

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.

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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 uniformitarianism 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 uniformitarianism 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 palaeoecologists 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 miner-

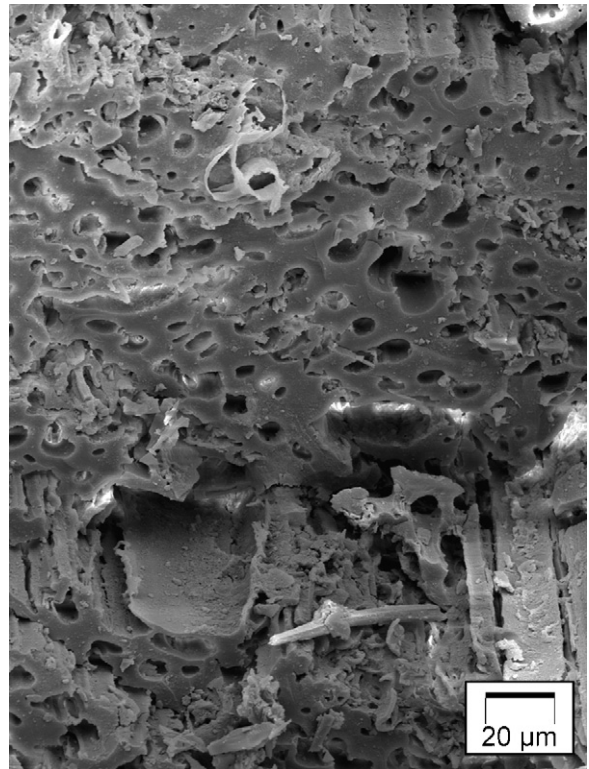


Fig. 1. Semi-transversal view in SEM of an angiosperm wood, Cenomanian of Gard (France).

alized 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.

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 megaremainings 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

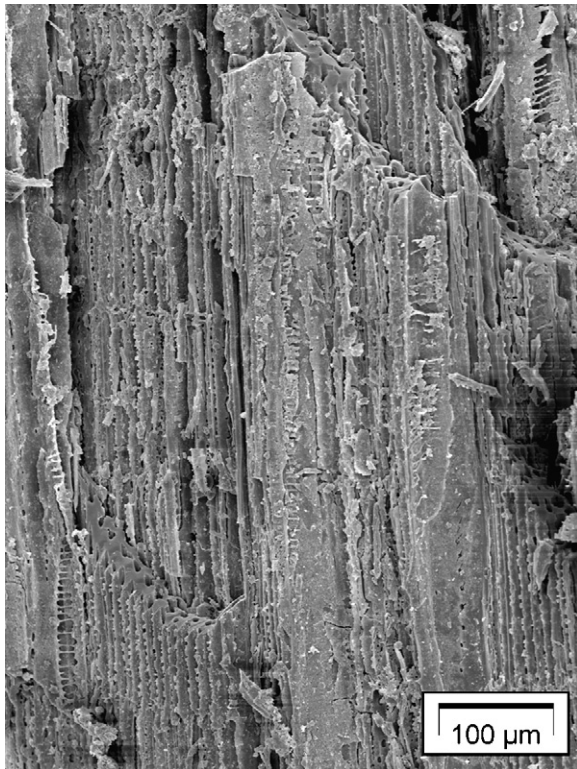


Fig. 2. Radial view in SEM of an angiosperm wood, Cenomanian of Gard (France).

the Early Cretaceous of Europe (Philippe et al., 2006). The older angiosperm wood specimens in Europe, of uncertain systematic position, were reported from the Albian (latest Early Cretaceous) in Hungary (Barale et al., 2002) and in the United Kingdom (Crawley, 2001). In Europe, angiosperm wood is exceedingly rare when compared to gymnosperm wood until the Cenomanian (Herendeen, 1991). Even during the Cenomanian, there is a sharp discordance of the angiosperm fossil records between woods and other remains (Falcon-Lang et al., 2001). Depending on the taxon, dicotyledonous wood is more or less resistant to decay than is that of the gymnosperms (Barghoorn and Spackman, 1950). Taphonomical biases can be, however, probably ruled out because, at almost all the localities bearing angiosperm leaves, araucaria-like wood co-occurs, which is usually not resistant to taphonomic processes (personal observation in Central Chile and Queensland).

