Geologica Acta, Vol.10, Nº 2, June 2012, 181-188
DOI: 10.1344/105.000001701
Available online at www.geologica-acta.com

geologica acta

Influence of latitude and climate on spread, radiation and rise to dominance of early angiosperms during the Cretaceous in the Northern Hemisphere

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ABSTRACT

Our aim is to evaluate the influence of climate and latitude on the rise to dominance of angiosperms in space and time during the Cretaceous. The main objectives of the study are: 1) to determine whether a relationship existed between plant biogeographical distribution and Cretaceous climate changes; 2) to explore latitude-dependent forcing on early angiosperm ecology; 3) to propose a mechanism explaining the observed stages of radiation in early angiosperms. The study focuses on 18 Cretaceous megafossil localities and reviews on microfossils in the Northern Hemisphere.

A database has been compiled using literature and personal unpublished data. The data document occurrences of micro- and megafossil plant remains including spores, pollen grains, leaves and whole plants. They are placed in context through the use of Cretaceous geographical maps and temperature curves or values. There is a clear correlation between latitude and the composition of Cretaceous floras. Latitudinal vegetation belts fluctuated in concert with climate changes during the Cretaceous. Differences in original plant associations may have driven the gradual plant turnover that resulted in the rise to dominance of early angiosperms during the Cretaceous. Cretaceous climate changes created dispersal bottlenecks. Bottlenecks induced the extinction of some plant groups and the radiation of others. Those that successfully radiated continued to spread.

KEYWORDS **Early angiosperms. Radiation. Rise to dominance. Palaeobotany. Palynology. Palaeogeography. Palaeoclimates. Cretaceous. North Hemisphere.**

INTRODUCTION

In 1875, Sir Charles Darwin wrote: “the sudden appearance of so many Dicotyledons in the Upper Chalk appears to me a most perplexing phenomenon” (see correspondence letters written by Charles Darwin compiled in Darwin and Seward, 1903). In the context of the theory of punctuated equilibrium (Gould and Eldredge, 1977), this sudden appearance may be explained by the substitution by peripheral taxa and their rapid spread, of and substitution by peripheral taxa, originating in areas in which allopatric speciation occurred. Darwin suggested a pre-Cretaceous angiosperm evolution "during long ages a small isolated continent in the S. Hemisphere which served as the birthplace of the higher plants" (see correspondence letters written by Charles Darwin compiled in Darwin and Seward, 1903). This proposal was supported by early Cretaceous tricolpate pollen grains (see review by Doyle and Hickey, 1976), suggesting that Eudicots first appeared in the low latitudes at or near the Barremian/Aptian boundary, and spread poleward during the Albian-Cenomanian. During the Cretaceous not only angiosperms, but also other plant clades experienced a radiation. It happened in core leptosporangiate ferns (Schneider *et al*., 2004), gnetales (Crane and Lidgard, 1989), and the conifer families Podocarpaceae (Kelch, 1998) and Pinaceae (Wang *et al*., 2000). The core leptosporangiate fern radiation was associated with the rise to dominance of angiosperms in forests, which established new plant communities and habitat traditions. In contrast other radiations were not definitively related to the rise to dominance of angiosperms. These radiations do not only share synchronism but they also probably had the same tropical origins. The Cretaceous was a period of tremendous climate changes, and so we also wonder about the role of climate in forcing vegetation changes and plant turnover during the Cretaceous.

PALYNOLOGICAL RECORD

The earliest unequivocal angiosperm records are pollen grains from the Valanginian of Israel and Morocco (see Barret and Willis, 2001 and references therein), between palaeolatitudes 5 and 25°N. By the Valanginian angiosperms spread poleward, and pollen grains were already widespread during the Barremian (Barret and Willis, 2001, Fig. 1). However, angiosperms did not become ecologically dominant during this Valanginian-Barremian early spread. At low latitudes, angiosperms remained a minor component of sporomorph assemblages during the Barremian (Hendriks and Schrank, 1990).

The second spread phase is characterized by the first occurrence of tricolpate pollen grains at low latitudes during the latest Barremian (Hickey and Doyle, 1977; Hughes, 1994; Fig. 1). Tricolpate pollen grains reached mid latitudes by the Albian (*e.g.* Heimhofer *et al*., 2005) and high latitudes during the Cenomanian (Hickey and Doyle, 1977). During the late Cretaceous, angiosperms represented 60-80% of sporomorph assemblages at low latitudes compared to 30-50% at high latitudes (Barret and Willis, 2001).

