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General Palaeontology (Taphonomy and Fossilisation)

Preservation and accumulation of biological inclusions in Lebanese amber and their significance

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Abstract

The amber is a fossilized vegetal resin ranging from a few millions to more than 300 million years in age. It constitutes a superb material for the conservation of biological inclusions in their minute three-dimensional details. This material not only preserves life forms, but also some aspects of their mode of life and their ecology such as swarming or mating, all kind of symbiotic associations like commensalism, mutualism, and parasitism. This paper deals with the aspects of preservation and accumulation of biological inclusions and their significance in the Lebanese amber. ***To cite this article: D. Azar, C. R. Palevol 6 (2007).***

Résumé

Conservation et accumulation des inclusions biologiques dans les ambres libanais et leur signification. L'ambre est une résine végétale fossile d'un âge allant de quelques millions à plus de 300 millions d'années. Il constitue un matériel superbe pour la conservation des inclusions biologiques dans leurs détails tridimensionnels minutieux. Ce matériel, non seulement préserve les formes, mais aussi les modes de vie et leur écologie, comme l'essaimage ou l'accouplement, tous les types d'associations symbiotiques comme le commensalisme, le mutualisme et le parasitisme. Cet article traite des aspects de la conservation et de l'accumulation des inclusions biologiques et leur signification dans l'ambre libanais. ***Pour citer cet article : D. Azar, C. R. Palevol 6 (2007).***

Keywords: Lebanon; Amber; Fossil insects; Palaeoenvironment; Palaeosymbiosis; Palaeoparasitism; Palaeobiogeography

Mots clés : Liban ; Ambre ; Insectes fossiles ; Paléoenvironnement ; Paléosymbiose ; Paléoparasitisme ; Paléobiogéographie

1. Introduction

The term 'fossil' is derived from a Latin word meaning 'dug up', and from the time of the ancient Greeks it was used to describe any distinctive objects or materials dug up from the Earth or found lying on the surface, including minerals, ores, rocks and stone implements, as well as organic remains. It was not until the 19th century that the word became restricted to the remains or traces of pre-existing life preserved in rocks by the natural processes.

Conditions conductive to the formation of fossils include quick burial in moist sediment or other material that tends to prevent weathering and to exclude oxygen and bacteria, thereby preventing decay.

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There are several reasons why fossils are significant for understanding the evolutionary history of organisms and the palaeoenvironment, as they offer direct information on the ages of lineages and a record of extinct ones; they assist in reconstructing the phylogeny of different groups [11]; and their assemblages provide exceptional knowledge and clues about the palaeoenvironments, palaeoecology and palaeobiogeography.

Fossils are usually found in sedimentary rocks, asphalt deposits, coal, and sometimes in amber which is also by itself a fossilized vegetal resin. Amber deposits occur all over the world and they range from a few millions to 300 million years in age. Amber is a gold mine for the palaeontologists as it contains a variety of biological inclusions in pristine, three-dimensional conditions [13]. The oldest amber containing intensive biological inclusions is the Lebanese one [2–5,12]. More than 375 outcrops have been recently discovered after intensive geological field researches made in the last decade. Curiously, only 15 outcrops yield to biological inclusions. Amber in Lebanon is found in lens of dark clay associated with lignite and plant debris, sometimes in purely fluvial deposition system, i.e. in channels, or riversides, and sometimes the deposition is subject to marine influences, i.e. in a deltaic zone, or on the littoral (in the intertidal area). In fluvial cases, no palynomorphs of marine origin are found and amber accumulation could mainly occur after storms, while several types of dinoflagellates and marine gastropods are incorporated into the sediments when the deposition undergoes marine influence. This type of accumulation could be continuous as long as resin producing forest exists aside. Lebanese amber is often buried in its primary deposit, with lignite and fossil leaves from the resin producing tree. When transported, it is for little distances, as confirmed by the exceptional preservation state of the palynomorphs. The amber is unique and extraordinary for 'bioaccumulation', as not only it constitutes a fossil vegetal accumulation by itself, but it also contains accumulation of well-diversified continental biological inclusions: till now, about 15 000 biological inclusions (mainly insects) have been found in the amber from the different outcrops. The age of Lebanese amber ranges from Late Jurassic to Albian. The fossiliferous outcrops have nearly the same age, viz. Late Barremian to Early Aptian [6]. This confirmed by the presence of the same entomofauna in the different fossiliferous outcrops. The different aspects of the accumulation of biological inclusions in the amber and their significance, discussed herein, are true for any kind of amber. However, this paper deals more specifically with the inclusions from the Lebanese one.

