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Review

Reconstructing the soil food web of a 100 million-year-old forest: The case of the mid-Cretaceous fossils in the amber of Charentes (SW France)

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ABSTRACT

Over the past decade, the mid-Cretaceous amber deposits of Charentes (SW France) have been intensively studied. The fossils investigated were not only limited to arthropods preserved in amber, but also included microorganisms, plant debris and vertebrate remains. This plethora of analyses provided important data about the ecology of the overall system, including sources of litter input into the soil and of the above-ground ecology. More precisely, they showed that most of the microfossils were those of soil organisms or organisms that participated in the ecology of the forest soil. This new discovery provided the opportunity to study the ecology of the soil as preserved in the 100 million years old Charentes amber. Indeed, the trophic links of the fossil forest soil have been reconstructed on the basis of the fossil assemblage discovered in amber outcrops and overlayed on a model ecological forest soil food web. We relied on existing phylogenetic information to discuss the absence of certain taxonomic groups in the fossilized specimens. Our synthesis shows that although the organisms of this ancient forest of Charentes were different from those of modern soils, the soil food web was organized functionally the same as modern soils. It also demonstrated that trophic links of the soil community were already diverse, including various means of predation, parasitism and organic matter decomposition. The most obvious differences are the absence of evidence for symbiotic root nitrogen fixation and mycorrhizae.

1. Introduction

Common attempts at reconstructing ancient forest habitats tend to focus on the above-ground vegetation and animals. Such descriptions have been used to recreate animated documentaries and graphics which can leave a lasting impression with the public. One neglected aspect of these reconstructions is the soil biota. Soils contain a diversity of species that contribute to decomposition of the organic matter and recycling of nutrients into plant available forms. Decomposition provides nutrients that roots compete for, and returns CO_2 to the air for photosynthesis. In addition, there are lessons that can be learned from the fossil record by reconstructing ancient communities, pertinent to our understanding of similar modern habitats (Jackson and Erwin, 2006).

Amber is a fossil tree resin that polymerized and fossilized over millions of years. The Charentes region (SW France) is known to be an important area providing amber of mid-Cretaceous age. This amber has been dated to be 100 million years old, from the uppermost Albian to the lowermost Cenomanian (Néraudeau et al., 2002, 2003, 2005, 2008, 2009; Perrichot et al., 2007b), and it has been used to describe many specimens from a variety of taxa. These include fossilized tissue fragments and individuals from prokaryotes and all the eukaryote super-groups of Archaeplastida, Animalia, Fungi, Amoebozoa, Stramenopila, Rhizaria, and Excavata (Adl et al., 2005).

This review attempts to reconstruct the food web of a forest soil community from fossilized specimens in mid-Cretaceous amber from SW France. One definition used in ecology for soil was proposed by Adl (2003) as “soil is the result of combined mixture of organic matter and unconsolidated minerals and it provides habitats for thousands of specific soil species”, which is different from that used in geology and familiar to paleontologists. In this definition, the inorganic part of the soil which is soil texture consists of clay, silt, gravel or sand. The organic part includes the litter such as fallen leaves, woody debris, and animal parts. It also contains secretions and excretions from living organisms such as coprolites

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or root exudates and more decayed organic matter (accumulating vertically). This review focuses on trophic functional groups, or ecological guilds, to reconstruct the soil food web into categories (Adl, 2003), rather than a taxonomic approach, so as to integrate the taxa into a putative interaction food web. All the fossils cited in this article correspond to already published specimens.

2. Origin of the amber specimen

The synthesis presented here is based on mid-Cretaceous fossil organisms from southwestern (SW) France. These fossils come mainly from paralic deposits that have been studied since the 19th century. The species of continental origin have recently been investigated under taxonomical, phylogenetic and palaeoecological approaches (Perrichot, 2005; Vullo, 2007; Vullo et al., 2007; Lak et al., 2008; Girard, 2009, 2010; Girard et al., 2009a,b). Most of the details used in this review are published, i.e. Néraudeau et al. (2002, 2003, 2005, 2008, 2009), Perrichot (2005), Schmidt et al. (2008), Girard (2009, 2010) and Girard et al. (2009a,b).

This review rallies the data on fossils from nine different amber deposits (Fig. 1). Mid-Cretaceous amber from Charentes was deposited in an estuarine to coastal marine sediments from the uppermost Albian to the early Cenomanian. Details about the nine amber deposits (sedimentology, stratigraphy, palaeoenvironments) can be found in Néraudeau et al. (2002) and Gomez et al. (2008) for Archingeay-les Nouillers, Néraudeau et al. (2008) for Cadeuil, Néraudeau et al. (2003) for Fouras-Bois Vert, Vullo et al. (2005) for Fouras-Vauban, Perrichot et al. (2007b) for La Buzinie, Néraudeau et al. (2005) for the quarries of Puy–Puy and Les Renardières at Tonnay-Charente and Néraudeau et al. (2009) for Aix island. Overall, about 120 kg of amber has been gathered from these sites and about 10–20% fragmented for screening at the microscope.

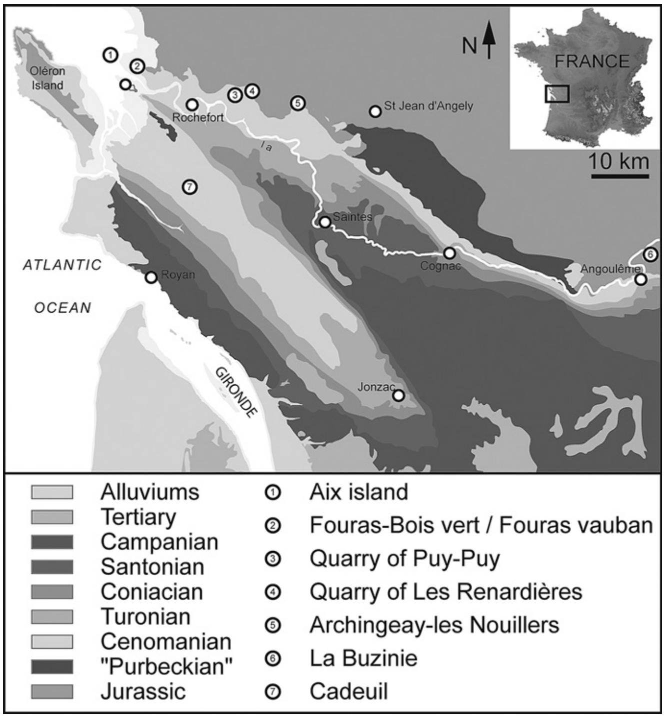

Fig. 1. Location map of the different amber outcrops of Charentes. Several amber layers are visible in the Charentes. The richest one comes from Archingeay-les Nouillers and corresponds to the Albian period. Albian amber is also present at the quarries of Puy–Puy and les Renardières and Cadeuil. Cenomanian amber is present at Aix island, Fouras-Bois vert, La Buzinie and Archingeay-les Nouillers.

