fossil studies

MDPI

Review

The Wasps (Hymenoptera) from Lower Cretaceous Lebanese and Spanish Ambers

Sergio Álvarez-Parra [1] and Dany Azar [1,2,*]

[1] State Key Laboratory of Palaeobiology and Petroleum Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing 210008, China; sergio@nigpas.ac.cn
[2] Natural Sciences Department, Faculty of Science II, Lebanese University, Fanar, Jdeidet, Beirut P.O. Box 90656, Lebanon
* Correspondence: danyazar@ul.edu.lb

Abstract: Hymenoptera is the fourth-most diverse insect order today, including wasps, bees, bumblebees, and ants. They show a wide panoply of modes of life, such as herbivory, predation, parasitoidism, pollination, and eusociality. This group also includes a great number of extinct species from both amber and compression outcrops. Hymenopterans probably originated in the Paleozoic, although their oldest record is from the Middle or Late Triassic, and their diversity expanded since the Cretaceous. Here, we present a review of the Hymenoptera in Lower Cretaceous ambers from Lebanon (Barremian) and Spain (Albian), which is pivotal for the study of hymenopteran evolution. Hymenoptera in Lebanese ambers are represented by 32 species in 22 genera within 15 families, while in Spanish ambers, they correspond to 49 species in 40 genera within 18 families. Most of these species belong to the 'Parasitica', and only a few species have been assigned to the Aculeata. The group 'Symphyta' is represented by one species in Spanish amber. The paleobiogeography and possible paleobiologies of the species in these ambers are reviewed. Furthermore, checklists for all Hymenoptera species in Lebanese and Spanish ambers are provided.

Keywords: Apocrita; Aculeata; diversity; parasitoidism; paleobiology; biogeography; Spain; Lebanon; Mesozoic; Early Cretaceous

Citation: Álvarez-Parra, S.; Azar, D. The Wasps (Hymenoptera) from Lower Cretaceous Lebanese and Spanish Ambers. *Foss. Stud.* **2024**, *2*, 110–122. https://doi.org/10.3390/fossils2020005

Academic Editor: Frank-Thorsten Krell

Received: 7 May 2024
Revised: 24 May 2024
Accepted: 4 June 2024
Published: 5 June 2024

1. Introduction

Hymenoptera are holometabolous insects, including wasps, bees, bumblebees, and ants [1], corresponding to the fourth-most diverse insect order, accounting for more than 150,000 living species [2]. The presence of hamuli, tiny hooks on the anterior margin of hind wings that allow their coupling with the forewings, is the main anatomical characteristic of Hymenoptera [3]. The ovipositor in some groups representing the Aculeata has evolved into a venomous sting [3,4]. Hymenopterans have a wide distribution and show a panoply of biologies, such as herbivory, predation, parasitoidism, pollination, and eusociality [1]. Phylogenetic studies have placed Hymenoptera as a sister group to the rest of the holometabolous insects [5]. The groups 'Symphyta' and Apocrita have been historically differentiated, the latter characterized by a narrowing (called petiole) between the first (fused to the thorax) and second segments of the abdomen [6]. Within Apocrita, 'Parasitica' and Aculeata have been distinguished, the latter characterized by the presence of a sting in the females [6]. However, both 'Symphyta' and 'Parasitica' have been recognized as paraphyletic groupings [6]. The 'Parasitica' were grouped together due to their parasitoid biology; however, not all members are parasitoids, and some groups of Aculeata also show this peculiar lifestyle [7].

With more than 3,500 known extinct species, Hymenoptera is one of the insect groups with a greater fossil diversity [3]. The oldest representative dates back to the Middle or Late Triassic, although molecular analyses point out that the group could have originated in the Carboniferous and diversified before the Triassic [7]. Hymenoptera are one of the

most abundant and diverse groups of insects found in amber, probably linked to their small size and habitats close to resiniferous trees, thus facilitating their entrapment in resin. Bees and ants, keystone insects in current ecosystems, probably emerged during the Early Cretaceous and diversified during the Late Cretaceous, simultaneously with the radiation of angiosperms [1,7], but still relatively rare in Cretaceous ecosystems [8]. The evolutionary history of the panoply of modes of life present in Hymenoptera is hitherto mostly unknown, and the study of extinct families is crucial to better understanding their present diversity. Cretaceous ambers are an excellent source of information for fossil hymenopterans, providing keys to a changing world that transitioned from ecosystems dominated by gymnosperms to angiosperms during the so-called Angiosperm Terrestrial Revolution [9].

Cretaceous ambers, linked to the Cretaceous Resinous Interval [10], are an important source of information on fossil Hymenoptera as they have provided numerous specimens belonging to diverse families [11,12]. Several Upper Cretaceous ambers have yielded abundant hymenopterans, such as the lower Cenomanian Kachin Burmese amber [13]. However, information on wasps from the Early Cretaceous is more restricted. They are represented from several compression outcrops, limiting the anatomical observations due to preservation [14,15]. Their record in Lower Cretaceous ambers is present in small number in ambers from Congo, Myanmar (Hkamti), and Japan [16–18]. In contrast, hymenopterans are highly numerous and diverse in Lebanese and Spanish ambers, highlighting their relevance and making them fundamental for the study of hymenopteran evolution. Here, we present a review of the Hymenoptera in both Lebanese and Spanish ambers, including checklists of described species and discussing the paleodiversity, paleobiogeography, and paleobiology.

2. Geological Settings

Amber has been found in more than 450 outcrops in Lebanon, with a timespan ranging from the Late Jurassic (Kimmeridgian) to the Late Cretaceous (Cenomanian), but bioinclusions have been only discovered in amber of 30 outcrops, all of them from the Barremian [19–21]. Most Lower Cretaceous ambers from Lebanon are found in the Sandstone of the Lebanon Unit, also known as the "Grès du Liban" Alloformation [19]. Amber (of the same early Barremian age) is found in thin levels of dark shales together with lignite and plant remains in three depositional intervals of the "Grès du Liban" [19,22]. The dating of these depositional intervals ranges from early to late Barremian based on charophytes, foraminifers, rudists, and echinoids [22]. It is considered that the resin pieces from the lower depositional interval underwent short-distance transport before burial [19], i.e., parautochthony. The remaining amber material found in mid- and upper depositional intervals was reworked in estuarian or margin-littoral shelves. The paleoenvironment of the amber outcrops has been inferred as dense resiniferous forests in a fluvial system with a marine influence under a warm and humid climate [19,22]. Until now, hymenopterans have been identified in amber from 17 outcrops in Lebanon (Figure 1A), being abundant in ambers from Bcharreh, Baskinta, Bouarij, Hammana-Mdeyrij, Ain Dara, and Jezzine. The relative rarity of hymenopteran from the remaining fossiliferous outcrops is certainly due to undersampling, as most of these outcrops have been visited once or a few times.

The Iberian Peninsula is also rich in amber outcrops. More than 150 possible amber deposits have been reported, but the presence of amber has been only confirmed in 67 outcrops from Spain and nine from Portugal. The oldest amber from the Iberian Peninsula is from the Triassic (Ladinian–Rhaetian) of Alicante Province [23]. There are a few Upper Cretaceous ambers from Spain, although most of the amber-bearing outcrops are dated as Early Cretaceous [23]. The Cretaceous amber outcrops from the Iberian Peninsula correspond to the western (Lusitanian Basin), northern (Central Asturian Depression and Basque Cantabrian Basin), and eastern (Maestrazgo Basin) coasts of the 'mid'-Cretaceous Iberia Island. They are considered parautochthonous, and the resin depositional environments are inferred as deltas, estuaries, or coastal swamps ranging from humid to arid

climatic contexts [23–25]. Bioinclusions have been found in amber from 12 outcrops of the Iberian Peninsula from the early Albian to the early Cenomanian [23–27]. Among them, the richest in bioinclusions are El Soplao, Peñacerrada I, San Just, and Ariño [23,26]. Hymenopterans have been found in ambers from nine outcrops so far (Figure 1B).