Crane and Lidgard (1989) noted the striking increase in gnetalean diversity, especially ephedroids, contemporaneous with the initial angiosperm diversification at low latitudes leading up to the Aptian. During the Aptian, Araucariaceae and ferns (Schizaeaceous) decreased, whereas drier conditions probably favoured the observed increase in proportion within the fossil conifer family Cheirolepidiaceae (Hendriks and Schrank, 1990). These trends lasted until the Cenomanian with a further drastic decrease in fern spores (down to less than 5% of total sporomorph assemblages), a more moderate decrease in ephedroids, and a rise to dominance of angiosperms (Hendriks and Schrank, 1990). An increase in humidity during the late Cenomanian-Turonian can be deduced from the drop in frequency of ephedroid pollen grains (Ibrahim, 1996). The Campanian-Maastrichtian palynology records a more humid tropical climate in Egypt. This is indicated by a slight increase in fern abundance as well as by the widespread occurrence of the pollen grain *Spinizonocolpites baculatus* Muller, which is related to the living tropical mangrove palm *Nypa* Steck (Hendriks and Schrank, 1990).

PALAEOBOTANICAL RECORD

Low latitudes (30°S-30°N)

The angiosperm fossil record from the Lower Cretaceous of low latitudes is sparse and hence poorly documented in the literature. The earliest angiosperm record at low latitudes is *Montsechia vidalii* (Zeiller) Teixeira from the Barremian of Las Hoyas (Spain, Fig. 2), which is interpreted as an aquatic plant (Gomez *et al*., 2006). Pons (1988) described angiosperms (*Monocotylophyllum heterophyllum* Pons, *Moutonia quetamensis* Pons, *M. sinuata* Pons) from the probable Aptian of Villavicencio (Columbia, Fig. 2). The Villavicencio locality yielded pollen assemblages exhibiting similar angiosperm morphologies and low levels

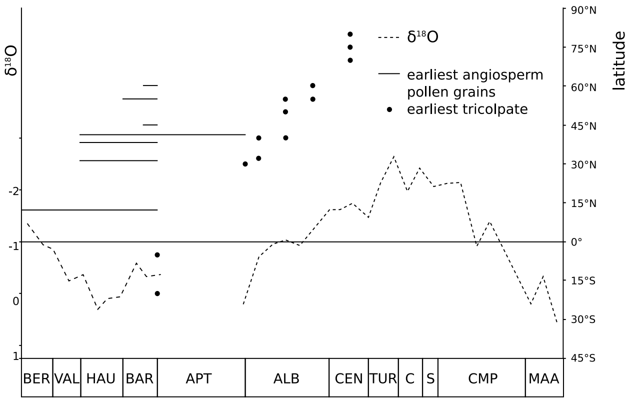

FIGURE 1 | Latitudinal distribution of earliest angiosperm monocolpate pollen grains (Barret and Willis, 2001) and tricolpate pollen grains (Doyle and Hickey, 1976) versus $\delta^{18}O$ variation (Veizer et al., 2000) during the Cretaceous.

of diversity to those from the Aptian-Albian of the Arundel Fm. and the Patuxent Fm. These latter assemblages were interpreted as representing floodplain understory floras (Hickey and Doyle, 1977).

In the Southern Hemisphere the most noteworthy locality is from the late Aptian-early Albian of the Crato Fm. in Brazil (Fig. 2), from which Mohr and collaborators described small-leaved Magnoliids (*Araripa* and *Endressinia*) and aquatic angiosperms (*Pluricarpellata*, *Klitzschophyllites*) (Mohr and Friis, 2000; Mohr and Eklund, 2003; Mohr and Bernardes-de-Oliveira, 2004; Mohr *et al*., 2008). Similar plant assemblages containing early aquatic angiosperms occur in southernmost Laurasia (Almargen Fm. in central Portugal, Teixeira, 1948, 1952; Mohr *et al*., 2006; Utrillas Fm. in north-eastern Spain, Gomez *et al*., 2009; Sender *et al*., 2010) and along the northern African margins of Gondwana (Fig. 2) (Abus Ballas Fm. in Egypt, Mohr *et al*., 2006; Bir El Karma in Tunisia, Barale and Ouaja, 2001; Kurnub Fm. in Jordan, Taylor *et al*., 2008). Mohr *et al*. (2006) suggested that these Aptian-Albian, low latitude regions experienced seasonal droughts. Under these conditions, angiosperms remained a minor component of the early Cretaceous vegetation and were restricted to floodplain understories and aquatic environments.

By the Cenomanian more diversified angiosperm floras appeared: from the Cenomanian of Nammouria in Lebanon (Krassilov and Bacchia, 2000) and of Bahariya Oasis in Egypt (Lyon, 2001), and from the Turonian of Gerofit (Israel; Dobruskina, 1997) (Fig. 2). These plant assemblages were dominated by angiosperms, which represented more than two-thirds of the species' richness. They showed systematical similarities to mid-latitude floras (*e.g.* presence of platanoid and lauroid leaves). The occurrence of platanoid leaves also suggested that tree angiosperms already existed (Dobruskina, 1997; Lyon, 2001). The Late Cretaceous plant record is very scarce but Upchurch *et al*. (1998) suggested that tropical rainforests existed during the Campanian?-Maastrichtian based on the occurrence of numerous coal deposits. An angiosperm-dominated tropical rainforest assemblage was also described from the Campanian/Maastrichtian of Coahuila in Northern Mexico (Upchurch *et al*., 2008; Estrada-Ruiz *et al*., 2009).