3. Paleoenvironment

3.1. Location and climate

The ancient mid-Cretaceous forests where the amber formed were located in the western part of Europe. It developed on the western coast of one of the islands (which vestiges is the modern Central Massif, France) that formed the European archipelago in the mid-Cretaceous period. Paleogeographical reconstruction of this period placed this part of Europe about 10° further south, at a latitude of 35–40° N.

On the base of §O_{18} data from oyster shells, Videt (2004) estimated the climate to be warm temperate to sub-tropical, with average temperature ranging from 20 to 40 °C. Comparison between these data and those obtained from §C_{13} of the same oyster shells emphasized a seasonality with warm and dry winters and warm and moist summers (Videt, 2004). The expected air humidity, as inferred by similar modern environments would have been above 75% all year especially under the forest canopy. The atmosphere at that time was similar to the modern one, with slightly elevated oxygen concentration at about 28 kPa compared to 21 kPa today, and elevated carbon dioxide concentration at about 70 kPa, compared to 30 kPa today (Berner, 1997; Berner et al., 2000). Different authors estimated that the increase in pCO_2 during the mid-Cretaceous was due to a relatively high velocity of seafloor spreading (Fluteau, 2003; Haworth et al., 2005).

3.2. The forest environment

The fossiliferous layers of the amber localities of Charentes provided a great amount of fossil plant from which the mid-Cretaceous forests of SW France may be reconstructed. Fossil woods (mainly lignite) provided not only evidence for the presence of Araucariaceae and/or Cheirolepidiaceae but also include some Gynkgoaceae and Pteridophyta (Perrichot, 2005). Only one angiosperm wood from the early Cenomanian layers has been found in the quarry of Puy–Puy (unpublished observation). Gomez et al. (2004, 2008) described the fossil leaf assemblage to be composed of three different Pteridophyta, some Coniferales (*Frenelopsis alata*, *Glenrosa* nov. sp., *Geinitzia*, other brachyphyllous and pagiophyllous leaves), Ginkgoales (*Nehvizdya andegavense*), Cycadales and many Angiosperm leaves (e.g., *Eucalyptolaurus deprei*, cf. *Pseudoasterophylites cretaceus*). They also mentioned the presence of a few fossil flowers and isolated stamens with in situ *Clavatipollenites hughesii* pollen. Peyrot et al. (2005) described two main types of forests based on the pollen record: the first one corresponds to a forest of xerophytic conifer (Cheirolepidiaceae) with a herbaceous stratum composed of Bennetitales, Cycadales and Pteridophyta; and the second one corresponds to a more humid forest of Araucariaceae and Cupressaceae with an undergrowth mainly composed of Pteridophyta. They also highlighted that a third formation (a riparian one composed of Ginkgoales and angiosperms) may have played an important role in mid-Cretaceous ecosystems of SW France. Coiffard et al. (2008) interpreted the different occurrences of plant remains in the Charentes region as evidence for the presence of a gallery forest on the coast. Finally, Batten et al. (2010) have recently confirmed by studying megaspores that these ancient forests developed in close proximity to water bodies. In these forests, the precise plant origin of amber was difficult to determine. Because of its Araucarian/Cheirolepediacean origin, amber of SW France could only have been produced in one of the two main forests or both defined by Peyrot et al. (2005).

Vertebrate remains found in the same localities have provided important data to understand the terrestrial fauna of Western Europe during the mid-Cretaceous. Dinosaurs are well represented by teeth and bones. Different Saurischia (including diverse theropods and sauropods) and Ornithischia (including some ankylosaurs and ornithopods) have been identified in diverse localities (Vullo et al., 2007). Associated with this dinosaur fauna, remains of frogs, turtles, crocodilians, snakes, lizards, pterosaurs and mammals have also been found (Vullo, 2007; Vullo and Néraudeau, 2008). The contribution of the decomposition of this type of vertebrates to the soil is considered below.

3.3. *The soil environment*

Soil organic matter would have originated from decomposing litter (Adl, 2003) from the plants and animals described above. The plant debris would have provided woody tissues with ligninocellulosic cell walls and non-lignified plant cell wall polysaccharides. The dominance of conifers, especially Araucariaceae and Cheirolepidiaceae, contributed to the resins that formed the amber deposits. The dominant above-ground invertebrates were various insects and other arthropods based on the number and diversity of specimens found (Perrichot, 2004, 2005; Lak et al., 2008). These invertebrates would have contributed frass, as undigested or excreted wastes, from above-ground habitats. In addition, they would have contributed uric acid, ammonia and guanidine crystals as nitrogenous wastes. The remains of the arthropods gave chitin, an amino-sugar polymer, from the exoskeletons.

The mineral component of the fossil forest soil is not understood. This is due to the amber deposits having originated away from their current location. Not much can be inferred from the pedology regarding depth of horizons, soil structure, and ped aggregates. However, with some certainty the soil could not be called arid, based on the vegetation and moisture regime. Soils in modern coniferous forests tend to be acidic at 4–5.5 pH (Fisher and Binkley, 1999). However, the presence of filaments resembling *Sphaerotilus* (Betaproteobacteria) at this site and other similar sites of the same period would indicate a pH of 6.5–7.5 (Holt et al., 2000). It could be that plant tissue chemistry at the time was slightly different, or that the *Sphaerotilus*-like filaments were adapted to an acidic pH. Alternative solutions to this conflict would be the presence of certain clays, such as smectites, which are saturated with base cations that would retard acidification and acted as buffers, or of calcite.

