Did dinosaurs invent flowers?
Dinosaur–angiosperm coevolution revisited

PAUL M. BARRETT[1]* and KATHERINE J. WILLIS[2]

[1] *Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK*
[2] *School of Geography and the Environment, University of Oxford, Mansfield Road, Oxford, OX1 3TB, UK*

ABSTRACT

Angiosperms first appeared in northern Gondwana during the Early Cretaceous, approximately 135 million years ago. Several authors have hypothesised that the origin of angiosperms, and the tempo and pattern of their subsequent radiation, was mediated by changes in the browsing behaviour of large herbivorous dinosaurs (sauropods and ornithischians). Moreover, the taxonomic and ecological radiation of angiosperms has been associated with the evolution of complex jaw mechanisms among ornithischian dinosaurs. Here, we review critically the evidence for dinosaur–angiosperm interactions during the Cretaceous Period, providing explicit spatiotemporal comparisons between evolutionary and palaeoecological events in both the dinosaur and angiosperm fossil records and an assessment of the direct and indirect evidence for dinosaur diets. We conclude that there are no strong spatiotemporal correlations in support of the hypothesis that dinosaurs were causative agents in the origin of angiosperms; however, dinosaur–angiosperm interactions in the Late Cretaceous may have resulted in some coevolutionary interactions, although direct evidence of such interactions is scanty at present. It is likely that other animal groups (insects, arboreal mammals) had a greater impact on angiosperm diversity during the Cretaceous than herbivorous dinosaurs. Elevated levels of atmospheric CO_2 might have played a critical role in the initial stages of the angiosperm radiation.

Key words: angiosperm, Ornithischia, Sauropoda, herbivory, coevolutionary interactions, spatiotemporal comparisons, Cretaceous palaeobotany, atmospheric CO_2.

CONTENTS

* Corresponding author: Paul M. Barrett. Tel: (01865) 271176; Fax: (01865) 281305; E-mail: paul.barrett@zoo.ox.ac.uk

I. INTRODUCTION

(1) General comments

Herbivory is one of the most fundamental of all trophic relationships, and the ecological and evolutionary interactions between herbivorous animals and plants have been the focus of intense study. In modern terrestrial ecosystems, it has been demonstrated that tetrapod herbivory exerts a strong influence on the structure and composition of plant communities (Crawley, 1983; papers in Werger *et al.*, 1989 and references cited therein), and on the dispersal of seeds (Janzen, 1983). In turn, plants impose reciprocal selection pressures on herbivorous tetrapods. Plant abundance, palatability, spatial distribution and temporal distribution affect the population density, migratory patterns, survival and reproductive success of herbivores (Crawley, 1983). This complex web of interactions has fostered the diffuse coevolution (*sensu* Herrera, 1985) of floral and faunal communities and has led to the development of sophisticated feeding adaptations in herbivores (including craniodental, physiological and behavioural modifications) and a wide range of defensive mechanisms (structural and chemical) in plants.

Given the importance of plant–tetrapod interactions over ecological time scales, it is not surprising that palaeobiologists have attempted to identify examples of similar phenomena over geological time. Changes in the taxonomic composition of tetrapod faunas through time, and changes in tetrapod anatomy and browsing behaviour, have been linked to the diversification or tabefaction of various plant lineages, changes in plant morphology and reproduction and large-scale ecological replacements in floral communities and *vice versa* (e.g. Swain, 1976; Regal, 1977; Bakker, 1978; Krassilov, 1981; Stebbins, 1981; Benton, 1983; Weishampel, 1984*a*, *b*; Coughenor, 1985; Norman & Weishampel, 1985; Coe *et al.*, 1987; Wing & Tiffney, 1987*a*, *b*; Weishampel & Norman, 1989; Fleming & Lips, 1991; Rayner, 1992; Tiffney, 1992; Zavada & Mentis, 1992; Taggart & Cross, 1997). Although the various scenarios proposed in these publications have been the subject of some discussion (see reviews in Behrensmeyer *et al.*, 1992; King, 1996), few of these hypotheses have been tested explicitly.

