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FOSSIL AMOEBAE (HEMIARCHERELLIDAE FAM. NOV.) FROM ALBIAN (CRETACEOUS) AMBER OF FRANCE

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Abstract: Two extraordinarily well-preserved testate amoebae are described from Late Albian age amber from south-western France. The specimens are attributed to a new family, the Hemiarcherellidae fam. nov., and are described as *Hemiarcherella christellae* gen. et sp. nov. The amoebae described herein originate from highly fossiliferous amber pieces. Based on syninclusions, *Hemiarcherella christellae* was a soil-dwelling organism, probably an active bacterivore. This taxon represents the third species of testate amoebae described from mid-Cretaceous French amber. Analysis of this fossil amoeba fauna illustrates the uniqueness of mid-Cretaceous French amber deposits. Indeed, most amoebae found in amber have been assigned to modern species, corroborating the hypothesis of morphological stasis in different microbial lineages. However, the well-preserved amoebae fauna found in French amber can be distinguished clearly from modern species and help us to better understand the fossil record of these organisms.

Key words: amber, Late Albian, forest soil, Amoebae, evolution.

AMOEBOID organisms are a group of protozoans, and some of them (thecamoebians) are protected by an organic or inorganic shell. Originally belonging to the subphylum Sarcodina, they are now placed in the super-group Amoebozoa of the new higher level classification of eukaryotes as defined by Adl *et al.* (2005). Shells of testate amoebae are rare in the fossil record. Porter and Knoll (2000) and Porter *et al.* (2003) described the oldest amoebae fauna (Neoproterozoic) from the Chuar Group (Grand Canyon). Bosak *et al.* (2011) recently reported agglutinated tests of Arcellinida (with possible affinities with modern family Heleoperidae, Plagiopyxidae and Difflugidae). Isolated reports of Carboniferous and Permian specimens have been made from Canada, Czech Republic and Germany (Vasicek and Ruzicka 1957; Thibaudeau *et al.* 1987; Medioli *et al.* 1990; Wightman *et al.* 1994; Wolf 1995). The Mesozoic amoeba fossil record is richer, due especially to the discovery of specimens preserved in amber. Schmidt *et al.* (2006) mentioned the presence of *Centropyxis hirsuta* Deflandre, 1929 in Carnian (Triassic) amber of Italy. Other amoebae were also described from Cretaceous ambers of Germany (Poinar *et al.* 1993; Schönborn *et al.* 1999; Schmidt *et al.* 2004), Canada (Waggoner 1996*a*) and France (Schmidt *et al.* 2010). Other Cretaceous specimens have been mentioned in Spanish amber, but their precise origin is debated (Schmidt *et al.* 2010; Girard and Adl 2011). Rare Mesozoic nonamber amoebae have been found, such as the specimens described in Jurassic black shale from Italy (Bassi *et al.* 2008) and in Late Albian clay-silt from Nebraska (van Hengstum *et al.* 2007). The Cenozoic amber fossil record is poor. Only a few amber specimens of Cyphoderiidae have been recorded from Dominican amber (Waggoner 1996*b*). The nonamber Cenozoic fossil record is richer with specimens from the Eocene (Bradley 1931; Schiller 1998), Oligocene (Schiller 1998), Miocene (Frenguelli 1933; Foissner and Schiller 2001) and Pliocene (Köváry 1956; Bœuf and Gilbert 1997). For more details about the amoebae fossil record, refer to Schmidt *et al.* (2010).

Analysis of the fossil record of amoebae, especially of the amber specimens, highlights one important aspect of the evolution of this group of organisms. Most of amber amoebae are morphologically indistinguishable from extant species. For example, the oldest amber specimens (from the Triassic amber of Italy) have been attributed to the extant species *Centropyxis hirsuta* (Schmidt *et al.* 2006). The most convincing example is the Cenomanian amber of Schliersee (Poinar *et al.* 1993; Schönborn *et al.* 1999; Schmidt *et al.* 2004). Of the eight species found in Schliersee amber, only two are fossil (*Triassamoeba alpha*

