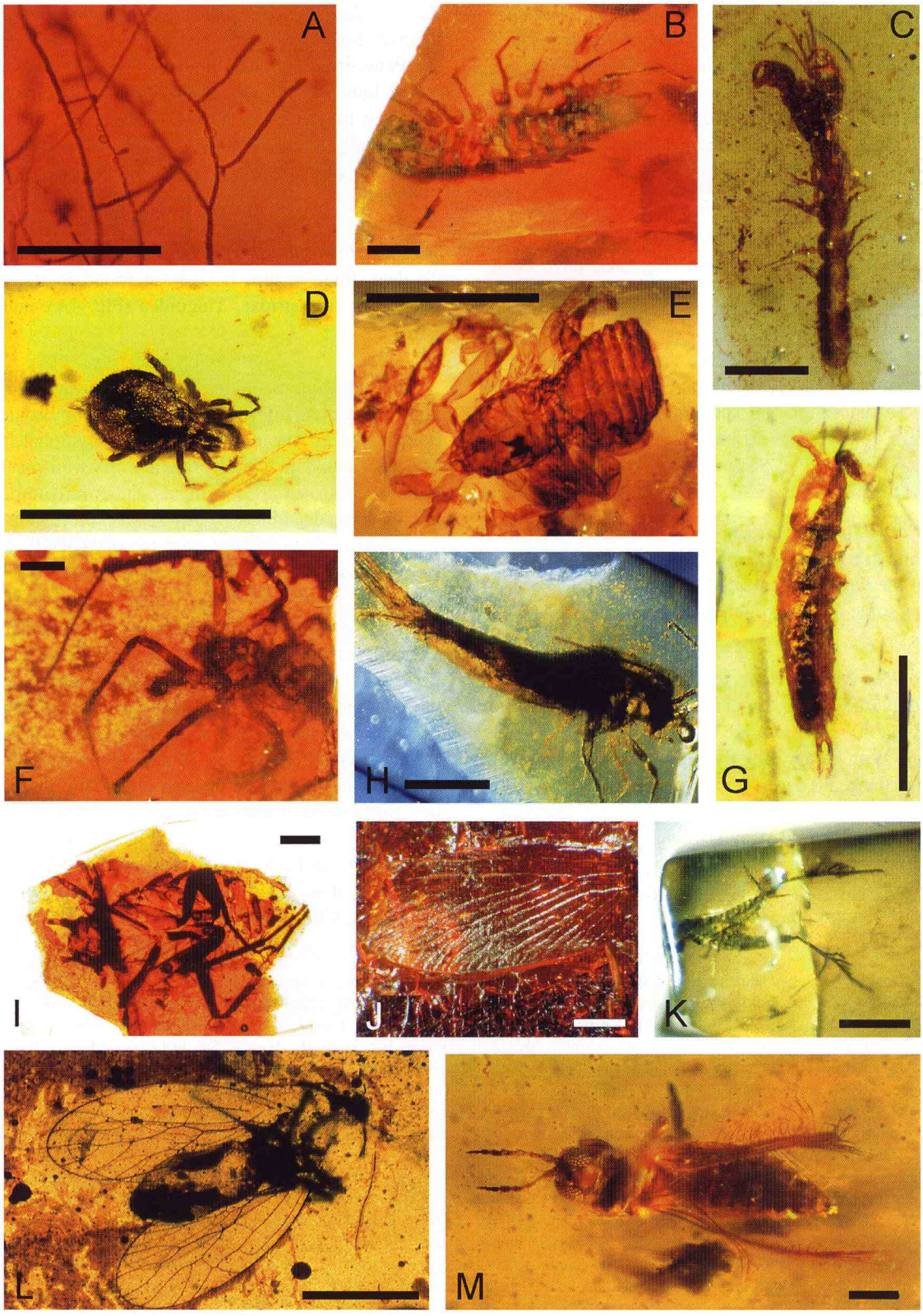
7.3.2. Arachnida

Arachnids are represented by three orders: Acari, Pseudoscorpionida, and Araneae. All the mites (Acari) known in the Peñacerrada-Moraza ambers (around 57 specimens) belong to the Acariformes (Fig. 3D), including the suborders Oribatida (Cryptostigmata) and Trombidiformes (Prostigmata). Among oribatids (beetle mites), two families have been recorded: Archaeorchestidae was described in Álava amber [6] with a new genus and species: *Archaeorchestes minguezae*. Family Cepheidae was also recorded [7], with the new species *Eupterotegaeus bitranslamellatus*. Several trombidid specimens have been found also but still remain undescribed, although parasitic larvae belonging to the genus *Leptus* (family Erythraeidae) have been recorded. The order Pseudoscorpionida has only very recently been discovered and only two specimens have been found in the Álava amber (Fig. 3E). One of the most remarkable discoveries in Spanish amber corresponds to Araneae web portions, which are found in the Álava and San Just ambers [38]. Body fossils of spiders (Order Araneae) are common, and to date 51 specimens have been found in the Peñacerrada–Moraza ambers; they include Mesozygiella dunlopi, the oldest true orb-weaving spider (Araneidae) [37], and also the oldest lagonomegopid spider [36]. Some spider specimens are also found in the amber of the Maestrat (Fig. 3F); nevertheless, in the majority of the specimens, their study is very difficult.

7.3.3. Hexapoda

Most of the inclusions found in Spanish ambers belong to Hexapoda. To date 17 orders of insects have been recognized.