4. The soil food web

The food web of a hypothetical modern forest soil (Figs. 2–4) was used (based on Adl, 2003; Coleman et al., 2004) to reconstruct the soil ecology of this ancient forest from the fossilized specimens found in these amber deposits. The model consisted of bacteria and fungi as the primary saprotrophs, responsible for the extracellular digestion of the litter and soil organic matter. The second trophic level constituted of consumers of the primary saprotrophs, and the partially digested organic matter. There are higher trophic levels that are consumers on these organisms, such as the predatory mites and small ground dwelling spiders. The main sources for the data used to reconstruct the soil food web are listed in Table 1. In Table 2, the expected feeding habits of the different arthropods are summarized where it was possible to determine them precisely.

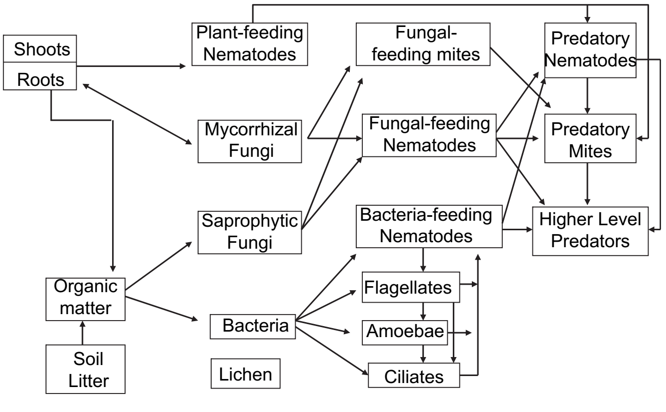

Fig. 2. Summary of the soil food web model used to interpret the data.

Several caveats must be stated in relation to the fossilized specimens found in amber. First, soft-bodied species are less likely to be preserved than those with an exoskeleton, cell wall or test. Second, larger or faster moving species may have tended to escape from the resin, so as to be under-represented. Third, some of the micro-arthropod specimens may be fossilized remains that were already dead. This would explain the presence of body parts or partially decomposed specimens penetrated with fungal hyphae. It is unclear whether the amber hardens to preserve the specimens rapidly enough to prevent decomposition. In this case, some faster decomposing species may be rare or absent in the amber. These factors would have revealed biased frequency of specimen found in ambers.

4.1. *Prokaryotes*

Certain filamentous bacteria have been identified to genera based on inclusions, sheaths, branching pattern or spores (Girard, 2010) among which we have identified nine bacteria. These include sheathed filaments with inclusions that resemble *Sphaerotilus* (Betaproteobacteria: Burkholderiales), diverse Actinobacteria morphologically close to some genera of groups 22, 26 and 29 *sensu* Holt et al. (2000). In particular, they include a *Nocardia* morphotype close to the genera *Amycolatopsis*- and *Pseudoamycolata*- (group 22), *Pseudonocardia*- (group 22) or *Saccharothrix*-like (group 29) filaments, and several other unidentified Actinobacteria morphotypes and spores. Most bacteria, however, could not be discerned from the debris or did not provide clues to determine their identity. Only evidence of rod-shaped bacteria has been obtained. Based on molecular phylogenies and the geochemical record, it seems likely that the modern bacteria metabolic pathways already existed; but it is unlikely that modern prokaryote genera were the same as the ancient genera, due to the instability of bacteria taxa on geological scales, and the frequency of lateral gene transfers (Doolittle, 1999; Ochman et al., 2000; Vishwanath et al., 2004). However, the geochemical environment for modern bacteria metabolisms and nutrient uptake developed long before in the Proterozoic, and the origin of bacteria metabolic pathways is dated from this period (Doolittle, 1999; Fennel et al., 2005; Saltzman, 2005). In particular, the parameters for nitrogen fixation 100 Mya were very similar to modern conditions (Raymond et al., 2004; Berman-Frank et al., 2003). It has been established that actinorhizal symbiosis of the nitrogen fixing *Frankia* (Actinobacteria) with eudicotyledon roots is estimated to the late Cretaceous based on the plant fossil record (Magallon et al., 1999). However, molecular phylogenies suggested that *Frankia* clades were established before the appearance of Angiosperms in the fossil record (Clawson et al., 2004). Thus, owing to an absence of fossil evidence, if there were any actinorhizal symbiosis 100 Mya at this site, it would have been early in the evolution of this association. Leguminous plants are not known to have existed until recently, about 60 Mya, and nodulation is dated at 58 Mya (Lavin et al., 2005; Sprent and James, 2006), so this mode of symbiotic nitrogen fixation can be discounted from our ecosystem. Lastly, nitrogen fixation in lichens would have occurred early in terrestrialization of eukaryote heterotrophy and these fungi

