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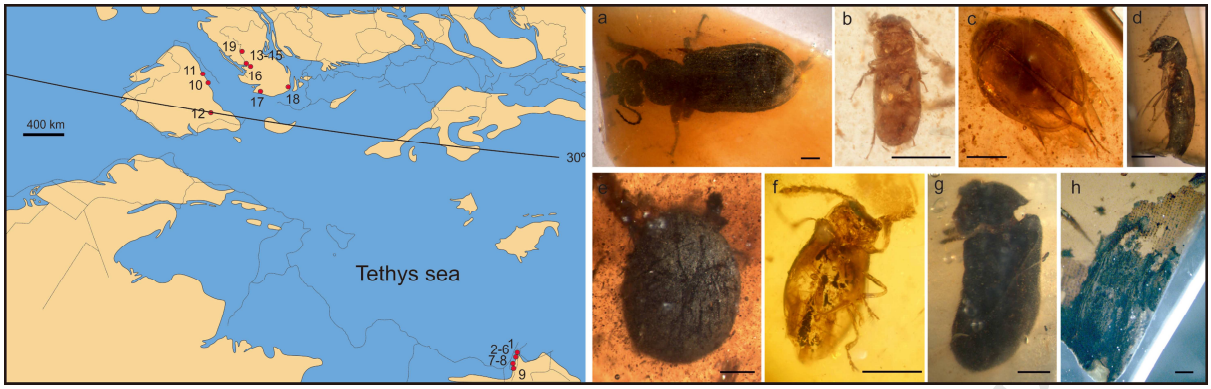
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# Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers

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## ABSTRACT

The intense study of coleopteran inclusions from Spanish (Albian in age) and French (Albian–Santonian in age) Cretaceous ambers, both of Laurasian origin, has revealed that the majority of samples belong to the Polyphaga suborder and, in contrast to the case of the compression fossils, only one family of Archostemata, one of Adephaga, and no Myxophaga suborders are represented. A total of 30 families from Spain and 16 families from France have been identified (with almost twice bioinclusions identified in

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Spain than in France); 13 of these families have their most ancient representatives within these ambers. A similar study had previously only been performed on Lebanese ambers (Barremian in age and Gondwanan in origin), recording 36 coleopteran families. Few lists of taxa were available for Myanmar (Burmese) amber (early Cenomanian in age and Laurasian in origin). Coleopteran families found in Cretaceous ambers share with their modern relatives mainly saproxylic and detritivorous habits in the larval or adult stages, rather than wood-boring behavior. Fifteen of the coleopteran families occur in both the Lebanese and Spanish ambers; while only five are present in both Spanish and French. Considering the paleogeographic proximity and similarity of age of the Spanish and French ambers, the small number of taxa found in common at both areas is surprising. The ancient origin for the Lebanese and Spanish ambers, the paleogeography (including some barriers for terrestrial biota) and the local paleohabitats are factors that may explain the dissimilarity with the French specimens. Wildfires are believed to be a more likely cause of resin production during the Cretaceous than infestation by beetles. Current knowledge of the beetle species found in the Cretaceous ambers is introduced.

KEYWORDS

Beetle, Fossil, Laurasia, Gondwana, resin production

## 1. Introduction

In the early Cretaceous, the Tethys Ocean occupied a vast paleogeographic area (Fig. 1a). It was flanked by passive margins to the southern side, while terrain that had started to drift away from that margin before the Cretaceous supported shallow carbonate

platforms in the central zone. The northern margin was characterized by a subduction zone that consumed oceanic crust alongside Laurasia (Skelton, 2003). The Tethyan margins were covered by vast gymnosperm-dominated forests (Ziegler et al., 1993; Burgoyne et al., 2005; Coiffard et al., 2012; Peralta-Medina and Falcon-Lang, 2012; Zhou et al., 2012). According to the evidence of the paleoenvironment and taphonomical factors, copious amounts of resin were produced and eventually fossilized to become amber in these forests (Martínez-Delclòs et al., 2004). The modern Myanmar amber deposit corresponds to the former eastern Tethys Ocean (Cenomanian in age, Figs. 1a and 3). Thousands of bioinclusions have been found in it and, at the moment, Myanmar is the area with the highest production of Cretaceous amber (also called Burmese amber) in the world (Shi et al., 2012). In the central part of the Tethys Ocean, close to the African continent, the Lebanese amber forests developed (Barremian in age, Figs. 1b and 3). A few thousand bioinclusions have been found in it at various localities, making Lebanese amber the most ancient that has yielded an important number of insects (Azar et al., 2010). Finally, along the western margin of the Tethys Ocean, in the proto-Atlantic, forests dominated by conifers developed and they gave rise to the Spanish (Albian in age) and French ambers (Albian–Santonian in age, Figs. 1b and 3) (Peñalver and Delclòs, 2010; Perrichot et al., 2010; Perrichot and Néraudeau, 2014).

Coleoptera (commonly known as beetles) is the most species-rich order of animals on Earth, with no less than 386,500 species described (Grimaldi and Engel, 2005; Ślipiński et al., 2011). Coleoptera is divided into four suborders: Archostemata, Adephaga, Myxophaga, and Polyphaga. Polyphaga contains the largest number of species (almost 90% of the whole Coleoptera order), characterized by extremely diverse feeding habits.

Beetles inhabit almost all available niches and exploit a huge variety of food. However, the major ecological contribution of coleopterans comes from their role in the decomposition of plant and animal debris and the formation of organic soil (Crowson, 1981). The term saproxylic has been established to refer to all dead-wood fauna, defined by Speight (1989) as: "species of invertebrate that are dependent, during some part of their life cycle, upon the dead or dying wood of moribund or dead trees (standing or fallen), or upon wood-inhabiting fungi, or upon the presence of other saproxylics". Hence, it refers to an entire functional group that has associations with an array of dead-wood habitats, including representatives from all the major insect orders, especially beetles and flies (Grove, 2002). It is important to note that variation in the host specificity of saproxylics may refer to the associated fungi, rather than of the beetles themselves (Kaila et al., 1994; Jonsell et al., 2001).

Beetles *s. l.* appeared around 290 million years ago (Ma) in the Permian (Hunt et al., 2007; Kirejtshuk et al., 2014), although putative stem-group Coleopterida have been proposed from the late Carboniferous (approximately 300 Ma) (Nel et al., 2013). Fossil beetle descriptions are often based on imprints or compressions of isolated elytra in rocks and their classification is sometimes unclear. Distinctive features, such as the rostrum of weevils, short elytra of staphylinids, and the elytral sculpturing of cupedoids, are not always detectable (Grimaldi and Engel, 2005). Consequently, a detailed interpretation of fossils is sometimes complex and left incomplete. The fauna clearly differs between the early and late Cretaceous, with the former being more similar to the Jurassic than the latter, and shows a divergence in some of the major polyphagan lineages present today (Ponomarenko, 2002; Grimaldi and Engel, 2005). Speculation as to whether flowering plants had any influence or coevolved with pollinators (including beetles) during the Cretaceous (Crowson, 1981; Farrell, 1998; Grimaldi, 1999; Grimaldi

and Engel, 2005; Hunt et al., 2007; Friis et al., 2011) or they were already present when angiosperms appeared (Labandeira and Currano, 2013; Wang et al., 2013; Smith and Marcot, 2015) is still debated.

The early Cretaceous yields the first amber inclusions of fossil coleopterans. This led to better morphological character preservation, and clearer definitions of the paleoecosystems (Martínez-Delclòs et al., 2004; Labandeira, 2014). Fossiliferous Cretaceous amber sites yielding beetles are known from the Lebanon and surrounding areas (Barremian; Maksoud et al., 2014), Spain (Albian; Peñalver and Delclòs, 2010; Barrón et al., 2015), France (Albian–Santonian; Perrichot et al., 2007, 2010; Perrichot and Néraudeau, 2014), Myanmar (Cenomanian; Cruickshank and Ko, 2003; Shi et al., 2012), Ethiopia (Cenomanian, although with some controversy; Schmidt et al., 2010), United States of America (Turonian; Grimaldi and Engel, 2005), Russia (Taymir–controversial Late Cretaceous; Rasnitsyn and Quicke, 2002) and Canada (Campanian; McKellar et al., 2008) (Fig. 3 and Appendix 2). Among them, the Lebanese, Spanish and French sites are particularly interesting due to their great abundance and diversity of arthropods, and their faunal compositions are well documented. By contrast, Myanmar amber fossils, as happens with other recent ambers such as Baltic *s. l.* (Eocene) or Dominican and Mexican (Miocene) (Fig. 3), are distributed in both public and private collections, and consequently the real proportions of their paleobiological content is difficult to establish. Coleoptera have been recorded in all Cretaceous ambers with bioinclusions (e.g., Poinar, 1992; Rasnitsyn and Ross, 2000; Grimaldi et al., 2000, 2002; Poinar and Milki, 2001; Penney, 2010; Schmidt et al., 2010); but the information that could be extracted after analysis of these collection has only recently begun to be exploited and it is still not included in recent compiling work (e.g., Smith and Marcot, 2015).

Historically, the involvement of xylophagous beetles in massive resin production has been suggested by several authors for different amber localities and ages (Poinar, 1992; Bright and Poinar, 1994; Martínez-Delclòs et al., 2004; Grimaldi and Engel, 2005; McKellar et al., 2011; Labandeira, 2014; Peris et al., 2015a). In fact, a great number of specimens from wood-borer groups (such as Scolytinae and Platypodinae) are known in Eocene and Miocene ambers (Bright and Poinar, 1994; Peris et al., 2015b). However, although this conclusion was extended to whole amber collections (Labandeira, 2014), such an unfounded observation was initially promoted by poor knowledge of which groups compose beetle communities in Cretaceous ambers. Wood-boring Platypodinae are, at the moment, not known from the Cretaceous and Scolytinae are very sparsely represented (Cognato and Grimaldi, 2009; Kirejtshuk et al., 2009) (see Appendix 2).