Sauropodomorph and ornithischian dinosaurs were the dominant vertebrate herbivores of Late Mesozoic terrestrial ecosystems. They were taxonomically, morphologically and ecologically diverse and employed many different solutions to the problems imposed by a diet of plants (Ostrom, 1961, 1964, 1966; Norman, 1984; Weishampel, 1984*a*; Norman & Weishampel, 1985, 1991; Galton, 1973, 1985*b*, 1986; Crompton & Attridge, 1986; Farlow, 1987; Calvo, 1994; Barrett & Upchurch, 1995; Barrett, 1998, in press; Upchurch & Barrett, 2000). Some herbivorous dinosaurs were able to chew or slice their food using sophisticated jaw mechanisms analogous to those employed by living mammals [e.g. ornithopods, ceratopians (Ostrom, 1966; Norman & Weishampel, 1985, 1991)], while others relied on gastric mills, lengthy digestive tracts and slow passage times to break down their plant food (e.g. prosauropods, sauropods; Farlow, 1987). A

minority of these animals were small, with adult body lengths of around 1–2 m and body masses of only a few kilograms (e.g. *Heterodontosaurus, Hypsilophodon*), but the majority of herbivorous dinosaurs were large, with body masses in excess of 1000 kg (Wing & Tiffney, 1987*a, b*; Farlow, Dodson & Chinsamy, 1995). As a result, they must surely be regarded as 'megaherbivores' (*sensu* Owen-Smith, 1988). The very largest herbivorous dinosaurs, the sauropods, are estimated to have consumed approximately 200 kg of fodder per day (Weaver, 1983; Colbert, 1993). Furthermore, herbivorous dinosaurs accounted for around 95 % of the vertebrate biomass in some, if not all, Late Mesozoic faunas (e.g. Bakker, 1978; Galton, 1985*b*). Consequently, dinosaurs must have had a considerable impact on contemporary vegetation.

While dinosaurs were the dominant vertebrate herbivores, several changes took place in the taxonomic and ecological composition of Mesozoic plant communities. The most obvious of these changes was the appearance of angiosperms in the Early Cretaceous and their subsequent radiation. Some of the most intriguing plant–herbivore coevolutionary scenarios are those that implicate herbivorous dinosaurs in the origin and early diversification of angiosperms (Bakker, 1978; Wing & Tiffney, 1987*a, b*; Weishampel & Norman, 1989).

The aim of this review is to assess critically hypotheses of dinosaur–angiosperm coevolution. In essence we ask two separate questions: can dinosaurs be implicated in the origin of angiosperms, and did changes in dinosaur browsing behaviour influence the subsequent angiosperm radiation? Current palaeobiological, palaeogeographical and stratigraphical data have been used in order to test the assumptions on which these hypotheses have been based, and to test the palaeobiogeographical and palaeoecological predictions made by these models.

Sereno (1997) presented a superficial analysis of dinosaur–angiosperm coevolution that attempted to test the temporal congruence of evolutionary events in clades of herbivorous dinosaurs and angiosperms. This analysis concluded that there was no strong evidence for dinosaur–angiosperm coevolution, but did not distinguish between the separate issues of angiosperm origin and angiosperm diversification. Moreover, Sereno's (1997) analysis was limited to a temporal comparison of the dinosaur and plant records and did not consider other lines of evidence (spatial comparisons, direct evidence of dinosaur diets, other palaeobotanical data on angiosperm biomass, physiognomy etc.). Taggart & Cross (1997)

have suggested that there was limited potential for dinosaur–angiosperm coevolution, due to the relatively short period of time during which angiosperms would have contributed significantly to the total amount of available dinosaur fodder, although they did not address this question in detail. A recent reassessment of ornithischian diversity patterns (Weishampel & Jianu, 2000) has also questioned some of the assumptions underlying angiosperm–dinosaur coevolution. These arguments, and others, are presented and assessed, below.

(2) Previous models of dinosaur–angiosperm coevolution

Bakker (1978, 1986) has proposed that the origin of angiosperms was correlated with large-scale changes in the composition of dinosaur faunas that occurred at the Jurassic/Cretaceous boundary. Concomitant changes in the prevailing regime of dinosaur browsing behaviour were suggested to have created ecological conditions that fostered the origin and diversification of angiosperms and enabled angiosperms to replace gymnosperms as the dominant component of Cretaceous floras. The main points in Bakker's argument are summarised below.

Late Jurassic terrestrial floras were composed of various gymnosperms, including plants of tree-stature, such as conifers (Araucariaceae, Cephalotaxaceae, Pinaceae, Podocarpaceae, Taxaceae etc.), gingkos and some bennettitaleans, and herbaceous plants like *Equisetum* and various pteridophytes and cycadophytes (Wing & Sues *et al.*, 1992). Sauropod dinosaurs were the dominant terrestrial vertebrate herbivores at this time, in terms of both diversity (McIntosh, 1992) and biomass (e.g. Dodson *et al.*, 1980; Russell, Béland & McIntosh, 1980), and Bakker (1978, 1986) regarded sauropods as high-browsers that used their elongate necks to reach foliage in tree canopies up to 12 m above ground-level. As a result, browsing pressure on the canopies of mature trees would have been high, but Bakker noted that living megaherbivores rarely cause the death of the adult sporophyte. The preponderance of high-browsing forms, which only infrequently browsed nearer ground level, permitted the development of gymnosperm saplings, which are slow growing and far less tolerant to herbivore damage than adult trees.