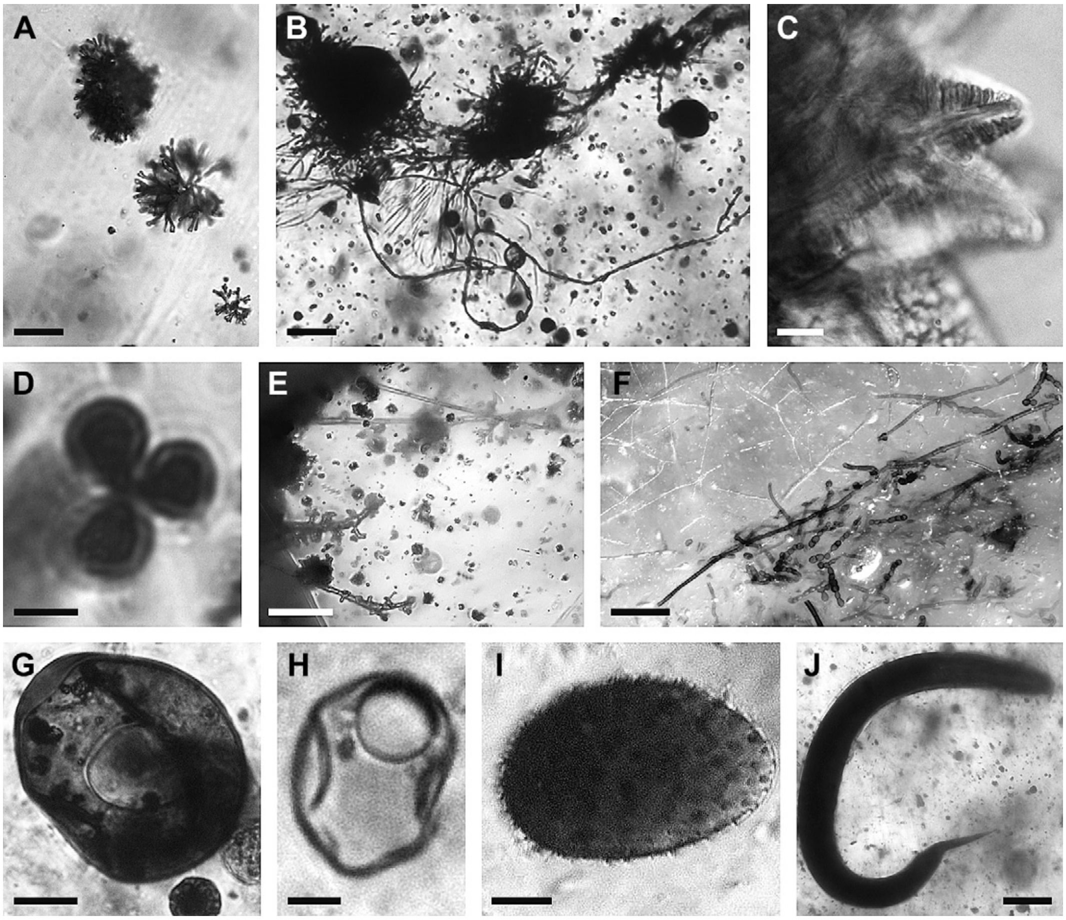

Fig. 3. Diverse microorganisms from mid-Cretaceous amber of Charentes. A – Actinomycetes indet. B – Actinomycetes of the family Pseudonocardiaceae. C – Sheathed bacterium of the genus *Sphaerotilus*. D – Green alga *Myrmecia*. E – Oomycetes of the family Peronosporaceae. F – Ascomycete morphologically close to the genus *Cladosporium*. G – Amoeba *Arcella discoides*. H – Amoeba of the genus *Hyalosphenia*. I – Possible ciliate of the genus *Grossglockneria*. J – Nematodes of the family Rhabditidae. Scale bars: 5 μm except in F (50 μm), A–B (40 μm), G (30 μm) and E (20 μm).

would have contributed to the mineralization of nutrients such as rock phosphate (Selosse and Le Tacon, 1998; Neaman et al., 2005; Senerivatne and Indrasena, 2006). There is no evidence for fungal associations with cyanobacteria or algal symbionts in lichens in the studied samples at this time. However, fungal taxa morphologically similar to modern lichen forming fungi existed. In the Cenomanian amber of Ecommoy (NW France; Breton and Tostain, 2005), an association of *Trentepohlia*-like filaments and fungal mycelia has been found (Breton and Tostain, 2005), indicating that lichens were present in some Cretaceous forests. The discovery of *Myrmecia* algae, known to be lichen gonidia, in the amber of Archingeay-les Nouillers is an indirect evidence of the presence of lichen in the mid-Cretaceous forest of Charentes (Girard et al., 2009b). Our results suggest that the contribution of prokaryotes to nutrient cycling and the availability of limiting nutrients in soil, such as nitrogen and phosphorous, were dissimilar to the modern period.

4.2. Fungi

The origin of fungal taxa are known to have occurred prior to the Cretaceous, based on fossil record and molecular phylogeny estimates (Lutzoni et al., 2004). Basidiomycota were the last group to appear, and hyphae with clamp connections were observed from 290 Mya and their basidiocarp from the Cretaceous (Hibbett et al., 1997a, 1997b). Fungal hyphae and spores were predominant in the mid-Cretaceous amber from Charentes (Girard et al., 2009b). Some specimens provide sufficient morphology to attempt identification. The identified specimens include chlamydospores of Glomeromycota, which suggested that arbuscular mycorrhizae may have occurred. However, as no forms of mycorrhizae were found in any sample from this region, we cannot know whether these fungi were mycorrhizal at the time in this forest. One Oomycete may belong to Peronosporales, which are identified as plant-parasites. Ascomycota are the most abundant fungi identified in the mid-Cretaceous amber from Charentes. Specimens of the Capnodiales, Mycosphaerellales, Eurotiales and Saccharomycetales have been found (Girard, 2010). Some are saprophytic, plant-parasites or lichen forming taxa. Several modern fungal genera capture micro-invertebrates, particularly nematodes, to supplement their nutrition with nitrogenous molecules that are otherwise deficient in the plant tissues (Barron, 1977; Adl, 2003). At least one Ascomycota specimen was a nematode-trapping fungus which revealed that it was probably a wood decomposer (Schmidt et al., 2008). Basidiomycota were rare in the amber. Hyphae of Polyporaceae have been identified in insect fecal pellets (Schmidt et al., 2010a); hyphae of Agaricales have also been found (Girard, 2010). A possible Uredinales, preserved on wood debris, have also been identified (Girard, 2010).

