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Evidence for marine microfossils from amber

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Amber usually contains inclusions of terrestrial and rarely limnetic organisms that were embedded in the places where they lived in the amber forests. Therefore, it has been supposed that amber could not have preserved marine organisms. Here we report the first known amber-preserved marine microfossils. Diverse marine diatoms as well as radiolarians, sponge spicules, a foraminifer, and a larval spine of a sea urchin were found in Late Albian and Early Cenomanian amber samples of southwestern France. The highly fossiliferous resin samples solidified ca. 100 million years ago on the floor of coastal mixed forests dominated by conifers. The amber forests of southwestern France grew directly along the coast of the Atlantic Ocean and were influenced by the nearby sea: shells and remnants of marine organisms were probably introduced by wind, spray or high tide from the beach or the sea onto the resin flows.

amber | Cretaceous | microfossils | paleoecology | taphonomy

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Amber contains some of the best preserved fossils of terrestrial arthropods, microorganisms and plants remains (1). Deposits of fossil resins are therefore considered exceptional Lagerstätten (2) that provide important data on the paleoecology of Triassic to Neogene forests (3-8). The presence of marine organisms in tree resin, however, seemed highly unlikely, and the absence of marine inclusions, which could serve as index fossils for dating of amber, had been emphasized in previous literature (6). Very few amber-preserved arthropods have been attributed to littoral or marine habitats so far (1, 9), but there are just speculations how they got trapped in the resin.

Here we present the first known marine microinclusions in a fossil resin: diatoms, radiolarians, sponge spicules, a foraminifer and a larval spicule of a sea urchin were found in 100 million-year-old amber from southwestern France. Our fossils originate from the Late Albian amber deposit of Archingeay/Les-Nouillers (10, 11) and from the Early Cenomanian deposit of La Buzinie (11, 12, Fig. 1). The newly found amber inclusions provide fresh insight into the paleoecology of the Cretaceous amber forests, and suggest that dating of amber by marine inclusions might become relevant in the future.

Results and Discussion

Marine microfossils. All fossils described herein were found inside the amber pieces and were entirely surrounded by the fossil resin. None of the specimens was located in microfissures or at the surface of the amber pieces. Moreover, few specimens were found in contact with filaments of fossil fungi that are preserved on arthropods. Consequently, our fossils are true amber inclusions that were enclosed by the resin in its liquid stage in the amber forests. Thus, any post-Cretaceous contamination can be excluded. Furthermore, the quarries with the amber-bearing sediments are about 30 and 100 km far from the sea which makes it unlikely to find remnants of modern marine organisms attached to the amber pieces from Archingeay/Les-Nouillers and from La Buzinie.

Planktonic colonial centric diatoms were the most diverse marine inclusions in the investigated amber samples (Fig. 2). About 70 specimens have been confidently attributed to 9 genera. The most diverse representatives are elliptical frustules of the genus *Hemiaulus*, which are connected by long horns (Fig. 2A). The most abundant diatom inclusions are frustules of the genus *Stephanopyxis* ranging from 8 to 20 μm in diameter (Fig. 2B). Other subspherical, discoid or cylindrical frustules were assignable to the genera *Basilicostephanus*, *Coscinodiscus*, *Melosira*, *Paralia*, *Rhizosolenia*, *Skeletonema*, and *Trochosira*. These discoveries extend the fossil record of the genera *Paralia*, *Rhizosolenia*, *Skeletonema* and *Trochosira* from the Late into the Early Cretaceous, whereas *Basilicostephanus*,

Coscinodiscus, *Hemiaulus*, *Melosira* and *Stephanopyxis* were already known from marine Aptian-Albian sediments (13). Some specimens could only be tentatively attributed to particular genera. A small diatom of 6 μm diameter with a strong central process of 16-18 μm length and two small marginal spines of 6-7 μm length resembles the genus *Syndetocystis* (Fig. 2D). A centric diatom 40 μm in diameter possesses strong costae on its edges; based on these features which are visible in valval view, it has been tentatively assigned to the Thalassiosirales (Fig. 2E). Cylindrical diatoms of 10 μm diameter with flat valve faces and a marginal ring of short spines resemble the genus *Aulacoseira*. Other diatoms were not identifiable because they are largely covered by organic debris (see, e.g. Fig. 2C).

Fossil and modern representatives of the amber-preserved diatom genera are typical taxa of marine nearshore shallow waters. These colonial genera are largely preserved as solitary frustules or as short chain fragments of 2 or 3 cells. Rarely, longer filaments of up to 20 frustules were found in the genera *Paralia* and *Stephanopyxis* (Fig. 2 B).