Mid latitudes (30°N-60°N)

The most complete record of earliest whole-plant angiosperms has been found at mid latitudes from the Hauterivian?-Barremian: *Archaefructus* spp. (Liaoning province, China, Sun *et al*., 1998, 2002; Ji *et al*., 2004), *Sinocarpus decussatus* Leng et Friis (Liaoning province, China, Leng and Friis, 2003), *Bevhalstia pebja* Hill (Weald Clay Group of Surrey and Sussex, southern England,, Hill, 1996) (Fig. 2). These occurrences postdate the earliest angiosperm pollen grains by about ten million years. They also provide key information about the gross morphology and ecology of the pre-tricolpate angiosperms. All of these assemblages were found in lacustrine deposits and most of the angiosperms present were aquatic (Friis *et al*. 2003 and references above).

During the Aptian-Albian, the ecological range of angiosperms at mid latitudes increased tremendously from only floodplain understories during the Aptian to colonisation of most environments during the Cenomanian (Coiffard *et al*., 2006, 2007). This apparently sudden increase in distribution and prevalence may be explained ecologically by the late spread of angiosperms that were settling into coastal environments and that therefore had an excellent fossilization potential. Hickey and Doyle (1977) proposed an ecological scenario for angiosperm radiation during the Aptian-Cenomanian in four stages: 1) during the Aptian angiosperms were restricted to floodplain understories; 2) during the mid Albian they invaded early successional thickets; 3) at about the Albian/Cenomanian boundary they spread among riparian trees, and 4) they settled in the forest canopy during the Late Cretaceous. During the Campanian-Maastrichtian especially, palms started to dominate coastal freshwater swamps (Marmi *et al*., 2008, 2010; Coiffard and Gomez, 2009; Villalba-Breva *et al*., 2012). Nevertheless, angiosperms remained a minor component of the terrestrial biomass until the end of the Cretaceous (Moldowan *et al*., 1994), and most forests remained dominated by conifers, particularly members of the Taxodiaceae. This scenario was based on the lowermost mid latitudes. However, according to Crabtree (1987), the earliest megafossil angiosperms at higher mid latitudes were *Sapindopsis* leaves from the middle Albian of Northern Rocky Mountains (about 40-60°N) similar to those characterising the second colonisation stage of Hickey and Doyle (1977). These angiosperms may represent lower latitude immigrants (Retallack and Dilcher, 1986).

High latitudes (60°N-90°N)

Until the end of the Albian, forests were dominated by conifers, with broad-leaved *Podozamites*-like trees being the most common source of foliage. Ginkgophytes were diverse but restricted to river margins or back levees, and cycads were relatively common but spatially restricted. Ferns and sphenophytes were early colonizers and were common ground cover elements (Askin and Spicer, 1995).

Rare angiosperms (*Cissites*) occurred in *Ginkgo*-dominated riparian environments from the Late Albian of Kukpowruk (Fig. 2, Spicer and Herman, 2001). Angiosperms started to diversify and established as shrubs or small trees in riparian

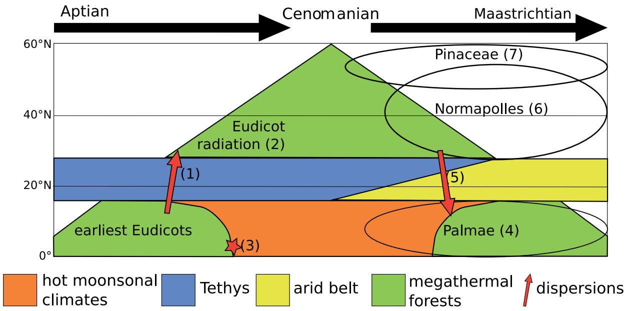

FIGURE 2 | Vegetation spread and evolutionary events during the Cretaceous. 1) Eudicot spread into mid latitudes, 2) Eudicot radiation at mid latitudes, 3) Extinction of megathermal forests, 4) Palmae province, 5) Return of megathermal forests to low latitudes, 6) Rise of Fagales under cooler climates, 7) Dominance of Pinaceae at high latitudes.

communities, mixing with cycadophytes and ferns (Spicer *et al.*, 2002). The most mature stages of serial successions were still dominated by conifers. By the Late Cenomanian, angiosperm diversity had risen to more than 60 leaf morphologies in Alaska (Spicer and Parrish, 1990). The vegetation was still dominated by conifers but needle-leaved conifers were less common. By the Coniacian, needle-leaved conifers and *Podozamites* had disappeared, whereas taxodiaceous foliage was common. Platanoid angiosperms were still dominant along river and lake margins, and began to penetrate into forests. By the Campanian, overall diversity had dropped in Northern Alaska (85°N). Angiosperms were mostly herbaceous, and conifers were only represented by two taxa (Askin and Spicer, 1995). The mega- and microfossil plants from the Maastrichtian of Hansen Point showed low to middle diversity. The vegetation was dominated by taxodiaceous conifers associated with subordinate angiosperms, bryophytes, conifers, cycads, ferns, ginkgos, lycopods and pines, co-existing in laterally and temporarily extensive peat mires and associated floodplain substrates (Falcon-Lang *et al.*, 2004).