This work reports information from the evolutionary and paleoecological analysis of the coleopteran collections in Cretaceous ambers (see Table 1 and Appendix 1 and 2). The characterization of the order represents a substantial advance in our understanding of the evolution of one of the most successful groups of animals, as well as in our knowledge of the structure of terrestrial Cretaceous ecosystems.

## 2. Paleontological setting

Western European Cretaceous ambers mainly consist of amber sites in Spain and France (Fig. 1). The material presented here as new comes from three Cretaceous amber sites in Spain and seven in France (Fig. 1b).

In Spain, there are more than 120 middle Cretaceous sites of amber deposits; most of them are dated as Albian in age (Peñalver and Delclòs, 2010; Barrón et al., 2015). However, only ten of them yield organic fossil inclusions. Only three sites have

provided a large number of bioinclusions so far, these are: Peñacerrada I in the province of Burgos (Alonso et al., 2000); El Soplao in the province of Cantabria (Najarro et al., 2009, 2010; Pérez-de la Fuente et al., 2013); and San Just in the province of Teruel (Peñalver et al., 2007). All these sites are in the northern or northeastern part of the Iberian plate.

Peñacerrada I is the most fossiliferous of all the Spanish amber sites to date; with more than 3200 catalogued bioinclusions. Samples from this locality are housed at the Museo de Ciencias Naturales de Álava (Vitoria-Gasteiz, Spain). El Soplao has yielded 549 bioinclusions; all housed at the Institutional amber collection of the El Soplao Cave laboratory (Celis, Spain). San Just has yielded 336 bioinclusions; all housed at the Conjunto Paleontologico de Teruel-Dinópolis (Teruel, Spain).

Despite there being 65 amber sites in France (Nel et al., 2004; Perrichot et al., 2007), bioinclusions have only been found at 13 of them; and the total number of bioinclusions remains lower than those in Spain: *ca*. 2000 arthropod fossils recorded to date (Perrichot and Néraudeau, 2014). This may be because a high proportion of the Cretaceous French amber is opaque: up to 80% of all the Charentese amber according to Lak et al. (2008). Therefore, a large proportion of French bioinclusions are not detectable without x-ray radiographic and tomographic imaging. Seven of these 13 sites have yielded fossil coleopterans; most fossils have been found in Albian–Cenomanian amber of the Charente-Maritime region (from the sites of Font-de-Benon quarry near Archingeay-Les Nouillers, Cadeuil, Fouras/Bois-Vert, and La Buzinie). A few others have been found in Cenomanian amber from the Eastern Pyrenees (Fourtou deposit) and the Alps (Salignac deposit), as well as in the late Cretaceous amber from Vendée (La Garnache deposit, Cenomanian–Early Santonian in age) (Perrichot and Néraudeau,

2014). The Cenomanian amber from Anjou (Durtal and Bezonnais sites) has also yielded a few beetles (Schlüter, 1983); but the specimens could not be examined and therefore they are not included in the present analysis. The French Cretaceous amber fossils are in a collection housed in the Department of Geosciences at the University of Rennes 1 (Rennes, France) and at the Muséum national d'Histoire naturelle (Paris, France).

Control of the entire collections and the existence of a regularly updated catalog of all the bioinclusions that are reported allows work such as that presented here is proceed.

## 3. Material and methods

The present study is based on 149 Coleoptera recorded from Spanish sites (84 out of the 3014 bioinclusions from Peñacerrada I (Burgos), 14 out of the 336 from San Just (Teruel) and 51 out of the 546 from El Soplao (Cantabria)) and 65 Coleoptera recorded from seven French sites (out of the *ca*. 2000 arthropod inclusions). Beetles represent 3.8% of the total bioinclusions in the Cretaceous amber from Spain and 3.3% of that from France. These data are in sharp contrast with the high diversity and disparity of beetles in forest ecosystems, and suggest that important taphonomical factors control their inclusion and preservation in plant resins.

The new information reported here is compared with the list of Coleoptera from Cretaceous amber from the Lebanon and Myanmar. The Coleoptera from Lebanese amber were reviewed by Kirejtshuk and Azar (2013) and represent approximately 3% of the bioinclusions found. In contrast, Myanmar amber contains the largest list of beetle taxa described to date (Appendix 2), representing 16% of all the studied inclusions from Burmese amber (Shi et al., 2012). The first list of families from this

deposit was published by Rasnitsyn and Ross (2000) based on a collection housed at the British Natural History Museum (BNHM). That study was later complemented by Grimaldi et al. (2002) with data from a second collection housed at the American Museum of Natural History (AMNH). However, one of us (DP) had the opportunity to examine some of the AMNH material, which revealed the need for a severe revision. A large proportion of the 48 specimens cited as Ptiliidae in Grimaldi et al. (2002) are in fact Staphylinidae: Scydmaeninae, which could be confused due to their tiny size. For this reason, the information on beetles from Burmese amber was mainly extracted from independent publications (Appendix 2) and not from lists.

Results are summarized in Table 1 which was later analyzed by cluster analysis with IBM SPSS software. The conducted analysis was a hierarchical conglomerate cluster using the chi-square distance and the Average Linkage between Groups method (Fig. 4).

The specimens reported in this work were examined under three different lenses: a Leica MS5 stereomicroscope and both a Motic BA310 and an Olympus BX–41 compound microscope with reflected and transmitted light. Photomicrographs were produced using a Canon EOS 7D digital camera attached to an Infinity K–2 long-distance microscope lens and a MOTICAM 2500 camera attached to the Motic BA310 microscope. All of them were arranged and sharpened using CombineZP and edited with Photoshop Elements 10 and CorelDraw X7.

The classification of families used here follows Bouchard et al. (2011).

## 4. Results

A total of 214 coleopteran specimens in 41 families were recorded from the Cretaceous amber collections from Spain and France (Table 1, Fig. 2 and Appendix 1). Among them, 25 families were exclusively found in the Spanish amber; while 11 families were exclusively found in the French amber (Table 1); and only five of them were observed in both paleobiogeographic areas.

The Spanish and French ambers clearly contain the oldest representatives of the Polyphagan families: Bostrichidae, Elmidae, Eucinetidae, Histeridae, Jacobsoniidae, Leiodidae, Limnichidae, Nosodendridae, Oedemeridae, Omethidae, Phalacridae (Fig. 2c), Ripiphoridae, and Tetratomidae. Furthermore, the records for the families Bostrichidae, Elmidae, Limnichidae, Nosodendridae, Omethidae and Phalacridae are the sole record for the whole Mesozoic; and the records for the family Jacobsoniidae and Tetratomidae in these western European Cretaceous ambers are the only fossil record known to date for their families. This means that all these families already existed at least in the late early Cretaceous and have persisted until now. In addition, several fossils with an unknown classification were checked and are probably ancient representatives of Recent groups, or maybe extinct lineages of Coleoptera. Vitalii (2014) transferred a fossil species previously described in Melandryidae to Tetratomidae, but he did not review the holotype because of that the change has not been considered. Bukejs et al. (2015) equally removing the specimen described in Elmidae from this family, they did not review the holotype or justify the change; thus, this specimen is considered within the original family (Peris et al., 2015c).

The Lebanese amber (Barremian) contains the most ancient representatives of the Recent families: Aderidae, Anthicidae, Cantharidae, Clambidae, Dasytidae, Dermestidae, Erotylidae, Kateretidae, Laemophloeidae, Latridiidae, Lebanophytidae, Melandryidae, Melyridae, Ptiliidae, Ptinidae, Ptilodactylidae, Salpingidae and

Throscidae from within the Polyphaga; as well as the record of the fossil family †Elodophalmidae (Kirejtshuk and Azar, 2013). The Burmese amber (Cenomanian) yielded the earliest representatives for the families: Lepiceridae (Kirejtshuk and Poinar, 2006; Ge et al., 2010) and Sphaeriusidae (Kirejtshuk, 2009) within the suborder Myxophaga, and for the family Prostomidae (Engel and Grimaldi, 2008) within the Polyphaga (Appendix 2).

The coleopteran taxonomic composition of the Laurasian ambers (from Spain, France, and Myanmar) is compared with that of a Gondwanian amber from the Lebanon in Table 1, and discussed thereafter.

## 5. Discussion

### 5.1. Beetles as vectors for the resin production during the Cretaceous

The beetles found at the Lebanese, Spanish, French and Myanmar amber sites had not participated in the resin production that resulted in early and mid-Cretaceous ambers.

Considering ambers exclusively from the Cretaceous period, McKellar et al. (2011) first demonstrated that resin production in the Cretaceous gymnosperm forest of New Jersey (Turonian, approximately 90 Ma) could have been promoted by continuous damage to resin producing trees. They hypothesized that bark beetles (Curculionidae: Scolytinae) could be responsible for this tree damage and based their ideas on carbon isotope analysis. Based on the high proportion of Ptinidae wood-boring beetles found in New Jersey amber, Peris et al. (2015a) hypothesized that they could have played the same role during the upper Cretaceous as bark beetles had in more recent paleoecosystems (Peris et al., 2015b). However, ptinids are not often cited among Cretaceous collections

in amber, and other hypothetical wood-boring families, such as Curculionidae, Cerambycidae or Buprestidae, have not been recorded in large proportions in any other Cretaceous amber in the world.

One argument against the idea of beetles attacking the trees is that, generally, the jaws that can be observed in amber specimens from Spain and France are not strong enough to damage wood. Furthermore, female genitalia are not cuticulized for direct deposition into live wood, so they would be expected to lay on herbaceous plants, or dead or decaying wood.

5.2. Wildfires and other paleoenvironmental processes as factors involved in the resin production in the Cretaceous

Apart from biotic influences, Martínez-Delclòs et al. (2004) proposed other abiotic factors that could have been involved in the resin production during the Cretaceous. Those factors are: reactions to physical damage, cellular metabolism or growth; and protective barriers to reduce temperature and water loss or to attract insect pollinators. Henwood (1993a) argues that periods of extensive production do not necessary reflected pathological tree situations but paleoenvironmental conditions.