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Poinar *et al.*, 1993 and *Hyalosphenia baurei* Schönborn *et al.*, 1999) and six correspond to extant species (*Centropyxis acuelata* var. *oblonga* Deflandre, 1929, *Centropyxis delicatula* Penard, 1902, *C. hirsuta*, *Cyclopyxis eurystoma* Deflandre, 1929, *Phryganella acropodia* (Hertwig and Lesser, 1874) Penard, 1902, *P. paradoxa* Penard, 1902). The discovery of extant species in Mesozoic ambers was interpreted as proof of morphological stasis in some microbial lineages (Martín-González *et al.* 2008). This conclusion based on amber specimens seems to be corroborated by a few nonamber species such as those discovered by van Hengstum *et al.* (2007). This Late Albian assemblage preserved in clay-silt is mostly composed of extant species (*Difflugia oblonga* Ehrenberg, 1832, *D. protaeiformis* Lamarck, 1816, *D. urens* Patterson, MacKinnon, Scott and Medioli, 1985, *Lagenidifflugia*? cf. *vas* Leidy, 1874, *Pontigulasia*? cf. *compressa* Carter, 1864, *Cucurbitella tricuspis* Carter, 1856, *Lesquereusia spiralis* Ehrenberg, 1840) and contains only one fossil species but belonging to an extant genus (*Difflugia baukalabastron* van Hengstum, Reinhardt, Medioli and Gröcke, 2007). Schmidt *et al.* (2010) interpreted this apparent morphological stasis as (1) possible evidence of convergent evolution and/or (2) the result of the largely asexual reproduction of testate amoebae. This latter hypothesis seems to be not supported by recent work that demonstrated the presence of sexual reproduction in many amoeboid organisms (Lahr *et al.* 2011).

Here, we described two new fossil amoeba specimens from mid-Cretaceous amber of south-western France. These amoebae are extremely well preserved, as even details of the filopodia are visible. The specimens are assigned to the new species, *Hemiarcherella christellae* gen. et sp. nov., and the new family, Hemiarcherellidae. *H. christellae* was probably a soil-dwelling organism, and its ecology is discussed in the light of associated syninclusions. This discovery speaks to the importance of the amoeba fauna from mid-Cretaceous amber from south-western France (mostly composed of fossil species) for elucidating the evolutionary history of testate amoebae. Fossil amoeba species from French amber (*Hemiarcherella christellae, Centropyxis perforata* and *Leptochlamys galippei*) form the basis of a discussion on the hypothesis of morphological stasis within amoeba lineages and the composition of fossil assemblages found in mid-Cretaceous amber of south-western France.

LOCALITY, MATERIAL AND METHOD

The amber piece was found in the quarry of Archingeay/Les-Nouillers in Charente-Maritime, south-western France (Fig. 1). The amber derives from alternating layers of estuarine sand and clay that contains many plant fragments (wood, cuticles, palynomorphs and amber). In the regional stratigraphy, the amber-bearing stratum corresponds to the subunit A1 *sensu* Néraudeau and Moreau (1989) and has been dated as Late Albian (100 million years old) by palynology (Néraudeau *et al.* 2002; Dejax and Masure 2005).

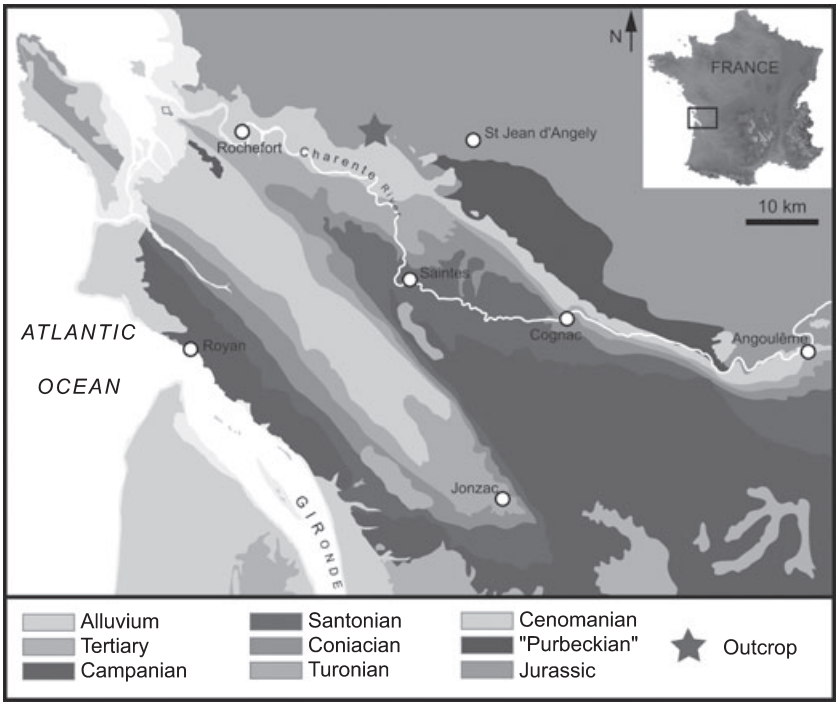

FIG. 1. Locality map of the outcrop of Archingeay/Les-Nouillers (Charente-Maritime, SW France).