3. A database to investigate the Berriasian–Cenomanian fossil wood record of Europe

To explore the question of the growth habit of Early Cretaceous angiosperms, we carried out an overview of the European fossil wood record over the interval of Berriasian–Cenomanian (i.e., the whole Early Cretaceous period plus the first stage of the Late Cretaceous). The time interval is chosen to encompass previously known palynological (e.g., Hughes, 1994) and palaeobotanical (e.g., Friis et al., 2001; Sun et al., 2002) first occurrences of early angiosperms, and as floras changed drastically after the Cenomanian (Doyle and Hickey, 1976; Retallack

and Dilcher, 1986; Crane and Lidgard, 1989; Brenner, 1996; Taylor and Hickey, 1996).

Europe is particularly suitable for such investigations as Lower and lowest Upper Cretaceous deposits are well developed, and their stratigraphy is usually well known. These deposits quite frequently yield plant remains, in a wide range of sedimentary contexts, which allows us to minimize taphonomic biases. European Arctic (Svalbard, Koenig's Karl Land) was not considered as the data from literature are not stratigraphically accurate (Philippe, 1995). For historical reasons the European palaeobotanical record for the Early Cretaceous is probably the most complete in the world.

Because fossil wood accumulations often show a low taxonomic diversity, we focused on generic diversity in fossil assemblages, disregarding the amount of samples relative to each datum.

The database (Appendix A) was compiled from a literature survey and personal identification data (either from museum collections or new field collections). Museum collections were investigated in Stockholm (Natur Historika Riksmuseet), Berlin (Museum für Naturkunde, Humboldt Universität), Copenhagen (Geologisk Museum), St.-Petersburg (Komarov Institute), Paris (Muséum national d'Histoire naturelle) and Lyon (Collections de Paléontologie de l'Université Claude Bernard).

To avoid taxonomic biases, we only dealt with the generic level. Several new data for Cenomanian angiosperm wood are with a question mark in Appendix A because they were obtained from charcoal, which often does not show all necessary characters for assigning fossil angiosperm wood to a morphogenus.

Each datum consists of the occurrence of one morphogenus at one locality, regardless of the number of specimens studied at each site. We studied an estimated number of about 620 new specimens, originating from about 120 localities, which is about 250% of the number of the specimens reported previously in the literature. Our database includes 185 data, of which 68 are new, increasing by 58% over the previously published record. All the referred new material is in MP's collection (Laboratoire de Paléobotanique de l'Université de Lyon), in the collections of the Réserve Géologique de Digne, or in JS's collection (Department of Geology and Palaeontology of Bratislava University).

Samples were studied with various methods, such as classical thin sectioning, SEM and cellulose acetate microcasting, and SEM and CAC accounting for 91% of new data.

4. Results

Fig. 3 summarizes Appendix A data of fossil wood record in the Berriasian–Cenomanian interval. Stratigraphically uncertain data were not considered for the construction of Fig. 3.

Data are unevenly distributed, with the record for Berriasian–Barremian being scarce. Even for these two stages, at least three (and up to 8) assemblages were considered, which were rich enough to allow collection of well-preserved woody fragments and were geographically distant. At least 30 specimens have been identified for each stage of the Berriasian–Cenomanian interval.

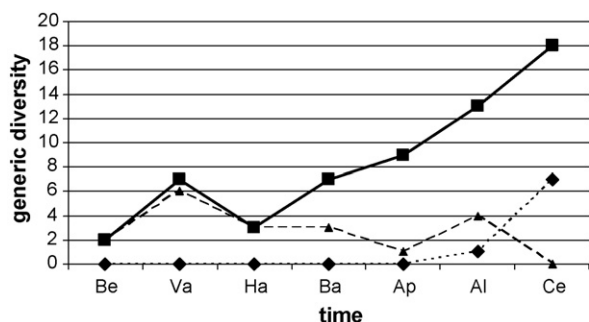


Fig. 3. Berriasian–Cenomanian fossil wood record in Europe: solid line and squares, total generic diversity; dashed line and triangles, number of new gymnosperm genera (i.e., not represented earlier in the record); dotted line and diamonds, number of new angiosperm wood genera.

Because of uneven data distribution, it seems logical to use relative diversity (i.e., number of genera/number of data) in order to get a more reliable assessment of wood generic diversity. As the number of data per stage is highly variable, we did not do so, however, assuming that it would have induced more biases than the assumption that sufficient specimens were analysed in each geological stage. In contrast, we preferred to analyse simultaneously (Fig. 3) a generic diversity curve (i.e., the number of morphogenera represented for each stage) and an “innovation” curve (i.e., the number of morphogenera with first occurrence in the same stage). The taphonomical bias, which is inherent to any fossil record, was limited here by the fact that analysed wood assemblages were collected from various settings (e.g., lacustrine, fluvial, deltaic, marine) for about all stages.