Gale (2000) described evidence of considerable formation of oceanic crust on Earth between 120 and 80 Ma, resulting from the middle-oceanic rifts and the formation of small Pacific plates. This process was called a “mantle superplume” by Larson (1991). Because of these processes, the mid-Cretaceous is associated with elevated $CO_2$ concentrations, a greenhouse effect and a relative rise in sea level globally (Caldeira and Rampino, 1991). Together with the increase in $CO_2$, the following parameters also increased: global average temperature, precipitation rate, extension of the areas with a

monsoon climate, tropospheric winds and plant growth over a wide latitudinal range (Gröcke, 2002; Skelton et al., 2003; Jarvis et al., 2011). The increase in volcanism together with that of $CO_2$ production can be associated with: (1) droughts that weaken trees; (2) high probability of fire; (3) increased rate of generation of insects; and (4) tsunamis (Gale, 2000). It is not at all difficult to associate these factors with the possible causes that Martínez-Delclòs et al. (2004) offered for the increased formation of resin.

Of all of them, wildfires constitute a very strong candidate as a cause of the increased resin production. Abundant charcoal and fusinite (inertinite) remains have been found in contemporary sediments with amber inclusions (personal observations, Sender et al., 2015) but also in the stratigraphic levels that contain amber (Najarro et al., 2010; Peñalver and Delclòs, 2010; Perrichot et al., 2010; Shi et al., 2012) and there is even charred plant material embedded within fossil resin (Fig. 2h) (Grimaldi et al., 2000; Perrichot, 2004). High levels of $CO_2$ during the Cretaceous increased average global temperatures, and when these factors are combined with high rates of volcanic eruptions, the result is more violent wildfires during the Cretaceous than during the Triassic and Jurassic (Belcher and McElwain, 2008; Scott, 2010).

Geological evidence supports this idea. Lebanese amber forests developed in an important volcanic area during the Mesozoic (Abdel-Rahman, 2002; Veltz et al., 2013); continental Lebanese early Cretaceous sites are interbedded with volcanic basaltic and lacustrine sites of volcanic origin (Walley, 1997; Ferry et al., 2007; Veltz et al., 2013). During the early Cretaceous volcanic events increased and were related with the development of plumes and superplumes that took place worldwide (Tatsumi et al., 1998; Jahren, 2002; Segev and Rybakov, 2010; Biggin et al., 2012). Associated with the kinematics of the formation of the Atlantic, magmatism and volcanism also affected the

Iberian plate during this period (Wilson, 1975; Prévot et al., 2000; Salas et al., 2005; Grange et al., 2010). Furthermore, Shi et al. (2012) clearly mention a volcanic environment in which Myanmar amber was buried. The paleobiological record also supports this: one anaxyelid woodwasps that laid eggs in recently burned wood (Ortega-Blanco et al., 2008) and the abundant gleicheniacean ferns trichomes, an invasive group of ferns after wildfires (Pérez-de la Fuente et al., 2012), became embedded in Spanish amber. Furthermore, one bostrichid coleopteran from genus *Stephanopachys* Waterhouse, 1888, that is particularly attracted by young trees damaged by wildfire, became embedded in French amber (Peris et al., 2014a). All these published taxa and some other unpublished specimens are related with primary succession pioneers following wildfires. In addition, some charred material embedded in amber is sometimes denoted (see an example in Fig. 2h).

Together with wildfires and the documented volcanic influence, some other factors such as pathogenic fungal growth or important annual periods of storms may be added to the hypothetical factors that influenced resin production. None of these hypotheses can be easily justified; but the conjunction of causes could have resulted in the increased resin production at that time (Seyfullah et al., 2012).

### 5.3. Beetles from Cretaceous resiniferous forests

Coleoptera is the most abundant and biodiverse order of insects in tropical and subtropical forests. Thanks to their evolutionary success, beetles have been able to colonize a large number of different habitats and environments, and feed on many different trophic resources. Xylophagous groups such as Ptinidae, Bostrichidae, Brentidae and Curculionidae have already been recorded in Cretaceous ambers, but

always in low numbers; except for the New Jersey amber deposit (Peris et al., 2015a). Cerambycidae, one of the best known xylophagous groups, has not been yet recorded in Cretaceous ambers (only in stone prints), possibly due to a taphonomic bias.

Most of the families in ambers from the Lebanon, Spain, France and Myanmar could be considered completely, or at least partially, saproxylic, playing an important role in wood processing and decomposition (Tate et al., 1993; Grove, 2002), in synergy with the activity of fungi and other microorganisms (Swift, 1977; Edmonds and Eglitis, 1989; Boberg, 2009; Strid, 2012). So, factors related with decaying wood and wood-inhabiting fungi, together with decomposers of the moist litter cover, are the most significant explanatory variables for the richness of Cretaceous species at those amber sites. Forest soil litter is an important habitat for beetles (Crowson, 1981). So it is then also possible that in the Cretaceous this litter allowed the development of a rich and highly diverse fauna. However, it is impossible to clearly identify or separate out which Coleoptera were strictly soil related groups or which were only transient visitors; in fact although many families are usually soil litter resident both at larval or adult stage, many others include adults that live and breed elsewhere, and are recorded in litter only occasionally.

Cretaceous ambers show, nonetheless, a wide diversity of ecological specializations: Phytophagous beetles such as Scarabeidae, Curculionidae and Buprestidae feeding on leaves or soft plant tissues; saprophagous / detritivores such as Zopheridae, Scarabeidae, Curculionidae and Tenebrionidae feeding directly on decaying plant matter; and microphagous families such as Erotylidae, and Curculionidae: Scolytiinae. Families such as Monotomidae, Silvanidae and Prosotomidae which have a flat body form, show clear adaptation and a strong relation with the subcortical arboreal environment. A few

other groups such as Histeridae, Hybosoridae and Cleridae are suspected of being predators of other invertebrates. Staphylinidae is one of the most abundant families in all the Cretaceous ambers. Staphylinids constitute up to a quarter of the beetle biomass in the Recent temperate forests and also a high proportion within amber fossils (Grimaldi and Engel, 2005). Nevertheless, Ripiphoridae is the most important group in French ambers and it seems that this parasitoid family had great success in French Cretaceous gymnosperm-dominated forests. Some of the families currently recorded in amber, such as Mordellidae, Scraptiidae and Oedemeridae, probably fed on nectar or pollen. It is therefore plausible that they were trapped in the resin accidentally or, in contrast, during the search for a suitable environment for oviposition, with larvae developing in rotten and decaying wood.

Beetle associations in Cretaceous ambers show a direct or indirect relation with resin producing tree (although in some cases it could be sporadic). Authors such as Henwood (1993b), Penney (2002) and Solórzano-Kraemer et al. (2015) experimentally analyzed different entrapment biases for arthropods in amber and arrived at different conclusions. Nevertheless, all the experimental work was performed by comparison with Cenozoic ambers and mainly produced by the genus *Hymenaea* (Angiospermae: Leguminoseae) which clearly differs from Cretaceous forest characteristics, as they were gymnosperm dominated. We should expect that most of beetles, since all are good or excellent fliers, may have been accidentally trapped in resin during flight. If that was the case, we would expect to find most of the specimens with their elytra opened and wings unfolded. However, only a small fraction of the samples clearly show open wings, indicating that the majority of beetles were probably trapped in the resin accidentally when walking on the wood or near the resin.

5.4. Beetle assemblages: similarities and dissimilarities

One of the most notable findings reported here is that the close associations expected between the beetles in the Spanish and French ambers, because of their similar paleogeography and age, were not observed. Only five families were found to be common to both areas. In contrast, the Laurasian Spanish ambers have more groups of beetles in common with the Gondwanan Lebanese ambers than to other Laurasian ambers of a similar age.

According to the cluster analysis performed with the "Total" values (T) for each area, the shortest distance is observed between France and Myanmar; Spain is closest to these two areas and Lebanon exhibits the highest distance to all the former (Table 2, Fig. 4). Only adult records with familial placement have been used – data representing immature stages, indeterminate groups and inconclusive fragmentary inclusions have not been considered (Appendix 2). As a result, missing data comprise 17% of total in Lebanon, 31% in Spain, 54% in France and 3% in Myanmar – these quite high values are namely explained by inconclusive fragmentary inclusions. Furthermore, data from Myanmar have been gathered from the literature, and many specimens that are currently under study will be described in the near future. Due to these reasons, and pending for a more refined data set, we refrained from using frequencies of specimens within each group to weight the cluster analysis; instead, herein we follow a presence/absence criterion. Different patterns in Spain and France during the Cretaceous were already observed due to the absence of ants (Hymenoptera: Formicidae) in Spanish amber, while several species and the same genera were found and described in French and Myanmar Laurasian ambers (Nel et al., 2004; Perrichot et al., 2008). Villanueva-Amadoz et al. (2010) studied the angiosperm pollen assemblages of the San Just

outcrop (Spain) and found important similarities with those of southern Laurasian localities; although taxa more typical of angiosperm palynofloras of northern Gondwana were also reported. When Barron et al. (2015) studied palynofloras from different Spanish Cretaceous amber-bearing sites, they proposed significant differences between the Spanish assemblages and others further north, in France (Peyrot et al., 2005) and Canada (Bujak and William, 1978).

Similarities between the Lebanese and Spanish bioinclusions are not exclusive to beetles (Peris et al., 2014b), but extend to other groups of flying insects too, such as dipterans (Borkent, 2012; Pérez de la Fuente, 2012) and hymenopterans (Ortega-Blanco et al., 2011). Kirejtshuk and Azar (2013) stated that some beetle specimens "belong to the groups rather different from those represented in the Recent fauna and they are very difficult to identify"; this observation can be extended to Spanish beetles too. Because of this, several new higher groups have been created that contain some of these fossils (see for example, Peris and Delclòs, 2015). In contrast, beetles from French and Myanmar ambers fit easily into Recent families and in several cases even in Recent genera, showing a remarkable stasis (Peris et al., 2014a; Peris and Háva, submitted). It seems that Lebanese and Spanish ambers contain proportions of specimens that are rather different from those of Recent faunas, which in some cases could be considered ancient, currently unknown or probably extinct. In fact, although Laurasia and Gondwana were classically understood in the context of a dual world, interchanges between Africa and Laurasia were not occasional or minor events from the Early Cretaceous (Gheerbrant and Rage, 2006).