The specimens originate from amber piece Arc115. The latter has been defined as litter amber by Perrichot (2004) because of its shape and fossiliferous content. The piece was initially 4 × 3 × 2 cm and had 'flattened and foliated lens-shaped structures that show a gradient of transparency ranging from a highly opaque brown side, whose surface is pockmarked by numerous pressure marks of sandstone grains, to a much more translucent yellow side, whose surface is smoother' (Perrichot 2004, p. 11). Analysis of the arthropod fauna and microfossil assemblage within the piece indicated that Arc115 was a resin flow that spread onto the forest floor soil. The piece has been divided into 39 fragments to investigate the different fossil inclusions (preparation after Perrichot 2004). To avoid contamination, the samples have been disinfected using the protocol described by Girard *et al.* (2009*b*).

The amber fragments were studied under a Nikon Eclipse TS100 microscope at the Soil Ecology Lab (Dalhousie University), on which interference contrast is available. The type material is housed in the amber collection of the Department of Geosciences of the University Rennes 1 (France) under the collection numbers IGR.ARC-115.12c and IGR.ARC-115.6. Requests for examination of the material should be addressed to Vincent Perrichot (vincent.perrichot@univ-rennes1.fr).

The classification scheme in Adl *et al.* (2005) was followed. Single dots (•) indicate the super-groups, double dots (••) correspond to first ranks, triple dots (•••) are second ranks, and so on.

SYSTEMATIC PALAEONTOLOGY

• RHIZARIA Cavalier-Smith, 2002
•• INCERTAE SEDIS *in* Adl *et al.*, 2005
Family HEMIARCHERELLIDAE fam. nov.

Derivation of name. Hemi for half and *Archerella* Loeblich and Tappan 1961 for the name of the morphologically closest genus of amoebae.

Type genus. Hemiarcherella gen. nov.

Geographical and stratigraphical range. Late Albian amber of south-western France.

Diagnosis. Amoebae with test morphologically similar to those of the family Amphitremidae. They differ from the Amphitremidae in that they have only one pseudostome. The shell is organic and translucent. The test is elliptical and compressed laterally. No external mineral particles are attached to the test. The unique aperture does not have a collar. The specimens have a row of many long and unbranched filopodia that emerge from the unique pseudostome.

Genus HEMIARCHERELLA gen. nov.

Derivation of name. Hemi for half and *Archerella* for the name of the morphologically closest genus of amoebae.

Type species. Hemiarcherella christellae sp. nov.

Geographical and stratigraphical range. Late Albian amber of south-western France.

Diagnosis. As for the family.

Hemiarcherella christellae sp. nov.
Figure 2

Derivation of name. The species epithet is dedicated to my ex-wife Christelle.

Holotype. IGR.ARC-115.12c (Fig. 2A), quarry of Archingeay/les-Nouillers (Charente-Maritime, France), Late Albian (subunit A1 in the local stratigraphy): well-preserved specimen with shell and filopodia.

Paratype. IGR.ARC-115.6, quarry of Archingeay/les-Nouillers (Charente-Maritime, France), Late Albian (subunit A1 in the local stratigraphy): specimen preserved in debris, shell visible with difficulty, but row of filopodia observable.

Diagnosis. As for the family.

Description. The specimens are preserved within organic debris in amber piece Arc115. They have a translucent shell that is laterally compressed (Fig. 2A, B). The shells do not exhibit any pore or xenosome. They have a length of *c.* 55 μm and a width of *c.* 17 μm. The pseudostome is nearly central and circular and has a diameter of about 9.6 μm. The filopodia are organised in a row around the pseudostome. The holotype (Fig. 2A, B) has 13 visible filopodia (others may be hidden in debris), while the paratype (Fig. 2C) has 17. They have a length between 100 and 110 μm, and their maximum diameter is about 1 μm close to the pseudostome. No photosynthetic endosymbionts are preserved in the specimens.