7.3.3.1. Collembola.. Springtails are common in Álava amber (Fig. 3H); with at least 80 specimens recorded. Up to 6 families and 8 genera were recognized [50], suggesting an important preservation of litter or tree bark fauna: Arrhopalitidae, Bourletiellidae, Isotomidae (sev-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eral specimens and three genera recognized), Neanuridae, Onychiuridae and Sminthuridae. All genera have recent species: *Micranurida* and *Onychiurus*, which are euedaphic, *Anurophorus, Proisotoma* and *Cryptopygus*, with a hemiedaphic habitat, two with an atmobious habitat, *Sminthurus* and *Fasciosminthurus*, and *Arrhopalites*, with a troglophilous one.

7.3.3.2. Archaeognatha. Only four specimens belonging to the order Archaeognatha (Fig. 3G) have been found and are still unstudied.

7.3.3.3. Blattodea. Cockroaches are represented in Spanish ambers as both juvenile and adult (winged) specimens. To date about 50 specimens are known from the Álava amber (Fig. 3I) and two from the La Hoya amber.

7.3.3.4. Orthoptera. This order is only known in the Álava amber as seven small juvenile individuals of one form of the family Elcanidae (Fig. 3K), mainly exuviae remains, some of them highly disarticulated.

7.3.3.5. Psocoptera. Book lice are a well-represented and widely studied order in the Álava amber (Fig. 3L). To date, about 80 specimens are known, and the following taxa have been recognized: the family Archaeatropidae, including the genus and species *Archaeatropos alavensis* [12]; family Manicapsocidae with the species *Manicapsocidus enigmaticus* [13], and two new genera and three new species, *Empheropsocus arilloi*, *Empheropsocus margineglabrus*, and *Preempheria antiqua* belonging to the family Empheriidae [14].

7.3.3.6. Thysanoptera. Thrips are recorded in diverse Spanish ambers (around 70 specimens in the Peñacerrada–Moraza amber). Possibly they belong to the family Stenurothripidae, like the specimen that has been found in the San Just amber (Fig. 3M) [39]. The family Aeolothripidae was previously cited in the Álava amber [1], but this identification must be reviewed.

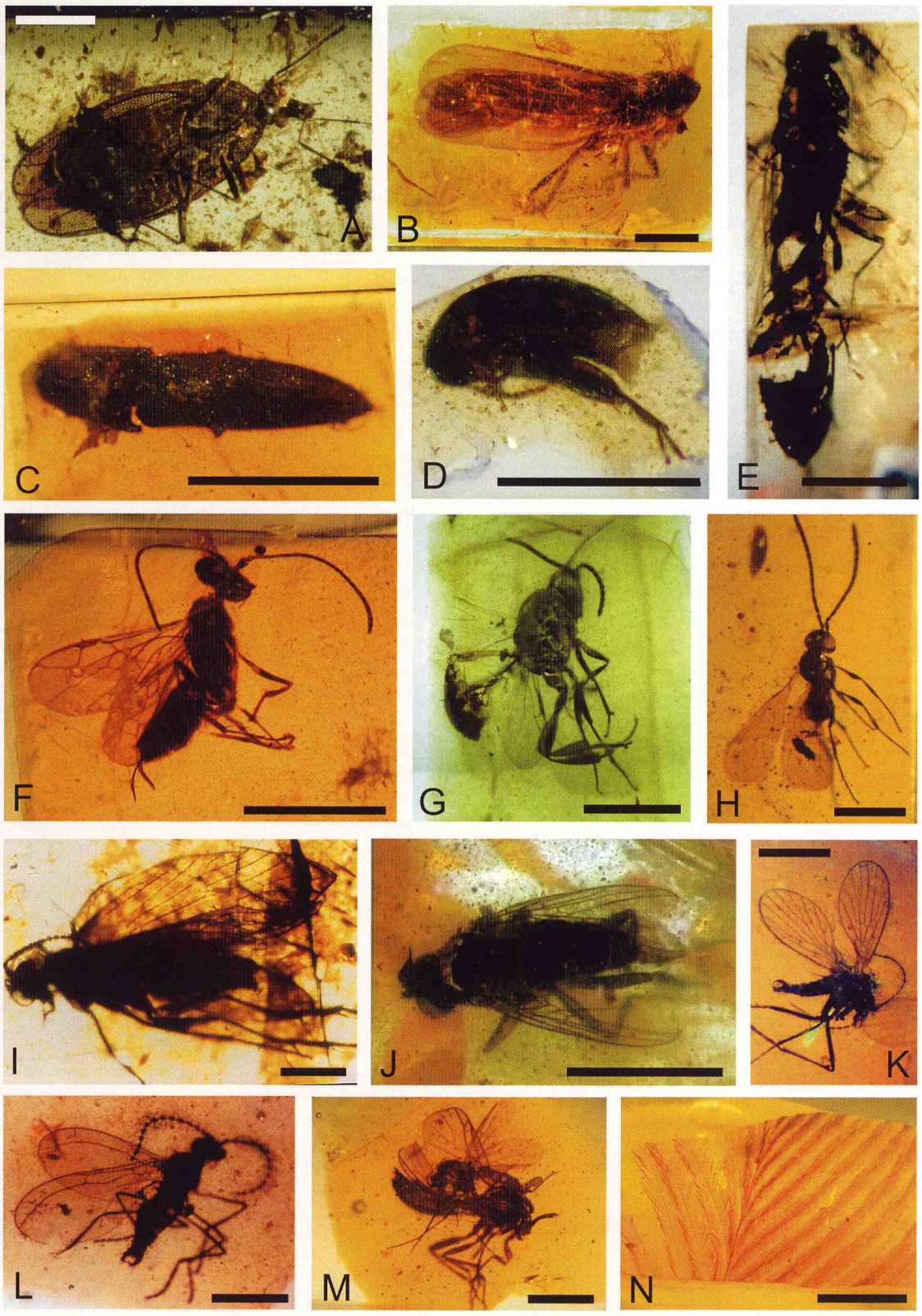
7.3.3.7. Heteroptera. True bugs are not very common. To date, three groups have been found in the Álava amber: Hydrometridae, Tingoidea (Fig. 4A), and Saldoidea.