Based on specimens found, it is likely that other fungal taxa not yet found in the amber also occurred, as they are known to be early diverging taxa (see Lutzoni et al., 2004). This would have included Chytridiomycetes which are common soil saprotrophs and

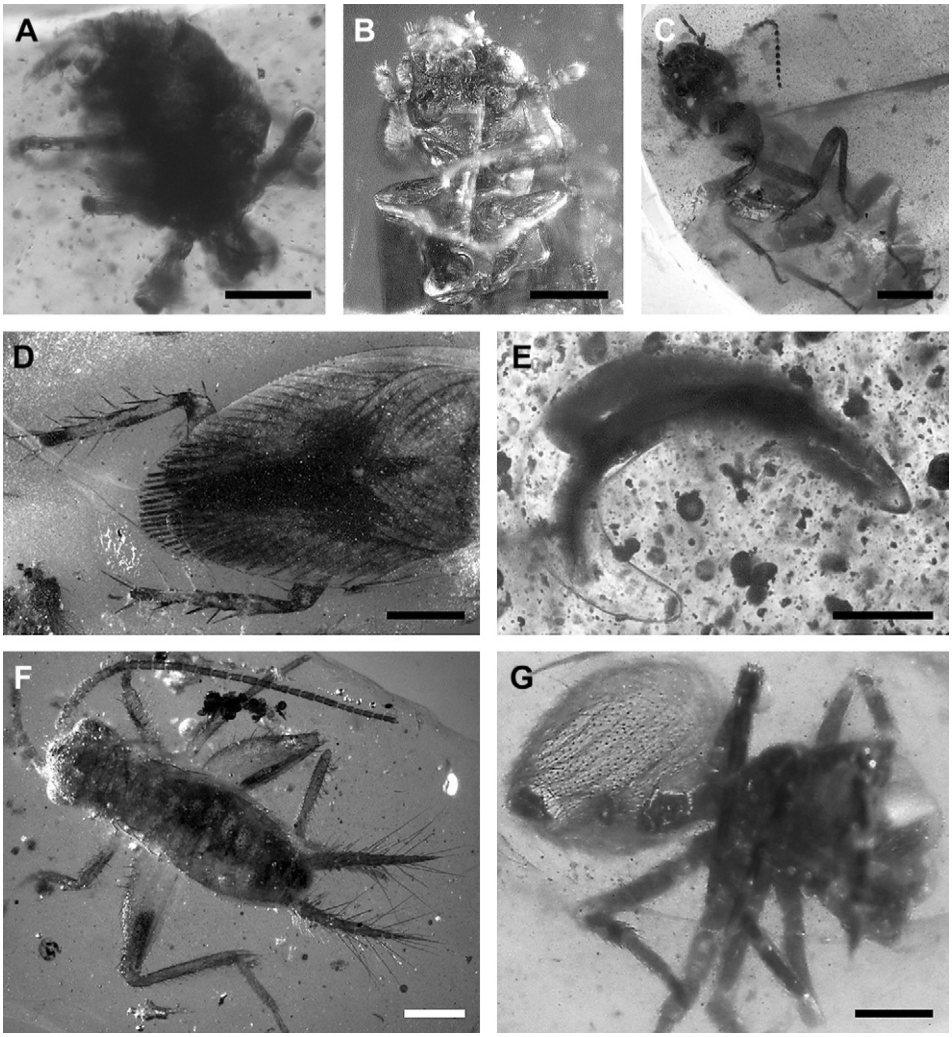

Fig. 4. Diverse metazoans from mid-Cretaceous amber of Charentes. A – Acari indet. B – Coleoptera Nitulidae. C – Isoptera. D – Posterior part of a cockroach (Blattaria). E – Enchytraeidae indet. F – Orthoptera Grylloidea. G – Araneae Mecysmaucheniidae. Scale bars: 0.1 mm (A, B, E), 0.5 mm (C, F, G) and 1 mm (D).

predators on invertebrates. Adl (2003) reviewed that some Chytridiomycetes are important in the decomposition of pollen, chitin, and many are parasites of amphibians or of plants. Other Fungi such as Entomophthorales would have occurred as free-living saprotrophic species, or as parasites of mites, spiders and insects. Other soil Zygomycota taxa are also likely to have been present, as these are also early diverging fungal taxa. Presence of Saccharomycetales in the amber was unexpected, since angiosperms were not common at that time and restricted to a specific environment (Coiffard et al., 2008). Thus the phyllosphere, flowers and fruit of angiosperms where they typically occur would not have been common, and Saccharomycetales probably relied on other sources of sugars.

4.3. *Bacterivores*

The main bacterivores in the soil are protists and nematodes. Some of the protists, such as the Testacealobosea (Amoebozoa) and Ciliophora (Alveolata), are convincingly present in the amber (Girard et al., 2009b; Girard, 2010; Schmidt et al., 2010b). Testacealobosea included morphotypes that resemble modern soil genera such as *Centropyxis*, *Arcella*, *Leptochlamys*, *Hyalosphenia*, *Microchlamys*, *Cryptodifflugia* (syn. *Difflugiella*) and *Archerella* (Girard, 2010; Schmidt et al., 2010b). Ciliophora are rare in the samples possibly due to the difficult preservation of protists without cell walls in conifer resins, as demonstrated by Foissner et al. (1999). To date, several unidentified specimens have been found. Only one specimen of Colpodea (similar to the genus *Grossglockneria*, a fungivore) has been identified in these samples, even though colpodids are the most common soil ciliates in modern times. There are many inclusions in the amber that resemble amoeboid forms and euglenids. Some authors attributed these similar inclusions in other amber deposits to amoeboid and euglenid species (Kedves and Párdutz, 2002; Ascaso et al., 2003, 2005; Veiga-Crespo et al., 2007; Martín-González et al., 2008, 2009a,b). The well preserved ultrastructure of these specimens would indicate rapid and efficient chemical fixation of the cytoplasm. If these inclusions are real fossils of protists, they would most probably be specimens of Amoebozoa and Heterolobosea (Excavata). However, one cannot ignore the possibility they might be pseudo-protists. However, considering the quantity of this kind of inclusions, their occurrence in often high, their broad range of dimensions but with similar shape, and the fact that they are always concentrated and oriented along amber flows would support the argument that they are pseudo-protists. Even though reconstructions of these inclusions show delicate vacuolated

Table 1
List of inclusions found in mid-Cretaceous French amber outcrops (# means "different taxa"). The classification used here is based on Adl et al. (2005).

