Rise to dominance of angiosperm pioneers in European Cretaceous environments

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The majority of environments are dominated by flowering plants today, but it is uncertain how this dominance originated. This increase in angiosperm diversity happened during the Cretaceous period (ca. 145–65 Ma) and led to replacement and often extinction of gymnosperms and ferns. We propose a scenario for the rise to dominance of the angiosperms from the Barremian (ca. 130 Ma) to the Campanian (ca. 84 Ma) based on the European megafossil plant record. These megafossil data demonstrate that angiosperms migrated into new environments in three phases: (i) Barremian (ca. 130–125 Ma) freshwater lake-related wetlands; (ii) Aptian–Albian (ca. 125–100 Ma) understory floodplains (excluding levees and back swamps); and (iii) Cenomanian–Campanian (ca. 100–84 Ma) natural levees, back swamps, and coastal swamps. This scenario allows for the measured evolution of angiosperms in time and space synthesizing changes in the physical environment with concomitant changes in the biological environment. This view of angiosperm radiation in three phases reconciles previous scenarios based on the North American record. The Cretaceous plant record that can be observed in Europe is exceptional in many ways. (i) Angiosperms are well preserved from the Barremian to the Maastrichtian (ca. 65 Ma). (ii) Deposits are well constrained and dated stratigraphically. (iii) They encompass a full range of environments. (iv) European paleobotany provides many detailed studies of Cretaceous floras for analysis. These factors make a robust dataset for the study of angiosperm evolution from the Barremian to the Campanian that can be traced through various ecosystems and related to other plant groups occupying the same niches.

vegetation turnover | early angiosperms | ecology | evolution in time and space

Less than 20 y after the publication of *The Origin of Species*, Charles Darwin wrote to Oswald Heer in a letter dated March 8, 1875: “The sudden appearance of so many Dicotyledons in the Upper Chalk appears to me a perplexing phenomenon” (1, p 539). A few years later, he wrote to Joseph Dalton Hooker in a letter dated July 22, 1879: “The rapid development as far as we can judge of all the higher plants within recent geological times is an abominable mystery” (1, p 378). Darwin was referring to the frequent appearance of leaves of the flowering plants with the beginning of the Late Cretaceous (Cenomanian Stage), as it was known at that time. Since then, paleobotanists have attempted to explain the “sudden” appearance of angiosperms in the fossil record based either on the present percentage and distribution of living primitive taxa in the tropics (2) or on fossils from the middle Cretaceous of North America (3–6). These publications have included many new finds on somewhat older Cretaceous strata. We present here a unique interpretation of the European Cretaceous record of angiosperms in their paleoenvironmental context. Our synthesis demonstrates that early angiosperms were at first successful invaders in only certain environments but expanded into others over an interval of ~45 million y (7). Three phases are clearly recognizable that represent different stages in the success story of flowering plants.

Phase 1: Barremian–Aptian Freshwater Lake-Related Wetlands

Worldwide, Barremian (ca. 130–125 Ma) angiosperm megafossils are very rare, represented by 11 genera, 5 of which apparently lived in freshwater lake/wetland habitats (8–15, *). In an aquatic community, these angiosperms competed with charophytes that dominated macrophytic associations since the Permian (10, 11, 13). In the Barremian of Europe (Figs. 1 and 2A), chloranthoid/*Afropollis* pollen indicate the presence of terrestrial angiosperms (16), although matoniaceous fern thickets and open conifer woodlands in floodplains dominated the terrestrial vegetation. The physiognomy of the megafossil plants from the Barremian (ca. 130 Ma) to the middle Aptian (ca. 118 Ma) is consistent with the fact that during that time Western Europe underwent an arid phase (17, 18). Diversified aquatic angiosperm megafossils (19) and terrestrial chloranthoid, lauralean, and magnolialean fossil pollen (16) appear in the late Aptian (Fig. 2B). This diversification was accompanied by the closure of canopy woodland, with conifers spreading over most environments and the near extinction of matoniaceous ferns (ref. 19; Fig. 2B). In contrast, terrestrial angiosperm leaf megafossils are very rare except for *Quercophyllum* from the Aptian/Albian of Arnal (Portugal) that probably grew along freshwater lakes or pond margins.