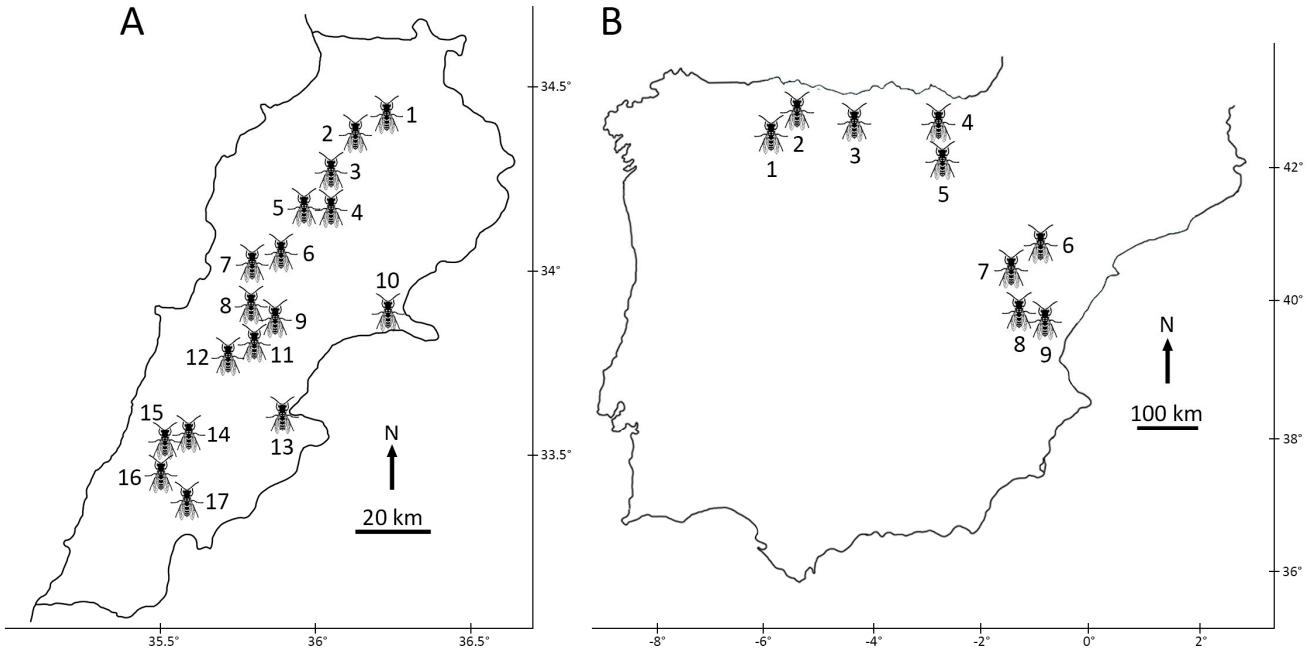

Figure 1. Schematic maps indicating the location of the Cretaceous amber outcrops yielding hymenopteran specimens as bioinclusions. (**A**) Lebanon: 1: Mechmech; 2: El-Dabsheh; 3: Bcharreh; 4: Beqaa Kafra; 5: Tannourine; 6: Bqaatouta; 7: Baskinta; 8: Kfar Selouan; 9: Bouarij; 10: Esh-Sheaybeh; 11: Hammana-Mdeyrij; 12: Ain Dara; 13: Aita El-Foukhar; 14: Jezzine; 15: Roum-Aazour-Homsiyyeh; 16: Maknouniyyeh; 17: Rihane. (**B**) Iberian Peninsula: 1: El Caleyu; 2: La Rodada; 3: El Soplao; 4: Peñacerrada I; 5: Peñacerrada II; 6: Ariño; 7: San Just; 8: Arroyo de la Pascueta; 9: La Hoya. Wasp silhouette from https://www.phylopic.org/ ("*Vespula alascensis* by Andy Wilson", CC0 1.0 Universal Public Domain Dedication, accessed on 1 May 2024).

3. Hymenoptera Paleodiversity in Lebanese and Spanish Ambers

3.1. Lebanese Ambers

Hymenoptera in Lebanese ambers are represented by 32 species in 22 genera within 15 families (Appendix A). Eight of the recorded families are extinct and restricted to the Cretaceous: †Protoitidae, †Spathiopterygidae, †Gallorommatidae, †Archaeoserphitidae, †Serphitidae, †Maimetshidae, †Stigmaphronidae, and †Holopsenellidae. Most of the species belong to the 'Parasitica' (78%), and Aculeata only correspond to seven species (Figure 2A, 3). The outcrops providing a higher number of species are Hammana-Mdeyrij and Bcharreh. Interestingly, all of the recorded species are only present in their type locality; therefore, there are no co-occurrences at the species level. There is only one genus identified from two outcrops, the genus *Protoita* from Hammana-Mdeyrij and Roum-Aazour-Homsiyyeh [28]. The most diverse family is the group of tiny chalcidoid wasps †Protoitidae (35% of the total species), followed by Evaniidae, †Serphitidae, and Scolebythidae.

The taxonomy of the hymenopterans from Lebanese ambers is mostly stable, and only a few taxonomic changes have been applied. The species *Cretaxenomerus jankotejai* Nel and Azar, 2005 was originally placed in the family Scelionidae [29], but an extensive study on chalcidoid wasps from Lebanese ambers has allowed transferring this species to the recently erected family †Protoitidae [28]. The monotypic genus *Eovernevania* was considered to be a junior synonym of *Cretevania* based on the lack of important anatomical differences [30], thus resulting in the species *Cretevania cyrtocerca* (Deans, 2004) being

derived from Hammana-Mdeyrij amber. The species *Aphelopus palaeophoenicius* Olmi, 2000 was transferred to a new genus in its own new subfamily, turning into *Archaeodryinus palaeophoenicius* (Olmi, 2000) based on its anatomical differences with the rest of the dryinids [31]. The species *Holopsenella primotica* Engel, Ortega-Blanco and Azevedo, 2016 was first considered the only member of its own subfamily within Bethylidae [32], the holopsenellines probably being the earliest diverging bethylids [33]. However, the status of this subfamily was raised into a family, †Holopsenellidae, and placed as *Incertae sedis* in Aculeata [34].