PALAEOCLIMATES THROUGH THE CRETACEOUS

During the Cretaceous, mid-oceanic ridge activity increased and large igneous provinces formed. This resulted in excessive greenhouse gas production and led to the warmest Phanerozoic interval during the early Late Cretaceous (Veizer *et al.*, 2000).

The Early Aptian and Late Aptian-Early Albian are marked by two oceanic anoxic events (OAE 1a and 1b) characterized by negative δ^3C excursions. The OAE 1a was linked to the Otong-Java super-plume (Leckie *et al.*, 2002), whereas the OAE 1b was related to a worldwide 5°C cooling (Steuber *et al.*, 2005). Weissert and Lini (1991) attributed this cooling to a positive feedback of carbon storage inducing a decrease in atmospheric CO_2.

It was during the Albian, that oceanic ridge spread produced high levels of CO_2. As a consequence global warming occurred, with temperatures increasing from 12-14°C to 22-26°C in the North Atlantic Ocean (Leckie *et al.*, 2002; Price and Hart, 2002). Temperatures increased by an additional 5°C during the Late Albian, coincident with a new worldwide OAE 1c (Stoll and Shrag, 2000).

The warmest temperatures of the Phanerozoic occurred during the Cenomanian interval (Veizer *et al.*, 2000). CLAMP analyses show that high latitudes had a temperate climate with Mean Annual Temperatures (MAT) of about 13°C in Grebenka (Russsia, about 70°N, Spicer *et al.*, 2002), whereas mid latitudes experienced a subtropical climate with a MAT of 17-20°C in Bohemia (Czech Republic, about 40°N, Kvaček *et al.*, 2000).

CLAMP analyses also indicated a post-Santonian cooling, especially those based on angiosperm leaves from the Campanian flora of Bohemia. These showed a MAT of about 14°C (Herman and Kvaček, 2002), indicating a 30° poleward latitudinal shift of temperate belts. During the Maastrichtian, high latitudes had a cold climate with a MAT of about 4-5°C (Spicer and Parrish, 1990).

DISCUSSION

Major Cretaceous plant turnover

Maslin *et al.* (2005) conducted a survey of the latitudinal distribution of vegetation during the last 100 million years, to determine how climate change disturbed tropical rainforests. They suggested that ice house megathermal forests were restricted to certain areas of tropical belts during the coolest periods, as occurred during the last Ice Age. As the global temperatures increased, megathermal forests could be expected to spread until they occupied most areas of tropical belts, as we can observe today in contemporary floras. Winter temperatures would then become warm enough to allow for the spread of megathermal forests into mid latitudes (*e.g.* during the Miocene, Maslin *et al.*, 2005). Under greenhouse climates (*e.g.* during the Cenomanian), megathermal forests at low latitudes would not exist, being strongly constrained by a warm, seasonally-marked, drought monsoonal climate.

The model of Maslin *et al.* (2005) can explain plant palaeogeography during the Cretaceous. The Aptian-Albian warming would have allowed tropical elements to spread into mid latitudes (*e.g.* Eudicots, Fig. 3). However, this spread implies long distance dispersal with few colonists that would have created an evolutionary bottleneck, especially in the Northern Hemisphere where the Tethys sea represented a large barrier. Taxa crossing the barrier would have experienced a rapid niche expansion as a result of ecological release, as takes place during mass extinction or island colonization. This would have led to an increase in the rate of species radiation (Fig. 3). Eudicots developed new ecological strategies during the Albian as they evolved new tree and shrub habits in ruderal environments (Hickey and Doyle, 1977; Coiffard *et al*., 2007). The Albian-Cenomanian warming would have driven the spread of megathermal forests into higher latitudes, allowing Eudicots to enter these new habitats, while they continued expanding their ecological ranges at low and mid latitudes (*e.g.* salt tolerant ecology, Coiffard *et al*., 2006; Gomez *et al*., 2008). By the Aptian, aridity had increased at low latitudes (Hendriks and Schrank, 1990), causing the extinction of megathermal forests before the Cenomanian (Fig. 3). This may have resulted in the extinction of some tropical clades at that time, because these were unable to adapt timeously to drier environmental conditions, and were unable to disperse into mid-latitudes. The Albian-Cenomanian global warming had, therefore, again played a major role in shaping the terrestrial vegetation, probably inducing much extinction in tropical areas and where geographical barriers occurred.