7.3.3.8. Homoptera. This order is represented in the Álava amber with numerous specimens. Fulgoroidea are represented in Álava amber as scarce nymphal forms. The most abundant homopterans are very well-preserved scale insects (over 20 specimens). Other rare homopterans are winged aphidoids. Only one fulgoroid individual from Arroyo de la Pascueta site and one Cicadomorpha from the San Just site (Fig. 4B) are known.

7.3.3.9. Coleoptera. Up to now, no systematic studies on beetle remains from Spanish amber outcrops has been performed. Nevertheless, several polyphagan families have been identified, most of them related to herbivorous or saproxylic habits, and some carnivorous or carrion feeders. In the Peñacerrada–Moraza amber outcrops has been found a record of at least eight families of beetles. Herbivorous beetles are represented by wood-boring forms of the families Elateridae (Fig. 4C), Bostrichidae, Dascillidae, and Scraptiidae, and probably by weevils (?Curculionidae family). Cucujoids are represented by the family Cucujidae, most probably with saproxylic

Fig. 3. Diverse palaeobiological inclusions in Spanish Lower Cretaceous ambers. (**A**) Fungi hyphae, La Hoya amber, Cortes de Arenós, Maestrat Basin, MGUV Coll., scale bar: 0.1 mm. (**B**) Isopoda individual, Álava amber, Basco-Cantabrian Basin, MCNA 9924, scale bar: 1 mm. (**C**) Crustacea Tanaidacea, Álava amber, MCNA 12704, scale bar: 1 mm. (**D**) Acari, Oribatida, Cepheidae, *Eupterotegaeus bitranslamellatus*, Álava amber, MCNA 9943a, scale bar: 1 mm. (**E**) Pseudoscorpionida, Álava amber, MCNA 13271, scale bar: 1 mm. (**F**) Araneae, San Just amber, Maestrat Basin, CPT Coll., scale bar: 1 mm. (**G**) Collembola Isotomidae, *Cryptopygus* sp., Álava amber, MCNA 9273, scale bar: 0.25 mm. (**H**) Archaeognathan specimen, Álava amber, MCNA 8638, scale bar: 1 mm. (**I**) Adult cockroach, La Hoya amber, MGUV Coll., scale bar: 1 mm. (**J**) Isopteran forewing, Álava amber, MCNA 12803, scale bar: 1 mm. (**K**) Forelegs of an orthopteran Elcanidae, Álava amber, MCNA-9150, scale bar: 0.5 mm. (**L**) Psocoptera Archaeotropidae, *Archaeatropos alavensis*, Álava amber, MCNA-8640, scale bar: 0.5 mm. (**M**) Thysanoptera Stenurothripidae, San Just amber, CPT-971, scale bar: 1 mm.

Fig. 3. Inclusions paléobiologiques dans les ambres du Crétacé inférieur d'Espagne. (**A**) Hyphe de champignon, ambre de La Hoya, Cortes de Arenós, bassin du Maestrat, coll. MGUV, échelle : 0,1 mm. (**B**) Isopode, ambre d'Álava, bassin Basque-Cantabrique, MCNA-9924, échelle : 1 mm. (**C**) Crustacea Tanaidacea, ambre d'Álava, MCNA-12704, échelle : 1 mm. (**D**) Acari, Oribatida, Cepheidae, *Eupterotegaeus bitranslamellatus*, ambre d'Álava, MCNA-9943a, échelle : 1 mm. (**E**) Pseudoscorpionida, ambre d'Álava, MCNA-13271, échelle : 1 mm. (**F**) Araneae, ambre de San Just, bassin du Maestrat, Coll. CPT, échelle : 1 mm. (**G**) Collembola Isotomidae, *Cryptopygus* sp., ambre d'Álava, MCNA-9273, échelle : 0,25 mm. (**H**) Spécimen d'archaeognathe, ambre d'Álava, MCNA-8638, échelle : 1 mm. (**I**) Adulte de blattidé, ambre de La Hoya, Coll. MGUV, échelle : 1 mm. (**J**) Aile antérieure d'isoptère, ambre d'Álava, MCNA-12803, échelle : 1 mm. (**K**) Patte antérieure d'orthoptère Elcanidae, ambre d'Álava, MCNA-9150, échelle : 0,5 mm. (**L**) Psocoptera Archaeotropidae, *Archaeatropos alavensis*, ambre d'Álava, MCNA-8640, échelle : 0,5 mm. (**M**) Thysanoptera Stenurothripidae, ambre de San Just, CPT-971, échelle : 1 mm.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habits. Carrion-beetles are composed by members of the families Staphyllinidae and Scydmaenidae. Even if the greater part of the latter families are usually found in Cretaceous ambers, there are certain forms found in this locality that are scarcely represented in other Mesozoic outcrops, such as Scirtidae (Fig. 4D) and Ptilodactylidae, whose adults are terrestrial, but present aquatic herbivorous larvae, and family Dascillidae, whose comparatively large body size makes their record in resins poor. At the moment, the San Just outcrop has only yielded one beetle specimen, identified as a member of the family Cucujidae [39]. Up to now, no members of the Archostemata or Adephaga suborders have been found in the Spanish ambers.

