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Research paper

Woody or not woody? Evidence for early angiosperm habit from the Early Cretaceous fossil wood record of Europe

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Abstract

The important question of early angiosperm growth habit (i.e., trees, shrubs or herbs?) remains unanswered. Various theories have been based on data from both living and fossil plants. The Early Cretaceous fossil wood record, however, was seldom used to investigate early angiosperm habit. We set up a database for the Early Cretaceous and Cenomanian of Europe, as this area has the most complete and stratigraphically well-constrained record. The database has 170 entries, based on a bibliographical survey and on the examination of more than 600 new fossil wood specimens from a wide range of palaeoenvironments. In our record the woody characteristic in angiosperms appeared during the Albian, whereas most of the angiosperm's early evolution took place earlier, during the earliest Cretaceous. From the European fossil wood record for the Early Cretaceous and Cenomanian, the global extension and dominance of angiosperms in the Cenomanian is concomitant with a sharp increase in heteroxylous wood diversity. It appears that small stature and weak wood limited the angiosperm ecological radiation for some time.

Keywords: Fossil wood; Cretaceous; Palaeobotany; Angiosperms; Evolution

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1. Introduction

The origin of angiosperms, as well as the causes of their subsequent success, is still a great mystery (Frohlich and Chase, 2007). Growth habit is a major factor in plant ecology and thus important in understanding angiosperm evolutionary success (Wing and Boucher, 1998). However, the growth habit of early angiosperms has been extensively discussed (Mabberley, 1984; Taylor and Taylor, 1993; Sun and Dilcher, 2002). Botanists have used both extant and fossil plant records to solve this part of Darwin's abominable mystery.

For a long time, neobotanists considered early angiosperms to be trees (Arber and Parkin, 1907; Thorne, 1992). Molecular phylogeny, however, indicates that basal habits are shrubs, and small trees and vines (APG, 2003; Feild et al., 2004). Recently, small aquatic annual plants were also found to occur early in the evolution of angiosperms from studies of both modern plants (Saarela et al., 2007) and fossil remains (Sun and Dilcher, 2002; Sun et al., 2002; Martín-Closas et al., 2007).

Turning to the fossil record, various lines of evidence have been used, such as flowers, fruits, leaves, pollen grains and wood (see review by Willis and McElwain, 2002; Friis et al., 2006) as well as geochemistry (Moldowan et al., 1994). Unfortunately, fossil plants are rarely preserved complete and almost exclusively isolated parts are known from the Cretaceous. As a whole, the potential of fossil wood has been underestimated up to now (Herendeen et al., 1999).

Because of the lack of fossil evidence, most current hypotheses on Early Cretaceous angiosperm growth habit were based on uniformitarism double hypothesis, i.e., deduced from the usual habit of the modern taxon that was supposed to be the nearest living relative (or equivalent) of the fossil suggested from living plants (Feild et al., 2004). This uniformitarism is absolutely unsatisfactory, as it becomes increasingly clear that early angiosperms were quite ecophysiologically and morpho-anatomically different from their modern relatives (Leroy, 1983; Mabberley, 1984; Dilcher, 2000).

Modern trees with woody axes dominate plant biomass, with wood making up to 90% of the total weight (Rollet, 1968). Thus, if early angiosperms were trees, they should have introduced some wood into the taphonomical processes, or in other words, the fossil record should have preserved angiosperm wood, provided that angiosperms were not too rare or not growing too far from deposition centres. In turn, wood features can be interpreted as indicators of original plant habit (Wheeler and Baas, 1991, 1993).

To optimize the probability of detecting the first angiosperm wood, large-scale scanning of Early Cretaceous fossil plant assemblages must be performed. Translucent permineralized material which can be examined under light microscope with thin sections as palaeoxylologists usually do, is relatively rare for this time interval and limited to few palaeoenvironmental settings. Lignite, fusinite and opaque material is much more common. Now that the scanning electron microscope (SEM) and cellulose acetate casts (CAC) are used in routine investigations (Philippe, 1995), these types of material provide a more reliable picture of the palaeofloras than that drawn from mineralized wood (Philippe, 1995; Herendeen et al., 1999). As shown in Figs. 1 and 2 under SEM, angiosperm wood is easily recognized by the co-occurrence of vessels and type of pitting even if the preservation is not good enough for systematic assignment.

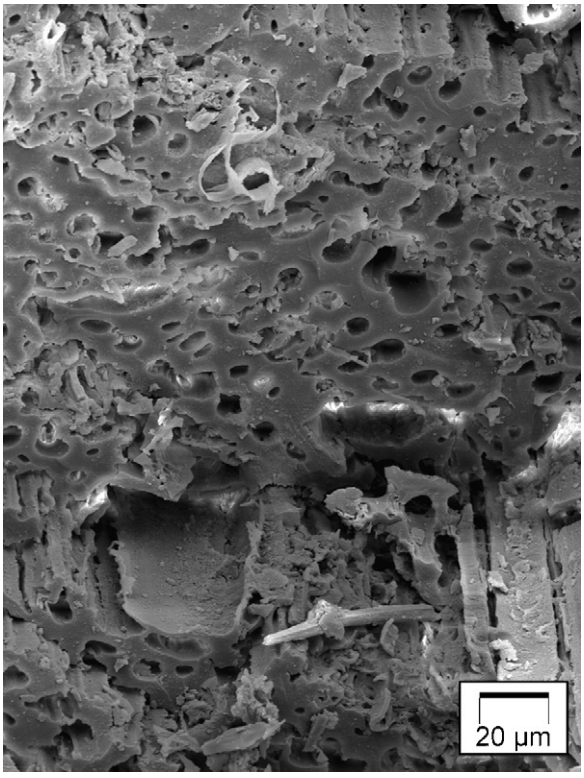

Fig. 1. Semi-transversal view in SEM of an angiosperm wood, Cenomanian of Gard (France).

SEM and CAC results are herein used for the first time for an extensive survey of an Early Cretaceous wood record in order to determine patterns associated with the beginning of the angiosperm woody habit. We focused on the European record between the Berriasian (earliest Cretaceous) and the Cenomanian (earliest Late Cretaceous). This choice is explained below, after a short synthesis of European angiosperm record for the Early Cretaceous.

2. Evidence of Early Angiosperms in Europe

Early angiosperms have been found at various localities in Europe. Small, dispersed, inaperturate to monoaperturate, columellate-reticulate pollen grains from the Valanginian–Hauterivian were found in southern England (Hughes and McDougall, 1987; Hughes, 1994). Very well-preserved fossil floras with stamens, flowers, fruits and seeds were described from the Aptian or Albian of Portugal (e.g., Friis et al., 2001, 2004, 2006; Heimhofer et al., 2005, 2007), some of these early European angiosperms being non-self-supporting aquatic plants. Some researchers pointed out the existence of dicotyledonous angiosperm leaf megaremains from the Albian of Europe (e.g., Saporta, 1894; Teixeira, 1948; Venzo, 1951; Alvarez-Ramiz and Lorenzo, 1979; Gomez et al., 2004; Sender et al., 2005). Published angiosperm fossil wood data are scarce for