2. Lebanese amber inclusions

The most fascinating aspects of the Lebanese amber are the abundance and the outstanding preservation of the biological inclusions. Inclusions could be found in amber every 25 to 30 pieces. This amber rarely includes vertebrate remains (one lizard *Baabdasaurus xenorus* Arnolds et al., 2002 [1]) and few feathers [4,15,16], but numerous arthropods and vegetal remains trapped while the resin exudation was fluid. Among arthropods, insects are largely dominant and most of the orders are represented [4]. A single piece of amber can contain one or several inclusions. Some of those that are found alone may provide important indirect hints of presence of other organisms, or reflect a specific habitat or palaeogeography. Regarding the specimens where several inclusions (or syninclusions) are found together, some of them are present only in a hazardous manner, but a considerable number of them are assembled for an ecological behaviour such as mating or parasitism, etc. In general, when the amber is in its primary deposition site, the inclusions are almost contemporaneous, while when the amber deposit has been reworked, the amber inclusions could have several ages. The inclusions found in a piece of amber are trapped mostly at the same time with a difference of very few days or weeks, depending on each flow of resin.

3. Providing indirect evidence of other organisms

There are size and habitat limitations to the types of organisms that can be trapped in amber [13]. Some arthropods that are specific to certain hosts can provide clues to other organisms that existed at that time. Engel and Grimaldi [10] described recently a sclerogibbid wasp (*Sclerogibbodes embioleia* Engel et Grimaldi, 2006). Sclerogibbidae are obligate parasitoids of webspinners (Embioptera), and thus the recovery of this lineage from the Lebanese amber implies that webspinners were probably present in the palaeofauna. Another example is the presence of the Acari of the family Smarididae, which are generally parasites of Psocids, relatively well represented in the Lebanese amber.

This situation is also the case of most of the parasitoids or parasites present in the Lebanese as in any amber; it simply indicates that some trophical specialization and relationship were most likely already established.

4. Providing indirect evidence of specific habitats

Some insects can provide indirect evidence of specific habitats, or climate. For example, chironomids (very common and diversified Diptera in the Lebanese amber), limonids, tipulids and psychodid flies, caddisflies (Trichoptera) provide evidence of aquatic or very humid habitats. In general, most of the Lebanese amber inclusions reflect a hot, dense and humid forest environment. The information given by the whole inclusions corroborate the dataset by the palynology: the palaeoenvironment of the amber deposits corresponds to a tropical dense, warm and humid forest with an intense complex fluvial system, altogether close to the sea. In addition, most of the fauna entombed in the Lebanese amber is the one living on the lower to mid part of trees. This could be explained by the fact that this type of fauna has more chance to be trapped, since normally all the resin drops falling down from the tree pass inevitably and more frequently by this area.

5. Amber insects and palaeobiogeography

The palaeobiogeographic analysis of Lebanese amber sites was established after examination of the relationship between the palynologic associations of these sites and the two microfloristic provinces of the peri-Tethys (southern Laurasia and northern Gondwana) of Brenner [7]. The palynologic association of the Lebanese amber sites shares some characters with the two microfloristic provinces of peri-Tethys, but is not really integrated into any of them; it however has a proper individuality [8,9]. The flora was probably subject to the 'influence' of these two rather remote provinces. The study of Lepidoptera: Micropterygidae from Lebanese amber enables to propose a hypothesis of a north-eastern position in the Gondwanaland for the future Lebanon during the Lower Cretaceous. These fossils have a constriction on the semi-length of the broad antennal scape, which is an apomorphic character proper to the Recent Micropterygidae of the southern hemisphere, which corresponds to the Lower Cretaceous continent of Gondwana.

6. Ecological behaviour

Amber is a mortal but a selective trap. Several factors affect the selectivity of the amber: (1) the size of the inclusion: it is evident that large organisms can only be partially trapped by the sticky resin and are strong enough to escape from it; (2) the attractive or repulsive character of the resin; (3) the action of seasons: in winter, the resin is relatively hard and therefore insects may rest on the resin without any harm, whereas in summer the resin is more fluid and sticky; (4) the living mode in proximity of the resin-producing tree – it is normal to find most of the amber biological inclusions among those that live directly on the resin producing tree; (5) some organisms live in symbiotic conditions (mutualism, commensalism, parasitism) or have a swarm behaviour, thus if they also live in proximity of the resinous tree, the chance to have a host with its parasite, or some conspecific individuals trapped is considerable. The two latter factors for the selectivity of amber will be developed below.