7.3.3.10. Hymenoptera. Two groups of Hymenoptera have been discovered, Symphyta and Apocrita [32,33]. Symphyta is represented by a single specimen of Anaxyelidae (Fig. 4E) and represents the latest record for this wood-boring Mesozoic family, except for a unique extant species found from California to southern central British Columbia. This specimen is the only one found in ambers and probably belongs to the genus *Eosyntexis*. The Apocrita is divided into Parasitica and Aculeata. The hymenopterans found in the Spanish ambers, as for all the Mesozoic ambers, belong mainly to Parasitica, with nine families recognized: Orussidae, Trigonalidae, Evaniidae, pre-Megaspilidae, Scelionidae, Stigmaphronidae, Serphitidae, Mymarommatidae, and Braconidae. Members are primary parasitoids or hyperparasitoids to other insect adults, larvae or eggs, or arthropods. Aculeata make up 4% of hymenopterans and belong to three or four families: Sphecidae, Chrysididae, Bethylidae, and possibly a new family of the superfamily Chrysidoidea.

Orussids are extremely scarce in the fossil record. Some individuals are found in the Spanish amber, and represent the earliest species of the family [56]. Recent orussids have a diet of woodboring insect larvae, primarily coleopterans. Trigonalids appear during the Lower Cretaceous, but are rare as amber inclusions, although common in compression fossil sites; the specimens found in Spanish ambers are the earliest representatives of the family (Fig. 4F). Evaniidae is another family that appears for the first time in the Lower Cretaceous record. The species of basal evaniids do not show all the synapomorphies of the recent representatives of the family, mainly related to the wing venation, antennal morphology and ovipositor length [21]. Four different species of the genera *Cretevania* and *Protoparevania* are recognized, which are close to those previously found in the Lebanese amber. The genus *Cretevania* is present in the ambers of Álava, San Just (Fig. 4G), Arroyo de la Pascueta and La Hoya. Only a few Megaspilids are found in the Cretaceous ambers. The specimens from Spanish ambers show some wing and body characters that are not observed in other fossil or recent forms; before their study, these forms have been named as pre-Megaspilidae group. Species of Stigmaphronidae are exclusive from the Cretaceous and are the second largest family collected (18% of hymenopterans). It appeared and developed profusely during the Lower Cretaceous, but decreased during the Late Cretaceous. Scelionidae is the largest hymenopteran family occurring in these ambers, which is recorded in six out of the seven sites, with more than 58% of hymenopteran individuals collected, and with more than five species represented. This family of parasitic wasps appears frequently in the Lower Cretaceous ambers, but decreases in importance in the Upper Cretaceous. Serphitidae is a fossil

Fig. 4. Diverse zoological inclusions in Spanish Lower Cretaceous ambers. (**A**) Heteropteran Tingoidea, Álava amber, Basco-Cantabrian Basin, MNCA-10656, scale bar: 0.5 mm. (**B**) Homoptera Cicadomorpha, San Just amber, Maestrat Basin, CPT. Coll., scale bar: 1 mm. (**C**) Coleoptera Elateridae, Álava amber, MNCA-9734, scale bar: 1 mm. (**D**) Coleoptera Scirtidae, Álava amber, MCNA-8995, scale bar: 1 mm. (**E**) Hymenoptera Anaxyelidae, Álava amber, MCNA-8756, scale bar: 1 mm. (**F**) Hymenoptera Trigonalidae, Álava amber, MCNA-9928, scale bar: 1 mm. (**G**) Hymenoptera Evaniidae, San Just amber, CPT-960, scale bar: 1 mm. (**H**) Hymenoptera Braconidae, San Just amber, CPT Coll., scale bar: 0.5 mm. (**I**) Lepidoptera Micropterygidae, Álava amber, MCNA-8642, scale bar: 0.5 mm. (**J**) Diptera Hybotidae, El Caleyu amber, Central Asturian Depression, MUO Coll., scale bar: 1 mm. (**K**) Diptera Psychodidae, Álava amber, MCNA-8647, scale bar: 1 mm. (**L**) Diptera Cecidomyiidae, *Eltxo cretaceous*, Álava amber, MCNA-8824, scale bar: 0.25 mm. (**M**) Diptera Mycetophilidae and Ceratopogonidae, San Just amber, CPT Coll., scale bar: 1 mm. (**N**) Isolated feather, Álava amber, MCNA-13332, scale bar: 1 mm.

Fig. 4. Inclusions zoologiques dans les ambres du Crétacé inférieur d'Espagne. (**A**) Heteroptera Tingoidea, ambre d'Álava, bassin Basque-Cantabrique, MNCA-10656, échelle : 0,5 mm. (**B**) Homoptera Cicadomorpha, ambre de San Just, bassin du Maestrat, Coll. CPT, échelle : 1 mm. (**C**) Coleoptera Elateridae, ambre d'Álava, MNCA-9734, échelle : 1 mm. (**D**) Coleoptera Scirtidae, ambre d'Álava, MCNA-8995, échelle : 1 mm. (**E**) Hymenoptera Anaxyelidae, ambre d'Álava, MCNA-8756, échelle : 1 mm. (**F**) Hymenoptera Trigonalidae, ambre d'Álava, MCNA-9928, échelle : 1 mm. (**G**) Hymenoptera Evaniidae, ambre de San Just, CPT-960, échelle : 1 mm. (**H**) Hymenoptera Braconidae, ambre de San Just, Coll. CPT, échelle : 0,5 mm. (**I**) Lepidoptera Micropterygidae, ambre d'Álava, MCNA-8642, échelle : 0,5 mm. (**J**) Diptera Hybotidae, ambre de El Caleyu, dépression centrale Asturienne, Coll. MUO, échelle : 1 mm. (**K**) Diptera Psychodidae, ambre d'Álava, MCNA-8647, échelle : 1 mm. (**L**) Diptera Cecidomyiidae, *Eltxo cretaceous*, ambre d'Álava, MCNA-8824, échelle : 0,25 mm. (**M**) Diptera Mycetophilidae et Ceratopogonidae, ambre de San Just, Coll. CPT, échelle : 1 mm. (**N**) Plume isolée, ambre d'Álava, MCNA-13332, échelle : 1 mm.