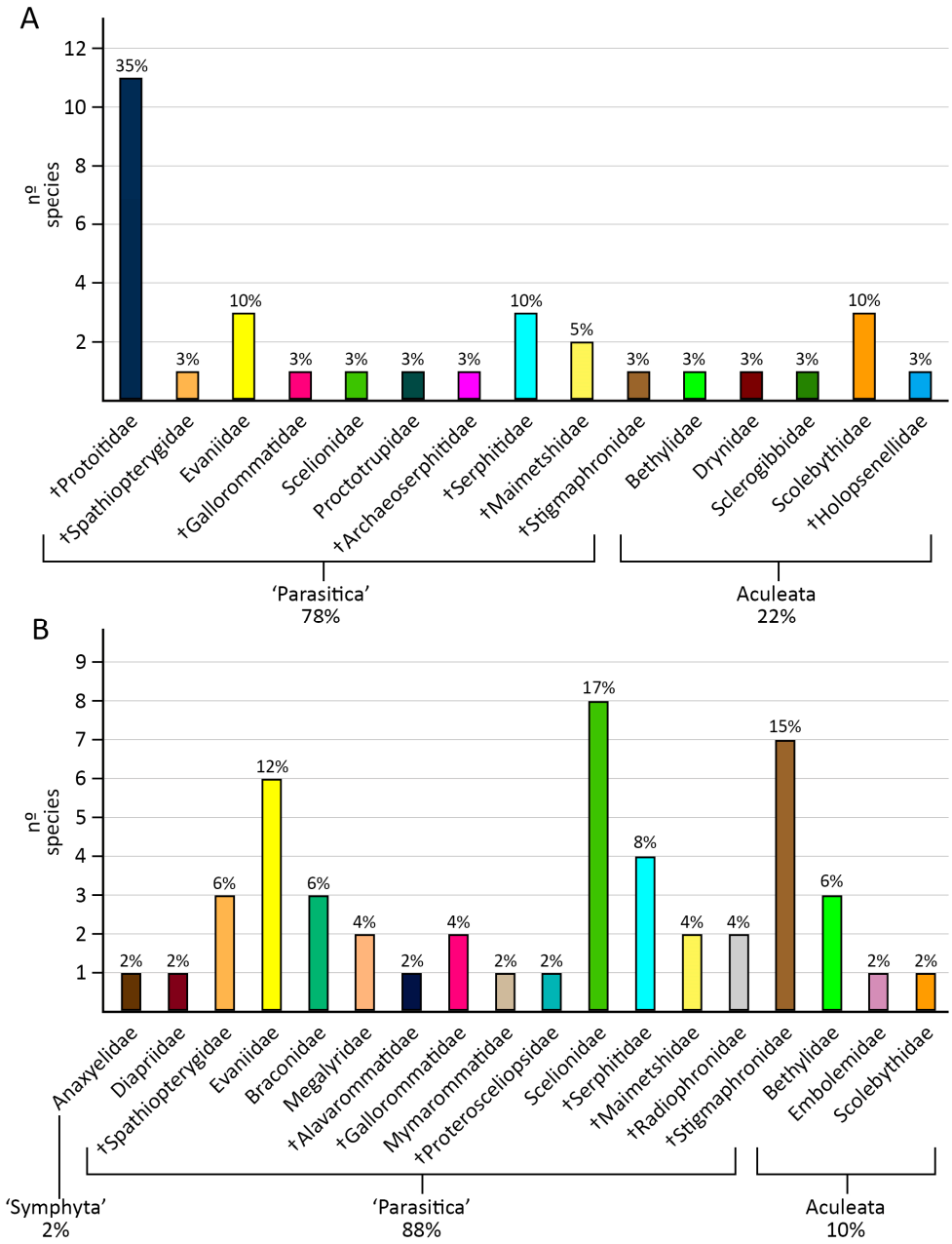

Figure 2. Paleodiversity at the species level of families within Hymenoptera. (**A**) Lebanese amber, Barremian; (**B**) Spanish amber, Albian.

Apart from the mentioned families, new specimens under study have been preliminarily assigned to the families †Baissidae, Braconidae, Megaspilidae, Mymarommatidae, and Chrysididae.

3.2. Spanish Ambers

Hymenoptera in Spanish ambers correspond to 49 species in 40 genera within 18 families (Appendix B). Among them, there are eight extinct families whose record is limited to the Cretaceous: †Spathiopterygidae, †Alavarommatidae, †Gallorommatidae, †Proterosceliopsidae, †Serphitidae, †Maimetshidae, †Radiophronidae, and †Stigmaphronidae. Similarly to Lebanese amber, most of the species belong to the 'Parasitica' (88%), while only five species form part of the Aculeata (Figure 2B, 3). Interestingly, there is one species, represented by the holotype, belonging to the sawfly family Anaxyelidae [35]. The ambers that have yielded the highest number of specimens are Peñacerrada I (782 specimens), El Soplao (276), San Just (111), and Ariño (34), although most of them are pending to be studied. Peñacerrada I is the type locality of 39 species, followed by San Just, type locality of 7 species. It is important to note that there are five co-occurrences at the species level among Spanish ambers: *Megalava truncata* Perrichot, 2009 (Megalyridae, in Peñacerrada I and El Soplao, [36,37]), *Alavaromma orchamum* (†Alavarommatidae, in Peñacerrada I and San Just, [38]), *Cretaceomma turolensis* (Ortega-Blanco, Peñalver, Delclòs and Engel, 2011) (†Gallorommatidae, in San Just and possibly in Ariño, [26,38]), *Archaeromma hispanicum* Ortega-Blanco, Peñalver, Delclòs and Engel 2011 (Mymarommatidae, in Peñacerrada I and El Soplao, [38]), and *Burmaphron jentilak* Ortega-Blanco, Delclòs and Engel, 2011 (†Stigmaphronidae, in Peñacerrada I and San Just, [39]). Furthermore, the genus *Cretevania* (Evaniidae) is present in the ambers from El Soplao, Peñacerrada I, San Just, and Arroyo de la Pascueta [30,40], and the genus *Serphites* (†Serphitidae) has been identified in the ambers from Peñacerrada I, San Just, and Ariño [26,41]. The most abundant and diverse wasp family in Spanish ambers is Scelionidae, accounting for 17% of the total species. The families †Stigmaphronidae, Evaniidae, and †Serphitidae are also highly diverse.

Some hymenopteran taxa from Spanish ambers have undergone taxonomic changes. The species *Iberopria perialla* Engel, Ortega-Blanco, and Delclòs, 2013 was originally assigned to Diapriidae [42], later it was transferred to †Cretacoformicidae [43], and subsequently, this family was synonymized under †Trupochalcididae, although returning *I. perialla* to Diapriidae [44]. The species *Galloromma turolensis* Ortega-Blanco, Peñalver, Delclòs and Engel, 2011 (†Gallorommatidae) [38] was transferred to the new genus *Cretaceomma* and is also present in Lebanese amber [45]. The genus *Proterosceliopsis*, described from a specimen of Peñacerrada I amber, was first considered to be a member of Scelionidae [46] but was later placed in its own family, †Proterosceliopsidae, based on their differential anatomical characteristics [47]. Both families †Radiophronidae and †Stigmaphronidae, the former described from specimens in Peñacerrada I amber, were placed in the superfamily Ceraphronoidea [39,48], although their relationships with this superfamily have been questioned, and they might belong to Aculeata [49]. The species *Lancepyris alavaensis* Ortega-Blanco & Engel, 2013 (Bethylidae) was transferred to the new genus *Zophepyris*, similarly to the species *Embolemus periallus* Ortega-Blanco, Delclòs and Engel, 2011 (Embolemidae), which was assigned to the genus *Ampulicomorpha*, clarifying the relationships within their corresponding families [32,50,51].

The families Baeomorphidae, Chrysididae, Sapygidae, Sierolomorphidae, and Tiphiidae have been preliminarily identified and the study of the specimens is in progress.

4. Discussion and Conclusions

Lebanese and Spanish ambers are among the most important sources of knowledge of fossil Hymenoptera based on the exceptional preservation of the specimens and their dating as Early Cretaceous (Figure 3), providing information from a crucial epoch for the Hymenoptera just prior to the Angiosperm Terrestrial Revolution [9,52]. 'Symphyta' are rare in Cretaceous ambers in comparison to the Apocrita. These wasps are not present yet in Lebanese ambers, and they are represented in Spanish ambers by only one species [35]. Most of the species in Lebanese and Spanish ambers are 'Parasitica', and the Aculeata correspond to only a few specimens (Figure 2). Wasps belonging to this group are represented by limited species in New Jersey, Taymyr, and Canadian ambers. This is surprising in

comparison to Kachin amber, where Aculeata include more than half of the whole studied hymenopteran diversity [13,34]. This fact may be explained by a research bias in which the study of hymenopterans from Kachin amber is focused on Aculeata, where the families Bethylidae, Dryinidae, Embolemidae, Formicidae, and Vespidae are highly diverse [13]. However, it is also possible that the differential diversity is linked to paleoenvironmental or paleobiogeographical factors, resulting in different wasp communities. Regarding the most diverse hymenopteran families today, Ichneumonidae are absent in Lebanese and Spanish ambers, while Braconidae are only represented by a few species [53].