Understandably, generic diversity rose from the Berriasian to the Valanginian (starting-point edge effect). Hauterivian generic diversity was low (three genera only). This is probably an effect of the small number of assemblages studied, as for the Barremian generic diversity reached seven genera again. The genera occurred during Berriasian–Barremian interval are the same as those during the Late Jurassic. The “innovation” curve only records the completeness of the database, and it is thus risky to interpret variations in systematic composition. In most assemblages, *Agathoxylon* was dominant, especially in the southern part of Europe.

From the Barremian to the Aptian, generic diversity did not change significantly, but a new genus was recorded, *Chamaecyparixylon* Chudajberdyev, which is unknown in the Jurassic and supposedly related to modern Cupressaceae *Chamaecyparis* Spach (False Cypress).

From the Aptian to the Cenomanian, generic diversity doubled, rising from 9 to 18. Some gymnosperm genera unrecorded before appeared: *Pityoxylon* Kraus in Schimper and *Pinuxylon* Gothan, both related to Pinaceae (and probably taxonomical synonyms); and *Ginkgoxylon* Saporta, with wood very similar to that of modern *Ginkgo* L. The Aptian–Cenomanian diversity rise was, however, mainly an effect of angiosperm apparition in the fossil wood record.

Angiosperm wood first appeared simultaneously in the Albian of France, Hungary and the United Kingdom (herein; Stopes, 1912; Crawley, 2001; Barale et al., 2002). In each of the corresponding assemblages, angiosperms constituted a minor

component of the wood floras, counting for less than 5% of the specimens. The specimens are generally poorly preserved, only allowing rough identifications. *Aptiana radiata* Stopes is based on well-preserved specimen, but its systematic affinities are dubious (Crawley, 2001; new observations in Stockholm). The safest inference that can be drawn from our record is that angiosperm wood diversity was very low in the Albian.

The picture changed dramatically in the Cenomanian, with at least seven co-occurring morphogenera of dicot wood. Among all assemblages, however, gymnosperm wood was still largely dominant in terms of both number of specimens and size. Just as in the Albian, most Cenomanian wood assemblages are devoid of dicot wood. In the Charentes (south western France), where angiosperms are known to occur, based on pollen and leaf evidence (Doyle et al., 1982; Gomez et al., 2004; Gomez, 2005; Peyrot et al., 2005; Néraudeau et al., 2005), only one dicot wood specimen was found after an intensive screening of more than 350 samples (Perrichot, 2005; new data).

5. Discussion

Like other types of remains, the fossil wood record indicates that the angiosperm ecological explosion lagged behind evolutionary novelty, in other words, angiosperm frequency in ecosystems rose significantly long after the appearance of this taxon.

The dicot wood samples found in the Albian and Cenomanian of Europe are all from axes less than 12 cm in diameter. The largest Albian sample for angiosperm wood, assigned to *A. radiata*, reaches 3.6 cm in diameter, all other samples being under 1 cm (Stopes, 1912; Crawley, 2001; our data). “Large” dicot axes have been mentioned from the Upper Cenomanian of Czech Republic (Falcon-Lang et al., 2001), with a sample assigned to *Icacinoxylon* Shilkina from an axis that could have been 10–12 cm in diameter. Nevertheless, most of the angiosperm material in this locality is from relatively small axes (Falcon-Lang, personal communication), including that related to *Paraphyllanthoxylon* Bailey (J. Kvaček, personal communication). In the USA, in the Cenomanian locality where Bailey’s *Paraphyllanthoxylon* came from, largest logs can reach as much as 60 cm in diameter (E. Wheeler, personal communication).

Our record indicates absence of large angiosperm tree trunks before the Cenomanian. Unfortunately, there are few data about sample sizes in the literature. Such data would be helpful to confirm that angiosperm woody axes were small (<5 cm) in the Albian and only slightly larger (ca. <12 cm) in the Cenomanian.