Other marine inclusions include a young foraminifer whose shell is not mineralized; it was found embedded in organic debris in the highly fossiliferous amber piece ARC115 from Archingeay/Les-Nouillers (Fig. 3A). It is weakly elongated in one direction, 35 μm x 29 μm in size, and is composed of 6 membranous rolled chambers. The panispiral shape of this foraminifer suggests that it belongs to the Nodosariidae (small benthic foraminifers). This amber piece also contains two specimens of marine radiolarians resembling the genera *Acanthosphaera* and *Carposphaera* (Fig. 3B). The spheres are 16 μm in diameter and possess a regular sub-hexagonal areolae network. Small spines are visible on their surface. One elongate calcitic inclusion of ARC115 has been identified as a spine of an echinopluteus, the planktotrophic larva of sea urchins (Fig. 3C). This spiny siliceous inclusion has a central canal of 1 μm diameter that branches several times into lateral canals which are 0.6 to 0.7 μm wide and reach the edges of the inclusion. Siliceous sponge spicules are the most abundant marine microfossils from the mid-Cretaceous French amber. Most of them correspond to oxea of demosponges (Fig. 4A) from which two different kinds could be distinguished. Eighty to hundred of these more or less curved spiny inclusions have been found in the six amber pieces containing marine fossils. One type is 7 to 12 μm and the other 17 to 24 μm in diameter. Their length ranges from 160 to 350 μm but they are mainly 230 to 290 μm long. Two acanthostyles have also been found. One is a 70 to 75 μm long curved siliceous inclusion (Fig. 4B) of 5 to 6 μm diameter. This inclusion has a central canal of 1-1.2 μm width that divides regularly into lateral canals of 0.35-0.4 μm width. The second has numerous small spines on its surface (Fig. 4C) and is just 50 to 55 μm long and 5 to 5.5 μm in diameter. Apart from these monoaxone spicules, an apparent triaxone sponge spicule has been found (Fig. 4D). Each large spine of these inclusions is 20 to 22 μm long and has a maximum diameter of 2 μm at its base. Detailed observation of this inclusion, however, revealed a very short spine emerging from the junction. We therefore interpret this fossil as a tetraxone calthrops with a reduced axis. A microscleire is also present in French amber. This multispiny inclusion is 35 x 24 μm in size. Because all spines are carried by a very small axis, this fossil is assignable to the strepaster type.

Numerous siliceous shell fragments and spicules are associated with these microfossils, but they remain unidentifiable.

Paleoecology and taphonomy. The sources of the amber were mixed coastal forests at the eastern rim of the young Atlantic Ocean (2, 14). These woods were dominated by the conifer families Araucariaceae and Cheirolepidiaceae (15, 16, 17). Furthermore, various representatives of the Ginkgoales and Lauraceae grew in these forests (15). All the different marine microfossils described above have been found in litter amber samples (14). Numerous

syninclusions of litter and soil dwelling arthropods and microorganisms (14, 18, 19) indicate that this resin flowed and solidified on the forest floor and not on the trees.

The occurrence of marine microfossils in the resin suggests that the amber forests were temporarily influenced by the nearby sea. Analysis of the depositional environment also supports the model of an estuarine, coastal landscape for the mid-Cretaceous amber forests of southwestern France. It has been suggested that a mangrove environment *sensu stricto* probably did not exist as early as the Albian-Cenomanian (20). But the French Cretaceous amber forests were clearly very close to the sea shore as also indicated by syninclusions of mangrove bugs whose modern representatives forage on forest floors during low tides (12). Also, teeth of sharks that are typical for mangroves occur in the amber-bearing layer (21). It has been shown that mangrove-like vegetation already existed at that time (20). Representatives of the Cheirolepidiaceae that are very abundant in the amber-bearing strata are considered to be the dominant trees in these Cretaceous mangroves. Under these conditions, different processes could have easily transported marine microorganisms to the forest floor where they were embedded in fresh resins flows. Marine organisms or their shells and spicules could have been introduced together with attached organic debris during high tides or by spray; later they became engulfed by tree resin. Since the inclusions occur in layers of successive resin flows within a single piece of amber, we assume the introduction of marine debris to the forest was a continuous process, rather than a single event. Because most marine microfossils are attached to tiny pieces of organic debris, it is likely that dried, marine organic matter with siliceous microfossil remnants was blown from the beach into the nearby woods. In this way, even long cell chains (see Fig. 2C) could have been transported onto the resin flows by attachment to detritus particles. Today, similar coastal resinous forests are difficult to find and only a few places in the world can be considered as a modern analogue. The *Araucaria columnaris* forests of New Caledonia (Fig. 5) may be a modern equivalent of the mid-Cretaceous amber forest of southwestern France. Some of these forests are growing directly at the sea shore. In this environment, wind, spray and high tides may easily transport shells and microremnants of marine organisms from the beach and sea onto the abundant resin flows of these woods.