During the Coniacian-Maastrichtian, the Palmae province developed at low latitudes (Friis *et al*., 2006, Fig. 3), while new extinctions occurred among gymnosperms, especially in the conifer family Cheirolepidiaceae. These trends may have been partly driven by the return of competitive megathermal forest taxa from mid latitudes to low latitudes predicted as a response to global cooling (Fig. 3). This return may have induced another bottleneck, which especially affected conifers negatively, and favoured woody angiosperm trees (Jacobs, 2004; Philippe *et al*., 2008). It has been suggested that tropical rainforests similar to those of the present day, occurred during the Maastrichtian (Upchurch *et al*., 1998; Morley, 2003). The increase in *Normapolles* pollen grains revealed a rise in Fagales, while angiosperms spread in cooler climates (Fig. 3). At the same time, Pinaceae became dominant at high latitudes (Falcon-Lang *et al*., 2004, Fig. 3).

Evolution of ecology

Plant turnover during the Cretaceous appears to have been driven by the spread of megathermal forests from low latitudes to mid latitudes. This spread would have induced bottleneck-driven evolutionary radiation. While climate warmed at high latitudes, taxa were driven from low latitudes to mid latitudes. Pollen grains from the Hauterivian suggest that angiosperms already existed before the mid Cretaceous plant turnover (Hughes *et al*., 1991). Thus, they had probably already evolved innovations allowing them to compete successfully with the dominant gymnosperm clades. The taxonomic composition of biomes was probably strongly influenced by the rarity of species transitions between biomes (Donoghue, 2008; Crisp *et al*., 2009) because most clades should be restricted to one biome. This latter assumption suggests that adaptations to major climate changes were dissimilarly accomplished in different lineages. As a consequence, when corridors allowed for the spread of plant taxa into newly emerging environments, these environments would be filled with species that had filtered through from areas where the relevant adaptations had already evolved, rather than remaining colonised by plants that evolved these adaptations *in situ*. In our scenario, the newly emerging environments were the megathermal forests at mid latitudes during the Mid-Cretaceous (during a period of global warming) and at low latitudes during the Late Cretaceous (during a period of global cooling).

From an adaptive point of view, equatorial rainforests are the most productive terrestrial environments on Earth today. However such productivity goes hand in hand with strong competition (Kadmon and Shmida, 1990; Grime, 2001). Thus, plants are subject to strong selection pressures while gathering resources (*e.g.* nutrients, light for growth in forests). Rich environments also lead to high phenotypic plasticity during times of stress (Grime, 2001), which can drive the evolution of new *Baupläne*. In contrast, plants growing up in resource-poor environments develop stress-tolerant strategies (to *e.g.* drought, coldness), and they usually display evolutionary convergences (*e.g.* succulency, rosette habits). Furthermore, mutation rates in tropical clades are higher and affect both coding and non-coding DNA, leading to a faster rate of evolution (Davies *et al*., 2004).

ACKNOWLEDGMENTS

B.G. received financial support from the CNRS-UMR 5276 Terre, Planètes, Environnement. This publication is a contribution to projects ANR AMBRACE (No BLAN07-1-184190) of the Agence Nationale de la Recherche and INSU NOVAMBRE of the Institut National des Sciences de l'Univers, and project CGL2008-00809/BTE and CGL2009-11838/BTE funded by the Ministerio de Ciencia e Innovación (Spain) and research group SGR2009-1451 funded by the Generalitat de Catalunya (Catalonia). C.C. received support from the Von Humboldt Foundation (Germany). The authors acknowledge revisions by B.A.R. Mohr, D.L. Dilcher, and J.M. de Gibert.

REFERENCES

Askin, R.A., Spicer, R.A., 1995. The Late Cretaceous and Cenozoic history of vegetation and climate at northern and southern high latitudes: a comparison. In: Stanley, S.M. (ed.). Effects of past global climate on life. Washington DC, National Research Council, National Academy Press, 156-173.

Barale, G., Ouaja, M., 2001. Découverte de nouvelles flores avec des restes à affinités angiospermiennes dans le Crétacé inférieur du Sud Tunisien. Cretaceous Research, 22, 131-143.

Barrett, P.M., Willis, K.J., 2001. Did dinosaurs invent flowers? Dinosaur-angiosperm coevolution revisited. Biological Reviews, 76, 411-447.

Blakey, R.C., 2007. Global paleogeographic views of Earth history-Late Precambrian to Recent. Website: http://jan.ucc.nau.edu/~rcb7/globaltext2.html. (Last updated March, 2011, Last checking 27th May 2011).

Coiffard, C., Gomez, B., 2009. The rise to dominance of the angiosperm kingdom: dispersal, habitat widening and evolution during the Late Cretaceous of Europe. Lethaia, 43, 164-169. Doi: 10.1111/j.1502-3931.2009.00181.x

Coiffard, C., Gomez, B., Thévenard, F., 2007. Early Cretaceous Angiosperm Invasion of Western Europe and Major Environmental Changes. Annals of Botany, 100, 545-553.

Coiffard, C., Gomez, B., Kvaček, J., Thévenard, F., 2006. Early Angiosperm Ecology: Evidence from the Albian-Cenomanian of Europe. Annals of Botany, 81, 495-502.

Crabtree, D.R., 1987. Angiosperms of the northern Rocky Mountains: Albian to Campanian (Cretaceous) megafossil floras. Annals of the Missouri Botanical Garden, 74, 707-747.