By contrast, Early Cretaceous dinosaur communities were dominated by low-browsing ornithischian dinosaurs, such as ornithopods and nodosaurid ankylosaurs, which had browse heights that rarely

exceeded 3 m. Sauropods, though still present, were severely reduced in numbers and generic-level diversity. Consequently, browsing pressure on low-stature vegetation was greatly increased from Late Jurassic levels. Bakker argued that this shift in dinosaur browsing behaviour facilitated the origin of angiosperms by creating highly disturbed environments from which gymnosperms, by virtue of their low tolerance to herbivory, had been excluded. It was suggested that the compressed life histories of angiosperms might have appeared in response to this vegetational disturbance, allowing them to colonise these areas. Continuing disturbance caused by low-browsing herbivores favoured the radiation of angiosperms and eventually led to their ecological dominance (Bakker, 1978, 1986).

Several other authors have extended and augmented Bakker's (1978, 1986) hypothesis. Comparison of the floral and faunal records led Weishampel & Norman (1989) to suggest that the rise of angiosperms may have been linked to the radiation of ornithopods with pleurokinetic jaw mechanisms. Pleurokinesis (slight lateral mobility of the upper jaws; see Norman, 1984; Weishampel, 1984a) allows the production of a transverse power stroke, analogous to that of mammals, during bilateral isognathous jaw closure, and it was suggested that the diversification of these more sophisticated low-browsers drove, or was driven by, the radiation of angiosperms. Analysis of various evolutionary metrics (speciation and extinction rates) seemed to confirm this hypothesis, as increases in angiosperm speciation rates coincided well with peaks in ornithopod speciation rates (Weishampel & Norman, 1989).

Wing & Tiffney (1987a, b) demonstrated that most Early Cretaceous dinosaur communities were dominated by animals with body masses in excess of 1000 kg. In modern faunas, large herbivores have generalist diets, and also require larger amounts of fodder than small herbivores (cf. Jarman, 1974). This observation led Wing & Tiffney (1987a, b) to suggest that Early Cretaceous herbivorous dinosaurs were generalist feeders, with high daily energy requirements. Such large herbivores would have caused major vegetational disturbance, and it was suggested that this dinosaur-mediated disturbance fostered the angiosperm radiation. Habitat disturbance prevented the dominance of large angiosperms and facilitated the growth of low-stature, high productivity plants, which may, in turn, have allowed the diversification of low-browsing herbivores (Wing & Tiffney, 1987a, b).

II. INTERPRETATION OF THE DATA – THE PROBLEM OF BIAS

Models of dinosaur–angiosperm coevolution are based upon a number of assumptions, namely: (i) that the known distribution data for Early Cretaceous herbivorous dinosaurs and angiosperms in both time and space is truly representative of Early Cretaceous ecosystems; (ii) that dinosaur and angiosperm taxonomies are essentially correct; and (iii) that all of the localities that have yielded the remains of Early Cretaceous dinosaurs and angiosperms are dated accurately. These assumptions are discussed below.

(1) Sampling problems

Macroevolutionary models that are based upon the presence or absence of taxa in particular geographical regions or time intervals face the problem of distinguishing between genuine absence and pseudo-absence. While a taxon may appear to be genuinely absent from a region/time interval in the fossil record, it may be that the region in question has not been fully sampled (Raup, 1979). This under-sampling may be due to a lack of exploration: for example, much of Gondwana is underexplored in comparison with North America and Europe and relatively few dinosaur localities are known from the southern continents (Weishampel, 1992). This situation is changing, however, and recent work in Gondwana is yielding spectacular results (e.g. Bonaparte, 1996; Novas & Molnar, 1996; Sereno et al., 1994, 1999; Sampson, Krause & Forster, 1997; Tomida, Rich & Vickers-Rich, 1999). New material from this region is likely to fuel an explosion in our knowledge of Mesozoic terrestrial ecosystems. The collection biases of individual palaeontologists might also be an important component of sampling error.

Aside from these artificial sampling errors there is the fundamental problem of a real lack of data (Raup, 1979). Some regions may not have surface deposits of either the appropriate age or representative of the appropriate palaeoenvironment to answer questions of presence or absence for some taxa. In these cases, it is possible that the taxon of interest may have been present in a region, but the deposits in which it was preserved are either buried well below the surface or have been eroded away. There are also taphonomic considerations (Raup, 1979; Behrensmeyer & Hook et al., 1992); if the conditions for preservation are not met, the taxon would appear to have been absent from the

region/time interval under scrutiny, even if it was actually present. Fuller discussions of sampling problems can be found in Raup (1979), King (1990) and Behrensmeyer & Hook *et al.* (1992).