Sedimentological contexts in which early angiosperm wood occurs are diverse. In the Albian, dicot wood was recorded in three localities (Lábatlan in Hungary, Escragnoles in France, and Kent in the United Kingdom). At all of these places, terrestrial plant material is quite abundant and diverse. It is found in marine sediments that, interestingly, are all glauconitic sandstones deposited in shallow sea with low sedimentation rate and significant input of terrestrial bioclasts. In the Cenomanian, dicot wood occurs again in marine glauconitic sands (as in Normandie, Lignier, 1907), but is more frequently found

Table 1

A summary of early angiosperm fossil wood worldwide record in the Albian–Cenomanian interval

Country	Aptian?–Albian?	Albian	Early Cretaceous	Cenomanian
Japan		<i>Icacinoxylon</i> (8, 9)	<i>Chionanthus</i> (7)	<i>Hamamelidoxylon</i> (9), <i>Icacinoxylon</i> (9), <i>Paraphyllanthoxylon</i> (9), <i>Platinium</i> (9)
Europe	<i>Aptiana</i> (3), dicot wood (2)			<i>Hamamelidoxylon</i> (6), <i>Icacinoxylon</i> (4), <i>Paraphyllanthoxylon</i> (4), <i>Salicinoxylon</i> (6), <i>Paraphyllanthoxylon</i> (3)
USA		<i>Aplectotremas</i> (7), <i>Icacinoxylon</i> (11, 13), <i>Paraphyllanthoxylon</i> (3, 11, 12)		
Africa				<i>Cassinium</i> (5), <i>Sladenioxylon</i> (1)

(1) Giraud et al. (1992); (2) Barale et al. (2002); (3) Crawley (2001); (4) Falcon-Lang et al. (2001); (5) Giraud and Lejal-Nicol (1989); (6) Lignier (1907); (7) Serlin (1982); (8) Spackman (1948); (9) Suzuki (1982); (10) Suzuki et al. (1996); (11) Takahashi and Suzuki (2003); (12) Thayn et al. (1983); (13) Thayn et al. (1985).

in terrestrial settings, like tide-influenced units (Czech Republic, Falcon-Lang et al., 2001), estuarine environment (Charente, France, new data) and coastal freshwater swamps (Gard, France, Ducreux, 1989). These types of terrestrial environments are rarely recorded in Albian sediments of Europe, which could explain, at least partially, the scarcity of Albian angiosperm wood record.

Worldwide, wood record for the Early Cretaceous shows angiosperm fossil wood was recorded in the Albian of Japan, Western USA (Colorado, Maryland, Texas and Utah) and Europe (see Table 1). Similar wood has not yet been found despite an extensive Early Cretaceous fossil wood record in India (Bose et al., 1990), Antarctica (Philippe et al., 1995), Thailand (Philippe et al., 2004), Tunisia (Barale et al., 1998) and Northeast China (Zhang et al., 2000). Our study confirms that angiosperm wood frequency evolved parallel in each area where recorded, appearing in the Albian and then increasing rapidly in the Cenomanian, just as did angiosperm wood anatomical diversity.

What has the woody habit changed regarding angiosperm evolution? A striking feature of Early Cretaceous angiosperm wood is that it usually lacked thick-walled fibres. In most of the specimens we studied, thin-walled cells occupied a large volume. Moreover, in the specimens we observed, vessels were large or small, solitary or in radial multiples, wood cells were relatively thin-walled, and porosity was diffuse. Trees with wood displaying such features were probably highly vulnerable to embolism and not very stiff, but probably capable of rapid growth (Wheeler and Baas, 1991). This fits the view that the first woody angiosperms grew in alluvial plains (Herman, 2002 and references therein; Coiffard et al., 2007) where they colonized disturbed areas and could have been heliophytes (Martín-Closas, 2003; Morley, 2003). Later, when angiosperms became able to build stiff wood, they could eventually colonized new ecosystems. The largest Cenomanian trunks are assigned to *Paraphyllanthoxylon* Bailey, a wood with relatively thick-walled cells possibly related to Lauraceae. Whatever the systematic relationships of this wood type (Martínez-Cabrera et al., 2006), the producing plants experienced a tremendous ecological radiation during the Cenomanian, occurring in several type of terrestrial environment, and may be related to an early successional tree strategy for Lauraceae (Coiffard et al., 2006, in press).

Viewing early angiosperms as small statured and with a wood vulnerable to embolism would also explain why the

angiosperm's rise to dominance was delayed until long after their first appearance(s). Indeed, the mid Early Cretaceous was globally quite dry (Skelton et al., 2003), and a group of plants vulnerable to embolism would have had few possibilities to radiate in such a dry world.