Discussion. The specimens have been placed in a new family because of the shape and aspect of the shell, its ornamentation and by the presence of a single pseudostome. The description of a new family is due to the fact that the closest modern family, the Amphitremidae, is characterised by the presence of two pseudostomes. If a certain morphological variability exists into modern amoebae (specimens with two apertures while the species should have only one and vice versa), this phenomenon cannot be demonstrated for fossil specimens. Because of their unique pseudostome, the specimens are thus placed in a new family deferring for the modern Amphitremidae

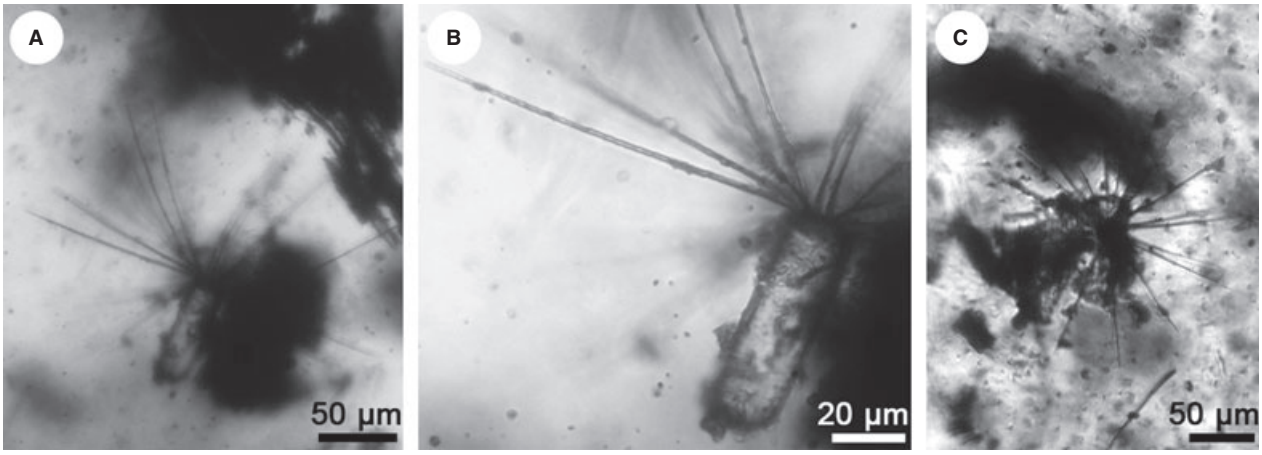

FIG. 2. *Hemiarcherella christellae* sp. nov. from Albian amber of France. A, holotype. B, detailed view of the shell of the holotype. C, aperture view of the paratype.

by the presence of only one pseudostome. The fossil specimens are morphologically similar to the genus *Archerella* (Amphitremidae) because they have a rigid and thick test with parallel sides and rounded ends (Lee *et al.* 2000). However, in contrast to the genus *Archerella*, the fossil specimens have only one pseudostome. *Archerella* and the genera of the family Amphitremidae are characterised by the presence of two pseudostomes, one at each extremity of the test (Lee *et al.* 2000). As for the Amphitremidae, the presence of real filopodia excludes any relation with the Granuloreticulosea (Lee *et al.* 2000).

Their similarities with the genus *Archerella* (Amphitremidae) (elliptical shell with a thick and rigid test with parallel sides and the presence of filopodia) and their specific character (one pseudostome) allow the creation of a new family of testate amoebae, the Hemiarcherellidae. The name is not meant to support any affinities with the genus *Archerella* and the Amphitremidae and merely reflects certain morphological similarities between these two families. The specimens are placed in the new genus *Hemiarcherella* to reflect their similarities to the genus *Archerella* within the Amphitremidae.

DISCUSSION

Palaeoecology

The two specimens described here were found in an amber piece labelled Arc115. Perrichot (2004) described this piece as litter amber because of its specific shape and fossil content. About 80 arthropods and several hundred microfossils have been found in the piece (Perrichot and Girard 2009). Most of these fossils belong to soil organisms such as schizopterid bugs (Perrichot *et al.* 2007), a mole cricket (Perrichot *et al.* 2002), a tanaupodid mite (Judson and Makol 2009), a carnivorous fungus (Schmidt *et al.* 2008), diverse testate amoebae (Schmidt *et al.* 2010) and other micro-organisms (Girard *et al.* 2009*a*). These syninclusions indicate that *Hemiarcherella christellae* was also a soil-dwelling organism, where it had a role as a consumer. Previous studies showed that the mid-Cretaceous amber forest of south-western France was a complex environment (at least as complex as modern forests) (Adl *et al.* 2011). The soil biocoenosis was organised with bacteria and fungi as primary consumers, feeding on plant debris that decomposed in the forest litter. In this environment, micro-organisms such as ciliates, amoebae and nematodes have been interpreted as consumers of bacteria, fungi and/or microalgae (Adl *et al.* 2011). *H. christellae* was probably an organism from the latter ecological group. A few photosynthetic micro-organisms, such as green algae (Girard 2009; Girard *et al.* 2009*c*) and cyanobacteria (Girard *et al.* 2009*b*), have also been found in amber from south-western France. Their presence has been interpreted as the function of flooding episodes, which allowed the transport of these photosynthetic organisms onto the forest floor (Girard 2009; Girard *et al.* 2009*b*). However, these episodes were quite infrequent, and we can thus conclude that *H. christellae* was not feeding on photosynthetic micro-organisms, or only sporadically. Predators of *H. christellae* were probably mites, juvenile spiders and/or collembolans. As highlighted by Adl *et al.* (2011), these organisms were the most probable predators of micro-invertebrates.