(2) Problems with taxonomy

Good taxonomy is essential in order to allow the proper identification of the specimens on which any evolutionary model is based. Incorrect identification of a specimen may artificially extend the spatial and/or temporal range of a taxon, or may provide misleading ecological or palaeobiological information. However, the taxonomy of herbivorous dinosaurs is fairly well established (see the relevant chapters in Weishampel, Dodson & Osmólska, 1992) and major misidentifications of dinosaur material are comparatively rare, although it is not always possible (or desirable) to identify scrappy material to higher taxonomic levels. The identification of specimens to the level of a major clade (e.g. iguanodontian ornithopod) is sufficient for the present analysis. Although the familial- and ordinal-level taxonomy of early angiosperms is poorly known, it is relatively easy to distinguish between angiosperm pollen and the pollen of other seed plants; this level of identification is adequate for dealing with questions regarding the time of origin for angiosperms. Further questions, relating to the subsequent radiation of angiosperms, require a more precise taxonomy. Fortunately, the fossil record of angiosperms in the mid – Late Cretaceous is rich enough to allow the construction of a working taxonomy. Many Late Cretaceous palynomorphs and macrofossils can be assigned to taxa with extant representatives, greatly reducing taxonomic uncertainty.

(3) Problems with stratigraphy and dating

The majority of dinosaur and angiosperm remains are recovered from terrigenous sediments, reflecting the terrestrial habitus of these taxa. As a result, correlation with the standard marine stages is difficult, relying in part on occasional marine transgressions. Radiometric dating is not usually applicable to sedimentary sequences unless they incorporate evidence of volcanic activity (such as extrusive lava flows or intrusive dykes and sills). Biostratigraphic correlation provides some constraints on the dating of these formations but is dependent on the identification of abundant, diagnostic index fossils.

In some cases, the stratigraphy of dinosaur- and angiosperm-bearing sediments can be highly re-solved and well constrained. Some formations can be dated to a stage or sub-stage with a high level of precision (see listings in Weishampel, 1992; D. B. Weishampel, J. Le Loeuff, R. A. Coria, E. M. Gomani, X.-J. Zhao, X. Xu, P. M. Barrett and A. Sahni, in preparation). In other cases, however, the stratigraphy is poorly resolved and poorly constrained leading to less precise age estimates: for example, many of the richly fossiliferous sedimentary deposits in Sichuan Province, People's Republic of China can only be dated to either Middle or Late Jurassic due to the lack of marine incursions and volcanics in these sequences (Dong, 1992). Imprecise dating can lead to erroneous data on the times of taxon origin and extinction. Furthermore, if a particular deposit cannot be dated with certainty, it becomes increasingly difficult to make meaningful comparisons between this deposit and other localities.

(4) Rationale

Despite the aforementioned constraints we believe that it is important to construct and test macro-evolutionary hypotheses in an attempt to gain a better understanding of the history of life. The discovery of new data, and the refinement of current data, allow for continuous testing of existing hypotheses and provide fertile ground for the germination of novel ideas. Moreover, several studies have suggested that the Mesozoic fossil record is complete enough to attempt to answer these kinds of macroevolutionary questions (Foote & Sepkoski, 1999; Benton, Wills & Hitchin, 2000; Fara & Benton, 2000).

Here, we use current data to test the bases and predictions of hypotheses of dinosaur–angiosperm coevolution, but acknowledge the fact that new data (e.g. the discovery of new taxa, extension of the geographical and spatial ranges of taxa, and additional direct evidence of dinosaur–angiosperm interactions) may necessitate a reappraisal of our conclusions at a later date.

III. SPATIOTEMPORAL COMPARISON OF THE FLORAL AND FAUNAL RECORDS

(1) The ecology and radiation of Cretaceous angiosperms

(a) *Time of angiosperm origin*

A number of authors have advocated a pre-Cretaceous origin for angiosperms, based on phylo-

genetic arguments (using both morphological and molecular data), palaeontological evidence and molecular clock studies.