Although reproductive features constitute major innovation in the early angiosperm history (Dilcher, 2000; Frohlich and Chase, 2007), the ability to develop efficient wood was a key point for the evolution of that group (Wheeler and Baas, 1991; Pittermann et al., 2005; Sperry et al., 2006). Whatever the habit of their Jurassic ancestors was, our record shows Early Cretaceous angiosperms were probably small non-woody or weak woody plants. They could have had a functional cambium, but this was probably not very active. It was only when early angiosperms acquired the ability to build thick and stiff trunks, presumably during or after the Albian that they really became significant competitors for conifers, and set roots in forests.

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Appendix A. A database to investigate the Berriasian–Cenomanian fossil wood record of Europe

Age	Identification	Locality	References
Tithonian–Berriasian	<i>Agathoxylon</i> , <i>Protocupressinoxylon</i>	FR, Ile d'Oléron	New data
Tithonian–Berriasian	<i>Taxodioxyton</i>	GB, Portland	New data, Stockholm collections
Tithonian–Berriasian	<i>Agathoxylon</i> , <i>Circoporoxylon</i> , <i>Protocupressinoxylon</i>	GB, Purbeck	Francis (1983)
Berriasian	<i>Circoporoxylon</i>	FR, Sully	Grambast (1953)
Berriasian	<i>Agathoxylon</i>	FR, Wimereux	New data
Berriasian	<i>Agathoxylon</i>	FR, Cherves de Cognac	Philippe in El Albani et al. (2004)
Berriasian	<i>Agathoxylon</i>	GB, Isle of Wight	New data, Stockholm collections
Berriasian–Valanginian	<i>Cupressinoxylon</i>	DK, Bornholm	Philippe et al. (2006)
Berriasian–Hauterivian	<i>Brachyoxylon</i>	PT, Cadriceira	Boureau (1949)
Berriasian–Hauterivian	<i>Cedroxylon</i>	FR, La Risle	Saporta (1880)
Valanginian	<i>Agathoxylon</i>	GB, Isle of Portland	Ward (1896)
Valanginian	<i>Brachyoxylon</i>	HU, Sümeg	Philippe et al. (2006)
Valanginian	<i>Cupressinoxylon</i> , <i>Keteleerioxylon</i> , <i>Phyllocladoxylon</i> , <i>Protocedroxylon</i> , <i>Taxaceoxylon</i>	RU, Kirov	Shilkina (1986, 1989)
Valanginian (Hauterivian?)	<i>Agathoxylon</i>	ES, La Rioja	Barale and Viera (1991)
Early Hauterivian	<i>Protocircoporoxylon</i>	DE, Harzvorland	Vogellehner (1966)
Hauterivian	<i>Cedroxylon</i>	FR, Haute-Marne	Fliche (1900)
Hauterivian	<i>Podocarpoxyton</i>	FR, Martignat	New data
Hauterivian–Barremian	<i>Pinites</i>	GB, Sussex	Seward (1895, 1896)
