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Blowin' in the wind… 100 Ma old multi-staged dinoflagellate with sexual fusion trapped in amber: Marine–freshwater transition

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ABSTRACT

Here we report the unexpected discovery of multi-staged dinoflagellates with organic cellular contents from a paralic habitat trapped in 100 million year (100 Ma) old amber. Amber formed from resin, a fluid medium, that trapped, then remarkably embedded and preserved soft parts of organisms usually destroyed by fossilization processes. We assume that the marine-costal dinoflagellates reached the sticky resin carried away by the wind, inside spray droplets. We answer to a fundamental question dealing with the Peridiniaceae: the paratabulation of Cretaceous cysts reflects the tabulation of Cretaceous thecae. We provide the first life cycle of the fossil record with evidence of cellulosic thecae, sexual fusion and zygote. We highlight an ancestral behaviour for the sexual phase: naked gametes complete fusion outside of gametic thecae, a process known in rare extant *Peridinium* species. The new taxon, *Succiniperidinium inopinatum* gen. et sp. nov., belongs to the Peridiniaceae and shares characters with extant marine-brackish *Scrippsiella* and two freshwater *Peridinium* clades identified by morphological characters (tabulation, cingular plates, ecdysis, plasmogamy) and molecular phylogenies. Understanding the processes of marine–freshwater transition in microbial lineages is a central goal in evolutionary ecology. Marine dinoflagellates passed through the osmotic barrier and the studies of marine-costal Cretaceous species help to understand the adaptation and the diversification of these species. We discuss the migration according to biological, paleontological and molecular phylogenies data and suggest that the freshwater colonization was the result of Cretaceous species adapted to costal habitats; their lineage isolated in ponds following the Cenozoic global sea-level fall passed through the osmotic barrier. A *Scrippsiella*-like group (i.e. *Subtilisphaera terrula, Palaeoperidinium cretaceum* and *Succiniperidinium inopinatum* gen. et sp. nov.) is suggested as intermediate species in the *Peridinium* freshwater colonization line.

1. Introduction

Extant dinoflagellates inhabit a large variety of environments (*i.e.* open sea, coastal domains, estuaries, rivers and lakes) which cover an extreme range of temperature, salinity and water chemistry and blooms may occur along their life cycle (Rodriguez et al., 1999; Leitao et al., 2001; Gribble et al., 2009). Observations on the tabulation of thecae and the paratabulation of cysts of extant Peridiniales have contributed to a better understanding of the nature of fossil dinoflagellates. The closest morphological resemblance (tabulation) of extant freshwater Peridiniaceae is with marine Mesozoic and Cenozoic representatives. The main difference between the marine extant species (Congruentidiaceae) and marine fossilized representatives, involves the cingular tabulation. Fensome et al. (1993, p. 208) hypothesized that the extant marine Congruentidiaceae evolved from the marine Peridiniaceae, perhaps during the latest Cretaceous.

Fossilized organic dinoflagellates recorded in sediments were up to now exclusively resistant dinosporin resting cysts (Fensome et al., 1993) named dinosporin-walled dinoflagellate cysts. The dinosporin is a complex biomacromolecular substance composed of phenolic, alcoholic and/or carboxylic hydroxides, fatty acids (C14–C16) with tocopherols and sterols (mostly cholesterol and dinosterol) (Kokinos et al., 1998; Versteegh et al., 2012). Resistant to diagenetic processes in environments with low pH, cysts are well preserved in sedimentary environments while siliceous and carbonaceous planktonic organisms are affected by dissolution.

Dinoflagellates play a key role in the evolution of microbial lineages because they are one of the few marine unicellular organisms that invaded freshwater habitats. Extant freshwater dinoflagellates belong to genera *Ceratium, Gymnodinium*, *Peridiniopsis* and mainly *Peridinium*. Along their evolution they are with diatoms, the only marine planktonic organisms which passed through the osmotic barrier. Phycologists,

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molecular biologists and paleontologists provide independent data estimating the marine-freshwater transition process.

The present study investigates dinoflagellates in 100 Ma old amber collected from a paralic black clay layer. The amber constitutes an exceptional medium to preserve soft parts of organisms. Complete dinoflagellates and half specimens show a very distinctive peridiniacean outline which was not observed among Cretaceous cysts. These dinoflagellates with cellular content are preserved as organic matter and cellulosic planktonic stages are suspected. Thanks to the exceptional preservation in amber, taphonomy and cellulosic multi-stages of Cretaceous species can be studied, allowing to precise the stability or instability of the tabulation of Cretaceous thecae and the behaviour of asexual and sexual phases of the life cycle. Furthermore, we discuss the present knowledge about marine–freshwater transitions and propose a new insight about how this may have happened.