Taphonomy

Preservation of delicate organisms such as amoebae requires ideal taphonomical conditions. Previous studies demonstrated that plant resin allows such a preservation

(Foissner *et al.* 1999; Schmidt *et al.* 2004, 2010). Contrary to all previous examples of amoebae from amber, the specimens described here exhibit well-preserved filopodia. The presence of these structures demonstrates that the preservation of the specimens was not a sudden phenomenon. A rapid contact between the resin and amoebae should cause contraction of the filopodia. The preservation of these structures on the specimens of *H. christellae* tends to indicate that the contact between the resin and the fossils was slow (perhaps very slow). Schmidt and Dilcher (2007) demonstrated that water slows down resin solidification and that inclusions of water drops in the resin flow increase the quality of preservation of the micro-organisms. The preservation of *H. christellae* was different than that of the organisms observed by Schmidt and Dilcher (2007). *H. christellae* was a soil-dwelling organism and not an aquatic organism. However, the soil of the Cenomanian amber forest of SW France was very humid as demonstrated by Girard *et al.* (2009*a*). Girard (2009, 2010) and Girard *et al.* (2009*c*) highlighted that piece IGR.ARC-115, which preserved *H. christellae*, also contains freshwater organisms (specimens of green algae of the genera *Quadrigula* Printz, 1915, *Myrmecia* Printz, 1920 and *Enallax* Pascher, 1943). This indicates that water, or at least humidity, was an important factor that influenced the resin flow and the preservation of the organisms into the piece IGR.ARC-115. This can explain the very good quality of preservation of *H. christellae*. Water, as in the example of Schmidt and Dilcher (2007), could have increased the preservation potential of the resin, and by its effect as a 'retarder' on the resin solidification, it allowed the preservation of fine structures such as the filopodia. Indeed, no rapid contact between the resin and the amoebae occurred. The fossils were probably protected by a fine water film that progressively evaporated during the resin solidification. Thanks to this phenomenon, the amoebae did not retract their filopodia before being engulfed in the dry resin. This fine water film could also explain the relative thickness of the filopodia. Evaporation of the film created a kind of cast around the filopodia and created an impression of greater relative thickness of these structures. In consequence, the diameter of the filopodia is perhaps overestimated.

Stasis in amoebae evolution?

Recently, research on amber microfossils has led to the discovery of amoebae that provide new data on the evolutionary history of terrestrial micro-organisms. Schmidt *et al.* (2006) recorded the presence of Centropyxidae and Difflugiidae in the Carnian amber of Italy. Members of the family Centropyxidae, Hyalosphenidae and Phryganellidae have also been found in Cenomanian amber of Schliersee and of Kansas (Waggoner 1996*a*; Schönborn *et al.* 1999; Schmidt *et al.* 2004). Other testate amoebae have been discovered in the Cretaceous of Spain and Kansas (Martín-González *et al.* 2008), but Schmidt *et al.* (2010) argued that these specimens have a nonmicrobial origin and probably represent pseudoprotists as defined by Girard *et al.* (2011).

Most of the aforementioned fossils have been attributed to extant genera or species. Indeed, the Centropyxidae from Carnian amber have been related to the extant species *Centropyxis hirsuta* Deflandre, 1929. The most abundant and diverse fossil amoebae fauna was found in the Cenomanian amber of Schliersee (Schönborn *et al.* 1999; Schmidt *et al.* 2004). Of the seven taxa of testate amoebae found in this amber, only one has been attributed to a new species (*Hyalosphenia baueri* Schönborn *et al.*, 1999). Such findings have led to the theory that morphological stasis exists in diverse microbial lineages (Martín-González *et al.* 2008, 2009). This apparent stasis can be due to real maintaining of microbial species though long periods or to evolutionary convergence that conducted to the resurgence of some phenotypes.