Crane, P.R., Lidgard, S., 1989. Angiosperm Diversification and Paleolatitudinal Gradients in Cretaceous Floristic Diversity. Science, 246, 675-678.

Crisp, M.D., Arroyo, M.T.K., Cook, L.G., Gandolfo, M.A., Jordan, G.J., McGlone, M.S., Weston, P.H., Westoby, M., Wilf, P., Linder, H.P., 2009. Phylogenetic biome conservatism on a global scale. Nature, 458, 754-756.

Darwin, F., Seward, A.C. (eds.), 1903. More letters of Charles Darwin. A record of his work in a series of hitherto unpublished letters. London, John Murray, volume 1 and 2, 494pp. and 508pp.

Davies, T.J., Savolainen, V., Chase, M.W., Moat, J., Barraclough, T.G., 2004. Environmental energy and evolutionary rates in flowering plants. Proceedings of the Royal Society, Biological Sciences, B, 271, 2195-2200.

Dobruskina, I.A., 1997. Turonian plants from the southern Negev, Israel. Cretaceous Research, 18, 87-107.

Donoghue, M.J., 2008. A phylogenetic perspective on the distribution of plant diversity. Proceedings of the National Academy of Sciences of the United States of America, 105, 11549-11555.

Doyle, J.A., Hickey, L.J., 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In: Beck, C.B. (ed.). Origin and Early Evolution of Angiosperms. New York, Columbia University Press, 139-206.

Estrada-Ruiz, E., Calvillo-Canadell, L., Cevallos-Ferriz, S.R.S., 2009. Upper Cretaceous aquatic plants from Northern Mexico. Aquatic Botany, 90, 282-288.

Falcon-Lang, H.J., MacRae, R.A., Csank, A.Z., 2004. Palaeoecology of Late Cretaceous polar vegetation preserved in the Hansen Point Volcanics, NW Ellesmere Island, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology, 212, 45-64.

Friis, E.M., Doyle, J.A., Endress, P.K., Leng, Q., 2003. *Archaefructus*-angiosperm precursor or specialized early angiosperm? Trends in Plant Science, 8, 369-373.

Friis, E.M., Pedersen, K.R., Crane, P.R., 2006. Cretaceous angiosperm flowers: Innovation and evolution in plant reproduction. Palaeogeography, Palaeoclimatology, Palaeoecology, 232, 251-293.

Gomez, B., Coiffard, C., Dépré, E., Daviero-Gomez, V., Néraudeau, D., 2008. Diversity and histology of a plant litter bed from the Cenomanian of Archingeay-Les Nouillers (southwestern France). Comptes Rendus Palevol, 7, 135-144.

Gomez, B., Coiffard, C., Sender, L.M., Martín-Closas, C., Villanueva-Amadoz, U., Ferrer, J., 2009. *Klitzschophyllites*, aquatic basal Eudicot (Ranunculales?) from the Albian (Lower Cretaceous) of north-eastern Spain. International Journal of Plant Sciences, 107, 1075-1085.

Gomez, B., Daviero-Gomez, V., Martín-Closas, C., de la Fuente, M., 2006. *Montsechia vidalii*, an early aquatic angiosperm from the Barremian of Spain. Prague, European Palaeobotany and Palynology Conference, abstract volume, 49pp.

Gould, S.J., Eldredge, N., 1977. Punctuated equilibria: the tempo and the mode of evolution reconsidered. Paleobiology, 3, 115-151.

Grime, J.P., 2001. Plant strategies, vegetation processes, and ecosystem properties. Chichester, John Wiley and Sons, 456pp.

Heimhofer, U., Hochuli, P.A., Burla, S., Dinis, J.M.L., Weissert, H., 2005. Timing of Early Cretaceous angiosperm diversification and possible links to major paleoenvironmental change. Geology, 33, 141-144.

Hendriks, F., Schrank, E., 1990. The marine Abu Ballas Formation of southern Egypt: a clay mineralogic and microfloral reconstruction of the Aptian paleoclimate. Journal of African Earth Sciences, 10, 471-481.

Herman, A.B., Kvaček, J., 2002. Campanian Grünbach flora of lower Austria: preliminary floristics and palaeoclimatology. Annalen des Naturhistorischen Museums in Vien, 113A, 1-21.

Hickey, L.J., Doyle, J.A., 1977. Early Cretaceous fossil evidence for angiosperm evolution. Botanical Review, 43, 538-589.

Hill, C.R., 1996. A plant with flower-like organs from the Wealden of the Weald (Lower Cretaceous), southern England. Cretaceous Research, 17, 27-38.

Hughes, N.F., 1994. The enigma of angiosperm origins. Cambridge, Cambridge University Press, 317pp.

Hughes, N.F., McDougall, A.B., Chapman, J.L., 1991. Exceptional new record of Cretaceous Hauterivian angiospermid pollen from southern England. Journal of Micropalaeontology, 10, 75-82.