The reasons for such patterns could be related to the ancient origin of the Lebanese and Spanish ambers. Located between Laurasia and Gondwana, the Iberian plate was a center of biotic interchange between the two areas (Heimhofer et al., 2007, and

references therein; Barrón et al., 2015). During the period of physical isolation, discontinuous and intermittent routes connected Africa more closely to Laurasia than to other Gondwanan continents (Gheerbrant and Rage, 2006). In contrast, the nearby southwestern coast of France, which contains a large part of the French ambers, is slightly more modern than the other two ambers. In fact, many of the coleopteran specimens found in French amber represent the most ancient record for their respective groups and have not been found among the numerous specimens from the Lebanon or Spain (see Results and Table 1).

Curculionidae (excluding Scolytinae), Ripiphoridae and Zopheridae are groups named equally in French and Myanmar ambers, while they are apparently absent from the other two areas (Zopheridae is doubtfully cited in the Lebanon). In contrast, Aderidae, Dermestidae, Latridiidae, Melandryidae (Figure 2d) and Monotomidae are families found abundantly at the Lebanese and Spanish sites that are completely absent or extremely scarcely represented at the French sites (Kirejtshuk and Azar, 2013; this work). It is possible that more local paleoclimatic or paleobotanical differences also influenced these patterns.

### 5.5. Paleoenvironment

All four paleogeographic areas considered in this work were under tropical/subtropical conditions during part of the Cretaceous (Gale, 2000). Moreover, all the sites in these areas developed in transitional–deltaic environments and are located close to the sea (Azar et al., 2010; Peñalver and Delclòs, 2010; Perrichot et al., 2010; Ross et al., 2010). The plant taxa that produced the resin which became amber in the Cretaceous are currently under discussion. They most likely belong to different groups of plants,

although there is consensus that the resin producers were gymnosperms. It has been suggested that ambers from the Tethys realm and of early Cretaceous age are representative of Araucariaceae (close to the Recent genus *Agathis*) or the extinct †Cheirolepidiaceae (Azar et al., 2010; Menor-Salván, 2013; Perrichot et al., 2010; Ross et al., 2010). However, it has been suggested that the sites of late Cretaceous age represent Cupressaceae (Nohra et al., 2015). Botanical remains associated with the amber are generally abundant at the sites and facilitate an overview of the paleoenvironment.

The palynological assemblage from the Lebanese amber deposit of Hammana shares some characters with the two microfloristic provinces of peri-Tethys (southern Laurasia and northern Gondwana) (Brenner, 1976). That suggests a rather individual community in the Lebanese paleoenvironment (Dejax et al., 1996) and allows us to hypothesize a northeastern position in the Gondwana continent for the Middle East during the Early Cretaceous (Azar et al., 2003). Different paleogeographical areas developed under diverse paleoenvironmental conditions, due to dissimilar subsidence rates; this also promoted an important diachrony between the amber-bearing sites (Massaad, 1975, 1976). In general, sandy-clay Lebanese amber sites are related with fluvio-lacustrine environments and contain lignite and plant debris. These sites are fewer in the north and disappear in Syria, where marine green clays with oolitic limestones or marly limestones with orbitolines dominate (Dubertret, 1975). The presence of dinoflagellate cysts in all the amber-bearing sites suggests a marine–brackish influence (Veltz et al., 2013) in deltaic or lagoon zones (Azar, 2007). Araucarian–†queirolepidiacean-dominated forests developed under a tropical or subtropical climate: moderate to hot and very wet (Azar et al., 2010).

An extensive explanation of paleohabitats at Spanish sites may be found in Peñalver and Delclòs (2010). In general, palynological assemblages from the amber-bearing sites in Spain consist of: spikemoss, clubmoss and fern spores; and araucariacean, cupressacean/taxodiacean, †cheirolepidiacean, cycadacean, ginkgoacean, †bennettitacean, pteridospemacean, gnetacean and angiosperm pollen grains. Dinoflagellate cysts, acritarchs, and phycomes of prasinophycean algae are also present (Delclòs et al., 2009; Najarro et al., 2009, 2010). These assemblages indicate gymnosperm-dominated forests that grew near the sea (Peñalver and Delclòs, 2010; Barron et al., 2015), sites such as El Soplao consist mainly of †Cheirolepidiaceae and Cupressaceae; while in Peñacerrada I, inaperturate pollen grains related to the family Araucariacea represent at least 50% of occurrences and in San Just, conspicuous percentages of tree fem spores of Cyatheaceae/Dicksoniaceae and Schizaeaceae, inaperturate pollen grains of Taxodiaceae/Cupressaceae are the most abundant taxa (Alonso et al., 2000; Barrón et al., 2001, 2015; Peyrot et al., 2007; Najarro et al., 2010).

At the French sites, abundant ferns and gymnosperms characterized the littoral flora, as they did throughout Europe (Gomez et al., 2008). In the Charentes region, coniferous forests were arranged in three main zones (Peyrot et al., 2005). The coastal margins were dominated by xerophytic conifers such as †Cheirolepidiaceae, with a rich undergrowth constituted of †Bennettitales, cycads and ferns of the families Gleicheniaceae and Schizaeaceae. Open formations of Araucariaceae and Cupressaceae developed in more humid places, presenting an understory dominated by ferns. Then, a community composed of Ginkgoales in association with primitive angiosperms developed in riparian zones. They were complemented with highly diversified fluvial angiosperms and rare brackish water-related angiosperms (Gomez et al., 2004; Coiffard et al., 2006). The Cenomanian amber forest of the eastern Pyrenees was apparently less

diverse and the only known taxa belong to xerophytic conifers of the families †Cheirolepidiaceae and Cupressaceae, which grew along the margins of a marine-dominated estuarine environment (Girard et al., 2013). Finally, the Santonian amber forest in Vendée was composed of various conifers (Cupressaceae, Pinaceae, †Cheirolepidiaceae and Podocarpaceae), with an understory of ferns and abundant angiosperms, as indicated by a *Normapolles*-dominated palynomorph. The association between the macroflora and microfloral indicates a coastal area of low marine-influenced lagoons and brackish swamps, under a subtropical or warm temperate climate (Legrand et al., 2006). In these different forest environments, the French Cretaceous ambers originated from varied plant sources (Nohra et al., 2015): the Albian–Cenomanian Charentese amber and Cenomanian Alpine amber were produced by †Cheirolepidiaceae and possibly Araucariaceae; the Cenomanian Pyrenean amber was produced by †Cheirolepidiaceae; and the Santonian Vendean amber was produced by Cupressaceae.

The paleohabitat of the Burmese amber has been considered to be a tropical forest with Cupressaceae (*Metasequoia*) or Araucariaceae as the resin source (Grimaldi et al., 2002; Poinar et al., 2007). It is also believed to have had a highly diverse understory including ferns (Polypodiales), mosses, liverworts, and angiosperms (bambusoid-like monocots and various eudicots). This is revealed by botanical inclusions in the amber (*e.g.*, Poinar, 2004; Poinar and Buckley, 2008; Poinar et al., 2013; Chambers et al., 2010; Hedenäs et al., 2014; Heinrichs et al., 2014).

Despite general tropical to subtropical gymnosperm-dominated environments, some differences existed in the taxonomic composition of the flora and the marine influence among the amber forests at each locality. Thus, contrasting environmental conditions could have had different influences on the taxonomic diversity.

## 6. Conclusions

The involvement of beetles in resin production during the Cretaceous has been reconsidered after the low presence of wood-borer families in the Cretaceous ambers from the Tethyan realm. Their involvement only seems plausible due to the major presence of ptinid beetles in the New Jersey Turonian amber (Peris et al., 2015a); and isotope analysis from this amber corroborates this possibility (McKellar et al., 2011). The beetle associations reported from Cretaceous ambers here (the Lebanon, Spain, France, and Myanmar) are rather related with a saproxylic and detritivorous lifestyle. A large quantity of plant debris is expected after recurrent wildfires, which is defended as one of the most important factors that influenced gymnosperm resin production in Cretaceous forests, in synergy with some other possible biotic or abiotic processes. Wildfires probably increased due to paleoenvironmental factors such as a higher average temperature than today or different levels of atmospheric gases; and due to geological processes, such as volcanism or superplumes. During volcanic episodes, climate may temporarily vary, inducing significant precipitation that can rework forest soils and their stocked resins.

The ancient origin for the Lebanese and Spanish ambers (Barremian and Albian in age, respectively) (Fig. 3), the insularity of the Iberian plate during part of the Mesozoic (Fig. 1), or the regional paleoenvironment could influence the similarities observed between the beetle collections from these two areas and, at the same time, the differences with other Cretaceous amber associations. Meanwhile, the amber from France, which is temporally and paleogeographically very close to the Spanish amber, shows very different insect composition; more closely related to the synchronic Laurasian Myanmar

amber. Nevertheless, many specimens remain as indeterminate groups and several new taxa are being studied from all the areas, and will result new for science soon. The increasing classification of taxa will probably allow the use of statistical methods more effectively to demonstrate conclusions here reported.

This work highlights the importance of studying fossil beetle associations as a whole, to discern paleobiology states, instead of taking them as isolated records. The conclusions may vary due to the lack of information if the community is fractionated. The study of syninclusions from the same piece can provide crucial data (for example, see Sánchez-García et al., 2014). On the other hand, complete analysis of the beetle fauna from amber sites clarifies several aspects of the paleoenvironments. Multiple lists of beetle families from different amber sites are published (e.g., Grimaldi et al., 2000, 2002; Ross and York, 2000), but they are in need of major revision. This work provides an updated list of beetle species found in Cretaceous ambers worldwide (Appendix 2).