Prokaryotes	#	Opisthokonta	#
Cyanobacteria	2	Fungi	
Actinomycetes	5	Ascomycotya	9
Other bacteria	2	Basidiomycota	2
		Glomeromycota	1
		Urediniomycetes	1
		Metazoa	
Eukaryotes	#	Animalia	
Amoebozoa		Annelida	1
Tubulinea		Nematoda	3
Testacealobosia		Arthropoda	
Arcellinida	10	Arachnids	
Archaeplastida		Acari	5
Chloroplastida		Araneae	3
Charophyta		Pseudoscorpionida	1
Streptophytina		Scorpionida	1
Plantae		Enthognata	
Coniferophyta	11	Collembola	3
Cycadophyta	1	Insecta	
Ginkgophyta	1	Blattodea	2
Gnetophyta	1	Coleoptera	9+
Lycophyta	4	Dermaptera	1
Magnollophyta	18	Diptera	15?
Pteridophyta	27	Hemiptera	13+
Chlorophyta		Hymenoptera	25
Chlorophyceae	4	Isoptera	1?
Chromalveolata		Lepidoptera	1
Stramenopiles		Mantodea	1
Peronosporomycetes	1	Neuroptera	4
Alveolata		Odonata	1?
Ciliophora	2	Orthoptera	5
Intramacronucleata		Psocoptera	4
Armophorea		Raphidioptera	1
Armophorida	1	Strepsiptera	1
Colpodea	1	Trichoptera	?1
Oligohymenophorea		Thysanoptera	1?
Peritrichia	1	Myriapoda	
Spirotrichea		Chilopoda	1
Stichostrichia	1	Diplopoda	1?
Excavata		Vertebrata	
Euglenozoa		Anoura	1
Euglenida		Chelonia	2
Euglena	2	Crocodilomorpha	2–6
Rhizaria		Dinosauria	6
Cercozoa		Mammalia	2–3
Silicofilosea		Pterosauria	1
Euglyphida	1	Squamata	6

structures, they seem not to have any preserved nuclei and other organelles, which are rather rigid organelles in amoebae (Raikov, 1982). There is no evidence that plant resin is an effective biological fixative. It also seems odd that if amoeboid specimen can be preserved in large numbers, that flagellates were not among them in the amber, and that the more robust ciliates are rare. Flagellated specimens are very rare to date from these amber deposits (few specimens of possible euglenids have been identified only). Because of the araucarian origin of the mid-Cretaceous amber of SW France, their rarity in this study of fossil assemblage could be a result of poor preservation as reported by Foissner et al. (1999). However, soil flagellates would certainly have been present based on molecular phylogenies (Berney and Pawlowski, 2006). These would have included a variety of free-living excavata that contain many groups with animal parasites that would have existed 100 Mya ago. There is one specimen of a filose testate amoeba, *Assulina* (Rhizaria: Silicofilosea) (Girard, 2010). Also expected to have been present are the Cercomonadida (Rhizaria) which in modern times constitute most of the soil bacterivorous flagellates.

There were four specimens of nematodes (Girard, 2010) including one Rhabditidae, one Aphelenchidae (fungi and root-feeders),

Table 2
Annelid and arthropod specimens found with expected feeding habits. #: number of different groups, D: detritivores, F: fungivore, P1: primary predator, P2: secondary and higher predator, R: parasite, H: herbivore, + indicates presence, ? indicates uncertainty about the identity or number found. Definitions as in Adl (2003).

Group	#	D	F	P1	P2	R	H
Annelida	**1**						
Haplotaxida							
Enchytraeidae	1	+					
Arachnida	**6?**						
Acari	?	+	+	+	+	+	+
Araneae	3			+	+		
Pseudoscorpionida							
Cheliferidae	1			+	+		
Scorpiones							
Palaeuscorpiidae	1			+	+		
Collembola	**3**						
Entomobryidae	1	+	+	+?			+
Onychiuridae	1	+	+	+?			+
other	1						
Crustacea	**4**						
Isopoda	1	+					+
Tanaidacea	3	+					+
Insecta	**85**						
Blattodea	**2**						
Umenocoleidae	1	+					
other	1						
Coleoptera	**9**						
Belidae	1						+
Buprestidae	1		+				+
Chrysomelidae	1						+
Curculionoidea	1		+				+
Elateridae	1		+		+		+
Nitidulidae	1		+				+
Ripiphoridae	1		+			+	
Scraptiidae	1						+
Staphylinoidea	1				+		+
Dermaptera							
Neodermaptera	1	+?	+?	+?	+?		+?
Diptera							
Brachycera	**6?**						
Bombyliidae	1						+
Dolichopodidae	2				+		
Hilarimorphidae	1						+
Phoridae	1	+	+				
Rhagionidae	1				+		
Other	?						
Nematocera	**8?**						
Cecidomiidae	1				+	+?	+
Ceratopogonidae	1	+	+		+		+
Chironomidae	1						
Limoniidae	1	+	+		+		+
Mycetophilidae	1		+		+		+
Psychodidae	2				+		
Tipuloidae	1						+
other	?						
Hemiptera	**13?**						
Auchenorrhyncha							
Achilidae	1?						+
Fulgoroidea	1?						+
Heteroptera							
Ebboidea	1				+?		+?
Gerridae	1				+		
other Geromorpha	1				+		
Pentatomidae	1				+?		+
Schizopteridae	1				+		
Tingidae	1						+
Homoptera							
Fulgoroidea	1						+
Sternorrhyncha							
Aleyrodidae	1						+
Aphidoidea	1						+
Coccidae	1		+				+
other	1?						
Hymenoptera	**25**						
Braconidae	2					+	

(*continued on next page*)

Table 2 (*continued*)