Ibrahim, M.I.A., 1996. Aptian-Turonian palynology of the Ghazalat-1 Well (GTX-1), Qattara Depression, Egypt. Review of Palaeobotany and Palynology, 94, 137-168.

Jacobs, B.F., 2004. Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. Philosophical Transactions of the Royal Society, Biological Sciences, B, 359, 1573-1583.

Ji, Q., Li, H., Bowe, L.M., Liu, Y., Taylor, D.W., 2004. Early Cretaceous *Archaefructus eoflora* sp. nov. with Bisexual Flowers from Beipiao, Western Liaoning, China. Acta Geologica Sinica, 78, 883-896.

Kadmon, R., Shmida, A., 1990. Patterns and causes of spatial variation in the reproductive success of a desert annual. Oecologia, 83, 139-144.

Kelch, D.G., 1998. Phylogeny of Podocarpaceae: comparison of evidence from morphology and 18S rDNA. American Journal of Botany, 85, 986-996.

Krassilov, V.A., Bacchia, F., 2000. Cenomanian florule of Nammoura, Lebanon. Cretaceous Research, 21, 785-799.

Kvaček, J., Spicer, R.A., Herman, A.B., 2000. Palaeoclimate of the Peruc-Koryčany flora and other Laurasian Cenomanian floras. Beijing, 6th International Organisation of Palaeobotany Conference, 3, abstract volume, 6.

Leckie, R.M., Bralower, T.J., Cashman, R., 2002. Oceanic anoxic events and plankton evolution: Biotic response to tectonic forcing during the mid-Cretaceous. Paleoceanography, 17, 1041.

Leng, Q., Friis, E.M., 2003. *Sinocarpus decussatus* gen. et sp. nov., a new angiosperm with basally syncarpous fruits from the Yixian Formation of Northeast China. Plant Systematics and Evolution, 241, 77-88.

Lyon, M.A., 2001. Late Cretaceous equatorial coastal vegetation: new megaflora associated with dinosaur finds in the Bahariya oasis, Egypt. Geological Society of America, Annual Meeting, November, 5-8, 2001.

Marmi, J., Gomez, B., Martín-Closas, C., 2008. Presencia de macrorestos parautóctonos de *Sabalites* cf. *longirhachis* (Unger, 1850) Kvaček and Herman, 2004 en facies parálicas del Cretácico superior del Pirineo oriental, Cataluña. Revista Española de Paleontología, 23, 7-14.

Marmi, J., Gomez, B., Martín-Closas, C., Villalba-Breva, S., 2010. A plant reconstruction of the early palm *Sabalites longirhachis* (Unger) J. Kvaček et Herman from the Maastrichtian of Pyrenees. Review of Palaeobotany and Palynology, 163, 73-83.

Maslin, M., Malhi, Y., Phillips, O., Cowling, S., 2005. New views on an old forest: assessing the longevity, resilience and future of the Amazon rainforest. Transactions of the Institute of British Geographers, 30, 477-499.

Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., 2004. *Endressinia brasiliana*, a magnolialean angiosperm from the Lower Cretaceous Crato Formation (Brazil). International Journal of Plant Sciences, 165, 1121-1133.

Mohr, B.A.R., Bernardes-de-Oliveira, M.E.C., Taylor, D.W., 2008) *Pluricarpellatia*, a nymphaealean angiosperm from the Lower Cretaceous of northern Gondwana (Crato Formation, Brazil). Taxon, 57, 1147-1158.

Mohr, B.A.R., Eklund, H., 2003. *Araripia florifera*, a magnoliid angiosperm from the Lower Cretaceous Crato Formation (Brazil). Review of Palaeobotany and Palynology, 126, 279-292.

Mohr, B.A.R., Friis, E.M., 2000. Early Angiosperms from the Lower Cretaceous Crato Formation (Brazil), a Preliminary Report. International Journal of Plant Sciences, 161, S155-S167.

Mohr, B.A.R., Bernardes-De-Oliveira, M.E.C., Barale, G., Ouaja, M., 2006. Palaeogeographic distribution and ecology of *Klitzschophyllites*, and early Cretaceous angiosperm in Southern Laurasia and Northern Gondwana. Cretaceous Research, 27, 464-472.

Moldowan, J.M., Dahl, J., Huizinga, B.J., Fago, F.J., Hickey, L.J., 1994. The molecular fossil record of oleanane and its relationship to angiosperms. Science, 265, 768-71.

Morley, R.J., 2003. Interplate dispersal paths for megathermal angiosperms. Perspectives in Plant Ecology, Evolution and Systematics, 6, 5-20.

Philippe, M., Gomez, B., Girard, V., Coiffard, C., Daviero-Gomez, V., Thévenard, F., Billon-Bruyat, J.-P., Guiomar, M., Latil, J.-L., Le Loeuff, J., Néraudeau, D., Olivero, D., Schlögl, J., 2008. Woody or not woody? Evidence for early angiosperm habit from the Early Cretaceous fossil wood record of Europe. Paleoworld, 17, 142-152.