family also restricted to the Cretaceous. Two out of the only three known genera (*Aposerphites* and *Serphites*) appear in Spanish ambers. Other specimens show a set of characters which are used to differentiate the Recent Mymarommatidae from other families of Chalcidoidea, such as Mymaridae. These specimens may allow an accurate analysis of the phylogenetic relationship within these groups. Braconidae is another new group that appears during the Lower Early Cretaceous, as Tenthredinidae, Ichneumonidae, Proctotrupidae, Cynipidae, Chalcidoidea, Pompilidae, Vespoidae, Scelionidae, and Sphecidae, which are characteristic of present-day communities. This group of hymenopterans is only found in the Moraza–Peñacerrada amber (Fig. 4H).

Chrysididae is the best represented Aculeata family in the amber of Peñacerrada–Moraza, and all individuals seem to belong to the Cleptinae subfamily. Species of this family are abundant during the Early Cretaceous, mainly in compression deposits, constituting a minor group in amber. Some of the individuals seem to belong to a new family of Chrysidoidea. Species of Bethylidae are commonly found in ambers since the Early Cretaceous. Nevertheless, they did not become dominant before the Late Cretaceous. Sphecidae species are more common in the Lower Cretaceous deposits than in the Upper Cretaceous and Tertiary ones. Four, possibly five individuals are found, but they have an unusual wing venation.

7.3.3.11. Lepidoptera. Moths are well represented in Álava amber with about 25 specimens found. All of them are rather 'primitive', with functional mandibles, belonging to the family Micropterygidae (Fig. 4I).

7.3.3.12. Diptera. True flies and mosquitoes are by far the best represented order in the amber outcrops, almost reaching 38% of all biological inclusions (Fig. 2). Several families are recognized and some of them have already been studied. The order is divided into two classical groups: Nematocera and Brachycera, both being represented in Spanish ambers. Nematocerans are represented by at least nine families: Limoniidae, Psychodidae, Chironomidae, Ceratopogonidae, Cecidomyiidae, Anisopodidae, Scatopsidae, Mycetophilidae, and Keroplatidae; some other specimens of the Sciaroidea have also been found. Brachycerans are represented by five families: Hybotidae, Phoridae, Dolichopodidae, Lonchopteridae, and Rhagionidae. The majority of them came from the Peñacerrada–Moraza ambers but some families, such as Ceratopogonidae, Empididae/Hybotidae, Dolichopodidae, Chironomidae and Mycetophilidae, are also found in other Spanish ambers (El Caleyu, San Just and La Hoya).

The family Limoniidae is represented by more than 10 specimens in the Álava amber and shows a great diversity; the larvae are associated with wet environments. Chironomidae are rather frequent but still remain unstudied; their larvae are aquatic and detritivorous, and the adults usually develop in swamps. Ceratopogonidae are very common in the Álava amber and have recently been found in the San Just amber also (Fig. 4M); several species have been described: *Archiaustroconops alavensis* and *Protoculicoides skalskii* (with long proboscis and haematophagous habits) [53], and *Leptoconops zherikhini* [54]. The genus *Austroconops* has also been recorded. Ceratopogonids have diverse habits with aquatic to terrestrial larvae; some adults can be haematophagous, others carnivorous and some feed on the nectar of flowers. Psychodidae are very frequent in Álava amber (Fig. 4K) but probably most of them belong to a single species close to the genus *Eophlebotomus*; the larvae of psychodids live in wet environments, and some species have haematophagous habits. Cecidomyiidae has barely appeared in the Álava amber, but all the specimens have been studied (Fig. 4L); the larvae are usually mycophagal, and develop in decaying organic matter. The forms already recognized are: *Cretohaplusia ortunoi* and *Eltxo cretaceous* [5], *Alavamanota hispanica* and *Allocotocera xavieri* from the family Mycetophilidae [17], and *Hegalari antzinako* and *H. minor*, belonging to the family Keroplatidae [17]; other specimens of Mycetophilidae are also found in San Just (Fig. 4M); this group is mainly mycophagal. Further specimens of Sciaroidea have been studied [8], but are still undescribed. Families Anisopodidae and Scatopsidae have also been recognized, but still remain undescribed; the larvae of both anisopodids and scatopsids are saprophagal from decaying organic matter. Family Bibionidae was first reported [1], but it was indeed erroneously recognized and remains to date unknown in Spanish ambers.

Brachycera present a high diversity in Álava amber, but the greater part of the specimens are still under study. Species already described are: *Alavesia subiasi* from the Hybotidae family [55] (this genus is also represented in El Caleyu amber, Fig. 4J), and *Euliphora grimaldii* from the family Phoridae [4]. Other Brachycera have been recognized as close to the genera *Microphorites* (Dolichopodidae) and *Chimeromyia* (undetermined family), but are still unpublished. The genus *Microphorites* is also represented in the San Just amber. Specimens of the families Lonchopteridae that live on decaying organic matter, and Rhagionidae (with carnivorous larvae inhabiting stagnant waters) have also been recognized.