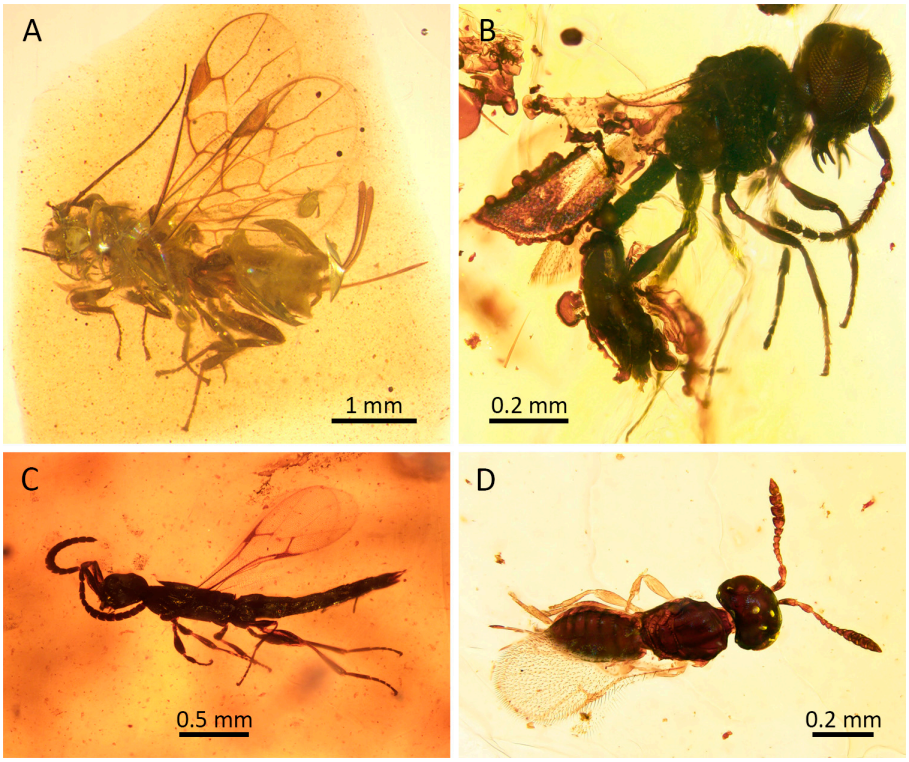

Figure 3. Hymenopterans in Lower Cretaceous Lebanese and Spanish ambers. (**A**) Braconid wasp (Braconidae) in amber from El Soplao, Spain; (**B**) Serphitid wasp (†Serphitidae) in amber from Hammana-Mdeyrij, Lebanon; (**C**) possible proterosceliopsid wasp (†Proterosceliopsidae) in amber from El Soplao; (**D**) possible scelionid wasp (Scelionidae) in amber from Hammana-Mdeyrij.

Five co-occurrences of hymenopterans at the species level between Spanish amber outcrops have been reported. The same species in different Spanish ambers have also been noticed for other insect groups, such as barklice, beetles, and midges [54–56]. These taxonomical coincidences may be linked to a great extension of the resiniferous forests along the northern and eastern coasts of the Iberia Island during the Albian, allowing entomofaunal dispersal. Interestingly, no hymenopteran species co-occurrences have been reported from Lebanese amber despite their close geographical and temporal distances, probably due to a research bias. In Lebanese and/or Spanish ambers, wasp genera with a wide distribution during the Cretaceous have been described, such as *Cretevania*, *Archaeromma*, and *Serphites*, all of them present in ambers from several distant provenances [30,38,41]. The genera *Eosyntexis*, from Spanish amber, and *Cretevania*, from both Lebanese and Spanish ambers, are also present in compression outcrops [30,35], evidencing that they thrived in diverse paleoenvironments and regions.

As discussed in previous articles, the entomofaunas from Lebanese and Spanish ambers shared similarities, as 20 insect genera co-occurrences have been reported [57–59]. In the case of the Hymenoptera, five genera have been identified from both provenances (Table 1): *Cretaceomma*, *Cretevania*, *Libanophron*, *Microserphites*, and *Mymaropsis*. This is surprising based on the geographical distance and the temporal separation of about

20 myr. Similar paleoenvironmental factors in these regions might explain the taxonomic coincidences, and land 'bridges' in western Tethys could facilitate the displacement of insect fauna, usually with low dispersal abilities [59]. The high co-occurrence of genera between Lebanese (four genera) and Spanish (eight genera) ambers with Kachin amber (Table 1) is thought-provoking. Furthermore, the presence of the same genera in Spanish ambers and New Jersey (four genera) and Yantardakh (six genera) ambers would not be expected, considering the great geographical and temporal separation (Table 1). However, Cretaceous hymenopteran biogeography is still not well known, and more information is required to understand the factors facilitating or hindering the long-distance movement of wasps during this period.

Table 1. Co-occurrences at the genus level of Hymenoptera between Lebanese and Spanish ambers with other Cretaceous ambers. Lebanon–Barremian, Congo–Aptian, Spain–Albian, Myanmar (Hkamti)–Albian, Myanmar (Kachin)–Cenomanian, France (Charentes)–Cenomanian, Russia (Nizhnyaya Agapa)–Cenomanian, USA (New Jersey)–Turonian, Japan (Iwaki)–Coniacian, Japan (Kuji)–Coniacian/Santonian, Russia (Yantardakh)–Santonian, Canada–Campanian.

Family	Genus	Lebanon	Congo	Spain	Myanmar (Hkamti)	Myanmar (Kachin)	France(Charentes)	Russia (Nizhnyaya Agapa)	USA (New Jersey)	Japan (Iwaki)	Japan (Kuji)	Russia (Yantardakh)	Canada
†Spathiopterygidae	*Mymaropsis*	X		X									
Evaniidae	*Cretevania*	X	X	X		X		X				X	
	Iberoevania			X		X							
†Gallorommatidae	*Cretaceomma*	X		X									
	Galloromma			X		X	X	X					
Mymarommatidae	*Archaeromma*			X		X			X	X	X	X	X
†Proterosceliopsidae	*Proterosceliopsis*			X		X							
Scelionidae	*Proteroscelio*	X				X							X
†Archaeoserphitidae	*Archaeoserphites*	X				X							
†Serphitidae	*Aposerphites*			X								X	
	Microserphites	X		X				X					
	Serphites			X		X	X		X			X	X
†Maimetshidae	*Iberomaimetsha*			X								X	
†Stigmaphronidae	*Burmaphron*			X		X							
	Elasmophron			X					X				
	Hippocoon			X								X	
	Tagsmiphron			X					X				X
	Libanophron	X		X									
Embolemidae	*Ampulicomorpha*			X	X	X							
†Holopsenellidae	*Holopsenella*	X			X	X							

Hymenoptera were abundant and diverse in the Early Cretaceous resiniferous forests of Iberia Island and Levantine regions, occupying key ecological niches and showing

a panoply of modes of life, probably mirroring those living in present-day ecosystems. The only representative of 'Symphyta' in Spanish amber, *Eosyntexis parva* Ortega-Blanco, Rasnitsyn and Delclòs, 2008, could lay eggs in burnt wood, similar to the living species of the family [35]. The rest of the extant families present in Lebanese and Spanish ambers are parasitoid, including the few aculeate families. Therefore, it is possible that their members in these ambers were also parasitoid. However, the wide diversity of modes of life present in Hymenoptera [1,7], and considering the high number of different types of parasitoidism behaviors and secondary reversals [60], makes it risky to assume a certain lifestyle for extinct species. Most of the extinct hymenopteran families, such as †Spathiopterygidae, †Serphitidae, †Radiophronidae, and †Stigmaphronidae, have been considered parasitoid based on phylogenetic inference [39,41,48,61], but an extensive morphological study is still required to better understand their possible paleobiologies.

Author Contributions: Conceptualization, S.Á.-P.; Investigation, S.Á.-P. and D.A.; Methodology, S.Á.-P.; Supervision, D.A.; Writing—original draft, S.Á.-P.; Writing—review and editing, S.Á.-P. and D.A. All authors have read and agreed to the published version of the manuscript.

Funding: This study is partly funded by the Consejería de Industria, Turismo, Innovación, Transporte y Comercio del Gobierno de Cantabria through the public enterprise EL SOPLAO S.L. (research agreement #20963 with Universitat de Barcelona and research contract Ref. VAPC 20225428 with CN IGME-CSIC, for the period 2022–2025).

Data Availability Statement: All the data used in the study are included in the paper.

Acknowledgments: It is a contribution to the project PID2022-137316NB-C21 (Spanish Ministry of Science and Innovation, AEI/FEDER, and the EU).

Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A. Checklist of the Wasp Species (Hymenoptera) Described from Lebanese Ambers

Group	Superfamily	Family	Genus and Species	Type Locality	Age	References
'Parasitica'	Chalcidoidea	†Protoitidae	*Cretaxenomerus brevis* Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
			Cretaxenomerus curvus Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
			Cretaxenomerus deangelis Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
			Cretaxenomerus jankotejai Nel and Azar, 2005	Hammana-Mdeyrij	Barremian	[28,29]
			Cretaxenomerus mirari Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
			Cretaxenomerus tenuipenna Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
			Cretaxenomerus vitreus Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
			Protoita bidentata Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
			Protoita istvani Ulmer and Krogmann, 2023	Roum-Aazour-Homsiyyeh	Barremian	[28]
			Protoita noyesi Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
			Protoita petersi Ulmer and Krogmann, 2023	Hammana-Mdeyrij	Barremian	[28]
	Diaprioidea	†Spathiopterygidae	*Mymaropsis baabdaensis* Krogmann, Azar, Rajaei and Nel, 2016	Hammana-Mdeyrij	Barremian	[61,62]
	Evanioidea	Evaniidae	*Cretevania cyrtocerca* (Deans, 2004)	Hammana-Mdeyrij	Barremian	[30,63]
			Lebanevania azari Basibuyuk and Rasnitsyn, 2002	Jezzine	Barremian	[64]
			Protoparevania lourothi Deans, 2004	Hammana-Mdeyrij	Barremian	[63]
	Mymarommatoidea	†Gallorommatidae	*Cretacomma libanensis* Rasnitsyn and Azar, 2022	Hammana-Mdeyrij	Barremian	[45]
	Platygastroidea	Scelionidae	*Proteroscelio gravatus* Johnson, Musetti and Masner, 2008	Hammana-Mdeyrij	Barremian	[65]
	Proctotrupoidea	Proctotrupidae	*Astarteserphus grimaldii* Engel, Herhold and Barden, 2022	Bcharreh	Barremian	[66]
	†Serphitoidea	†Archaeoserphitidae	*Archaeoserphites melqarti* Engel, 2015	Bcharreh	Barremian	[67]
		†Serphitidae	*Leptoserphites iriae* Rssnitsyn and Azar, 2022	Baskinta	Barremian	[45]
			Leptoserphites pabloi Rasnitsyn and Azar, 2022	Baskinta	Barremian	[45]
			Microserphites libanensis Rasnitsyn and Azar, 2022	Hammana-Mdeyrij	Barremian	[44]
	Trigonalyoidea	†Maimetshidae	*Ahiromaimetsha najlae* Perrichot, Azar, Nel and Engel, 2011	Maknouniyyeh	Barremian	[68]
			Zorophratra corynetes Engel, 2016	Hammana-Mdeyrij	Barremian	[69]
	Incertae sedis	†Stigmaphronidae	*Libanophron astarte* Engel and Grimaldi, 2009	Hammana-Mdeyrij	Barremian	[70]

Group	Superfamily	Family	Genus and Species	Type Locality	Age	References
Aculeata	Chrysidoidea	Bethylidae	*Lancepyris opertus* Azevedo and Azar, 2012	Ain Dara	Barremian	[71]
		Drynidae	*Archaeodryinus palaeophoenicius* (Olmi, 2000)	Jezzine	Barremian	[31,72]
		Sclerogibbidae	*Sclerogibbodes embioleia* Engel and Grimaldi, 2006	Bcharreh	Barremian	[73]
		Scolebythidae	*Libanobythus milkii* Prentice and Poinar, 2006	Jezzine	Barremian	[74,75]
			Uliobythus terpsichore Engel and Grimaldi, 2007	Hammana-Mdeyrij	Barremian	[75]
			Zapenesia libanica Engel and Grimaldi, 2007	Hammana-Mdeyrij	Barremian	[75]
	Incertae sedis	†Holopsenellidae	*Holopsenella primotica* Engel, Ortega-Blanco and Azevedo, 2016	Bcharreh	Barremian	[32]

Appendix B. Checklist of the Wasp Species (Hymenoptera) Described from Spanish Ambers

Group	Superfamily	Family	Genus and Species	Type Locality	Age	References
'Symphyta'	Siricoidea	Anaxyelidae	*Eosyntexis parva* Ortega-Blanco, Rasnitsyn and Delclòs, 2008	Peñacerrada I	late Albian	[35]
'Parasitica'	Diaprioidea	Diapriidae	*Iberopria perialla* Engel, Ortega-Blanco, and Delclòs, 2013	Peñacerrada I	late Albian	[42]
		†Spathiopterygidae	*Diameneura marveni* Santer and Álvarez-Parra, 2022	San Just	late Albian	[61]
			Mymaropsis turolensis Engel and Ortega-Blanco, 2013	San Just	late Albian	[42,61]
			Spathiopteryx alavarommopsis Engel and Ortega-Blanco, 2013	Peñacerrada I	late Albian	[42]
	Evanioidea	Evaniidae	*Cretevania alcalai* Peñalver, Ortega-Blanco, Nel and Delclòs, 2010	San Just	late Albian	[30]
			Cretevania alonsoi Peñalver, Ortega-Blanco, Nel and Delclòs, 2010	Peñacerrada I	late Albian	[30]
			Cretevania montoyai Peñalver, Ortega-Blanco, Nel and Delclòs, 2010	San Just	late Albian	[30]
			Cretevania rubusensis Peñalver, Ortega-Blanco, Nel and Delclòs, 2010	Rubielos de Mora	late Albian	[30]
			Cretevania soplaensis Pérez-de la Fuente, Peñalver and Ortega-Blanco, 2012	El Soplao	middle Albian	[41]
			Iberoevania roblesi Peñalver, Ortega-Blanco, Nel and Delclòs, 2010	Peñacerrada I	late Albian	[30]
	Ichneumonoidea	Braconidae	*Archephedrus stolamissus* Ortega-Blanco, Bennett, Delclòs, and Engel, 2009	Peñacerrada I	late Albian	[76]
			Protorhyssalopsis pernicote Ortega-Blanco, Delclòs, and Engel, 2011	Peñacerrada I	late Albian	[77]
			Utrillabracon electropteron Álvarez-Parra and Engel, 2022	San Just	late Albian	[53]
	Megalyroidea	Megalyridae	*Megalava truncata* Perrichot, 2009	Peñacerrada I	late Albian	[36,37]
			Valaa delclosi Perrichot, 2009	Peñacerrada I	late Albian	[36]
	Mymarommatoidea	†Alavarommatidae	*Alavaromma orchamum* Ortega-Blanco, Peñalver, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[38]
		†Gallorommatidae	*Cretaceomma turolensis* (Ortega-Blanco, Peñalver, Delclòs and Engel, 2011)	San Just	late Albian	[38,45]
			Gallоromma alavaensis Ortega-Blanco, Peñalver, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[38]
		Mymarommatidae	*Archaeromma hispanicum* Ortega-Blanco, Peñalver, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[38]
	Platygastroidea	†Proterosceliopsidae	*Proterosceliopsis masneri* Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46,47]
		Scelionidae	*Alavascelio delvallei* Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46]
			Amissascelio temporarius Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46]
			Bruescelio platycephalus Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46]
			Electroteleiopsis hebdomas Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46]
			Juxtascelio interitus Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46]
			Perimoscelio confector Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46]
			Perimoscelio tyrbastes Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46]
			Tithonoscelio resinalis Ortega-Blanco, McKellar and Engel, 2014	Peñacerrada I	late Albian	[46]
	†Serphitoidea	†Serphitidae	*Aposerphites angustus* Ortega-Blanco, Delclòs, Peñalver and Engel, 2011	Peñacerrada I	late Albian	[41]
			Microserphites soplaensis Ortega-Blanco, Delclòs, Peñalver and Engel, 2011	El Soplao	middle Albian	[41]
			Serphites lamiak Ortega-Blanco, Delclòs, Peñalver and Engel, 2011	Peñacerrada I	late Albian	[41]
			Serphites silban Ortega-Blanco, Delclòs, Peñalver and Engel, 2011	San Just	late Albian	[41]
	Trigonalyoidea	†Maimetshidae	*Iberomaimetsha nihtmara* Ortega-Blanco, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[68]
			Iberomaimetsha rasnitsyni Ortega-Blanco, Perrichot 2011 Engel, 2011	Peñacerrada I	late Albian	[68]
	Incertae sedis	†Radiophronidae	*Microcostaphron parvus* Ortega-Blanco, Rasnitsyn and Delclòs, 2010	Peñacerrada I	late Albian	[48]
			Radiophron ibericus Ortega-Blanco, Rasnitsyn and Delclòs, 2010	Peñacerrada I	late Albian	[48]
	Incertae sedis	†Stigmaphronidae	*Burmaphron jentilak* Ortega-Blanco, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[39]
			Burmaphron iratxoak Ortega-Blanco, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[39]
			Burmaphron sorginak Ortega-Blanco, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[39]
			Elasmophron mari Ortega-Blanco, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[39]
			Hippocoon basajauni Ortega-Blanco, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[39]
			Libanophron sugaar Ortega-Blanco, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[39]
			Tagsmiphron olentzero Ortega-Blanco, Delclòs and Engel, 2011	Peñacerrada I	late Albian	[39]