Amoebae from mid-Cretaceous French amber seem to be one exception to the theory of stasis. Most of the specimens found are not well preserved and have only been tentatively attributed to genera (Girard 2010). Only a few are very well preserved and allow for precise systematic placements, but those that have been definitively assigned are all distinguishable from modern taxa. *Centropyxis perforata* Schmidt, Girard and Schönborn, 2010 and *Leptochlamys galippei* Schmidt, Girard and Schönborn, 2010 have pores on their tests, a characteristic never observed in modern species of the genera *Centropyxis* Stein, 1857 and *Leptochlamys* West, 1901. The specimens described here also have characteristics (such as the unique pseudostome) that place them in a new species, a new genus and even a new family. The amoeba fauna from French amber thus appears atypical compared to the other amber amoeba faunas. Several hypotheses can explain the composition of the amoeba fauna from mid-Cretaceous amber of south-western France. First, chance may have led to the discovery of these new fossil taxa. That is to say, fossil taxa were equally abundant in all deposits, but contingency has played a role in what has been found and described. Second, the mid-Cretaceous amber forest of south-western France was perhaps an area of endemism, allowing for rapid diversification and evolution of species compared to other Cretaceous forests. Third, very few scientists are studying microfossil inclusions, creating a paucity of published data, particularly when compared with the body of knowledge on arthropod inclusions. Additional research on these fossils will probably lead to the discovery of new testate amoebae that will clarify the evolutionary history of these organisms and/or the

uniqueness of the mid-Cretaceous amber of south-western France.

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REFERENCES

ADL, S. M., SIMPSON, A. G. B., FARMER, M. A., ANDERSEN, R. A., ANDERSON, O. R., BARTA, J. R., BOWSER, S. S., BRUGEROLLE, G., FENSOME, R. A., FREDERICQ, S., JAMES, T. Y., KARPOV, S., KUGRENS, P., KRUG, J., LANE, C. E., LEWIS, L. A., LODGE, J., LYNN, D. H., MANN, D. G., MCCOURT, R. M., MENDOZA, L., MOESTRUP, Ø., MOZLEY-STRANDBRIDGE, S. E., NERAD, T. A., SHEARER, C. A., SMIRNOV, A. V., SPIEGEL, F. W. and TAYLOR, M. F. J. R. 2005. The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. *Journal of Eukaryotic Microbiology*, **52**, 399–451.

—— GIRARD, V., BRETON, G., LAK, M., MAHARNING, A., AARON, M., PERRICHOT, V., TRIONNAIRE, M., VULLO, R. and NÉRAUDEAU, D. 2011. 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). *Soil Biology and Biochemistry*, **43**, 726–735.

BASSI, D., FUGAGNOLI, A., POSENATO, R. and SCOTT, D. B. 2008. Testate amoebae from the Early Jurassic of the Western Tethys, North-East Italy. *Palaeontology*, **51**, 1335–1339.

BŒUF, O. and GILBERT, D. 1997. Présence de thécamoebiens du genre *Trinema*, au Pliocène supérieur, découverte à Chilhac (Haute-Loire, France). *Comptes Rendus de l'Académie des Sciences, Paris*, **325**, 623–627.

BOSAK, T., LAHR, D. J. G., PRUSS, S. B., MACDONALD, F. A., DALTON, L. and MATYS, E. 2011. Agglutinated tests in post-Sturtian cap carbonates of Namibia and Mongolia. *Earth and Planetary Sciences Letters*, **308**, 29–40.

BRADLEY, W. H. 1931. Origin and microfossils of the oil shale of the Green River Formation of Colorado and Utah. *United States Geological Survey, Professional Paper*, **168**, 58.

DEJAX, J. and MASURE, E. 2005. Analyse palynologique de l'argile lignitifère à ambre de l'Albien terminal d'Archingeay (Charente-Maritime, France). *Comptes Rendus Palevol*, **4**, 53–65.

FOISSNER, W. and SCHILLER, W. 2001. Stable for 15 million years: scanning electron microscope investigation of Miocene euglyphid thecamoebians from Germany, with description of the new genus Scutiglypha. *European Journal of Protistology*, **37**, 167–180.

—— SCHÖNBORN, W., WRIGHT, A. D. G. and LYNN, D. H. 1999. Further studies on fossilized ciliates (Protozoa, Ciliophora) from Triassic amber. *In* TAJOVSKÝ, K. and PIL, V. (eds). *Soil zoology in Central Europe. Proceedings of the 5th Central European Workshop on Soil Zoology held in České Budějovice, Czech Republic, April 27–30, 1999*. Academy of Sciences of the Czech Republic, České Budějovice, 377 pp.