Hauterivian–Barremian	<i>Agathoxylon</i> , <i>Cupressinoxylon</i> , <i>Protocedroxylon</i>	FR, Féron-Glageon	Carpentier (1927); Lemoigne and Demarcq (1967); Koeniguer in Alvarez-Ramis et al. (1981)
Hauterivian–Barremian	Conifer wood	FR, Forges-les-Eaux	Koeniguer in Alvarez-Ramis et al. (1981)
Hauterivian–Barremian	Conifer wood	FR, St.-Germain-la-Poterie	Koeniguer in Alvarez-Ramis et al. (1981)
Hauterivian–Barremian	Conifer wood	FR, Cuy-St.-Fiacre	Koeniguer in Alvarez-Ramis et al. (1981)
Early Barremian	<i>Agathoxylon</i> , <i>Xenoxylon</i>	ES, Ladrunan	Lemoigne and Marin (1972)
Barremian	<i>Agathoxylon</i>	BU, Oborichte	Philippe et al. (2006)
Barremian	<i>Agathoxylon</i>	PO, Stempiny	Reymanówna (1956)
Barremian	<i>Agathoxylon</i>	FR, Haute-Marne	Fliche (1900)
Mid-Barremian (Aptian?)	<i>Brachyoxylon</i> , <i>Podocarpoxyton</i> , <i>Taxodioxyton</i> , cf. <i>Cupressinoxylon</i>	BE, Hautrage	New data (from T. Gerards, personnel communication)
Mid-Barremian (Aptian?)	<i>Protopodocarpoxyton</i>	BE, Bernissart	New data, Stockholm collections
(Barremian?)–Aptian	<i>Agathoxylon</i> , <i>Protopodocarpoxyton</i>	ES, Cameros	García-Esteban et al. (2006)
Early Aptian	<i>Brachyoxylon</i>	ES, Mas de la Paretta	New data
Mid Aptian	<i>Agathoxylon</i> , <i>Taxodioxyton</i>	FR, Col de Vallouse	New data
Late Aptian	<i>Agathoxylon</i> , <i>Protopodocarpoxyton</i>	HU, Tata	Greguss (1967); Philippe et al. (2006); new data
Aptian	<i>Pityoxylon</i>	FR, Boulogne	Carpentier (1943)
Aptian	<i>Agathoxylon</i>	SK, Benatina	New data
Aptian	Conifer wood	FR, Cap d'Antifer	Koeniguer in Alvarez-Ramis et al. (1981)
Aptian	Conifer wood	FR, Rosans	Barale and Bréhéret (1995)
Aptian	<i>Podocarpoxyton</i>	FR, Haute-Marne	Bertrand (1954)
Aptian	<i>Cupressinoxylon</i>	GB, Wight	Barber (1898)
Aptian	<i>Brachyoxylon</i> , <i>Protopodocarpoxyton</i>	RO, Medgidia	Iamandei (2004)
Aptian	<i>Chamaecyparixylon</i> , <i>Protocupressinoxylon</i>	RO, Tibrinu	Iamandei and Iamandei (1999)
Aptian	<i>Protocupressinoxylon</i> , <i>Protopodocarpoxyton</i>	RO, Cuza Voda	Iamandei (2004)
Aptian	<i>Protocupressinoxylon</i>	RO, Cernavoda	Iamandei and Iamandei (1999); new data
Aptian–Early Albian	Conifer wood	ES, Álava	Suárez Ruiz (2003)
Late Aptian–Albian	<i>Agathoxylon</i> , <i>Brachyoxylon</i> , <i>Cedroxylon</i> , <i>Cupressinoxylon</i>	FR, Normandie	Lignier (1913)
Late Aptian–Albian	<i>Agathoxylon</i>	FR, Moutier-en-Cinglais	Lignier (1913)
Late Aptian–Albian	<i>Agathoxylon</i>	FR, Lisieux	Lignier (1913)
Aptian–Albian	<i>Podocarpoxyton</i>	FR, Sauvage-Magny	Bertrand (1954)