Phase 2: Albian Understory Floodplains (Excluding Levees and Back Swamps)

The total taxa count in the vegetation of Europe became very diverse during the Albian (ca. 112–100 Ma). For example in the floodplains, there were ca. 4 angiosperms per 11 taxa in total per locality during the Albian vs. 0 angiosperms per 8 taxa in total during the Barremian and 0 angiosperms per 6 taxa in total during the Aptian. This angiosperm increase coincided with a warming period beginning in the early Albian (20, 21), when angiosperms exhibited widening ecological ranges (Fig. 2C). They continued to dominate the aquatic vegetation (22, 23) but also occurred in significant numbers in the floodplains for the first time (ref. 19; Fig. 2C). From the Barremian, angiosperms competed with Osmundaceae taxa (e.g., *Cladophlebis* Brongniart), which nearly disappeared during the Albian.

In contrast to the small-leaved, highly ramified angiospermous habit, the ferns and gymnosperms, which were replaced by the angiosperms, often showed a large-leaved, monocaulous habit. The small-leaved, ramified habit is more resilient than those with a single apical meristem that may be damaged or lost. If the meristem of a monocaulous plant is destroyed, it may die or recover only very slowly, whereas a ramified plant can use many active meristems that

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Fig. 1. Pie diagrams representing the vegetation changes in Europe from the Barremian to the Santonian. The paleoenvironmental reconstructions correspond to Barremian (A), Aptian (B), Albian (C), Cenomanian (D), and Turonian–Santonian (E). BM, brackish marsh; BR, braided river; EM, estuary mouth; FP, floodplain; FS, freshwater swamp; L, levee; LP, lake/pond.

will allow the plant to recover quickly. In closed forests of the floodplains, angiosperms occupied the understory, and conifers formed the canopy (ref. 19; Fig. 2C). In contrast, matoniaceous fern thickets were exclusive to the open vegetation of floodplains (19). Most floodplain angiosperms belonged to core angiosperms (i.e., Eudicots and Magnoliids; ref. 19). Besides the rare occurrence of floodplain angiosperms before (12, 14, 15, 24), the increase of Eudicots in the Albian could be due to a poleward dispersion driven by global warming. This dispersion is also supported by the poleward dispersion of tricolpate (Eudicot) pollen grains shown by Hickey and Doyle (25) and Lidgard and Crane (26). This poleward dispersion may be related to the poleward shift of the megathermal forest during the Aptian–Albian (27).

Phase 3: Cenomanian–Campanian Levees, Back Swamps, and Coastal Swamps

At the beginning of the Cenomanian (ca. 100 Ma), angiosperms were already widespread in Europe and inhabited most environments, except marine-dominated estuary river mouths (ref. 28; Fig. 2D). In the back swamps, they replaced Cycadales and, to a lesser extent, matoniaceous and dicksoniaceae ferns. In the coastal swamps, they competed with matoniaceous ferns (e.g., *Weichselia* Stiehler) and constitute the earliest record of halophytic angio-

sperms (28, 29). Angiosperms exhibited clear tree habit, especially trees of Lauraceae and Platanaceae, which inhabited disturbed channel margins (Fig. 2D). In such a niche, they may have displaced conifers due to a faster seedling growth rate in agreement with Bond's hypothesis (28, 30, 31). Angiosperm abundance in various Cenomanian environments would have been enhanced by their shorter life cycles compared with those of the gymnosperms.

From the Turonian (ca. 94 Ma), various genera of the Platanaceae spread over more stable floodplain environments, whereas Bennettitales and Dicksoniaceae decreased (ref. 32; Fig. 2E). Palms competed with Cupressaceae (*Taxodium* affinities) in the back swamps (33). The palm seedlings developed large leaf crowns that shaded understory weeds, and conifer seedlings must compete with the weeds. During the later growth stage, palm monocaulous habit represents a lower energetic cost than Cupressaceae

Fig. 2. Vegetation changes in Europe from the Barremian to the Santonian put into an environmental context. The paleoenvironmental reconstructions correspond to Barremian (A), Aptian (B), Albian (C), Cenomanian (D), and Turonian–Santonian (E). The dashed circles indicate the environments/habitats as follows: BM, brackish marsh; BR, braided river; EM, estuary mouth; FP, floodplain; FS, freshwater swamp; L, levee; LP, lake/pond. The red circles and numbers (1–10) indicate the major ecological changes as follows: 1, turnover between ferns and conifers in braided river environments (vegetation closure); 2, diversification of angiosperms in wetland-related habitats; 3, diversification of the vegetation in brackish marsh; 4, oldest record of angiosperms in floodplains; 5–7, oldest record of angiosperms in brackish marsh, levee, and swamp environments; 8, turnover between conifers and angiosperms in braided river environments; 9, increase in platanoid occurrence; and 10, oldest record of woody monocotyledons.

trunks, resulting in either a faster growth or higher allocation to reproduction. Cupressaceae were maintained in cooler areas, whereas palms do poorly in cool and cold temperate climates.