Cladistic analyses using morphological characters have provided strong support for the 'anthophyte hypothesis' – the suggestion that angiosperms form a monophyletic clade with Gnetales, Bennettitales, Pentoxylales and Caytoniales. In this scheme, angiosperms are regarded as either the sister-taxon to a monophyletic clade of Gnetales + Bennettitales + Pentoxylales (Doyle & Donoghue, 1993; Doyle, 1998 a, b), the sister-taxon to a monophyletic Gnetales (Crane, 1985) or are nested within a paraphyletic Gnetales (Nixon et al., 1994; Hickey & Taylor, 1996). Several molecular phylogenies support the anthophyte hypothesis and provide evidence for a monophyletic Gnetales that is the sister-taxon of the angiosperms (Hamby & Zimmer, 1992; Stefanovic et al., 1998). As Gnetales and bennettitaleans are present in pre-Cretaceous floras, many of these phylogenies imply that the divergence between Gnetales and angiosperms occurred in the Triassic or Jurassic (Crane, 1985; Hamby & Zimmer, 1992; Doyle & Donoghue, 1993; Doyle, 1998 a, b; Stefanovic et al., 1998). However, if angiosperms are nested within Gnetales it is possible that they diverged as recently as the Early Cretaceous (Nixon et al., 1994; Hickey & Taylor, 1996).

The close relationship of angiosperms and Gnetales has been questioned recently by several studies that have proposed seed plant phylogenies on the basis of mitochondrial, nuclear, chloroplast and plastid gene sequences (Qui et al., 1999; Bowe, Coat & de Pamphilis, 2000; Chaw et al., 2000). These phylogenies either nest the Gnetales within the conifers or place Gnetales as the sister-taxon to Coniferales, implying that the divergence between angiosperms and other seed plants might have occurred during the Carboniferous, around 290 million years ago (Kenrick, 1999; Bowe et al., 2000).

Molecular clock studies have suggested a Triassic (Li et al., 1989) or Permian (Martin, Gierl & Saedler, 1989) origin for angiosperms. Recent estimates, based on a phylogeny of monocotyledonous angiosperms calibrated with minimum divergence times from fossils, led Bremer (2000) to conclude that the major radiation of monocots occurred during the late Early Cretaceous and that the monocot/dicot split had occurred sometime earlier in either the Jurassic or the Triassic, although the latter was considered less likely.

A great deal of phylogenetic evidence therefore postulates a long pre-Cretaceous history for the angiosperms. However, no convincing fossil evidence of pre-Cretaceous angiosperms has been found to date. Many putative pre-Cretaceous angiosperm palynomorphs and megafossils have been shown to pertain to other plant groups (Scott, Barghoorn & Leopold, 1960), although several of these taxa, such as the Late Triassic Sanmiguelia (Cornet, 1989) remain enigmatic. It seems likely that Sanmiguelia and several other Late Triassic taxa with 'angiospermoid' features are basal members of the anthophyte radiation (Wing & Boucher, 1998).

In a recent report, Sun et al. (1998) announced the discovery of an angiosperm megafossil (Archaefructus liaoningensis) from the lower part of the Yixian Formation of Liaoning Province, People's Republic of China. This find was hailed as the earliest-known angiosperm as the lower part of the Yixian Formation was considered to be of Late Jurassic age on the basis of biostratigraphical correlations (Sun et al., 1998). Several lines of evidence, however, indicate that the Yixian Formation is of late Early Cretaceous age (Luo, 1999; Swisher et al., 1999; Barrett, 2000). A recent radiometric study, which used ^{40}Ar–^{39}Ar techniques to date tuffs collected from extrusive volcanic strata within the lower part of the Yixian Formation, has provided a well-constrained age of 124.6 ± 0.1 million years (Ma) placing this unit within the Barremian stage of the Early Cretaceous (Swisher et al., 1999). Some palaeontological evidence also supports a late Early Cretaceous age for these deposits. Material referable to the ceratopian dinosaur Psittacosaurus has been reported from the Yixian Formation (Xu & Wang, 1998), and there is a general consensus that Psittacosaurus is restricted to late Early Cretaceous (Barremian–Albian) units, a conclusion supported by radiometric dating of several Psittacosaurus localities (Eberth et al., 1993). This evidence casts serious doubts on the supposed Late Jurassic age of the lower part of the Yixian Formation, and on the claim that this unit has yielded the first undoubted pre-Cretaceous angiosperm megafossil (Swisher et al., 1999; Barrett, 2000). If the lower part of the Yixian Formation is of late Early Cretaceous age, the presence of angiosperms would hardly be surprising as the angiosperm radiation was well underway by this time (see below). Moreover, the affinities of several putative angiosperm taxa from the Early Cretaceous of China (including Archaefructus, Eragrosites and Chaoyangia) have been questioned, and it is likely that some or all of these taxa are referable to Gnetales (Sun et al., 1998; J. Hilton, personal communication). [Some geologists regard the lower

beds of the Yixian Formation as a separate litho-logical unit that has been referred to as the Chaomidianzi Formation (e.g. Chiappe *et al.*, 1999). In this scheme, the Yixian Formation *sensu stricto* conformably overlies the Chaomidianzi Formation. The radiometric ages quoted for the main fossili-ferous horizons of this series are based on measure-ments from the tuff layers in the lower beds of the Yixian Formation *sensu lato* (Swisher *et al.*, 1999) which are considered to be equivalent to the strata of the Chaomidianzi Formation (e.g. Chiappe *et al.*, 1999). Consequently, in this scheme the Chao-midianzi Formation is considered to be of Barremian age (Luo, 1999; Swisher *et al.*, 1999; Barrett, 2000), while the overlying Yixian Formation (*sensu stricto*) must be of late Early Cretaceous (?Aptian) age.]