Appendix A (Continued)

Age	Identification	Locality	References
Aptian–Albian	<i>Cupressinoxylon</i>	FR, Louvemont	Bertrand (1954)
Aptian–Albian	<i>Aptiana</i> , <i>Brachyoxylon</i> , <i>Cedroxylon</i> , <i>Cupressinoxylon</i> , <i>Phyllocladoxylon</i> , <i>Pityoxylon</i> , <i>Podocarpoxyton</i> , <i>Protopiceoxyton</i> , <i>Protopodocarpoxyton</i>	GB, diverse Greensands localities	Stopes (1915)
Aptian–Albian	<i>Agathoxyton</i> , <i>Podocarpoxyton</i> , dicotyledon wood	HU, Lábatlan	Greguss (1952); Barale et al. (2002)
Early Albian	<i>Pinuxylon</i> , <i>Cupressinoxylon</i>	FR, Aube	Pons et al. (1993)
Early–Mid Albian	<i>Agathoxyton</i>	ES, Rubielos de Mora	New data
Early–Mid Albian	<i>Agathoxyton</i>	FR, St.-André-de-Rosans	New data
Early–Mid Albian	<i>Agathoxyton</i>	FR, Rosans	New data
Mid Albian	<i>Podocarpoxyton</i>	FR, Chabrières	Cotillon and Lemoigne (1967a)
Mid Albian	<i>Agathoxyton</i>	FR, Escragnolles	Cotillon and Lemoigne (1967b); new data
Mid Albian	<i>Agathoxyton</i>	FR, Hyèges 1	Cotillon and Lemoigne (1971)
Mid Albian	Conifer wood	FR, Andon	Cotillon and Lemoigne (1971)
Mid Albian	Conifer wood	FR, Comps	Cotillon and Lemoigne (1971)
Mid Albian	Conifer wood	FR, Marvillon	Cotillon and Lemoigne (1971)
Mid Albian	Conifer wood	FR, Vergons	Cotillon and Lemoigne (1971)
Mid Albian	<i>Agathoxyton</i>	FR, Logis-du-Pin	New data
Mid Albian	<i>Brachyoxylon</i>	FR, Digne	New data
Mid Albian	<i>Podocarpoxyton</i>	FR, Hyèges 2	New data
Mid Albian	<i>Agathoxyton</i>	FR, Bevons	New data
Mid Albian	Conifer wood	FR, Sisteron	New data
Mid Albian	Conifer wood	FR, Château-Arnoux	New data
Mid–Late Albian	<i>Protopodocarpoxyton</i>	GB, Folkestone	New data, Stockholm collections
Late Albian	<i>Agathoxyton</i>	FR, Blieux	Lemoigne (1967)
Late Albian	<i>Brachyoxylon</i>	FR, St.-Anne-d'Evenos	Machhour and Pons (1992)
Late Albian	<i>Agathoxyton</i> , dicotyledon wood	FR, Escragnolles	New data
Late Albian	Conifer wood	FR, Dives-sur-Mer	New data
Late Albian	<i>Agathoxyton</i>	FR, Salazac	New data
Late Albian	<i>Agathoxyton</i>	FR, Revest-des-brousses	New data
Late Albian	<i>Agathoxyton</i> , <i>Podocarpoxyton</i>	FR, Blieux	New data
Late Albian	<i>Agathoxyton</i> , <i>Brachyoxylon</i> , <i>Podocarpoxyton</i> , <i>Protopodocarpoxyton</i>	FR, Cadeuil	Perrichot (2005)
Late Albian	<i>Agathoxyton</i> , <i>Brachyoxylon</i> , <i>Podocarpoxyton</i> , <i>Protopodocarpoxyton</i>	FR, Les Renardières	Perrichot (2005)
Late Albian	<i>Agathoxyton</i> , <i>Brachyoxylon</i> , <i>Podocarpoxyton</i>	FR, Archingeay	Perrichot (2005)
Late Albian	<i>Agathoxyton</i>	FR, Cap de la Hève	New data
Albian	<i>Brachyoxylon</i> , <i>Taxodioxyton</i>	UK, Kanev	Philippe et al. (2006)
Albian	<i>Cupressinoxylon</i>	ES, Oliete	Lemoigne and Marin (1972)
Albian	<i>Taxodioxyton</i>	FR, Bédouin	New data
Albian	<i>Agathoxyton</i>	FR, Prads	New data
Albian	<i>Agathoxyton</i>	FR, Digne	New data
Albian	<i>Agathoxyton</i> , <i>Podocarpoxyton</i>	FR, Cauville	New data
Albian	<i>Brachyoxylon</i> , <i>Cupressinoxylon</i> , <i>Protocedroxylon</i> , <i>Taxodioxyton</i>	FR, Ardennes	New data, in Nancy collections
Albian	Conifer wood	FR, Cricqueboeuf	Riout (1966)
Albian	Conifer wood	FR, Villerville	Riout (1966)
Albian	Conifer wood	FR, Hennequeville	Riout (1966)
Albian	Conifer wood	FR, Villers-sur-mer	Riout (1966)
Albian	Conifer wood	FR, Houlgate	Riout (1966)
Albian	Conifer wood	FR, Fresville	Riout (1966)
Albian	<i>Pityoxylon</i>	FR, Villers-St.-Barthélémy	Koeniguer in Alvarez-Ramis et al. (1981)
Albian	Conifer wood	FR, St.-Jouin	Koeniguer in Alvarez-Ramis et al. (1981)
Albian	<i>Cupressinoxylon</i> , <i>Protopodocarpoxyton</i> , conifer wood	FR, Cap de la Hève	Lignier (1907); Riout (1966); new data

Appendix A (Continued)