Reconciliation of Previous Scenarios

Several hypotheses based mainly on North American records have been proposed to explain the dispersal and rise to dominance of the angiosperms. In this work, we focus our attention on the dispersal of the angiosperms through time with special reference to when angiosperms came to occupy the niches of particular environments as demonstrated by the Cretaceous sedimentary record preserved in Europe. This view of angiosperm rise to domination during Cretaceous time can be seen in three phases that typify their diversification and occupation of more varied habitats (Fig. 1).

This record is contrasted with the angiosperm record through time and space in North America. The scenario by Doyle and Hickey (3) and Hickey and Doyle (25) proposed that fossil angiosperms from the Aptian–Lower Albian of Potomac Zone I were understory shrubs and grew on levees and in floodplains. These were followed by pinnately compound leafed platanoid trees–shrubs (e.g., *Sapindopsis* Fontaine) during the Upper Albian (Potomac Zone IIB) in the same environments. This change in angiosperm vegetation corresponds to phase 2 of our scenario (Fig. 1C). Platanoids (e.g., *Araliopsoides* Berry) evolved along disturbed channel margins from the Cenomanian of the Potomac Zone III and colonized floodplains from the Cenomanian–Turonian of the Potomac Zone IV. The latter two Zones are in agreement with our phase 3 (Fig. 2D). Doyle and Hickey (3) and Hickey and Doyle (25) hypothesized that early angiosperms were riparian weeds before the Aptian but had no fossil record to support this interpretation.

Retallack and Dilcher (4) proposed a reconstruction of the late Albian Dakota Formation flora and showed that angiosperms occupied a variety of environments. Lauraceous trees/shrubs (e.g., *Prisca/Magnoliaephyllum*) occupied swampy woodlands and margins of coastal lagoons; angiospermous shrubs (e.g., “*Acerites*”) colonized margins of tide-dominated deltas; platanoids were common around freshwater lakes, levees, and swales of freshwater coastal stream sides (e.g., *Araliopsoides*); and conifers forested dry continental floodplains (4). Closer inspection shows some differences from Europe (34). However, although slightly older, overall the Dakota floras and their ancient environments fit well with the beginning of the phase 3 of our scenario (Fig. 2D), even though there were some differences. In addition, the Magnoliales (e.g., *Liriophyllum* Lesquereux, *Didromophyllum* Upchurch and Dilcher) found in North America were lacking in Europe, and the Laurales were represented by different taxa (e.g., *Pabiana* Upchurch and Dilcher in Northern America vs. *Cocculophyllum* Velenovský in Europe).

Taylor and Hickey (35) suggested that early angiosperms were perennial rhizomatous plants resembling herbaceous Magnoliids such as Piperaceae and that they competed with ferns and sphenopsids in disturbed areas such as stream margins. These angiosperms then invaded the aquatic niche in the Early Cretaceous due to their rhizomatous growth habit and efficient seedlings, thus creating a stable environment.

Feild et al. (36) and Feild and Arens (37, 38) hypothesized a disturbed forest understory and/or streamside shrubby ecology similar to the ecology of extant basal angiosperm lineages (i.e., Amborellaceae, Nymphaeales, Austrobaileyales, and Chloranthaceae). Retallack and Dilcher’s (4) “coastal hypothesis,” Taylor and Hickey’s (35) “paleoherb,” and Feild et al.’s (36) “dark and disturbed” hypotheses are supported by the occurrence of angiosperms in disturbed floodplain environments from the Aptian (e.g., lower zone I of the Potomac group, United States; refs. 25, 39). This early angiosperm ecology may fit our phase 2, but is unlike our phase 1 (Fig. 2A and B). One may question whether the earliest angiosperms

were shade tolerant as proposed by the “damp, dark, and disturbed habitats” hypothesis (36, 38). An ecophysiological study of hypothetical living relatives of the zone I Potomac (Aptian–Albian) group angiosperms indicates that, if the assumed living related angiosperms are a good model of the physiology of the earliest angiosperms, they may have been shade tolerant (40). Furthermore, the three phases proposed here for the angiosperm rise to dominance show an interesting synchronism with the progressive increase of escalation in angiosperm leaf hydraulic capacity also noted by Feild et al. (41) that reflects an escalation in ecological range.