Group	Superfamily	Family	Genus and Species	Type Locality	Age	References
Aculeata	Chrysidoidea	Bethylidae	*Cretepyris martini* Ortega-Blanco and Engel, 2013	Peñacerrada I	late Albian	[50]
			Liztor pilosus Ortega-Blanco and Engel, 2013	Peñacerrada I	late Albian	[50]
			Zophepyris alavaensis (Ortega-Blanco and Engel, 2013)	Peñacerrada I	late Albian	[32,50]
		Embolemidae	*Ampulicomorpha perialla* (Ortega-Blanco, Delclòs and Engel, 2011)	Peñacerrada I	late Albian	[51,78]
		Scolebythidae	*Ectenobythus iberiensis* Engel, Ortega-Blanco and McKellar, 2013	Peñacerrada I	late Albian	[79]

References

1. Blaimer, B.B.; Santos, B.F.; Cruaud, A.; Gates, M.W.; Kula, R.R.; Mikó, I.; Rasplus, J.-Y.; Smith, D.R.; Talamas, E.J.; Brady, S.G.; et al. Key innovations and the diversification of Hymenoptera. *Nat. Commun.* **2023**, *14*, 1212. [CrossRef] [PubMed]
2. Aguiar, A.P.; Deans, A.R.; Engel, M.S.; Forshage, M.; Huber, J.T.; Jennings, J.T.; Johnson, M.F.; Lelej, A.S.; Longino, J.T.; Lohrmann, V.; et al. Order Hymenoptera. In: Zhang, Z.-Q. (Ed.) Animal Biodiversity: An Outline of Higher-level Classification and Survey of Taxonomic Richness (Addenda 2013). *Zootaxa* **2013**, *3703*, 51–62. [CrossRef]
3. Grimaldi, D.A.; Engel, M.S. *Evolution of the Insects*; Cambridge University Press: New York, NY, USA, 2005; 755p.
4. Goulet, H.; Huber, J.T. *Hymenoptera of the World: An Identification Guide to Families*; Research Branch Agriculture Canada: Ottawa, ON, Canada, 1993; 668p.
5. Misof, B.; Liu, S.; Meusemann, K.; Peters, R.S.; Donath, A.; Mayer, C.; Frandsen, P.B.; Ware, J.; Flouri, T.; Beutel, R.G.; et al. Phylogenomics resolves the timing and pattern of insect evolution. *Science* **2014**, *346*, 763–767. [CrossRef] [PubMed]
6. Sharkey, M.J.; Carpenter, J.M.; Vilhelmsen, L.; Heraty, J.; Liljeblad, J.; Dowling, A.P.G.; Schulmeister, S.; Murray, D.; Deans, A.R.; Ronquist, F.; et al. Phylogenetic relationships among superfamilies of Hymenoptera. *Cladistics* **2012**, *28*, 80–112. [CrossRef] [PubMed]
7. Peters, R.S.; Krogmann, L.; Mayer, C.; Donath, A.; Gunkel, S.; Meusemann, K.; Kozlov, A.; Podsiadlowski, L.; Petersen, M.; Lanfear, R.; et al. Evolutionary history of the Hymenoptera. *Curr. Biol.* **2017**, *27*, 1013–1018. [CrossRef] [PubMed]
8. Solórzano-Kraemer, M.M.; Peñalver, E.; Herbert, M.C.; Delclòs, X.; Brown, B.V.; Aung, N.N.; Peretti, A.M. Necrophagy by insects in *Oculudentavis* and other lizard body fossils preserved in Cretaceous amber. *Sci. Rep.* **2023**, *13*, 2907. [CrossRef] [PubMed]
9. Benton, M.J.; Wilf, P.; Sauquet, H. The Angiosperm Terrestrial Revolution and the origins of modern biodiversity. *New Phytol.* **2022**, *233*, 2017–2035. [CrossRef] [PubMed]
10. Delclòs, X.; Peñalver, E.; Barrón, E.; Peris, D.; Grimaldi, D.A.; Holz, M.; Labandeira, C.C.; Saupe, E.E.; Scotese, C.R.; Solórzano-Kraemer, M.M.; et al. Amber and the Cretaceous Resinous Interval. *Earth-Sci. Rev.* **2023**, *243*, 104486. [CrossRef]
11. Zhang, Q.; Rasnitsyn, A.P.; Wang, B.; Zhang, H. Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: A review of the fauna. *Proc. Geologist. Assoc.* **2018**, *129*, 736–747. [CrossRef]
12. Rasnitsyn, A.P.; Öhm-Kühnle, C. Non-aculeate Hymenoptera in the Cretaceous ambers of the world. *Cretac. Res.* **2021**, *124*, 104805. [CrossRef]
13. Ross, A.J. Complete checklist of Burmese (Myanmar) amber taxa 2023. *Mesozoic* **2024**, *1*, 21–57. [CrossRef]
14. Rasnitsyn, A.P.; Jarzembowski, E.A.; Ross, A.J. Wasps (Insecta: Vespida = Hymenoptera) from the Purbeck and Wealden (Lower Cretaceous) of southern England and their biostratigraphical and palaeoenvironmental significance. *Cretac. Res.* **1998**, *19*, 329–391. [CrossRef]
15. Rasnitsyn, A.P.; Martínez-Delclòs, X. Wasps (Insecta: Vespida = Hymenoptera) from the Early Cretaceous of Spain. *Acta Geol. Hisp.* **2000**, *1–2*, 65–96.
16. Bouju, V.; Perrichot, V. A review of amber and copal occurrences in Africa and their paleontological significance. *Bull. Soc. Geol. Fr.* **2020**, *191*, 17. [CrossRef]
17. Xing, L.; Qiu, L. Zircon UPb age constraints on the mid-Cretaceous Hkamti amber biota in northern Myanmar. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2017**, *558*, 109960. [CrossRef]
18. Perkovsky, E.E.; Martynova, K.V.; Mita, T.; Olmi, M.; Zheng, Y.; Müller, P.; Zhang, Q.; Gantier, F.; Perrichot, V. A golden age for ectoparasitoids of Embiodea: Cretaceous Sclerogibbidae (Hymenoptera, Chrysidoidea) from Kachin (Myanmar), Charentes (France) and Choshi (Japan) ambers. *Gondwana Res.* **2020**, *87*, 1–22. [CrossRef]
19. Maksoud, S.; Azar, D. Lebanese amber: Latest updates. *Palaeoentomology* **2020**, *3*, 125–155. [CrossRef]
20. Maksoud, S.; Granier, B.R.; Azar, D. Palaeoentomological (fossil insects) outcrops in Lebanon. *Carnets Geol.* **2022**, *22*, 699–743. [CrossRef]
21. Maksoud, S.; Iskandar-Tabib, D.; Azar, D. Tannoura: A new early Barremian fossiliferous amber outcrop from South Lebanon. *Mesozoic* **2024**, *1*, 90–98. [CrossRef]
22. Maksoud, S.; Azar, D.; Granier, B.; Gèze, R. New data on the age of the Lower Cretaceous amber outcrops of Lebanon. *Palaeoworld* **2017**, *26*, 331–338. [CrossRef]
23. Peñalver, E.; Delclòs, X. Spanish amber. In *Biodiversity of Fossils in Amber from the Major World Deposits, Vol. 13*; Penney, D., Ed.; Siri Scientific Press: Manchester, UK, 2010; pp. 236–270.
24. Barrón, E.; Peyrot, D.; Rodríguez-López, J.P.; Meléndez, N.; López del Valle, R.; Najarro, M.; Rosales, I.; Comas-Rengifo, M.J. Palynology of Aptian and upper Albian (Lower Cretaceous) amber-bearing outcrops of the southern margin of the Basque-Cantabrian basin (northern Spain). *Cretac. Res.* **2015**, *52*, 292–312. [CrossRef]