Pons, D., 1988. *Le Mésozoïque de Colombie: macroflores et microflores*. Cahiers de Paléontologie, Paris, Editions du Centre National de la Recherche Scientifique, 168pp.

Price, G.D., Hart, M.B., 2002. Isotopic evidence for Early to Mid-Cretaceous ocean temperature variability. Marine Micropalaeontology, 46, 45-58.

Retallack, G.J., Dilcher, D.L., 1986. Cretaceous angiosperm Invasion of North America. Cretaceous Research, 7, 227-252.

Schneider, H., Schuettpelz, E., Pryer, K.M., Cranfill, R., Magallon, S., Lupia, R., 2004. Fern diversified in the shadow of angiosperms. Nature, 428, 553-557.

Sender, L.M., Gomez, B., Diez, J.B., Coiffard, C., Martín-Closas, C., Villanueva-Amadoz, U., Ferrer, J., 2010. *Ploufolia cerciforme* gen. et comb. nov.: aquatic angiosperm leaves from the upper Albian of north-eastern Spain. Review of Palaeobotany and Palynology, 161, 77-86.

Spicer, R.A., Herman, A.B., 2001. The Albian-Cenomanian flora of the Kukpowruk River, western North Slope, Alaska: stratigraphy, palaeofloristics, and plant communities. Cretaceous Research, 22, 1-40.

Spicer, R.A., Parrish, J.T., 1990. Late Cretaceous-early Tertiary palaeoclimates of northern high latitudes: a quantitative view. Journal of the Geological Society, 147, 329-341.

Spicer, R.A., Herman, A.B., Ahlberg, A.T., Raikevich, M.I., Rees, P.M.A., 2002. Mid-Cretaceous Grebenka flora of North-eastern Russia: stratigraphy, palaeobotany, taphonomy and palaeoenvironment. Palaeogeography, Palaeoclimatology, Palaeoecology, 184, 65-105.

Steuber, T., Rauch, M., Masse, J.P., Graaf, J., Malkoč M., 2005. Low-latitude seasonality of Cretaceous temperatures in warm and cold episodes. Nature, 437, 1341-1344.

Stoll, H.M., Schrag, D.P., 2000. High-resolution stable isotope records from the Upper Cretaceous Rocks of Italy and Spain: Glacial episodes in a greenhouse planet? Geological Society of America Bulletin, 112, 308-319.

Sun, G., Dilcher, D.L., Zheng, S., Zhou, Z., 1998. In Search of the First Flower: A Jurassic Angiosperm, *Archaefructus*, from Northeast China. Science, 282, 1692-1695.

Sun, G., Li, Q., Dilcher, D.L., Zheng, S., Nixon, K.C., Wang, X., 2002. Archaefructaceae, a new basal angiosperm family. Science, 296, 899-904.

Taylor, D.W., Brenner, G.J., Basha, S.H., 2008. *Scutifolium jordanicum* gen. et sp. nov. (Cabombaceae), an aquatic fossil plant from the Lower Cretaceous of Jordan, and the relationships of related leaf fossil to living genera. American Journal of Botany, 95, 340-352.

Teixeira, C., 1948. Flora Mesozóica Portuguesa. Parte I. Lisboa, Serviços Geológicos de Portugal, 118pp.

Teixeira, C., 1952. Notes sur quelques gisements de végétaux fossiles du Crétacé des environs de Leiria. Revista da Facultade de Ciencias, Universidade de Lisboa, C2, 133-154.

Upchurch, G.R., Otto-Bliesner, B.L., Scotese, C., 1998. Vegetation-atmosphere interactions and their role in global warming during the latest Cretaceous. Philosophical Transactions of the Royal Society, B: Biological Sciences, 353, 97-112.

Upchurch, G.R., Estrada-Ruiz, E., Cevallos-Ferriz, S.S., 2008. Did tropical rainforest vegetation exist during the Late Cretaceous? New data from the late Campanian to early Maastrichtian Olmos Formation, Coahuila, Mexico. Eos Transactions of the American Geophysical Union, 89(53), Fall Meeting Supplement Abstract PP11D-07.

Veizer, J., Godderis, Y., Francois, L.M., 2000. Evidence for decoupling of atmospheric CO_2 and global climate during the Phanerozoic eon. Nature, 408, 698-701.

Villalba-Breva, S., Martín-Closas, C., Marmi, J., Gomez, B., Fernández-Marrón, M.T., 2012. Peat-forming plants of the Pyrenean Maastrichtian coal. Geologica Acta*,* 10, 189-207

Wang, X.Q., Tank, D.C., Sang, T., 2000. Phylogeny and Divergence Times in Pinaceae: Evidence from Three Genomes. Molecular Biology and Evolution, 17, 773-781.

Weissert, H., Lini, A., 1991. Ice Age interludes during the time of Cretaceous greenhouse climate? In: Muller, D.W., McKenzie, J.A., Weissert, H. (eds.). Controversies in Modern Geology. London, Academic Press, 173-191.

Manuscript received March 2010;
revision accepted December 2010;
published Online May 2011.