7.3.3.13. Other orders with scarce and unstudied recorded data. Ten fragments of termite wings are recognized in Álava amber (Fig. 3J); to date no complete specimens have been found. Only one specimen of Plecoptera, or stone flies, has been recently recorded in the Álava amber. Neuropterans are rare, with only 16 adult specimens and one larva found in the Álava amber. Three very fragmentary specimens are believed to belong to the order Raphidioptera, but further studies are needed. Lastly, five individuals of caddisflies have been found in the Álava amber.

7.4. Vertebrates

Vertebrates are only represented by a small number of little feathers from dinosaurs or Aves in the amber of Peñacerrada–Moraza (Fig. 4N). This material is currently under study.

8. Conclusions

Mesozoic amber-bearing deposits have been traditionally considered as scarce in the geological record, but several new amber outcrops have been discovered around the world in the last few years. In Spain, more than 100 localities of Early Cretaceous age have been located, seven of them with palaeobiological inclusions. All these outcrops are located in a strip curve that corresponded to the coastal line during the Early Cretaceous (in deltaic and swamp environments).

The geochemical analysis of the fossiliferous amber indicates *Agathis* or another genus close to Coniferales as one of the resin producers.

Plants are not only preserved in the amber, they are also preserved in the sediments. This circumstance allows the reconstruction of the ancient forests where the fauna later preserved in the amber developed. These forests were formed by different groups of Coniferales, with a rich undergrowth of ferns, other gymnosperms and angiosperms.

Outcrops from Álava have been more exhaustively sampled than the rest of the amber-bearing outcrops, but the fauna assemblage found in all the outcrops preserves some similarities. As in the greater part of the amber faunas, the one recorded from the Spanish Lower Cretaceous localities is dominated by arthropods, mainly hexapods, and among them dipterans, hymenopterans, and coleopterans. The greater part of the animals found in the amber is related to trees, both directly (wood-eating or saproxylic forms such as some dipterans and beetles) and indirectly (parasitoids or hunters on the forms related with the wood, as hymenopterans or spiders). Other forms suggest a root-produced resin, with the important presence of litter forms, such as springtails or isopods. In the Spanish amber, sites, there is also an important record of forms related to water during their larval stages (such as some beetles or dipterans groups), which suggests a certain proximity with at least partially inundated areas.

Finally, and as shown by the current knowledge of the amber-bearing localities from the Spanish Lower Cretaceous, with well-preserved, abundant and diverse palaeoflora and palaeofauna, and the discovery of more than a hundred new localities, the collection of new amber samples in these outcrops and the study of their palaeobiological content will allow the reconstruction of the forests that evolved during this period in Spain.

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References

[1] J. Alonso, A. Arillo, E. Barrón, J.C. Corral, J. Grimalt, J.F. López, X. Martínez-Delclòs, V. Ortuño, E Peñalver, P.R. Trincaõ, A new fossil resin with biological inclusions in Lower Cretaceous deposits from Álava (Northern Spain, Basque-Cantabrian Basin), J. Paleontol. 74 (2000) 158–178.

[2] M. Arbizu, E. Bernárdez, E. Peñalver, M.A. Prieto, El ámbar de Asturias, Est. Mus. Cien. Nat. Álava 14 (1999) 245–254.

[3] A. Arillo, Paleoethology: fossilized behaviours in amber, Geol. Acta (in press).

[4] A. Arillo, M. Mostovski, A new genus of Prioriphorinae (Diptera, Phoridae) from the Lower Cretaceous amber of Alava (Spain), Stud. Dipterol. 6 (1999) 251–255.

[5] A. Arillo, A. Nel, Two new fossil Cecidomyiid flies from the Lower Cretaceous amber of Alava (Spain) (Diptera, Cecidomyiidae), Bull. Soc. Entomol. 105 (2000) 285–288.

[6] A. Arillo, L.S. Subías, A new fossil oribatid mite, *Archaeorchestes minguezae* gen. nov., sp. nov. from the Spanish Lower Cretaceous amber. Description of a new family, Archaeorchestidae (Acariformes, Oribatida, Zetorchestoidea), Mitt. Geol. Paläontol. Inst. Univ. Hamburg 84 (2000) 231–236.

[7] A. Arillo, L.S. Subías, Second fossil oribatid mite from the Spanish Lower Cretaceous amber. *Eupterotegaeus bitranslamellatus* n. sp. (Acari, Oribatida, Cepheidae), Acarologia 42 (2002) 403–406.

[8] A. Arillo, H. Hippa, A new genus and species of sciaroid fly from Lower Cretaceous amber of Spain (Diptera: Sciaroidea), Abstracts on Fossilsx3 Congress, Pretoria, South Africa, 2005, p. 11.

[9] C. Ascaso, J. Wierzchos, J.C. Corral, R. López, J. Alonso, New applications of light and electron microscopic techniques for the study of microbiological inclusions in amber, J. Paleontol. 77 (2003) 1182–1192.

[10] C. Ascaso, J. Wierzchos, M. Speranza, J.C. Gutiérrez, A. Martín-González, A. De Los Ríos, J. Alonso, Fossil protist and fungi in amber and rock substrates, Micropaleontology 51 (2005) 59–72.

[11] E. Barrón, M.J. Comas-Rengifo, L. Elorza, Contribuciones al estudio palinológico del Cretácico Inferior de la Cuenca Vasco-Cantábrica: los afloramientos ambarígenos de Peñacerrada (España), Col. Paleont. 52 (2001) 135–156.

[12] A. Baz, V.M. Ortuño, Archaeatropidae, a new family of Psocoptera from the Cretaceous amber of Álava, northern Spain, Ann. Entomol. Soc. Am. 93 (2000) 367–373.