European, Chinese, and North American records (10, 11, 42, 43, *) all show that angiosperms occurred in aquatic environments from at least the Barremian. The occurrence of early aquatic angiosperms opens the way for a reinterpretation of the North American records such as the Aptian peltate leaves of *Proteaephyllum reniforme* Fontaine. This leaf also agrees with the early aquatic angiosperms that appeared in the European phase 1 that we recognize (Fig. 2A).

Darwin’s Abominable Mystery

Darwin’s “abominable mystery” concerning the sudden appearance of rather modern genera of flowering plants can now be understood. What most bothered Darwin was “the sudden appearance of so many extant taxa of flowering plants in the Upper Chalk” (1). At that time, he was relying on a paleobotanical record produced by people who approached the study of angiosperm fossils with the intent of relating them to extant taxa by using only gross leaf form as a basis for their systematic determinations. More recently, numerous Early Cretaceous angiosperm remains have been described as extinct angiosperm leaf and fruit morphotypes based upon critical observations and evaluations of many leaf and fruit characters. Our scenario supports the view by Darwin that “the presence of even one true angiosperm in the Lower Chalk makes [one] inclined to conjecture that plant[s] of this great division must have been largely developed in some isolated area, whence owing to geographical changes, they at last succeeded in escaping, and spread quickly over the world” (1, p 539). Thus, the rise to dominance of angiosperms was a process that lasted >45 million years. Dilcher (44, 45) pointed out that the modern nature of the fossil angiosperms identified in the Cretaceous were products of the use of limited characters combined with the goal of finding extant angiosperm genera. Probably there are no extant angiosperm genera that extend back to the Cretaceous when careful and detailed character analysis is used.

Angiosperms became abundant and diversified worldwide in coastal environments by the Albian as proposed in the “coastal hypothesis of angiosperm dispersal” (4). The so-called “sudden appearance of angiosperms” is really a series of ecological successions captured by exceptional depositional and preservational environments. At this time, there are also important rapid changes in the biotic environment as angiosperm and insect coevolution gains momentum (46, 47). The biotic changes and habitat changes may seem to be sudden events, but in geological time these, events can be seen as occurring in distinct phases as outlined here (Fig. 2).

By mid-Cretaceous time, some early ancestors of major taxa can be recognized. This diversification and local abundance in particular environments explains why Friis and colleagues (e.g., refs. 48–51) found very diverse and abundant angiosperm mesofossil flowers, fruits, and seeds in Portuguese stratigraphic horizons now considered as Late Aptian–Early Albian in age (16), whereas older Aptian mesofossil floras (e.g., Torres Vedras, Catefica) were less diversified and mainly consisted of the early diverging clades [e.g., Austrobaileyales (*Anacostia*) and Chloranthaceae (*Pennipollis*) plant; refs. 51 and 52]. The fossil angiosperms reported by Friis et al. (50, 51) are diverse, abundant, and well preserved so that some can be linked to extant major angiosperm lineages. Their occurrence in fluvial deposits demonstrates the occupation of

understory floodplains in phase 2 (Fig. 2C). Overall, the ecological diversification of angiosperms parallels the progressive systematic diversification of angiosperms evidenced from mesofossils (51, 52).

Crepet et al. (53), Crepet and Nixon (54), Grimaldi (55), and Hu et al. (46, 47) have called attention to angiosperm coevolution with insects. This coevolution appears to have been a crucial step in the rise to dominance of angiosperms (46, 47, 56). For example, the increase in ecological range and richness of conifers from the beginning of the Albian suggests closed vegetation under humid climates that encouraged the rise of understory angiosperms. This situation implies that angiosperms did not simply overtop other plant groups in different environments, but they benefited from any opportunities offered by global vegetation and climate changes. Furthermore angiosperms were not the only clade that experienced a diversification during the Cretaceous: Core Leptosporangiate ferns, Pinaceae, Gneta-

ceae, and Podocarpaceae also underwent extensive diversification (57–62). In addition, the heterosporous ferns originated and radiated at this same time (63, 64). It is important to appreciate the extent of vegetation turnover during the Cretaceous. We need to expand our focus when dealing with angiosperm evolution to consider also angiosperm evolution in time and space as they pioneered changing physical and biotic environments through Cretaceous time.

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