7. Organisms that share the same ecological niche

A biocoenosis (biocoenose or biocenose), termed by the German ecologist Karl August Möbius in 1877, describes all the interacting organisms living together in a specific habitat or biotope. The amber tree constitutes a biotope by itself where several populations and communities of organisms are living together beside the extruded resin. This event increases the possibility to have several organisms trapped in the same amber piece. Each population is the result of procreations between individuals of the same species and cohabitation in a given place for a given time. Two kinds of relationships result from the cohabitation: intra- and interspecific relations.

7.1. Intraspecific relations

The intraspecific relations are those established between individuals of the same species, like living in a group (Figs. 1–3), swarms, mating (Figs. 4–6), cooperation or competition, and sometimes organization in hierarchical societies.

Fig. 1. Two larvae of mites belonging to the same species, found in a piece of amber with 54 similar mite larvae. The scenario to explain this assemblage is a resin drop that falls on the mites just after egg hatching.
Fig. 1. Deux larves d'acariens appartenant à la même espèce, trouvées dans un morceau d'ambre contenant 54 larves identiques. Le scénario expliquant cette accumulation fait appel à une goutte de résine tombée juste après l'éclosion des œufs.

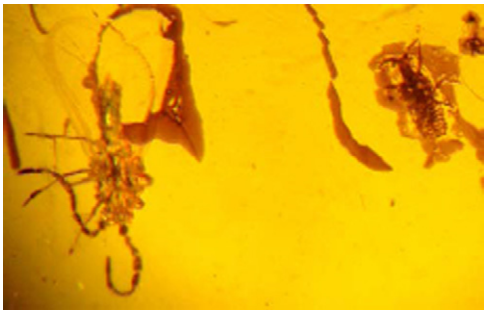

Fig. 2. Two coccids, a male and a larva, almost certainly belonging to the same species. Such assemblage is very important to study the real diversity of the scale insects, as this group presents a great polymorphism between adults and larvae, and among adults, even between sexes. Even in recent fauna, it is normally impossible to tell whether a male coccid and a female one correspond to the same species, except if they are found together.
Fig. 2. Deux cochenilles, un mâle et une larve, appartenant vraisemblablement à la même espèce. Ce rassemblement est très important pour l'étude de la véritable diversité des cochenilles, puisque ce groupe présente un important polymorphisme entre les adultes et les larves et même, parmi les adultes, entre les deux sexes. Dans la faune moderne, il est normalement impossible de dire qu'un mâle et une femelle correspondent à la même espèce, sauf s'ils sont trouvés ensemble.

Fig. 3. Two male coccids that might have lived in a group aside females and larvae.
Fig. 3. Deux cochenilles mâles qui auraient vécu en groupe à côté des femelles et des larves.

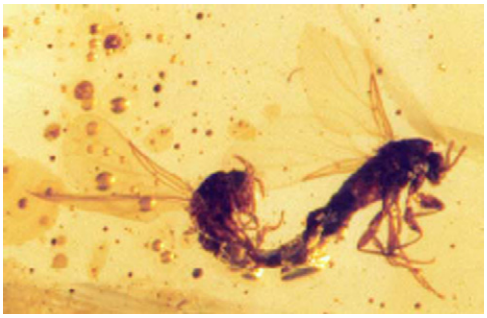

Fig. 4. A mating pair of scatopsid flies. This is the oldest ever known preserved mating pair in the animal realm.
Fig. 4. Accouplement de diptères de la famille des Scatopsidae. C'est le plus ancien accouplement conservé dans le règne animal.

Fig. 5. Two ceratopogonid flies that were mating when the drop of resin surprised them.
Fig. 5. Deux cératopogonides qui étaient en cours d'accouplement quand la goutte de résine les a surpris.

7.2. *Interspecific relations*

The interspecific relations, between different species, are numerous, and usually described according to their beneficial, detrimental or neutral effect. The most significant relation is the predation, which leads to the essential concepts in ecology of food chains. Other interspecific

Fig. 6. A couple of enicocephalid bugs (*Enicocephalinus acragrimaldii* Azar et al. 1999).
Fig. 6. Un couple de punaises de la famille des Enicocephalidae (*Enicocephalinus acragrimaldii* Azar et al. 1999).

Fig. 7. An aleyrode (Hemiptera) on the left and a thrips (Thysanoptera) on the right. These insects usually occupy the same ecological niche.
Fig. 7. Un aleurode (Hemiptera) à gauche et un thrips (Thysanoptera) à droite. Ces insectes occupent normalement la même niche écologique.