Group	#	D	F	P1	P2	R	H
Ceraphronoidae	1					+	
Chalcidoidea	1					+	+?
Chrysidoidae	?1					+	
Cynipoidae	1					+	+
Diapriidae	2					+	
Falsifomicidae	1		+?		+?		+?
Formicidea	2		+		+		+
Ibaliidae	1					+	
Ichneumoidea	1					+	
Mymarommatidae	1					+	
Proctotrupidae	1					+	
Scelionidae	4					+	
Scolebythidae	1						
Siricidae	1						+
Sphecidae	1				+		
Stigmaphronidae	?1						
Trigonalidae	1					+	
other	?						
Isoptera	**1?**	**+**	**+**				**+**
Lepidoptera	**1**				**+**		**+**
Mantodea	**1**				**+**		
Neuroptera	**4**						
Ascalaphidae	1				+		
Coniopterygidae	1				+		
Myrmeleontidae	1				+		+
Rhachiberothidae	1				+?		+?
Odonata							
Aeshnoptera	1?				+		
Orthoptera	**5**						
Acridoidea?	1				+?		+?
Elcanidae	1						+
Gryllidae	1	+	+		+		+
Gryllotalpidae	1	+	+		+		+
Tridactyllidae	1						+
Psocoptera	**4**						
Trogiomorpha	4	+	+				+
Raphidioptera							
Mesoraphidiopteriidae	1				+		
Strepsiptera	**1**					**+**	
Trichoptera	?1	**+?**	**+?**		**+?**		**+?**
Thysanoptera							
Thripidae	1?						+
Myriapoda	**2**						
Chilopoda	1				+		
Diplopoda							
Polyxenida							

and two undetermined morphotypes as there are insufficient preserved morphological traits to observe the oral structures.

It is surprising that no slime mould has been discovered, despite forming resistant plasmodia and sporangia. These organisms would have been important bacterivores (and fungivores) of the forest. Their fossil record is very scarce. No slime mould may have existed in their modern form until the Tertiary, as the oldest specimen is of the Eocene (34–55 Mya) in Baltic amber (Domke, 1952; Dörfelt et al., 2003), even though this group of amoebae is supposedly ancient.

4.4. *Fungivores*

The main fungivores in soils are typically found in several genera of nematodes, mites, springtails, some insects and a small number of amoeboid genera. Only one fungivorous or root feeding nematode, an Aphelenchidae, was found. The other fungivores found so far appear to be a number of mites, springtails, flies, and beetle larvae. The identity of the mites remains to be determined, but they include Tanaupodidae (Judson and Makol, 2009). Some psocopterans of the sub-order Trogiomorpha (Perrichot et al., 2003) were also active fungivorous organisms.

4.5. *Other secondary saprotrophs*

Scarce fossil evidence for osmotrophy in these samples is quite obvious. There would have been some osmotrophy by protists, but it is a minor contribution to the feeding habit of most terrestrial species. Yeasts are normally the most common soil eukaryotic osmotrophs but they are not common in these samples, except Saccharomycetales (Girard, 2010) and Deuteromycotina (Schmidt et al., 2008). Cytotrophy (feeding on protists) would have occurred through the bacterivorous nematodes (some are also cytotrophs). Most cytotrophy tends to occur indirectly, through ingestion of detritus. Detritivores included a variety of mites, one enchytraeid, and numerous insects including beetles, woodlice and termites (Perrichot et al., 2007a) (Table 2). Although most insect fossil remains are from adults, their larvae are soil detritivores that ingest decaying organic matter. Termites, as other wood digesting insects require bacteria and protist (Excavata) gut symbionts to digest the wood, or require a mutual association with fungi. Termite coprolites are abundant in the outcrops, suggesting an important role in wood decomposition. Cockroaches are also very abundant in the mid-Cretaceous French amber, suggesting that they played an important role in the decomposition of the organic matter. A specimen of earthworm (Enchytraeidae) has been found (Girard, 2010), representing the oldest specimen preserved in amber. Other invertebrates are likely to have been present in the forest soil, such as Lecithoepitheliata flatworms (Adl et al., 2006) that occurred in forest soils and are known to have diverged early in the invertebrate fossil record.

4.6. *Plant-feeders*

Many fossil arthropods from Charentes amber were active plant-feeders in the soil. Between them, the most abundant group corresponds to the coleopterans (Soriano, 2009); specimens of Belidae, Buprestidae, Chrysomelidae, Curculionoidea, Elateridae and Nitidulidae, found in amber, probably ate wood, leaves, seeds, fruits and sap. Hemiptera (Coccidae, Pentatomidae, Tingidae, Sternorrhyncha and Auchenorrhyncha) and Thysanoptera were also probably active plant-feeders, eating leaves and/or sap. Other putative plant-feeders belong to diverse groups of arthropods such as Polyxenida, Dermaptera, Tricoptera and Orthoptera (Elcanidae, Gryllidae, Gryllotalpidae, Tridactylidae). Several specimens of this last order are particularly interesting. Mole crickets played a significant important role in the soil structure (Perrichot et al., 2002). The functions of mole crickets are to build tunnels in wet soils and they can destroy many roots and tubercles. Their activity in forest soil should have provided significant quantity of plant debris to the soil.

The most important plant-feeders of the forest were the dinosaurs. Teeth of three groups of herbivorous dinosaurs have been found, belonging to the Titanosauriformes (at least Brachiosauridae), the Iguanodontoidea and the Nodosauridae (Vullo et al., 2007; Vullo and Néraudeau, 2010). These dinosaurs would have eaten the plants but it is difficult to determine their precise interactions with the soil. They provided diverse cellulosic wastes that contributed to the soil ecology, and undigested plant debris that they broke while eating. Some of them would have also eaten herbaceous plants such as some ferns, and locally disturbed the soil structure.

4.7. *Predators*

Taxa that contain first order predators included mites, juvenile spiders (especially of the smaller species), and possibly collembolans (Table 2). These species would prey on secondary saprotrophs and other micro-invertebrates. The second order trophic level predators included larger species that are predatory on a diversity of consumers and first order predators. They include diverse orders of insects and arachnids. Among them, four groups are particularly abundant in Charentes amber. Primitive ants have been found, that were likely predators at the surface of the soil (Perrichot et al., 2008b) although ants can be omnivorous generalists. Orthopterans primarily classified as plant-feeders could have also been predators of insect larvae and earthworms. Many heteropterans have been found (Perrichot et al., 2005, 2006; Solórzano Kraemer et al., 2010). Except specimens in the family Tingidae which are plant-feeders, the other families (Gerridae, Mesoveliidae, Schizopteridae and Veliidae) were probably active predators of small insects and small invertebrates. Many neuropterans should have also been predators (Nel et al., 2005a,b). Specimens of the family Ascalaphidae were insect predators whilst the Myrmeleontidae, at their larval stage, fed on ants and others insects. The other supposed predatory consumers belong to the raphidiopterans and dermapterans (Perrichot and Engel, 2007; Engel, 2009).