The earliest unequivocal angiosperms are rep-resented by pollen grains from the late Valanginian–Hauterivian (approximately 134–127 Ma) of Israel (Brenner, 1996). The pattern of angiosperm diversi-fication, as revealed by the fossil record, begins with the appearance of primitive magnoliid pollen in the earliest Cretaceous (Valanginian) and is followed by the radiation of basal angiosperms and the origin and diversification of monocots and eudicots in the late Early Cretaceous and early Late Cretaceous (e.g. Drinnan, Crane & Hoot, 1994; Friis, Crane & Pedersen, 1997; Friis, Pedersen & Crane, 1999; Gandolfo *et al.*, 1998; Magallon, Crane & Heren-deen, 1999; Pole, 1999). Angiosperm remains are rare in Hauterivian sediments, but increase in both diversity and abundance through the Barremian, culminating in speciose Albian–Cenomanian palyno-floras and megafloras (see reviews in Wing & Sues *et al.*, 1992; Wing & Boucher, 1998 and references cited therein). This sequence of events is congruent with the majority of proposed angiosperm phylo-genies (which suggest that monocots and eudicots are derived from several 'primitive' dicot clades; see Crane, Friis & Pedersen, 1995; Doyle, 1998*b*; Soltis, Soltis & Chase, 1999; Qui *et al.*, 1999) and does not imply the presence of significant pre-Cretaceous ghost lineages (Hughes, 1994; Crane *et al.*, 1995; Wing & Boucher, 1998). The apparent absence of unequivocal angiosperm pollen or megafloral re-mains in Triassic and Jurassic sediments and the observation that the earliest-known angiosperms are also the most primitive has convinced many authors that the origin of angiosperms occurred sometime in the lowermost Cretaceous (e.g. Crane *et al.*, 1995; Wing & Boucher, 1998).

Moreover, the results of the molecular phylo-genetic studies mentioned above must be treated with caution as they cannot access data from those extinct plants that are thought to be closest to the origin of angiosperms, the Caytoniales, Bennettitales, most members of the Gnetales and the stem-group angiosperms (Doyle, 1998*a*). Comparison of the gene sequences of a few derived representatives of one of these groups (only Gnetales can yield molecular data – all Caytoniales and Bennettitales are extinct) with those of extant conifers and angiosperms might be expected to give different results from those proposed by morphological studies that are based largely on extinct 'primitive' taxa. The deep divergences within seed plant phylogeny are also subject to the errors inflicted by long-branch attraction, a phenomenon that may cause distantly related, anciently separated lineages to cluster in a phylogenetic analysis (Felsenstein, 1978; Doyle, 1998*a*, *b*). Moreover, refutation of the anthophyte hypothesis requires an unprecedented amount of morphological homoplasy (Doyle, 1998*b*). Parsi-mony suggests that the anthophyte hypothesis is preferable to the alternatives in which angiosperms are the sister-taxon of all other seed plants as the latter hypotheses require a large number of ad-ditional evolutionary steps (Doyle, 1998*b*), including either the convergent acquisition of double fertili-sation and flower-like structures in Gnetales and angiosperms, or the multiple loss of these characters in many disparate gymnosperm lineages (Bowe *et al.*, 2000; Chaw *et al.*, 2000). A close relationship between angiosperms and Gnetales accords well with evolutionary scenarios for the origin of many angiosperm features, such as flowers (Hickey & Taylor, 1996). Finally, if these molecular phylo-genies are correct, the resulting angiosperm ghost lineage spans more than 150 million years. By comparison, many morphological analyses yield much shorter ghost lineages that extend into the Jurassic or Triassic (assuming that Gnetales is monophyletic; Crane, 1985; Doyle & Donoghue, 1993; Doyle, 1998*a*, *b*). If Gnetales is paraphyletic with respect to angiosperms (Nixon *et al.*, 1994; Hickey and Taylor, 1996) then the presence of the gnetaleans *Gnetum* and *Welwitschia* in Early Cre-taceous sediments would indicate that there was no notable lag between the divergence of these taxa and the earliest-known angiosperms and there would be no significant ghost lineage. Consequently, mor-phological phylogenies [particularly those of Nixon *et al.* (1994) and Hickey & Taylor (1996)] show a greater degree of congruence with the stratigraphical distribution of angiosperms, gnetaleans, bennetti-taleans and gymnosperms than those phylogenies