[13] A. Baz, V.M. Ortuño, A new electrentomoid psocid (Psocoptera) from the Cretaceous amber of Alava (Northern Spain), Dtsch. Entomol. Z. 48 (2001) 27–32.

[14] A. Baz, V.M. Ortuño, New genera and species of empheriids (Psocoptera: Empheridae) from the Cretaceous amber of Álava, northern Spain, Cretaceous Res. 22 (2001) 575–584.

[15] E. Bernárdez, Unidades litoestratigráficas del Cretácico de la Depresión Central Asturiana, Bol. Geol. Min. 18 (1994) 11–25.

[16] E. Bernárdez, Los dientes de seláceos del Cretácico de la Depresión Central Asturiana, unpublished PhD thesis, Universidad de Oviedo, Spain, 2002 (p. 476).

[17] V.A. Blagoderov, A. Arillo, New Sciaroidea (Insecta: Diptera) in Lower Cretaceous amber from Spain, Stud. Dipterol. 9 (2002) 31–40.

[18] G. Casal, Historia natural y médica del Principado de Asturias, Servicio de Publicaciones, Principado de Asturias, Oviedo, facsimile edition, 1762.

[19] R. Chaler, J. Grimalt, Fingerpinting of Cretaceous higher plant resins by infrared spectroscopy and gas chromatography coupled to mass spectrometry, Phytochem. Anal. 16 (2005) 446–450.

[20] J.C. Corral, R. López del Valle, J. Alonso, El ámbar cretácico de Álava (Cuenca Vasco-Cantábrica, Norte de España): su colecta y preparación, Est. Mus. Cien. Nat. Álava 14 (1999) 7–21.

[21] A.R. Deans, H.H. Basibuyuk, D. Azar, A. Nel, Descriptions of two new Early Cretaceous (Hauterivian) ensign wasp genera (Hymenoptera: Evaniidae) from Lebanese amber, Cretaceous Res. 25 (2004) 509–516.

[22] X. Delclòs, E. Peñalver, A. Arillo, V. Ortuño, R. López del Valle, C. Soriano, Spanish Mesozoic amber localities, Abstracts on Fossilsx3 Congress, Pretoria, South Africa, 2005, p. 43.

[23] J.B. Díez, L.M. Sender, U. Villanueva-Amadoz, J. Ferrer, C. Rubio, New data regarding *Weichselia reticulata*: Soral clusters and the spore developmental process, Rev. Palaeobot. Palynol. 135 (2005) 99–107.

[24] F.T. Fursich, Fossil concentrations and life and death assemblages, in: D.E.G. Briggs, P.R. Crowther (Eds.), Palaeobiology: A Synthesis, Blackwell Scientific, London, 1990, pp. 235–239.

[25] B. Gomez, G. Barale, C. Martín-Closas, F. Thévenard, M. Philippe, Découverte d'une flore à Ginkgoales, Bennettitales et Coniférales dans le Crétacé inférieur de la formation Escucha (chaîne ibérique orientale, Teruel, Espagne), N. Jahrb. Geol. Paläontol. Mh. (1999) 661–675.

[26] B. Gomez, C. Martín-Closas, N. Solé de Porta, G. Barale, F. Thévenard, Précisions géologiques, paléobotaniques, taphonomiques et paléoenvironnementales sur le gisement à cuticules végétales du Crétacé inférieur de Rubielos de Mora (chaîne Ibérique, Espagne), Monograf. Acad. Cien. Exactas Fis. Nat. Zaragoza 16 (1999) 32–34.

[27] B. Gomez, C. Martín-Closas, G. Barale, F. Thévenard, A new species of *Nehvizdya* (Ginkgoales) from the Lower Cretaceous of the Iberian Ranges (Spain), Rev. Palaeobot. Palynol. 111 (2000) 49–70.

[28] B. Gomez, C. Martín-Closas, G. Barale, N. Solé de Porta, F. Thévenard, G Guignard, *Frenelopsis* (Coniferales: Cheirolepidiaceae) and related male organ from the Lower Cretaceous of Spain, Palaeontology 45 (2002) 997–1036.

[29] B. González-Fernández, E. Menéndez-Casares, M. Gutiérrez-Claverol, J.C. García-Ramos, Litoestratigrafía del sector occidental de la cuenca cretácica de Asturias, Trab. Geol. 24 (2004) 43–80.

[30] J.O. Grimalt, B.R.T. Simoneit, P.G. Hatcher, A. Nissenbaum, The molecular composition of ambers, Org. Geochem. 13 (1988) 677–690.

[31] R. Martínez, A. Grauges, R. Salas, Distribución de los ammonites del Cretácico inferior de la Cordillera Costera Catalana e Ibérica Oriental, Cuad. Geol. Iber. 18 (1994) 337–354.

[32] X. Martínez-Delclòs, E. Peñalver, A. Rasnitzyn, Los Hymenoptera del ámbar del Cretácico Inferior de Álava (País Vasco, España), Abstract World Congress on amber inclusions, Vitoria-Gasteiz, Spain, 1998, p. 119.

[33] X. Martínez-Delclòs, E. Peñalver, A. Rasnitzyn, Hymenopteran insects from the Lower Cretaceous amber of Álava (Spain), Abstract VII Internacional Symposium on Mesozoic Terrestrial Ecosystems, Buenos Aires, Argentina, 1999, p. 42.

[34] X. Martínez-Delclòs, D.E.G. Briggs, E. Peñalver, Taphonomy of insects in carbonates and amber, Palaeogeogr., Palaeoclimatol., Palaeoecol. 203 (2004) 19–64.