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**Figure captions**

**Figure 1.** Main Cretaceous sites with beetles embedded in amber from the Lebanon, Spain, France, and Myanmar. They are indicated by circles and numbered. The deposits in Lebanon are: (1)Nabaa Es-Sukkar-Brissa; (2)Hammana-Mdeyrij; (3)Bouarij; (4)Ain Dara; (5)Kfar Selouane; (6)Falougha; (7)Bkassine; (8)Roum-Aazour-Homsiyyeh; and (9)Rihane. The deposits in Spain are: (10)Peñacerrada I; (11)El Soplao; and (12)San Just. The deposits in France are: (13)Archingeay-Les Nouillers; (14)Cadeuil; (15)Fouras/Bois-Vert;(16) La Buzinie; (17)Fourtou; (18)Salignac; and (19) La Garnache. Finally, the deposits in Myanmar are found near Tanai in the Hukawng Valley (20). (a) World paleogeographical map that corresponds to the Aptian (125 Ma) for the Lebanese sites and the Albian (100 Ma) for the rest. (b) Detail of the western margins of the Tethys Ocean showing the deposits in the Lebanon, Spain and France. Modified from Blakey (2011).

**Figure 2.** Bioinclusions embedded in Cretaceous amber. (a) CES–515, Ommatidae; (b) MCNA–12747, Salpingidae; (c) MCNA–9730, Phalacridae; (d) CES–577, Melandryidae; (e) MCNA–14250, Histeridae; (f) MCNA–13334, Endomychidae?; (g) CES–489, Dermestidae; (h) MCNA-13850, charred plant material.

**Figure 3.** Cretaceous amber areas with beetle record (Appendix 2) and other Cenozoic sites cited in the text. Chronostratigraphy following Cohen et al. (2013; updated). Spanish and French ambers are indicated with a circle. [1] La Garnache deposit is a French deposit with a beetle record that is Turonian–Santonian in age.

**Figure 4**. Dendrogram showing the result of the clustering analysis for the countries.

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**Appendix 1**

Samples of Coleoptera reviewed from Cretaceous ambers from Spain and France. Sample have been classified by coleopteran groups, mainly families but also some superfamilies, larva, fragments, or indeterminates group have been considered as posible groups. The Spanish deposits are: Peñacerrada I ("MCNA–"), El Soplao ("CES–") and San Just ("CPT–" or "SJNB–"). The French deposits are: Archingeay-Les Nouillers ("IGR.ARC–"), Cadeuil ("CDL–"), Fouras/Bois-Vert ("FRS–"), La Buzinie ("Buz–"), Fourtou ("FOU–"), Salignac ("Sis–" ) and La Garnache ("GAR–" ). The family classification is following criteria in Bouchard et al. (2011), although families appear in alphabetical order in this work in order to facilitate the search of further information.

| Group | Amber from Spain | Amber from France |
|---|---|---|
| Aderidae | MCNA-9795, CES-019, CES-574, CES-583 | - |
| Artematopodidae | - | IGR.ARC-331.4 |
| Bostrichidae | - | IGR.ARC-270 |
| Buprestidae | - | IGR.ARC-50.3 |
| Cantharidae | CES-522 | - |
| Carabidae | - | IGR.ARC-254.5 |
| Caridae | CES-432 | IGR.ARC-328.2 |
| Cleridae | - | IGR.FRS-7.6 |
| Cleroidea | - | IGR.ARC-227, IGR.FRS-7.2 |
| Cryptophagidae | MCNA-9194, MCNA-14303, CES-571, CES-575, SJNB2012-42 | - |
| Curculionidae | - | IGR.ARC-331.2 |
| Dermestidae | MCNA-9736, MCNA-9738, MCNA-13025, MCNA-14924, CES-057.2, CES-489, CES-512, CES-589, SJNB2012-41? | - |
| Elateridae | MCNA-9734 | - |
| Elmidae | CES-567 | - |
| Erotylidae | CES-587 | - |
| Eucinetidae | MCNA-14638, CES-519, CES-600, CPT- | - |

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| | 4129 | |
| Histeridae | MCNA-14250 | - |
| Jacobsoniidae | - | IGR.CDL-2.42 |
| Latridiidae | MCNA-9611, CES-361, CES-488, CES-490 | - |
| Leiodidae | MCNA-9423, MCNA-14496 | - |
| Limnichidae | - | IGR.ARC-393.1 |
| Melandryidae | MCNA-9551, MCNA-9845, MCNA-14310, CES-507, CES-518, CES-577 | - |
| Monotomidae | MCNA-8655, MCNA-9158, MCNA-9184, MCNA- 9317, MCNA- 9552, MCNA-15127 | - |
| Mordellidae | MCNA-8839, MCNA-8985, MCNA-9480 | - |
| Nemonychidae | CES-576, CPT-4106 | - |
| Nitidulidae | MCNA-9424, CES-525.1 | - |
| Nosodendridae | CES-520 | - |
| Oedemeridae | MCNA-11229 | - |
| Omethidae | MCNA-12771 | - |
| Ommatidae | CES-515 | - |
| Phalacridae | MCNA-9730, MCNA-9733, | - |
| Ptinidae | MCNA-9369, MCNA-14401, SJ-10-18 | IGR.GAR-010, IGR.GAR-107 |
| Pyrochroidae | MCNA-9380 | - |
| Ripiphoridae | - | IGR.ARC-115.11, IGR.ARC-164.1, IGR.ARC-181, IGR.ARC-254.6, IGR.ARC-254.10, IGR.ARC-387.4, IGR.Sis-2.1 |
| Salpingidae | MCNA-12747 | - |
| Scraptiidae | MCNA-9974.1, MCNA-9974.2, MCNA-10056, MCNA-14226 | IGR.ARC-205.1 |
| Silvanidae | MCNA-9315, MCNA-9729, CPT-4105, SJ-10-51 | - |
| Staphylinidae | MCNA–8654, MCNA–8912, MCNA–9990, MCNA–12663, MCNA–12683, MCNA–12752, MCNA–13254, | IGR.ARC-194.3, IGR.ARC-260.1, IGR.ARC-370.6, IGR.ARC-370.10 + LOST |

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|---|---|---|
| | MCNA–13611, MCNA–13823, MCNA–14190, MCNA–14247, MCNA–14251, MCNA–14265, MCNA–14948, MCNA–14933, CES–059.3, CES–433.1, CES–433.2, CES–463, CES–487, CES–566.2, CES–572, CES–601, SJNB2012–40, SJNB2012–43 | |
| Tenebrionoidea | MCNA-14188, CES-570 | - |
| Tenebrionidae | MCNA-9331, CES-529.1 | - |
| Tetratomidae | - | IGR.ARC-60.2, IGR.ARC-330.1 |
| Trogossitidae | MCNA-9259 | IGR.FRS-5.1 |
| Zopheridae | - | IGR.GAR-007.2 |
| Larva | MCNA-8658 | IGR.ARC-331.5, IGR.ARC-204, IGR.ARC-237.12, IGR.GAR-012, IGR.FOU-106 |
| Fragments | MCNA-8965, MCNA-8986, MCNA-9501, MCNA-9786, MCNA-9850, MCNA-9975, MCNA-10026, MCNA-12525, MCNA-13628, MCNA-14030, MCNA-14192, MCNA-14279, MCNA-14323, MCNA-14643, MCNA-14659, CES-057.1, CES-420.2, CES-420.7, CES-425, CES-521, CES-524, CES-525.2, CES-529.2, CES-553, CES-580, SJ-10-48, SJNB2012-39-01 | IGR.ARC-87.3, IGR.ARC-121, IGR.ARC-167.1, IGR.ARC-186.3, IGR.ARC-198.1, IGR.ARC-215, IGR.ARC-244, IGR.ARC-263.4, IGR.ARC-285, IGR.ARC-417, IGR.CDL-2.23, IGR.FRS-7.23, IGR.GAR-127, IGR.Sis-4.1, IGR.Sis-6.1, IGR.Sis-17.2 |
| Indeterminated group | MCNA-9622, MCNA-9739, MCNA-10763, MCNA-12596, MCNA-13032, MCNA-13334, MCNA-14273, , MCNA-14656, | IGR.ARC-22, IGR.ARC-32, IGR.ARC-188.1, IGR.ARC-198.5, IGR.ARC-271.3, IGR.ARC-318.4, IGR.ARC-369.4, |

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| | MCNA-15103, CES-315.1 , CES-391.3, CES 391.4, CES-530.2, CES-585, CES-602, CPT-965, CPT-4060, SJNB2012-01-02 | IGR.ARC-393.5, IGR.ARC-394, IGR.Buz-1.16, IGR.FRS-7.3, IGR.FRS-7.9, IGR.Sis-21.1, IGR.Sis-23.2 |