based on molecular data. The results of several molecular clock studies (Li *et al.*, 1989; Martin *et al.*, 1989) are subject to doubt as their phylogenetic methodology is flawed (Crane *et al.*, 1989), they have not adequately justified the assumption that rates of molecular evolution in angiosperms have remained constant through time, and they suffer from a lack of congruence with the angiosperm fossil record. Although certain aspects of Bremer's (2000) study are congruent with the fossil record [several lineages of monocots are now known from both palynofloras and megafloras of late Early Cretaceous (Barremian–Albian) age; e.g. Friis *et al.* (1999); Pole (1999)], the predicted presence of pre-Cretaceous angiosperm lineages cannot be confirmed by palaeontological data at present.

At this time, we accept an earliest Cretaceous origin (?Valanginian) for flowering plants on the basis of current palaeontological evidence (Brenner, 1996), a conclusion that is supported by some stratigraphically congruent morphological phylogenetic evidence (Nixon *et al.*, 1994; Hickey & Taylor, 1996). Alternative hypotheses in which angiosperms originated prior to the Cretaceous are not supported by the fossil record (Crane *et al.*, 1995; Wing & Boucher, 1998), require an unprecedented amount of morphological homoplasy (Doyle, 1998*b*) and conflict with the predictions made by several phylogenetic studies (Nixon *et al.*, 1994; Hickey & Taylor, 1996).

(b) Early angiosperm ecology and physiognomy

Evidence of pre-Aptian angiosperms is found mainly in the palynological record (e.g. Traverse, 1988; Crane & Lidgard, 1989; Brenner, 1996), although rare macrofossils are also known (e.g. Sun *et al.*, 1993). From the Aptian onwards, angiosperm leaves, fruits and flowers (Taylor & Hickey, 1990; Endress, 1987; Friis & Crepet, 1987) become much more abundant, allowing reconstruction of both the morphology and ecology of these early flowering plants.

Early angiosperms are morphologically conservative and are usually referred to the extant sub-class Magnoliidae (Hughes, 1976, 1994; Hickey & Doyle, 1977; Dilcher & Crane, 1984; Friis & Crepet, 1987; Traverse, 1988; Taylor & Hickey, 1990; Crane *et al.*, 1995). More precise taxonomic assignments can be made on the basis of floral anatomy, and two broad groups can be recognised (Endress, 1987); those with relatively few floral components and small

(< 1 mm in diameter), possibly unisexual, flowers, and those with numerous floral components and large bisexual flowers (up to 65 mm in diameter). The former have been compared with the extant dicotyledonous families Chloranthaceae, Piperaceae and Platanaceae, and the latter are usually included within the Magnoliaceae, Degeneraiaceae and Winteraceae (Endress, 1987; Friis & Crepet, 1987).

Since most of these families have both arborescent and non-arborescent forms, the question of whether the first angiosperms were predominately trees, shrubs or herbs has been contentious. Early angiosperm wood is rare in the fossil record; all of the large-diameter stems recovered from major Early and early Late Cretaceous fossiliferous deposits are attributed to coniferous taxa (Doyle & Hickey, 1976; Hickey & Doyle, 1977; Herendeen, 1991), and it is not until the latest Cretaceous or early Tertiary that a diverse angiosperm wood flora becomes established (Wing & Tiffney, 1987*b*; Wheeler & Baas, 1993; Wing, Hickey & Swisher, 1993). However, this may reflect taphonomic bias; for example, early angiosperm wood may have been less resistant to decay and more prone to damage by low-browsing herbivores than conifer wood or the wood of more advanced angiosperms.

Other features of early angiosperms, however, appear to support a primitive herbaceous habit (for a review see Taylor & Hickey, 1996). These features include small seed sizes (1–40 mm in length), thin seed walls (Tiffney, 1984; Wing & Tiffney, 1987*a, b*) and small leaves (2–4 cm in diameter) with expanded laminae and reticulate venation patterns (Hughes, 1994). In extant plant groups, these features are typical of small, weedy plants with a rapid life cycle. Such plants are usually found in highly disturbed environments like riparian channels. Sedimentological evidence demonstrates that most early angiosperm fossils are recovered from over-bank and stream-channel deposits (Taylor & Hickey, 1996), an observation that adds further support to the suggestion that the majority of the earliest angiosperms were probably early colonisers, situated in sites of relatively high physical disturbance.