25. Barrón, E.; Peyrot, D.; Bueno-Cebollada, C.A.; Kvaček, J.; Álvarez-Parra, S.; Altolaguirre, Y.; Meléndez, N. Biodiversity of ecosystems in an arid setting: The late Albian plant communities and associated biota from eastern Iberia. *PLoS ONE* **2023**, *18*, e0282178. [CrossRef] [PubMed]
26. Álvarez-Parra, S.; Pérez-de la Fuente, R.; Peñalver, E.; Barrón, E.; Alcalá, L.; Pérez-Cano, J.; Martín-Closas, C.; Trabelsi, K.; Meléndez, N.; López Del Valle, R.; et al. Dinosaur bonebed amber from an original swamp forest soil. *eLife* **2021**, *10*, e72477. [CrossRef] [PubMed]
27. Solórzano-Kraemer, M.M.; Sinclair, B.J.; Arillo, A.; Álvarez-Parra, S. A new genus of dance fly (Diptera: Empidoidea: Hybotidae) from Cretaceous Spanish ambers and introduction to the fossiliferous amber outcrop of La Hoya (Castellón Province, Spain). *PeerJ* **2023**, *11*, e14692. [CrossRef] [PubMed]
28. Ulmer, J.M.; Jansta, P.; Azar, D.; Krogmann, L. At the dawn of megadiversity–Protoitidae, a new family of Chalcidoidea (Hymenoptera) from Lower Cretaceous Lebanese amber. *J. Hymenopt. Res.* **2023**, *96*, 879–924. [CrossRef]
29. Nel, A.; Azar, D. The oldest parasitic Scelionidae: Teleasinae (Hymenoptera: Platygastroidea). *Pol. Pis. Entomol.* **2005**, *74*, 333–338.
30. Peñalver, E.; Ortega-Blanco, J.; Nel, A.; Delclòs, X. Mesozoic Evaniidae (Insecta: Hymenoptera) in Spanish amber: Reanalysis of the phylogeny of the Evanioidea. *Acta Geol. Sin.* **2010**, *84*, 809–827. [CrossRef]
31. Olmi, M.; Perkovsky, E.E.; Martynova, K.V.; Contarini, M.; Bückle, C.; Guglielmino, A. An important intermediate step in the evolution of pincer wasps: An extraordinary new type of chela from mid-Cretaceous Burmese amber (Hymenoptera, Dryinidae). *Cretac. Res.* **2020**, *111*, 104420. [CrossRef]
32. Engel, M.S.; Ortega-Blanco, J.; Azevedo, C.O. A new bethylid wasp in Lebanese Early Cretaceous amber (Hymenoptera: Chrysidoidea), with comments on other Mesozoic taxa. *Am. Mus. Novit.* **2016**, *2016*, 1–14. [CrossRef]
33. Jouault, C.; Ngô-Muller, V.; Pouillon, J.M.; Nel, A. New Burmese amber fossils clarify the evolution of bethylid wasps (Hymenoptera: Chrysidoidea). *Zool. J. Linn. Soc.* **2021**, *191*, 1044–1058. [CrossRef]
34. Lepeco, A.; Melo, G.A. The wasp genus† *Holopsenella* in mid-Cretaceous Burmese amber (Hymenoptera: †Holopsenellidae stat. nov.). *Cretac. Res.* **2022**, *131*, 105089. [CrossRef]
35. Ortega-Blanco, J.; Rasnitsyn, A.P.; Delclòs, X. First record of anaxyelid woodwasps (Hymenoptera: Anaxyelidae) in Lower Cretaceous Spanish amber. *Zootaxa* **2008**, *1937*, 39–50. [CrossRef]
36. Perrichot, V. Long-tailed wasps (Hymenoptera: Megalyridae) from Cretaceous and Paleogene European amber. *Paleont. Contr.* **2009**, *2009*, 1–19. [CrossRef]
37. Pérez-de la Fuente, R. Description of the male of *Megalava truncata* Perrichot (Hymenoptera: Megalyridae) in Early Cretaceous amber from El Soplao (Spain). *Zootaxa* **2012**, *3274*, 29–35. [CrossRef]
38. Ortega-Blanco, J.; Peñalver, E.; Delclòs, X.; Engel, M.S. False fairy wasps in early Cretaceous amber from Spain (Hymenoptera: Mymarommatoidea). *Palaeontology* **2011**, *54*, 511–523. [CrossRef]
39. Ortega-Blanco, J.; Delclòs, X.; Engel, M.S. Diverse stigmaphronid wasps in Early Cretaceous amber from Spain (Hymenoptera: Ceraphronoidea: Stigmaphronidae). *Cretac. Res.* **2011**, *32*, 762–773. [CrossRef]
40. Pérez-de la Fuente, R.; Peñalver, E.; Ortega-Blanco, J. A new species of the diverse Cretaceous genus *Cretevania* Rasnitsyn, 1975 (Hymenoptera: Evaniidae) from Spanish amber. *Zootaxa* **2012**, *3514*, 70–78. [CrossRef]
41. Ortega-Blanco, J.; Delclòs, X.; Peñalver, E.; Engel, M.S. Serphitid wasps in early Cretaceous amber from Spain (Hymenoptera: Serphitidae). *Cretac. Res.* **2011**, *32*, 143–154. [CrossRef]
42. Engel, M.S.; Ortega-Blanco, J.; Soriano, C.; Grimaldi, D.A.; Delclòs, X. A new lineage of enigmatic diaprioid wasps in Cretaceous amber (Hymenoptera: Diaprioidea). *Am. Mus. Novit.* **2013**, *2013*, 1–23. [CrossRef]
43. Rasnitsyn, A.P.; Öhm-Kühnle, C. Revision of the Cretaceous Proctotrupomorpha (Insecta: Hymenoptera) of Australia. *Cretac. Res.* **2019**, *100*, 91–96. [CrossRef]
44. Rasnitsyn, A.P.; Öhm-Kühnle, C. Taxonomic revision of the infraorder Proctotrupomorpha (Hymenoptera). *Palaeoentomology* **2020**, *3*, 223–234. [CrossRef]
45. Rasnitsyn, A.P.; Maalouf, M.; Maalouf, R.; Azar, D. New Serphitidae and Gallorommatidae (Insecta: Hymenoptera: Microprocta) in the Early Cretaceous Lebanese amber. *Palaeoentomology* **2022**, *5*, 120–136. [CrossRef]
46. Ortega-Blanco, J.; McKellar, R.C.; Engel, M.S. Diverse scelionid wasps from Early Cretaceous Álava amber, Spain (Hymenoptera: Platygastroidea). *Bull. Geosci.* **2014**, *89*, 553–571. [CrossRef]
47. Talamas, E.J.; Johnson, N.F.; Shih, C.; Ren, D. Proterosceliopsidae: A new family of Platygastroidea from Cretaceous amber. *J. Hymenopt. Res.* **2019**, *73*, 3–38. [CrossRef]
48. Ortega-Blanco, J.; Rasnitsyn, A.P.; Delclòs, X. A new family of ceraphronoid wasps from Early Cretaceous Álava amber, Spain. *Acta Palaeontol. Pol.* **2010**, *55*, 265–276. [CrossRef]
49. Mikó, I.; van de Kamp, T.; Trietsch, C.; Ulmer, J.M.; Zuber, M.; Baumbach, T.; Deans, A.R. A new megaspilid wasp from Eocene Baltic amber (Hymenoptera: Ceraphronoidea), with notes on two non-ceraphronoid families: Radiophronidae and Stigmaphronidae. *PeerJ* **2018**, *6*, e5174. [CrossRef] [PubMed]
50. Ortega-Blanco, J.; Engel, M.S. Bethylidae from Early Cretaceous Spanish amber (Hymenoptera: Chrysidoidea). *J. Kans. Entomol. Soc.* **2013**, *86*, 264–276. [CrossRef]
51. Olmi, M.; Rasnitsyn, A.P.; Brothers, D.J.; Guglielmino, A. The first fossil Embolemidae (Hymenoptera: Chrysidoidea) from Burmese amber (Myanmar) and Orapa Kimberlitic deposits (Botswana) and their phylogenetic significance. *J. Syst. Palaeontol.* **2014**, *12*, 623–635. [CrossRef]