Age	Identification	Locality	References
Albian	<i>Cedroxylon</i>	FR, Gault-de-Bléville	Lignier (1907)
Albian	<i>Protopodocarpoxyton</i>	FR, Bléville	Lignier (1913)
Albian	<i>Agathoxyton, Brachyoxylon, Cupressinoxylon, Piceoxylon, Podocarpoxyton, Tetraclinoxylon, Widdringtonioxylon</i>	FR, Wissant	Desplats (1976a,b, 1978, 1979); new data
Albian	<i>Agathoxyton, Cupressinoxylon, Pityoxylon</i>	FR, Aube	Fliche (1897)
Late Albian–Early Cenomanian	<i>Cupressinoxylon</i>	ES, Seno	Lemoigne and Marin (1972)
Early Cenomanian	<i>Hamamelidoxylon</i>	FR, Vimoutiers	Lignier (1913)
Early Cenomanian	<i>Salicinoxylon</i>	FR, Cap de la Hève	Lignier (1913)
Early Cenomanian	<i>Pityoxylon</i>	FR, Fresville	Lemoigne and Rioult (1971)
Early Cenomanian	<i>Agathoxyton, Protopodocarpoxyton, dicotyledon wood</i>	FR, Puy-Puy	Perrichot (2005); new data
Early Cenomanian	<i>Agathoxyton</i>	FR, Archingey	Perrichot (2005)
Early Cenomanian	<i>Agathoxyton, Brachyoxylon</i>	FR, Ile d'Aix	Koeniguer (1980); Perrichot (2005)
Early Cenomanian	<i>Agathoxyton, Brachyoxylon, Ginkgoxylon, Podocarpoxyton, Protopodocarpoxyton</i>	FR, Fouras	Néraudeau et al. (2003); Perrichot (2005)
Early–Mid Cenomanian	<i>Ginkgoxylon, ?Hamamelidoxylon, ?Icacinoxylon, Podocarpoxyton</i>	FR, St.-Laurent-la-Vernède	New data
Early–Mid Cenomanian	<i>?Hamamelidoxylon, ?Ulmium, ?Icacinoxylon, ?Magnoliaceoxylon, ?Fagoxylon, Podocarpoxyton</i>	FR, St.-André-d'Olérargues	New data
Early–Mid Cenomanian	<i>?Icacinoxylon</i>	FR, Rodières	New data
Early–Mid Cenomanian	<i>?Ulmium</i>	FR, St.-Laurent-de-Carniols	New data
Early–Mid Cenomanian	<i>?Magnoliaceoxylon</i>	FR, le-Pin	New data
Mid Cenomanian	<i>Circoporoxylon</i>	DK, Arnager	New data, Stockholm collections
Mid–Late Cenomanian	<i>?Icacinoxylon, Paraphyllanthoxylon, Pinuxylon</i>	CZ, Pecinov unit 2	Falcon-Lang et al. (2001)
Mid–Late Cenomanian	<i>Cupressinoxylon, Protocupressinoxylon</i>	CZ, Pecinov unit 3	Falcon-Lang et al. (2001)
Mid–Late Cenomanian	<i>Cupressinoxylon, Paraphyllanthoxylon, Protocupressinoxylon</i>	CZ, Pecinov unit 4	Falcon-Lang et al. (2001)
Mid–Late Cenomanian	<i>Cupressinoxylon</i>	CZ, Pecinov unit 5	Falcon-Lang et al. (2001)
Mid Cenomanian	<i>Agathoxyton</i>	FR, Ile Madame	Perrichot (2005)
Mid Cenomanian	<i>Agathoxyton</i>	FR, Cubrières-sur-Cinobre	New data
Mid Cenomanian	<i>Agathoxyton</i>	FR, Fourtou	New data
Mid–Late Cenomanian	<i>Ginkgoxylon</i>	FR, Angers	Pons and Vozenin-Serra (1992)
Late Cenomanian	<i>Podocarpoxyton</i>	FR, Vachères	New data
Late Cenomanian	<i>Agathoxyton, Podocarpoxyton</i>	FR, Ile d'Aix	Crié (1890); Perrichot (2005)
Cenomanian	Conifer wood	FR, St.-Paulet-de-Caisson	Defretin (1943)
Cenomanian	<i>Agathoxyton</i>	FR, Dives	Lignier (1913); new data, Berlin collections
Cenomanian	<i>Protopodocarpoxyton</i>	FR, Montigné	Boureau and Veillet-Bartoszewska (1955)
Cenomanian	<i>Cedroxylon, Cupressinoxylon</i>	FR, Argonne	Fliche (1896)
Cenomanian	<i>Agathoxyton</i>	FR, St.-Georges	New data

Country-codes: BE, Belgium; BG, Bulgaria; CZ, Czech Republic; DE, Germany; DK, Denmark; ES, Spain; FR, France; GB, Great Britain; HU, Hungary; PO, Poland; PT, Portugal; RO, Romania; RU, Russia; SK, Slovakia; UK, Ukraine.

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