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| **Lebanon** | | |
| Anthicidae | *Camelomorpha longicervix* Kirejtshuk and Azar, 2008 | [30] |
| Cerophytidae | *Lebanophytum excellens* Kirejtshuk and Azar, 2008 | [30] |
| Chelonariidae | *Eochelonarium belle* Kirejtshuk, 2013 | [31] |
| Clambidae | *Eoclambus rugidorsum* Kirejtshuk and Azar, 2008 | [30] |
| Curculionidae | *Cylindrobrotus pectinatus* Kirejtshuk, Azar, Beaver, Mandelshtam and Nel, 2009 | [33] |
| Dermestidae | *Cretonodes antounazari* Kirejtshuk and Azar, 2009 | [32] |
| Elodophthalmidae | *Elodophthalmus harmonicus* Kirejtshuk and Azar, 2008 | [30] |
| | *Elodophthalmus gracilis* Kirejtshuk and Azar, 2008 | [30] |
| Hybosoridae | *Libanochrus calvus* Kirejtshuk, Azar and Montreuil, 2011 | [34] |
| Kateretidae | *Lebanoretes andelmani* Kirejtshuk and Azar, 2008 | [30] |
| Latridiidae | *Tetrameropsis mesozoica* Kirejtshuk and Azar, 2008 | [30] |
| | *Archelatrius marinae* Kirejtshuk and Azar, 2009 | [32] |
| | *Atetrameropsis subglobosa* Kirejtshuk, 2013 | [31] |
| Micromalthidae | *Cretomalthus acracrowsonorum* Kirejtshuk and Azar, 2008 | [30] |
| Monotomidae | *Rhizophtoma elateroides* Kirejtshuk and Azar, 2009 | [32, 51] |
| | *Rhizophtoma synchrotronica* Kirejtshuk, 2013 | [31, 51] |
| | *Rhizobactron marinae* Kirejtshuk, 2013 | [31, 51] |
| Nemonychidae | *Libanorhinus succinus* Kuschel and Poinar, 1993 | [38] |
| Ptismidae | *Ptisma zasukhae* Kirejtshuk and Azar, 2016 | [36] |
| Sphindidae | *Libanopsis poinari* Kirejtshuk, 2015 | [35] |
| | *Libanopsis impexa* Kirejtshuk, 2015 | [35] |
| | *Libanopsis limosa* Kirejtshuk, 2015 | [35] |
| | *Libanopsis straminea* Kirejtshuk, 2015 | [35] |
| | *Libanopsis slipinskii* Kirejtshuk, 2015 | [35] |
| Staphylinidae | *Libanoeuaesthetus pentatarsus* Lefebvre, Vincent, Azar and Nel, 2005 | [39] |
| Throscidae | *Potergosoma gratiosa* Kovalev and Kirejtshuk, 2013 | [36] |
| | *Rhomboaspis laticollis* Kovalev and Kirejtshuk, 2013 | [36] |
| **Jordan*** | | |
| Mordellidae? | *Bruchitypus anonymus* [nomen dubium] Kaddumi, 2005 | [27] |
| Anthicidae? | *Petratypus nigri* [nomen dubium] Kaddumi, 2005 | [27] |
| Staphylinidae | *Scaphylinus ammanicus* [nomen dubium] Kaddumi, 2005 | [27] |
| **Spain** | | |
| Caridae | *Albicar contriti* Peris, Davis, Engel and Delclòs, 2014 | [54] |
| Curculionidae | *Antiquis opaque* Peris, Davis, Engel and Delclòs, 2014 | [54] |
| Elmidae | *Elmadulescens rugosus* Peris, Maier and Sánchez-García, 2015 | [58, 5] |
| Mordellidae | *Mediumiuga sinespinis* Peris and Ruzzier, 2013 | [49, 50] |
| Staphylinidae | *Archeutheia magnifica* (Peris, Chatzimanolis and Delclòs, 2014) | [53, 26] |
| | *Cretasonoma corinformibus* Peris, Chatzimanolis and Delclòs, 2014 | [53] |
| | *Penarhytus tenebris* Peris, Chatzimanolis and Delclòs, 2014 | [53] |
| | *Prosolierius parvus* Peris, Chatzimanolis and Delclòs, 2014 | [53] |
| Monotomidae | *Cretakarenni hispanicus* Peris and Delclòs, 2015 | [51] |
| | *Rhizophtoma longus* Peris and Delclòs, 2015 | [51] |
| Nemonychidae | *Arra legalovi* Peris, Davis and Delclòs, 2015 | [54] |
| Ptinidae | *Actenobius magneoculus* Peris, Philips and Delclòs, 2015 | [59] |
| Oedemeridae | New genus and species | [48] |
| **France** | | |
| Bostrichidae | *Stephanopachys vetus* Peris, Delclòs and Perrichot, 2014 | [55] |
| Caridae | *Gratshevbelus erici* Soriano, 2009 | [41, 72, 54] |
| Ripiphoridae | *Paleoripiphorus deploegi* Perrichot, Nel and Néraudeau, 2004 | [21, 60] |
| | *Macrosiagon ebboi* Perrichot, Nel and Néraudeau, 2004 | [60] |
| Staphylinidae | *Duocalcar geminum* Peris and Thayer, 2014 | [57] |
| | *Stenus inexpectatus* Schlüter, 1978 | [71] |

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| Trogossitidae | *Cretamerus vulloi* Peris, Kolibáč and Delclòs, 2014 | [56] |
| Tetratomidae | *Synchrotronia idinineteena* Soriano and Pollock, 2014 | [73] |
| **Myanmar** | | |
| Carabidae | *Oodes kachinensis* Liu, 2015 | [43] |
| Caridae | *Mesophyletis calhouni* Poinar, 2006 | [42, 54, 62, 63] |
| | *Anchineus dolichobothris* Poinar and Brown, 2009 | [42, 54, 66] |
| Curculionidae | *Palaeocryptorhynchus burmanus* Poinar, 2009 | [42, 54, 64] |
| | *Microborus inertus* Cognato and Grimaldi, 2009 | [17] |
| Dermestidae | *Dermestes larvalis* Cockerell, 1917 | [14] |
| Elateridae | *Elater burmitinus* Cockerell, 1917 | [15] |
| | *Acmaeodera burmitina* Cockerell, 1917 | [3, 15, 74] |
| Histeridae | *Pantostictus burmanicus* Poinar and Brown, 2009 | [67] |
| Hybosoridae | *Hybosorus ocampoi* Bai and Zhang, 2015 | [2] |
| Lepiceridae | *Haplochelus georissoides* Kirejtshuk and Poinar, 2006 | [22, 29] |
| Monotomidae | *Cretakarenni birmanicus* Peris and Delcòs, 2015 | [49] |
| Nemonychidae | *Burmonyx zigrasi* Davis and Engel, 2014 | [18] |
| Prostomidae | *Vetuprostomis consimilis* Engel and Grimaldi, 2008 | [20] |
| Ptilodactylidae | *Aphebodactyla rhetine* Chatzimanolis, Cashion, Engel and Falin, 2012 | [10] |
| Pyrochroidae | *Eurygenius wickhami* Cockerell, 1917 | [15] |
| Ripiphoridae | *Cretaceoripidius burmiticus* (Cockerell, 1917) | [13, 21] |
| | Possible larva | [4, 24] |
| Scirtidae | *Mesernobius anawrahtai* Engel, 2010 | [19, 59] |
| Silvanidae | *Pleuroceratos burmiticus* Poinar and Kirejtshuk, 2008 | [68] |
| Sphaeriusidae | *Burmasporum rossi* Kirejtshuk, 2009 | [28] |
| Staphylinidae | *Cretodeinopsis aenigmatica* Cai and Huang, 2014 | [6] |
| | *Hapsomela burmitis* Poinar and Brown, 2004 | [9, 65] |
| | *Octavius electrospinosus* Clarke and Chatzimanolis, 2009 | [12] |
| | *Ektatotricha paradoxa* Chatzimanolis, Engel and Newton, 2010 | [9] |
| | *Electroatopos castaneus* Chatzimanolis, Engel and Newton, 2010 | [9] |
| | *Kachinus antennatus* Chatzimanolis, Engel and Newton, 2010 | [9] |
| | *Prosolierius crassicornis* Thayer, Newton and Chatzimanolis, 2012 | [75] |
| | *Prosolierius mixticornis* Thayer, Newton and Chatzimanolis, 2012 | [75] |
| | *Prosolierius tenuicornis* Thayer, Newton and Chatzimanolis, 2012 | [75] |
| | *Prosolierius spp. indet.* | [75] |
| | *Protopeplus cretaceus* Cai and Huang, 2014 | [7] |
| | *Mesallotrochus longiantennatus* Cai and Huang, 2015 | [8] |
| | *Protodasycerus aenigmaticus* Yamamoto, 2016 | [76] |
| | *Megalopinus extinctus* Yamamoto and Solodovnikov, 2016 | [77] |
| Zopheridae | *Cryphalites rugosissimus* Cockerell, 1917 | [16, 70] |
| Unknown | Possibly coleopteran | [24] |
| **New Jersey** | | |
| Attelabidae | *Sayrevilleus grimaldii* Gratshev and Zherikhin, 2000 | [23, 40, 69] |
| Caridae | *Cretocar luzii* Gratshev and Zherikhin, 2000 | [23, 41, 54] |
| Dermestidae | New species | [52] |
| Melandryidae | *Archaeserropalpus cretaceus* Nikitsky, 2002 | [46] |
| | *Pseudocuphosts tnstzs* Nikitsky, 2002 | [46] |
| Ptinidae | *Stegobium raritanensis* Peris, Philips and Delclòs, 2014 | [59] |
| Staphylinidae | *Mesotachyporus puer* Gusarov, 2000 | [25] |
| | *Phloeocharis agerata* Chatzimanolis, Newton and Engel, 2013 | [11] |
| **Canada** | | |
| Chrysomelidae | *Mesopachymerus antiqua* Poinar, 2005 | [61] |
| Staphylinidae | *Palaeoleptochromus schaufussi* O'Keefe, 1997 | [47] |

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| **Taimyr** | | |
|---|---|---|
| Acanthocnemidae | *Acanthocnemoides sukatshevae* Zherichin, 1977 | [1] |
| Cerophytidae | *Aphytocerus communis* Zherichin, 1977 | [1, 31] |
| | *Aphytocerus dolganicus* Zherichin, 1977 | [1] |
| Cryptophagidae | *Nganasania khetica* Zherichin, 1977 | [1] |
| | *Nganasania taymyrica* Lyubarsky and Perkovsky, 2014 | [44] |
| Latridiidae | *Succinimontia infleta* Zherichin, 1977 | [1] |
| Melandryidae | *Archaeoxylita zherichini* Nikitsky, 1977 | [45] |
| | *Pseudohallomenus cretaceous* Nikitsky, 1977 | [45] |