52. Peris, D.; Condamine, F.L. The angiosperm radiation played a dual role in the diversification of insects and insect pollinators. *Nat. Commun.* **2024**, *15*, 552. [CrossRef]
53. Álvarez-Parra, S.; Peñalver, E.; Delclòs, X.; Engel, M.S. A braconid wasp (Hymenoptera, Braconidae) from the Lower Cretaceous amber of San Just, eastern Iberian Peninsula. *ZooKeys* **2022**, *1103*, 65–78. [CrossRef]
54. Arillo, A.; Peñalver, E.; Delclòs, X. *Microphorites* (Diptera: Dolichopodidae) from the Lower Cretaceous amber of San Just (Spain), and the co-occurrence of two ceratopogonid species in Spanish amber deposits. *Zootaxa* **2008**, *1920*, 29–40. [CrossRef]
55. Peris, D.; Davis, S.R.; Engel, M.S.; Delclòs, X. An evolutionary history embedded in amber: Reflection of the Mesozoic shift in weevil-dominated (Coleoptera: Curculionoidea) faunas. *Zool. J. Linn. Soc.* **2014**, *171*, 534–553. [CrossRef]
56. Álvarez-Parra, S.; Peñalver, E.; Nel, A.; Delclòs, X. New barklice (Psocodea, Trogiomorpha) from Lower Cretaceous Spanish amber. *Pap. Palaeontol.* **2022**, *8*, e1436. [CrossRef]
57. Peris, D.; Ruzzier, E.; Perrichot, V.; Delclòs, X. Evolutionary and paleobiological implications of Coleoptera (Insecta) from Tethyan-influenced Cretaceous ambers. *Geosci. Front.* **2016**, *7*, 695–706. [CrossRef]
58. Álvarez-Parra, S.; Peñalver, E.; Nel, A.; Delclòs, X. Barklice (Insecta: Psocodea) from Early Cretaceous resiniferous forests of Iberia (Spanish amber): New Troctomorpha and a possible Psocomorpha. *Cretac. Res.* **2023**, *148*, 105544. [CrossRef]
59. Davranoglou, L.R.; Pérez-de la Fuente, R.; Baňař, P.; Peñalver, E. The first unique-headed bug (Hemiptera, Enicocephalomorpha) from Cretaceous Iberian amber, and the Gondwanan connections of its palaeoentomological fauna. *Pap. Palaeontol.* **2024**, *10*, e1550. [CrossRef]
60. Polaszek, A.; Vilhemsen, L. Biodiversity of hymenopteran parasitoids. *Curr. Opin. Insect Sci.* **2023**, *56*, 101026. [CrossRef] [PubMed]
61. Santer, M.; Álvarez-Parra, S.; Nel, A.; Peñalver, E.; Delclòs, X. New insights into the enigmatic Cretaceous family Spathiopterygidae (Hymenoptera: Diaprioidea). *Cretac. Res.* **2022**, *133*, 105128. [CrossRef]
62. Krogmann, L.; Azar, D.; Rajaei, H.; Nel, A. *Mymaropsis baabdaensis* sp. n. from Lower Cretaceous Lebanese amber–the earliest spathiopterygid wasp and the first female known for the family. *C. R. Palevol* **2016**, *15*, 483–487. [CrossRef]
63. Deans, A.R.; Basibuyuk, H.H.; Azar, D.; Nel, A. Descriptions of two new Early Cretaceous (Hauterivian) ensign wasp genera (Hymenoptera: Evaniidae) from Lebanese amber. *Cretac. Res.* **2004**, *25*, 509–516. [CrossRef]
64. Basibuyuk, H.H.; Fitton, M.G.; Rasnitsyn, A.P.; Quicke, D.L. The limits of the family Evaniidae (Insecta: Hymenoptera) and a new genus from Lebanese Amber. *Insect Syst. Evol.* **2002**, *33*, 23–34. [CrossRef]
65. Johnson, N.F.; Musetti, L.; Masner, L. The Cretaceous scelionid genus *Proteroscelio* Brues (Hymenoptera: Platygastroidea). *Am. Mus. Novit.* **2008**, *2008*, 1–7. [CrossRef]
66. Engel, M.S.; Herhold, H.W.; Barden, P. A proctotrupid wasp in Lebanese Lower Cretaceous amber (Hymenoptera: Proctotrupidae). *Palaeoentomology* **2022**, *5*, 439–444. [CrossRef]
67. Engel, M.S. A new family of primitive serphitoid wasps in Lebanese amber (Hymenoptera: Serphitoidea). *Novit. Paleoentomol.* **2015**, *13*, 1–22. [CrossRef]
68. Perrichot, V.; Ortega-Blanco, J.; McKellar, R.C.; Delclòs, X.; Azar, D.; Nel, A.; Tafforeau, P.; Engel, M.S. New and revised maimetshid wasps from Cretaceous ambers (Hymenoptera, Maimetshidae). *ZooKeys* **2011**, *130*, 421–453. [CrossRef] [PubMed]
69. Engel, M.S. A new genus and species of maimetshid wasps in Lebanese Early Cretaceous amber (Hymenoptera: Maimetshidae). *Novit. Paleoentomol.* **2016**, *18*, 1–14. [CrossRef]
70. Engel, M.S.; Grimaldi, D.A. Diversity and phylogeny of the Mesozoic wasp family Stigmaphronidae (Hymenoptera: Ceraphronoidea). *Denisia* **2009**, *26*, 53–68.
71. Azevedo, C.O.; Azar, D. A new fossil subfamily of Bethylidae (Hymenoptera) from the Early Cretaceous Lebanese amber and its phylogenetic position. *Zoologia (Curitiba)* **2012**, *29*, 210–218. [CrossRef]
72. Olmi, M. New fossil Dryinidae from Baltic and Lebanese amber (Hymenoptera Chrysidoidea). *Frustula Entomol.* **2000**, *21*, 48–67.
73. Engel, M.S.; Grimaldi, D.A. The first Cretaceous sclerogibbid wasp (Hymenoptera: Sclerogibbidae). *Am. Mus. Novit.* **2006**, *2006*, 1–7. [CrossRef]
74. Prentice, M.A.; Poinar, G.O., Jr.; Milki, R. Fossil scolebythids (Hymenoptera: Scolebythidae) from Lebanese and Dominican amber. *Proc. Entomol. Soc. Wash.* **1996**, *98*, 802–811.
75. Engel, M.S.; Grimaldi, D.A. Cretaceous Scolebythidae and phylogeny of the family (Hymenoptera: Chrysidoidea). *Am. Mus. Novit.* **2007**, *2007*, 1–16. [CrossRef]
76. Ortega-Blanco, J.; Bennett, D.J.; Delclòs, X.; Engel, M.S. A primitive aphidiine wasp in Albian amber from Spain and a Northern Hemisphere origin for the subfamily (Hymenoptera: Braconidae: Aphidiinae). *J. Kans. Entomol. Soc.* **2009**, *82*, 273–282. [CrossRef]
77. Ortega-Blanco, J.; Delclòs, X.; Engel, M.S. A protorhyssaline wasp in Early Cretaceous amber from Spain (Hymenoptera: Braconidae). *J. Kans. Entomol. Soc.* **2011**, *84*, 51–57. [CrossRef]

78. Ortega-Blanco, J.; Delclòs, X.; Engel, M.S. The wasp family Embolemidae in Early Cretaceous amber from Spain (Hymenoptera: Chrysidoidea). *J. Kans. Entomol. Soc.* **2011**, *84*, 36–42. [CrossRef]
79. Engel, M.S.; Ortega-Blanco, J.; McKellar, R.C. New scolebythid wasps in Cretaceous amber from Spain and Canada, with implications for the phylogeny of the family (Hymenoptera: Scolebythidae). *Cretac. Res.* **2013**, *46*, 31–42. [CrossRef]