2. Material and method

2.1. Material

Our amber samples were collected from a quarry located in Charente-Maritime department, SW France (Fig. 1). The region has been well known for a long time, related with the black clay and lignite amber-bearing layers (d'Archiac, 1837; Manès, 1853; Coquand, 1856; Arnaud, 1877; Crié, 1890). The Archingeay-Les Nouillers quarry is located on the northern margin of the Aquitaine basin, where Cenomanian sediments are widely spread over both Rochefort-Saintes and Jonzac synclines. The Cenomanian has been divided into seven units (A–G) (Moreau, 1978; Moreau, 1993; Néraudeau et al., 1997). Our material comes from the lower unit A, described in detail (Néraudeau et al., 2002); unit A, lying in slight unconformity over Late Jurassic sediments, is a transgressive whole which is composed of marl and sand of continental to lagoonal origin (paralic habitat), dated to the Lowermost Cenomanian (Meunier et al., 1999; Moreau, 1977, 1978, 1993; Néraudeau et al., 1997). Black clay layer embedding amber, the A1sl2 layer of sub-unit A1, was attributed to the Late Albian by palynological analysis (Néraudeau et al., 2002; Dejax and Masure, 2005). Amber of the same level yields arthropods and a variety of freshwater and marine microfossils (diatoms, a foraminifer, radiolarians, crustaceans, testate amoebas and sponge spicules) studied previously, transported by wind, spray or high tide onto the resin flow (Perrichot, 2005; Girard et al., 2008, 2009b, 2009c; Struwe, 2008).

2.2. Methods

Four very small (Table 1) pieces of translucent yellow amber were prepared from the same larger amber sample [ARC 76, Muséum national d'Histoire naturelle, Paris (MNHN)]. Three pieces from ARC 76 were sawed and polished to obtain a clean and plane surface, then mounted on two standard slides, embedded with Canada balsam inside a round cell sealed with a cover-slip; two pieces (# 1 and # 2) are located on slide # 40092, the third piece (# 3) is on slide # 40093. Another amber sample [ARC 130, MNHN] (Table 1) from the same A1sl2 layer has also been sawed and polished, located on slide # 40095. These four pieces have been studied under a light microscope (Nikon Eclipse 80i with differential interference contrast objectives) and piece # 1 has also been observed under a digital microscope (Keyence VHX-600). We encountered more than sixty isolated dinoflagellate specimens in the three pieces of the amber sample ARC 76 and more than a hundred inside the amber sample ARC 130, which were studied under the light microscope; the location of all figured specimens are given in Table 2 after the "England Finder" reference slide. Successive foci of sexual reproduction were photographed and a single combined view is provided using CS 4 Photoshop software; sexual reproduction 3-D modeling was performed using 2.60 Blender software. The last piece of the amber sample ARC 76 (# 4), which is located on

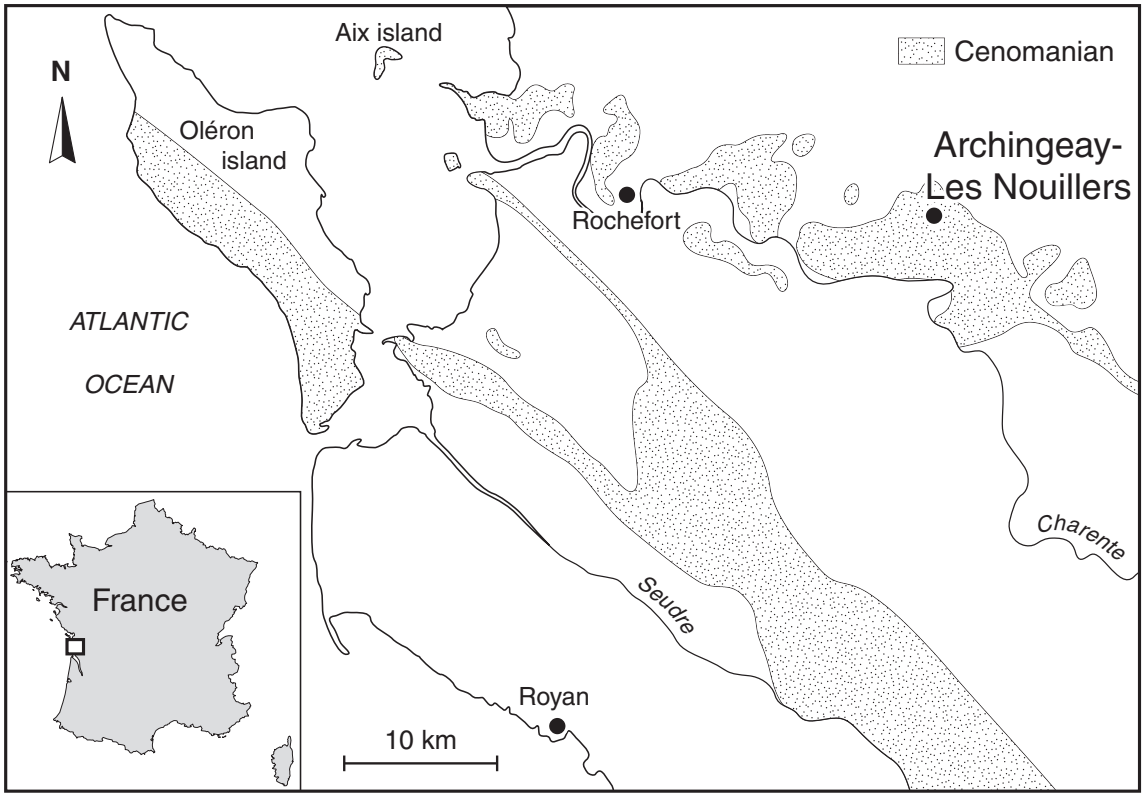

Fig. 1. Geological map and geographical location of the Archingeay–Les Nouillers quarry.