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Table 1. Groups of Coleoptera found in the Cretaceous amber collections from Lebanon (Barremian in age), Spain (Albian in age), France (Albian-Santonian in age) and Myanmar (Cenomanian in age). Information about Lebanese amber has been obtained in Kirejtshuk and Azar (2013) and Kirejtshuk et al. (2015). Information about the Spanish and French amber is newly presented here. Information about the Myanmar amber is after beetle taxa publications (Appendix 2). Deposits from Lebanon are: Nabaa Es-Sukkar-Brissa (Na), Hammana-Mdeyrij (Ha), Bouarij (Bo), Ain Dara (Ai), Kfar Selouane (Kf), Falougha (Fa), Bkassine (Bk), Roum-Aazour-Homsiyyeh (Ro), Rihane (Ri), a reference for the unknown deposit (Un) is necessary to housed fragments; deposits from Spain are: Peñacerrada I (Pe), El Soplao (So) and San Just (SJ); deposits from France are: Archingeay-Les Nouillers (Ar), Cadeuil (Ca), Fouras/Bois-Vert (Fs), La Buzinie (Bu), Fourtou (Fu), Salignac (Sa ) and La Garnache (Ga); deposit from Myanmar are: Kachin (Ka). The information for each area is summarized in the column Total (T). The family classification is following criteria in Bouchard et al. (2011), although families appear in alphabetical order. [(1)] Family not considered in Bouchard et al. (2011).

| | Lebanon | | | | | | | | | | | Spain | | | | France | | | | | | | | Myanmar |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Superfamily/Family | Na | Ha | Bo | Ai | Kf | Fa | Bk | Ro | Ri | Un | T | Pe | So | SJ | T | Ar | Ca | Fs | Bu | Fu | Sa | Ga | T | Ka |
| Archostemata | | | | | | | | | | | | | | | | | | | | | | | | |
| Micromalthidae | | | | | | | 1 | | | | 1 | | | | - | | | | | | | | - | - |
| Ommatidae | | | | | | | | | | | - | | 1 | | 1 | | | | | | | | - | - |
| Adephaga | | | | | | | | | | | | | | | | | | | | | | | | |
| Carabidae | | | | | | | 1 | | | | 1 | | | | - | 1 | | | | | | | 1 | 1 |
| Myxophaga | | | | | | | | | | | | | | | | | | | | | | | | |
| Lepiceridae | | | | | | | | | | | - | | | | - | | | | | | | | - | 1 |
| Sphaeriusidae | | | | | | | | | | | - | | | | - | | | | | | | | - | 1 |
| Polyphaga | | | | | | | | | | | | | | | | | | | | | | | | |
| Aderidae | 1 | 6 | | 1 | | | 1 | | | | 9 | 1 | 3 | | 4 | | | | | | | | - | - |
| Anthicidae | | 1 | | | | | | | | | 1 | | | | - | | | | | | | | - | - |
| Artematopodidae | | | | | | | | | | | - | | | | - | 1 | | | | | | | 1 | - |
| Boganiidae | | 3 | | | | | | | | | 3 | | | | - | | | | | | | | - | - |
| Bostrichidae | | | | | | | | | | | - | | | | - | 1 | | | | | | | 1 | - |
| Buprestidae | | | | | | | | | | | - | | | | - | 1 | | | | | | | 1 | - |
| Cantharidae | | 1 | | | | | | | | | 1 | | 1 | | 1 | | | | | | | | - | - |
| Caridae | | | | | | | | | | | - | | 1 | | 1 | 1 | | | | | | | 1 | 2 |
| Chelonariidae | | | | | 1 | | | | | | 1 | | | | - | | | | | | | | - | - |
| Clambidae | | 2 | | | | | | | | | 2 | | | | - | | | | | | | | - | - |
| Cleridae | | 1 | | | | | | | | | 1 | | | | - | | | 1 | | | | | 1 | - |
| Cleroidea | | | | | | | | | | | - | | | | - | 1 | | 1 | | | | | 2 | - |

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cryptophagidae | | | | | | | | | | | - | 2 | 2 | 1 | 5 | | | | | | | | - | - |
| Curculionidae | | 1 | | | | | | | | | 1 | | | | - | 1 | | | | | | | 1 | 2 |
| Decliniidae | | 1 | | | | | | | | | 1 | | | | - | | | | | | | | - | - |
| Dermestidae | | 4 | 1 | | | | | | | | 5 | 4 | 4 | 1 | 9 | | | | | | | | - | 1 |
| Elateridae | | 1 | | | | | 6 | | | | 7 | 1 | | | 1 | | | | | | | | - | 2 |
| Elmidae | | | | | | | | | | | - | | 1 | | 1 | | | | | | | | - | - |
| Elodophthalmidae | | 3 | 1 | | | | | | | | 4 | | | | - | | | | | | | | - | - |
| Erotylidae | | | | | | | 1 | | | | 1 | | 1 | | 1 | | | | | | | | - | - |
| Eucinetidae | | | | | | | | | | | - | 1 | 2 | 1 | 4 | | | | | | | | - | - |
| Histeridae | | | | | | | | | | | - | 1 | | | 1 | | | | | | | | - | 1 |
| Hybosoridae | | 1 | | | | | | | | | 1 | | | | - | | | | | | | | - | - |
| Jacobsoniidae | | | | | | | | | | | - | | | | - | | 1 | | | | | | 1 | - |
| Kateretidae | | 1 | | | | | | | | | 1 | | | | - | | | | | | | | - | - |
| Laemophloeidae | | 1 | | | | | | | | | 1 | | | | - | | | | | | | | - | - |
| Latridiidae | | 2 | 1 | | | | | | | | 3 | 1 | 3 | | 4 | | | | | | | | - | - |
| Lebanophytidae[1] | | 1 | | | | | | | | | 1 | | | | - | | | | | | | | - | - |
| Leiodidae | | | | | | | | | | | - | 2 | | | 2 | | | | | | | | - | - |
| Limnichidae | | | | | | | | | | | - | | | | - | 1 | | | | | | | 1 | - |
| Lymexylidae | | 1 | 1 | | | | | | | | 2 | | | | - | | | | | | | | - | - |
| Melandryidae | | 2 | | | | | 1 | | 1 | | 4 | 3 | 3 | | 6 | | | | | | | | - | - |
| Melyridae | | 1 | 1 | | | | | | | | 2 | | | | - | | | | | | | | - | - |
| Monotomidae | 1 | 4 | | | | | 2 | | | | 7 | 6 | | | 6 | | | | | | | | - | 1 |
| Mordellidae | | | | | | | | | 1 | | 1 | 3 | | | 3 | | | | | | | | - | - |
| Nemonychidae | | | 1 | | | | 1 | | | | 2 | | 1 | 1 | 2 | | | | | | | | - | 1 |
| Nitidulidae | | | | | | | | | | | - | 1 | 1 | | 2 | | | | | | | | - | - |
| Nosodendridae | | | | | | | | | | | - | | 1 | | 1 | | | | | | | | - | - |
| Oedemeridae | | | | | | | | | | | - | 1 | | | 1 | | | | | | | | - | - |
| Omethidae | | | | | | | | | | | - | 1 | | | 1 | | | | | | | | - | - |
| Phalacridae | | | | | | | | | | | - | 2 | | | 2 | | | | | | | | - | - |
| Prostomidae | | | | | | | | | | | - | | | | - | | | | | | | | - | 1 |
| Ptiliidae | 1 | 1 | 1 | | | | | | | | 3 | | | | - | | | | | | | | - | - |
| Ptilodactylidae | | 1 | | | | | | | | | 1 | | | | - | | | | | | | | - | 1 |
| Ptinidae | | | | | | | | | 1 | | 1 | 2 | | 1 | 3 | | | | | | | 2 | 2 | - |
| Pyrochroidae | | | | | | | | | | | - | 1 | | | 1 | | | | | | | | - | - |
| Ripiphoridae | | | | | | | | | | | - | | | | - | 6 | | | | | 1 | | 7 | 1 |
| Salpingidae | | | | | | | | | 5 | | 5 | 1 | | | 1 | | | | | | | | - | - |
| Scarabaeoidea | | 1 | 1 | | | | 1 | | | | 3 | | | | - | | | | | | | | - | - |
| Scirtidae | | | 1 | | | | 1 | 1 | | | 3 | | | | - | | | | | | | | - | 1 |
| Scraptiidae | | 1 | | | | | | | 1 | | 2 | 4 | | | 4 | 1 | | | | | | | 1 | - |

ACCEPTED MANUSCRIPT

| | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Silvanidae | 1 | 1 | | | | | | | | | 2 | 2 | | 2 | 4 | | | | | | | | - | 1 |
| Sphindidae | 1 | 2 | 1 | | | | 1 | | | | 5 | | | | - | | | | | | | | - | - |
| Staphylinidae | | 4 | 3 | 1 | | | 2 | | | | 10 | 15 | 8 | 2 | 25 | 5 | | | | | | | 5 | 12 |
| Tenebrionoidea | | 1 | 1 | | | | | | | | 2 | 1 | 1 | | 2 | | | | | | | | - | - |
| Tenebrionidae | | | | | | | | | | | - | 1 | 1 | | 2 | | | | | | | | - | - |
| Tetratomidae | | | | | | | | | | | - | | | | - | 2 | | | | | | | 2 | - |
| Throscidae | | 2 | 1 | | | 1 | 3 | | | | 7 | | | | - | | | | | | | | - | - |
| Trogossitidae | | | | | | | | | | | - | 1 | | | 1 | | | 1 | | | | | 1 | - |
| Zopheridae | | | | | | | | | | | - | | | | - | | | | | | | 1 | 1 | 1 |
| Larva | | 1 | | | | | 1 | | 1 | | 3 | 1 | | | 1 | 3 | | | | 1 | | 1 | 5 | 1 |
| Fragments | | | | | | | | | | 16 | 16 | 16 | 10 | 2 | 28 | 10 | 1 | 1 | | | 3 | 1 | 16 | - |
| Indeterminate group | | 2 | | | | | 1 | | 1 | | 4 | 9 | 6 | 3 | 18 | 9 | | 2 | 1 | | 2 | | 14 | - |
| Total | 9 | 55 | 15 | 2 | 1 | 1 | 24 | 1 | 11 | 16 | 135 | 84 | 51 | 14 | 149 | 45 | 2 | 6 | 1 | 1 | 6 | 5 | 65 | 32 |