[35] L.M. Martínez-Torres, V. Pujalte, S. Robles, Los yacimientos de ámbar del Cretácico Inferior de Montoria-Peñacerrada (Álava, Cuenca Vasco-Cantábrica): estratigrafia, reconstrucción paleogeográfica y estructura tectónica, Est. Mus. Cien. Nat. Álava 18 (2003) 9–32.

[36] D. Penney, The oldest lagonomegopid spider, a new species in Lower Cretaceous amber from Álava, Spain, Geol. Acta 4 (2006, in press).

[37] D. Penney, V.M. Ortuño, Oldest true orb-weabing spider (Araneae: Araneidae), Biol. Lett. (2006 published online).

[38] E. Peñalver, D.A. Grimaldi, X. Delclòs, Early Cretaceous Spider Web with its prey, Science 312 (2006) 1761.

[39] E. Peñalver, X. Delclòs, C. Soriano, A new and rich amber outcrop with palaeobiological inclusions from the Lower Cretaceous of Spain, Cretaceous Res. (in press).

[40] V. Perrichot, Early Cretaceous amber from south-western France: insight into the Mesozoic litter fauna, Geol. Acta 2 (2004) 9–22.

[41] D. Peyrot, J.P. Rodríguez-López, E. Barrón, N. Meléndez, A.R. Soria, Nuevas aportaciones a la Palinología del Cretácico Inferior

de la Subcuenca de Oliete (Fm. Escucha, Teruel), Fundamental 6 (2005) 165–168.

[42] G. Poinar, R. Poinar, The Amber Forest. A Reconstruction of a Vanished World, Princeton University Press, Princeton, NJ, USA, 1999 (p. 239).

[43] X. Querol, R. Salas, El sistema deposicional deltaico del Albiense medio en la cuenca del Maestrazgo. Cordillera Ibérica Oriental, II Congreso Geológico de España, Granada, Sec. Estratigrafía-Sedimentología (1988) 173–176.

[44] X. Querol, R. Salas, G. Pardo, L. Ardevol, Albian coal-bearing deposits of the Iberian Range in northeastern Spain, in: P.J. McCabe, J.T. Parrisch (Eds.), Controls on the Distribution and Quality of Cretaceous Coals, Geological Society of America, Boulder, Colorado Spec. Pap. 267 (1992) 193–208.

[45] R. Salas, J. Guimerá, Estructura y estratigrafía secuencial de la cuenca del Maestrazgo durante la etapa de rift Jurásica superior-Cretácica inferior (Cordillera Ibérica Oriental), Bol. Geol. Min. 108 (1997) 393–402.

[46] R. Salas, J. Guimerà, R. Mas, C. Martín-Closas, A. Meléndez, A. Alonso, Evolution of the Mesozoic Central Iberian Rift System and its Cainozoic inversion (Iberian chain) in: P.A. Ziegler, W. Cavazza, A.H.F. Robertson, S. Crasquin-Soleau (Eds.), Peri-Tethys memoir 6: Peri-Tethyan Rift/Wrechn Basins and Passive Margins, Mém. Mus. natl Hist. nat. 186 (2001) 145–185.

[47] A.R. Schmidt, U. Schafer, *Leptotrichites resinatus*: new genus and species, A fossil sheathed bacterium in alpine Cretaceous amber, J. Paleontol. 79 (2005) 175–184.

[48] A. Seilacher, Begriff und Bedeutung der Fossil-Lagertstätten, N. Jahrb. Geol. Paläontol. Mh. (1970) 34–39.

[49] L.M. Sender, J.B. Díez, J. Ferrer, D. Pons, C. Rubio, Preliminary data on a new Albian flora from the Valle del Río Martín, Teruel, Spain, Cretaceous Res. 26 (2005) 898–905.

[50] J.C. Simón-Benito, V.M. Ortuño, D. Espantaleón, Colémbolos, (Collembola, Insecta) del ámbar cretácico de Álava, Est. Mus. Cien. Nat. Álava 17 (2002) 83–91.

[51] N. Solé de Porta, X. Querol, R. Cabanes, R. Salas, Nuevas aportaciones a la Palinología y Paleoclimatología de la Formación Escucha (Albiense inferior-medio) en las Cubetas de Utrillas y Oliete. Cordillera Ibérica Oriental, Cuad. Geol. Iber. 18 (1994) 203–215.

[52] G. Stampfil, G. Borel, W. Cavazza, J. Mosar, P.A. Ziegler, The Paleotectonic Atlas of the PeriTethyan Domain, European Geophysical Society, 2004 (CD).

[53] R. Szadziewski, A. Arillo, Biting midges (Diptera: Ceratopogonidae) from the Lower Cretaceous amber from Alava, Spain, Pol. Pis. Entomol. 67 (1998) 291–298.

[54] R. Szadziewski, A. Arillo, The oldest fossil record of the extant subgenus *Leptoconops (Leptoconops)* (Diptera: Ceratopogonidae), Act. Zool. Crac. 46 (2003) 271–275.

[55] S.B. Waters, A. Arillo, A new genus of Hybotidae (Diptera, Empidoidea) from Lower Cretaceous amber of Alava (Spain), Stud. Dipterol. 6 (1999) 59–66.

[56] L. Wilhemlsen, The old wasp and the tree: fossils, phylogeny and biogeography in the Orussidae (Insecta, Hymenoptera), Biol. Linn. Soc. 82 (2003) 139–160.

[57] M.W.H. Wilson, Taphonomic Processes: Information Loss and Information Gain, Geosci. Can. 15 (1988) 131–148.