FRENGUELLI, G. 1933. Tecambiani e Biatomee nel Miocene del Neuquen (Patagonia settentrionale). *Bollettino della Società Geologica Italiana*, **52**, 33–43.

GIRARD, V. 2009. Evidence of Scenedesmaceae (Chlorophyta) from 100 million-year-old amber. *Geodiversitas*, **31**, 145–151.

——2010. Microcénoses des ambres médio-crétacés français. Taphonomie, Systématiques, Paléoécologie et Reconstitution du paléoenvironnement. *Mémoires Géosciences Rennes*, **134**, 1–294.

—— and ADL, S. M. 2011. Amber microfossils: on the validity of species concept. *Comptes Rendus Palevol*, **10**, 189–200.

—— BRETON, G., BRIENT, L. and NÉRAUDEAU, D. 2009*a*. Sheathed prokaryotic filaments, major components of mid Cretaceous French amber microcoenoses. *Journal of Paleolimnology*, **42**, 437–447.

——NÉRAUDEAU, D., BRETON, G., SAINT MARTIN, S. and SAINT MARTIN, J. P. 2009*b*. Contamination of amber samples by recent microorganisms and remediation evidenced by Mid-Cretaceous amber of France. *Geomicrobiology Journal*, **26**, 21–30.

—— SCHMIDT, A. R., STRUWE, S., PERRICHOT, V., BRETON, G. and NÉRAUDEAU, D. 2009*c*. Taphonomy and palaeoecology of mid-Cretaceous amber-preserved microorganisms from south-western France. *Geodiversitas*, **31**, 153–162.

—— NÉRAUDEAU, D., ADL, S. M. and BRETON, G. 2011. Protist-like inclusions in amber, as evidenced by Charentes amber. *European Journal of Protistology*, **47**, 59–66.

JUDSON, M. L. I. and MAKOL, J. 2009. A mite of the family Tanaupodidae (Acari, Parasitengona) from the Lower Cretaceous of France. *Geodiversitas*, **31**, 41–47.

KÖVÁRY, J. 1956. Thékamöbák (Testaceák) a magyarországy alsòpannòniai koru üled ékelböl. *Földtani Közlöny*, **86**, 266–273.

LAHR, D. J. G., WEGENER PARFREY, L., MITCHELL, E. A. D., KATZ, L. A. and LARA, E. 2011. The chastity of amoebae: re-evaluating evidence for sex in amoeboid organisms. *Proceedings of the Royal Society B*, **278**, 2081–2090.

LEE, J. J., LEEDALE, G. F. and BRADBURY, P. 2000. *An illustrated guide to the protozoa. Second edition. Organisms traditionnally referred to as protozoa, or newly discovered groups*, Vol. II. Society of Protozoologists, Lawrence, 743 pp.

MARTÍN-GONZÁLEZ, A., WIERZCHOS, J., GUTIÉRREZ, J. C., ALONSO, J. and ASCASO, C. 2008. Morphological stasis of protists in Lower Cretaceous amber. *Protist*, **159**, 251–257.

——————————2009. Microbial Cretaceous park: biodiversity of microbial fossils entrapped in amber. *Naturwissenschaften*, **96**, 551–564.

MEDIOLI, F. S., SCOTT, D. B., COLLINS, E. S. and MCCARTHY, F. M. G. 1990. Thecamoebians from the early Cretaceous deposits of Ruby Creek, Alberta (Canada). 793–812. *In* HEMLEBEN, C., MAMINSKI, M. A., KUHNT, W. and SCOTT, D. B. (eds). Paleoecology, biostratigraphy, paleopceanography and taxonomy of agglutinated foraminifera. *Proceedings of the NATO Advanced Study Institute, Kluwer, NATO ASI Series C*, **327**, 1–1017.

NÉRAUDEAU, D. and MOREAU, P. 1989. Paléoécologie et paléobiogéographie des faunes d'échinides du Cénomanien nord-aquitain (Charente-Maritime, France). *Geobios*, **22**, 293–324.

—— PERRICHOT, V., DEJAX, J., MASURE, E., NEL, A., PHILIPPE, M., MOREAU, P., GUILLOCHEAU, F. and GUYOT, T. 2002. Un nouveau gisement à ambre insectifère et à végétaux (Albien terminal probable) : Archingeay (Charente-Maritime, France). *Geobios*, **35**, 233–240.

PERRICHOT, V. 2004. Early Cretaceous amber from southwestern France: insight into the Mesozoic litter fauna. *Geologica Acta*, **2**, 9–22.