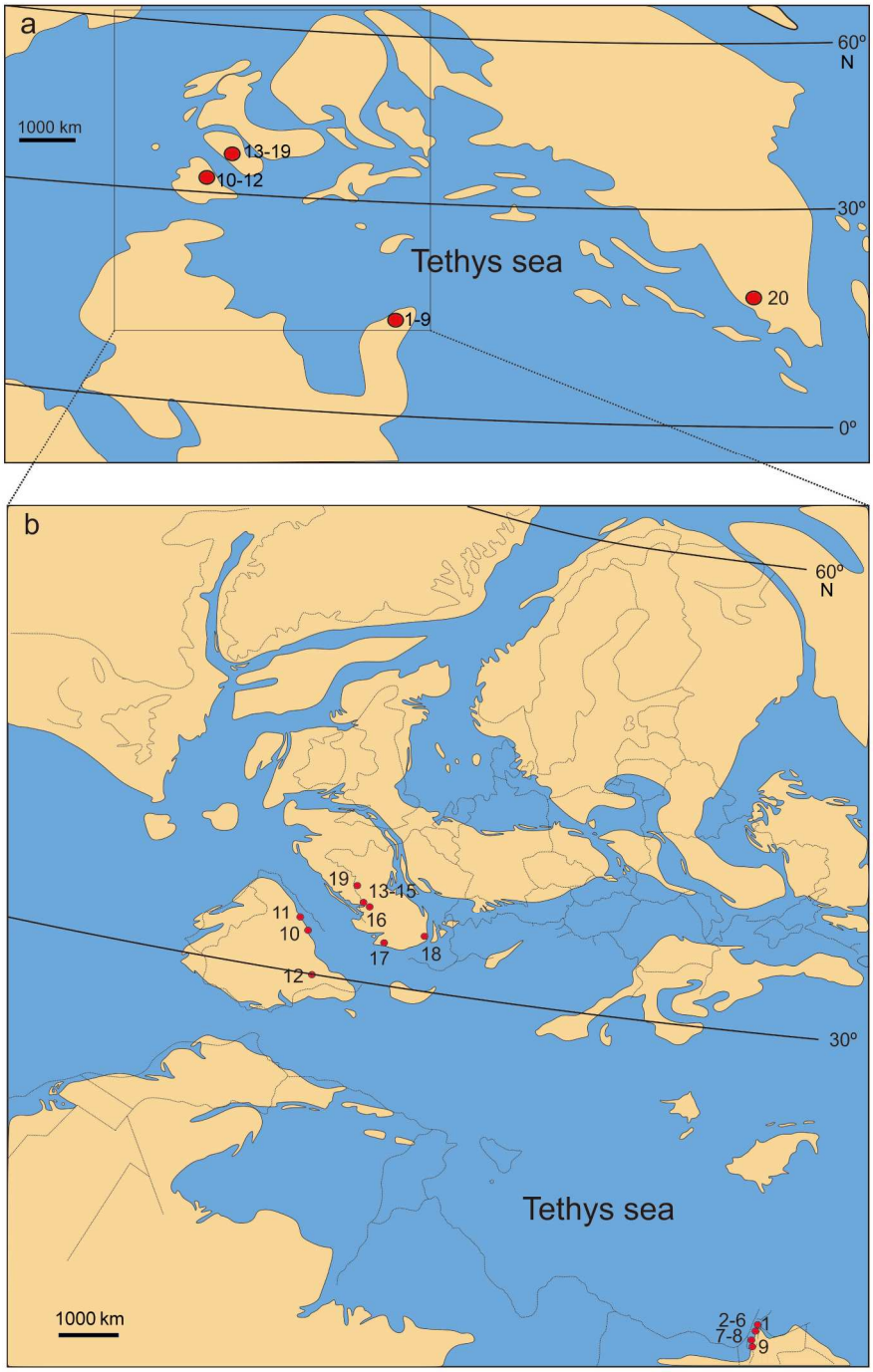
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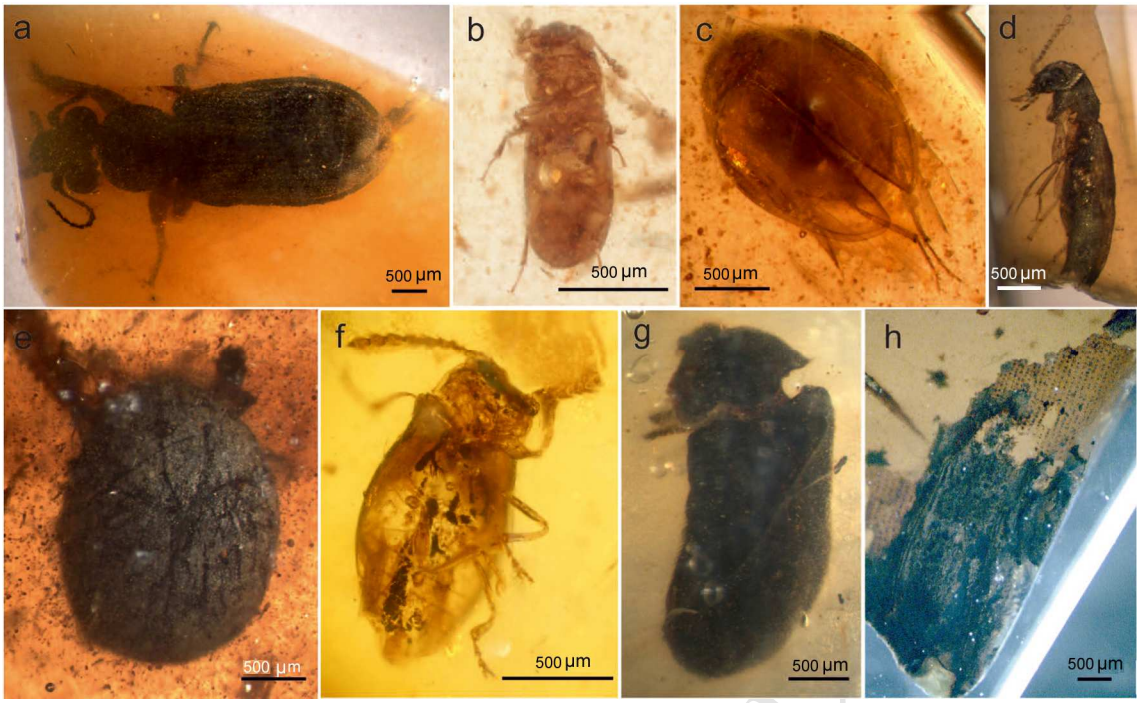
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Table 2. Chi-square distance matrix between countries

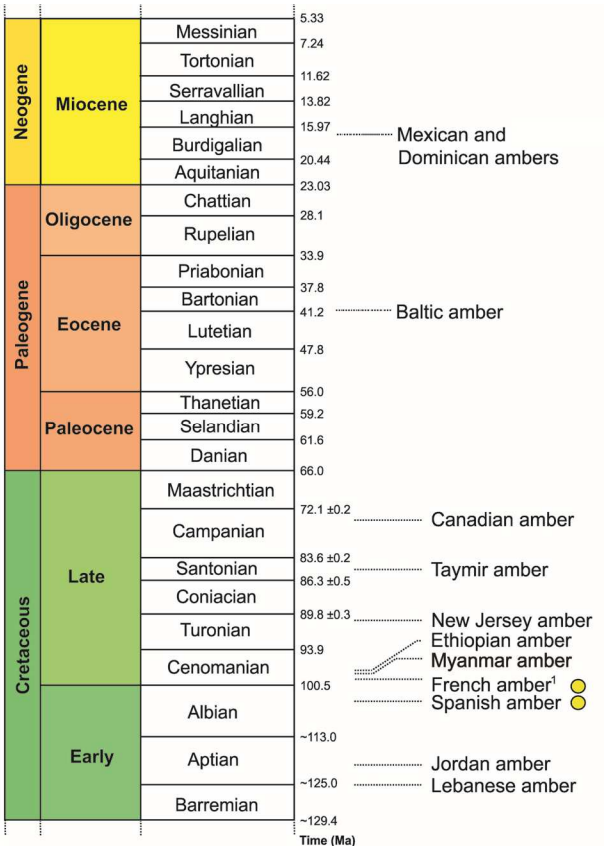
| | Spain | Lebanon | France | Myanmar |
|---|---|---|---|---|
| Spain | ,000 | 9,619 | 9,549 | 7,704 |
| Lebanon | 9,619 | ,000 | 10,087 | 8,188 |
| France | 9,549 | 10,087 | ,000 | 5,835 |
| Myanmar | 7,704 | 8,188 | 5,835 | ,000 |

ACCEPTED MANUSCRIPT

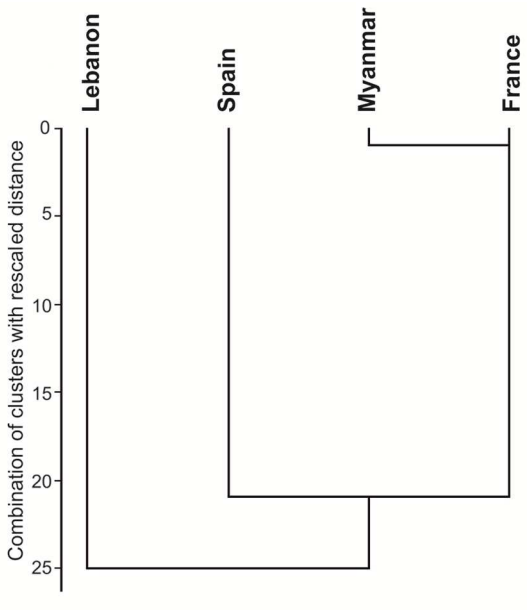

a
60°
N
1000 km
13-19
10-12
30°
Tethys sea
20
1-9
0°
b
60°
N
19
13-15
11
16
10
17
18
12
30°
Tethys sea
1000 km
2-6
7-8
1
9




ACCEPTED MANUSCRIPT




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RESEARCH HIGHLIGHTS

- Coleoptera were not vectors for the resin production that resulted in Early-Middle Cretaceous ambers
- Ancient representatives of at least 13 families are embedded in these ambers
- Age, paleogeography or local paleohabitat could influence dissimilar communities
- Current knowledge of the beetles in Cretaceous ambers is established

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