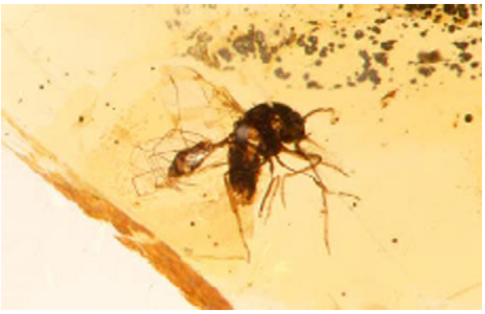

Fig. 8. A ceratopogonid fly parasitized by a mite. In Lebanese amber, the animal–animal parasitisms are the oldest preserved ones.
Fig. 8. Un cératopogonide parasité par un acarien. Dans l'ambre du Liban, les parasitismes entre animaux sont les plus anciens qui soient conservés.

Fig. 9. A chironomid fly parasitized by a mite. This peculiar chironomid is haematophagous *contra* the recent chironomids.
Fig. 9. Un chironome parasité par un acarien. Ce chironome est particulier, car il est hématophage à l'encontre des chironomes modernes.

relations include species that share the same ecological niche (Fig. 7) and symbiotic associations, like commensalism, parasitism (Figs. 8–12), infectious disease and competition for limiting resources.

7.2.1. Phoresis

Phoresis (when an organism is carried or transported by another organism) is one of the classical types of

Fig. 10. The oldest preserved parasitism on vertebrates: a mite is parasitizing a reptile skin.
Fig. 10. Le plus ancien parasitisme conservé chez les Vertébrés : un acarien qui parasite une peau de reptile.

Fig. 11. A rhagionid fly parasitized by a mite. The arrow indicates the mite.
Fig. 11. Un rhagionide parasité par un acarien. La flèche indique l'acarien.

palaeocommensalism found in amber. Most of the time, it involves mites or pseudoscorpions being carried by insects. The carrier is not harmed and serves as a transporting agent. An example of this kind of symbiotic association in the Lebanese amber consists of mites

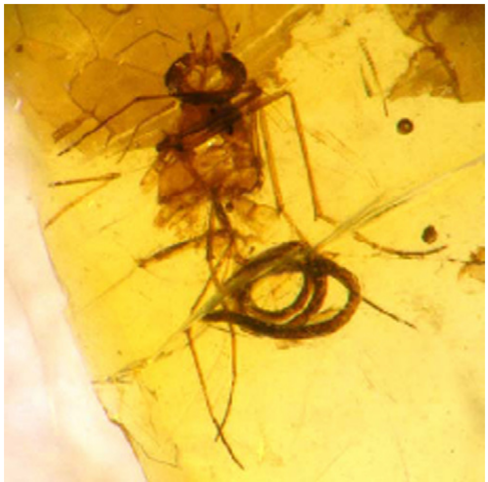

Fig. 12. The earliest fossil nematode (Mermithidae), parasitizing a chironomid fly. This nematode was living in the abdomen of the chironomid when the latter was trapped. The worm is still coiled inside the abdomen of its insect host. This association represents the oldest known example of animal–animal internal parasitism in a terrestrial environment.
Fig. 12. Le plus ancien nématode fossile (Mermithidae), parasitant un chironome. Ce nématode vivait dans l'abdomen du chironome quand ce dernier a été englué. Le ver est enroulé à l'intérieur de l'insecte hôte. Cette association représente, en ce qui concerne l'environnement terrestre, le plus ancien exemple connu de parasitisme interne d'un animal envers un autre.

(Acari: Astigmata) carried by a termite (Hodotermitidae). Such behaviour is necessary for the subsistence of the mite that lives in the termite nest and requires effective dispersal mechanism for survival.

7.2.2. Ecto- and endoparasitism

In parasitism, two modes are known, ecto- and endoparasitism, both identified in Lebanese amber. For ectoparasitism, a numerous number of parasitizing mites are recorded: one on a reptile skin (Fig. 10) and the others on several entomological groups like, in Diptera: Trichoceridae, Eoptychopteridae, Chironomidae (Fig. 9), Rhagionidae (Fig. 11), Ceratopogonidae (Fig. 8); in Lepidoptera: Micropterygidae; in Hemiptera: Aleyrodidae; Psocoptera; etc.

8. Conclusion

Amber is a material that fascinated so much and forever will not cease doing it. It constitutes a wonderful 'natural time capsule' as termed by Ross [14], and an original vegetal and animal bioaccumulation that not only preserves biological inclusions in their pristine three-dimensional details, but also aspects of their mode of life and their ecology. Life forms' preservation and accumulation in amber increase significantly our knowledge of the palaeobiodiversity, the palaeoenvironment, and the palaeoecology, and give the amber its attribute of exceptional 'window to the past'.

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