—— and GIRARD, V. 2009. A unique piece of amber and the complexity of ancient forest ecosystems. *Palaios*, **24**, 137–139.

—— NÉRAUDEAU, D., AZAR, D., MENIER, J. J. and NEL, A. 2002. A new genus and species of fossil mole cricket in the Lower Cretaceous amber of Charente-Maritme, SW France (Insecta: Orthoptera: Gryllotalpidae). *Cretaceous Research*, **23**, 307–314.

—— NEL, A. and NÉRAUDEAU, D. 2007. Schizopterid bugs (Insecta : Heteroptera) in Mid-Cretaceous ambers from France and Myanmar (Burma). *Palaeontology*, **50**, 1367–1374.

POINAR, G. O. J., WAGGONER, B. M. and BAUER, U. 1993. Description and paleoecology of a Triassic amoeba. *Naturwissenschaften*, **80**, 566–568.

PORTER, S. M. and KNOLL, A. H. 2000. Testate amoebae in the Neoproterozoic era: evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon. *Paleobiology*, **26**, 360–385.

—— MEISTERFELD, R. and KNOLL, A. H. 2003. Vase-shaped microfossils from the Neoproterozoic Chuar Group, Grand Canyon: a classification guided by modern testate amoebae. *Journal of Paleontology*, **77**, 409–429.

SCHILLER, W. 1998. Kieselige mokrofossilien aus dem Unter-Oligozän von Sieblos/Rhön. *Geologische Abhandlungen Hessen*, **104**, 173–199.

SCHMIDT, A. R. and DILCHER, D. J. 2007. Aquatic organisms as amber inclusions and examples from a modern swamp forest. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 16581–16585.

—— SCHÖNBORN, W. and SCHÄFER, U. 2004. Diverse fossil amoebae in German Mesozoic amber. *Palaeontology*, **47**, 185–197.

—— RAGAZZI, E., COPPELLOTTI, O. and ROGHI, G. 2006. A microworld in Triassic amber. *Nature*, **444**, 835.

——DÖRFELT, H. and PERRICHOT, V. 2008. *Palaeoanellus dimorphus* gen. et sp. nov. (Deuteromycotina): a Cretaceous predatory fungus. *American Journal of Botany*, **95**, 1328–1334.

—— GIRARD, V., PERRICHOT, V. and SCHÖNBORN, W. 2010. Testate amoebae from a Cretaceous forest floor of France. *Journal of Eukaryotic Microbiology*, **57**, 245–249.

SCHÖNBORN, W., DÖRFELT, H., FOISSNER, W., KRIENITZ, L. and SCHÄFER, U. 1999. A fossilized microcoenosis in Triassic amber. *Journal of Eukaryotic Microbiology*, **46**, 571–584.

THIBAUDEAU, S. A., MEDIOLI, F. S. and SCOTT, D. B. 1987. Carboniferous marginal-marine rhizopods, a morphological comparison with recent correspondents. Abstract, GSA Annual Meeting, Phoenix, 866 pp.

VAN HENGSTUM, P. J., REINHARDT, E. G., MEDIOLI, F. S. and GRÖCKE, D. R. 2007. Exceptionally preserved Late Albian (Cretaceous) Arcellaceans (Thecamoebians) from the Dakota Formation Near Lincoln, Nebraska, USA. *Journal of Foraminiferal Research*, **37**, 300–308.

VASICEK, M. and RUZICKA, B. 1957. Namurian Tech-amoebina from the Ostraxa-Karxina coal district. *Sbornik Naradniho Museav Praze, Rada B, Prirodni Vedy Acta Musei Nationalis Pragae, Series B*, **13**, 333–340.

WAGGONER, B. M. 1996*a*. Bacteria and protists from Middle Cretaceous amber of Ellsworth County, Kansas. *Paleobios*, **17**, 20–26.

—— 1996*b*. The first fossil cyphoderiid testate amoeba in Dominican Republic amber (Eocene–Oligocene). *Paleobios*, **17**, 17–19.

WIGHTMAN, W. G., SCOTT, D. S., MEDIOLI, F. S. and GIBLING, M. R. 1994. Agglutinated foraminifera and thecamoebians from the late Carboniferous Sydney coalfield, Nova Scotia: paleoecology, paleoenvironments and paleogeographical implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **106**, 187–202.

WOLF, M. 1995. Verkieste amöben in steinkohlen aus dem Ruhrgebiet–erster Nachweis von Arcella Ehrenberg im Paläozoikuma. *Paläontologische Zeitschrift*, **69**, 1–6.