Among the other arthropods, some chilopodans that were predators of several groups of insects and of small invertebrates were also found. The arachnid predators were represented by three different groups. The Cheliferidae (Pseudoscorpionida) ate small insects and Acari. Palaeoeuscorpiidae (Scorpionida) would have been predators of several insects and arachnids (Lourenço, 2003). Spiders were represented by several specimens, but not all have been identified. The supposed presence of Zodariidae spiders is interesting as they are known to be ant predators (Perrichot et al., 2007b). The presence of ants implied that this prey–predator relationship was already established by the mid-Cretaceous (Nel et al., 2004; Perrichot et al., 2008b). However, a reinvestigation of the so-called Zodariid specimens suggests that they may not belong to this family (Paul Selden and Erin Saupe, Pers. Comm.).

5. Links with the above-ground food web

Links with the above-ground food web are difficult to rebuild. It is difficult to establish precisely the links between the permanent soil inhabitants and the temporary soil species, most of which correspond to flying insects such as dipterans, hymenopterans and lepidopterans. Dipterans represent more than 40% of the arthropods found in the Charentes amber (Perrichot, 2005). These organisms would have played an important role in the ecology of the ancient forest. Most of them correspond to cosmopolitan families that prefer wet forest environments. Some families at their larval stage may have been inhabitants of soils rich in organic matter. Some families such as the Bombyliidae would have been important in the propagation of plants as they are known to be important pollinating agents. However, as angiosperms were rare, it is not clear which plants were being pollinated. Other families such as Dolichopodidae would have been one of the most important groups of predators, especially in the wet areas of the forest. The hymenopterans were also very abundant. Most of them were probably parasites of other groups of insects and arthropods such as Braconidae and Scelionidae (Perrichot, 2005). Lepidopterans were mostly represented by isolate scales, but some complete specimens have also been found. These insects would have played an important role in the dispersion of the pollen in the ancient forest.

The flying insects are the most abundant arthropods in Charentes amber. Different reasons can explain it. First, most of these insects (such as dipterans) fly in swarm. When close to the resin, some of them could have been trapped, explaining why they are so abundant. Secondly, the cadavers already trapped in the resin could have attracted some flying scavengers. Finally, we suppose the flying insects could have been attracted by the odour of the resin.

The other temporary soil actors mainly correspond to vertebrates. Diverse remains have been found in amber, including feathers (Perrichot et al., 2008a), reptile skin (Perrichot and Néraudeau, 2005) and mammal hair (Vullo et al., 2009). Many vertebrate remains have also been found in sediments (mostly isolated teeth) belonging to diverse herbivorous and carnivorous dinosaurs, crocodiles, squamate reptiles, turtles, pterosaurs, frogs and marsupialiform mammals (Néraudeau et al., 2005; Vullo et al., 2005, 2007; Vullo et al., 2010; Vullo, 2007; Vullo and Néraudeau, 2008, 2010). All these organisms should have played a more or less important role in the ecology of the forest soil. As already mentioned, they provided diverse substances such as uric acid, urea and amino acids. But they probably also played a more direct role. Indeed some of them (the small carnivorous dinosaurs, the frogs and the mammals) should have been insectivorous. They probably preyed both on flying insects and on soil dwelling arthropods.

6. Conclusion

Palaeoecological reconstructions are often based on very partial data. They mostly take into consideration vertebrate, shelled invertebrate and plant remains. Soft-bodied organisms such as arthropods, nematodes and protists are often neglected because they are rarely preserved. They need specific conditions to be preserved, and amber is a rare medium that allows such preservation.

Over 10 years, a broad variety of descriptive studies was performed on mid-Cretaceous amber localities of Charentes (SW France), including micropalaeontological, macropalaeontological and sedimentological studies. This particularity provides more complete data about the ecology of a fossil environment than previous studies.

All the fossils identified in the mid-Cretaceous amber layers of Charentes permit a reconstruction of the trophic links of a 100 million-year-old forest soil. One of the main lessons of this study is that the mid-Cretaceous soil food web worked in the same way than those of modern forests. The different trophic categories of organisms that are represented in modern environments are also present in the fossils of Charentes. Perhaps the most important concern is the scarcity of soluble sugars as Angiosperms were scarce in Charentes forest, or at least restricted to specific environments. They were mainly developed close to rivers and the first European brackish water-related angiosperms just appeared during the mid-Cretaceous (Coiffard et al., 2006, 2008). This particularity should have influenced the soil community and the soil development (indeed conifer soils are generally less developed than angiosperm soils). These differences would have greatly influenced the abundance of the diverse soil organisms. However, the biases introduced by the kind of organisms trapped and preserved in amber cannot allow us to evaluate the relative abundance of the different soil organisms. Actuotaphonomical studies are in progress in order to quantify the abundance of microorganisms in the amber from the ancient forest. This study should help to characterize the development of the soil and the importance of its disturbance to specimen fossilization. Indeed it has been demonstrated that the soil of the Charentes forest was regularly flooded, perhaps because of a seasonal effect (Girard et al., 2009a).

All the results presented in this study are valid only if all the fossil organisms really lived in the same environment. Actually, it is impossible to say that two organisms found in two different amber pieces lived closed together. However, the discovery of certain amber pieces allows us to be confident with the outcome of this research. Several very rich amber pieces, named litter amber, have been found (Perrichot, 2004, 2005). One of these amber pieces contains 274 syninclusions including 86 arthropods, 181 microorganisms, 7 feathers, and various plant remains (mostly wood fibres and stellate hairs) (Perrichot and Girard, 2009). These peculiar amber fragments have preserved organisms representing all the different trophic categories cited above, and are the best proofs that all the organisms cited in this article could have interacted together in the 100 Mya forests of Charentes.

Since the Triassic, many amber-bearing sediments were deposited all over the world (Schmidt et al., 2006). Most of them have been studied for the arthropods trapped in the amber. Only few have been investigated for other fossils such as vertebrate remains and amber microorganisms. Lack of sufficient evidence from these other regions makes it impossible to compare the soil food web of the Charentes amber with those of other forests.

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