Conclusions

Our findings show that tree resin of coastal forests is not exclusively a trap for terrestrial and limnetic organisms, and that the occurrence of marine fossils should seriously be considered when interpreting amber inclusions. Dating of ambers and their terrestrial inclusions is often difficult since they may be redeposited in sedimentary rocks which are younger than the fossil resin itself (e.g. 22). The newly found marine microorganisms reveal that, contrary to common opinion, dating of amber by enclosed index fossils might become relevant in the future.

Materials and Methods

The amber pieces no. ARC60, ARC115, ARC226, and ARC263 were found in the quarry of Archingeay/Les-Nouillers in Charente-Maritime, and the amber pieces no. BUZ1 and BUZ2 were collected in 2002-2003 during road works near the locality of La Buzinie in Charente (southwestern France). The amber is derived from alternating layers of estuarine sand and clay containing mixed fragments of fossil plants (cuticles and lignitic wood). The amber-bearing stratum from Archingeay/Les-Nouillers corresponds to the regional stratigraphic subunit A1 and was dated as latest Albian (10), while the amber-bearing stratum from La Buzinie corresponds to the subunit B2 and is dated as mid Early Cenomanian (12). The reconstructed paleoenvironment corresponds to a coastal tropical forest, and representatives of the Araucariaceae and Cheirolepidiaceae were probably the main resin-

producing trees (18).

The marine microfossils were found in the six highly fossiliferous amber pieces mentioned above. These pieces also contained more than 200 arthropods and numerous microorganisms such as bacteria, algae and testate amoebae. Most syninclusions of arthropods and microorganisms are litter and soil dwelling taxa. Particularly, the finds of a mole cricket (23), carnivorous soil fungi and nematodes (19) and actinomycetes indicate that the resin solidified in a soil habitat, not on the tree bark. The different pieces of amber were fragmented into smaller portions in order to separate the inclusions for investigation. This preparation followed the method described by Perrichot (12). The polished fragments were investigated using transmitted-light differential-interference-contrast microscopes. The siliceous or calcitic nature of the microfossils described above has been proofed under a polarized microscope at the University of Rennes 1.

The different amber fragments containing the marine microfossils are deposited in the amber collection of the Department of Earth History in the National Museum of Natural History (MNHN) in Paris and in the collection of the Geosciences Laboratory of the University of Rennes 1.

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Figures legends

Fig. 1. Geological map of Charentes (southwestern France) showing both mid-Cretaceous amber localities with marine microfossils.

Fig. 2. Marine diatoms preserved in the mid-Cretaceous amber of southwestern France. (A) Diatom genus *Hemiaulus* (MNHN ARC263.9). (B) A 18-cells chain of *Stephanopyxis* (arrows; collection Géosciences Rennes BUZ1.1). (C) Centric diatom attached to organic debris (MNHN ARC115.19). (D) Centric diatom morphologically close to the genus *Syndenocystis* (MNHN ARC115.22). (E) Centric diatom belonging to Thalassiosirales (MNHN ARC115.13). [Scale bars: 100 µm (B), 20 µm (A, C and F) and 5 µm (D)].

Fig. 3. Diverse marine microfossils from mid-Cretaceous amber of southwestern France. (A) Foraminifer (MNHN ARC115.1). (B) Radiolarian (MNHN ARC115.20). (C) Larval spine of a sea urchin (MNHN ARC115.24). [Scale bars: 10 µm].

Fig. 4. Spicules of demonsponges from mid-Cretaceous amber of southwestern France. (A) Slightly curved oxea (MNHN ARC226.36). (B) Acanthostyle with a central canal (MNHN ARC115.12). (C) Spiny acanthostyle (MNHN ARC115.26). (D) Tetraxone calthrops (ARC60). (E) Microsclere (streaster, ARC115.2). [Scale bars: 50 μm (A), 15 μm (B, C) and 5 μm (D, E)].

Fig. 5. A possible modern analogue of the Cretaceous amber forest of southwestern France: a coastal forest of *Araucaria columnaris* at Maré, New Caledonia. Shells and remnants of marine microorganisms can be introduced by wind, spray or high tide from the beach or sea water onto the resin flows in the nearby woods.