Although the earliest angiosperms are present in the geological record from approximately 135 Ma, in terms of species numbers and overall abundance they remained a minority group until approximately 100 Ma (Hughes, 1994; Niklas, 1997; Niklas, Tiffney & Knoll, 1983, 1985). Between 100 and 70 Ma, however, angiosperms rapidly increased in species-level diversity. This increase in diversity has

often been taken as a proxy for an increase in ecological importance or biomass, but this may not be the case. The biomass of Early Cretaceous angiosperms seems to have been extremely low, and did not increase significantly until the Late Cretaceous (Wing & Sues *et al.*, 1992; Wing, Hickey & Swisher, 1993; Lupia, Lidgard & Crane, 1999). Although mid-Cretaceous angiosperms are reasonably diverse taxonomically, remains of conifers and other plant groups continue to make up the majority of plant macrofossils at many localities. Angiosperms appear to have been subdominant members of mid- and early Late Cretaceous floras, and were present as an understory of shrubs and small trees in forests and open forests dominated by large coniferous trees. Ferns continued to be important constituents of low-level vegetation (e.g. Wing & Sues *et al.*, 1992; Wing et al. 1993; see also comments on Indian and South American floras below).

(c) Geographical distribution of Early Cretaceous angiosperms

There has been considerable debate in the palaeobotanical literature as to (i) the identity of the geographical area in which angiosperms originated and (ii) the biogeographical pattern of their subsequent radiation. Two approaches have been adopted in various attempts to answer these questions. The first approach has examined the present day distribution of primitive dicotyledonous families (e.g. Winteraceae and Magnoliaceae) and assumes that the area which possesses the greatest diversity of these primitive groups will also be the area of their origination (Takhtajan, 1969); the second approach uses evidence from the fossil record (palynofloras and macrofloras) to examine the geographical distribution of angiosperms through time (Schuster, 1972, 1976; Hughes, 1973; Lidgard & Crane, 1988, 1990; Crane & Lidgard, 1989; Drinnan & Crane, 1990). Both approaches have yielded broadly similar conclusions regarding the latitudes at which angiosperms evolved, but differ in their identification of the region in which angiosperms originated (see below).

Studies on the distribution of extant angiosperm taxa have led botanists to suggest that the geographical origin of angiosperms lay somewhere in south-east Asia (Takhtajan, 1969). This conclusion is based on three main observations [see Briggs (1995) for a summary of the evidence in support of this hypothesis]. Firstly, the greatest diversity of extant angiosperm families occurs in south-east Asia.

Secondly, members of those extant families that are considered to be the most primitive are most abundant and most diverse in south-east Asia, or in areas immediately adjacent to this region. Finally, many evolutionary lineages, each representing an almost continuous phylogeny from extremely primitive to derived taxa, are found in south-east Asia. The conclusion based upon these observations relies upon the following assumption: that the region which harbours the greatest diversity of angiosperms must *ipso facto* be the region in which angiosperms have had the greatest length of time in which to radiate into the greatest number of taxa (*c.f.* Briggs, 1995). Although this assumption may appear to be logically sound, it overlooks several factors that may have had a strong influence on angiosperm diversification and dispersal. These factors may include climatic changes through time, continental movements, extinction of a taxon in a part of its original range, and differential rates of evolution in various angiosperm lineages (Schuster, 1972, 1976). All of these factors are time-dependent and require knowledge of angiosperm history; this information is lacking from the essentially time-independent approach of biogeographic models based exclusively on extant material.

During the Early Cretaceous much of south-east Asia lay between palaeolatitudes of 0° and 30° North (Smith, Smith & Funnell, 1994). If the fossil record can substantiate the conclusions made on the basis of modern biogeography, this would suggest that angiosperms originated in the palaeotropics.

In our view, the fossil record presents much more compelling data on the geographical origins of angiosperms, as it provides information on what was actually happening during the Early Cretaceous at the time of the initial angiosperm radiation. Theoretically, this source of evidence is less prone to the problems associated with the use of extant angiosperm biogeography (see above) as it is essentially time-dependent. This approach is not without drawbacks, however, particularly as regards various forms of bias in the fossil record (see above).

The fossil record supports a low-palaeolatitudinal (palaeotropical) origin for angiosperms, as the earliest-known unequivocal angiosperm remains have been recovered from a number of localities with palaeolatitudes of between 0 and 30° North (Brenner, 1976; Hickey & Doyle, 1977). Fig. 1 represents a compilation of pre-Aptian (> 121 Ma) angiosperm occurrences (both palynological and macrofloral). The earliest well-dated angiosperm remains are palynomorphs from the late Valanginian
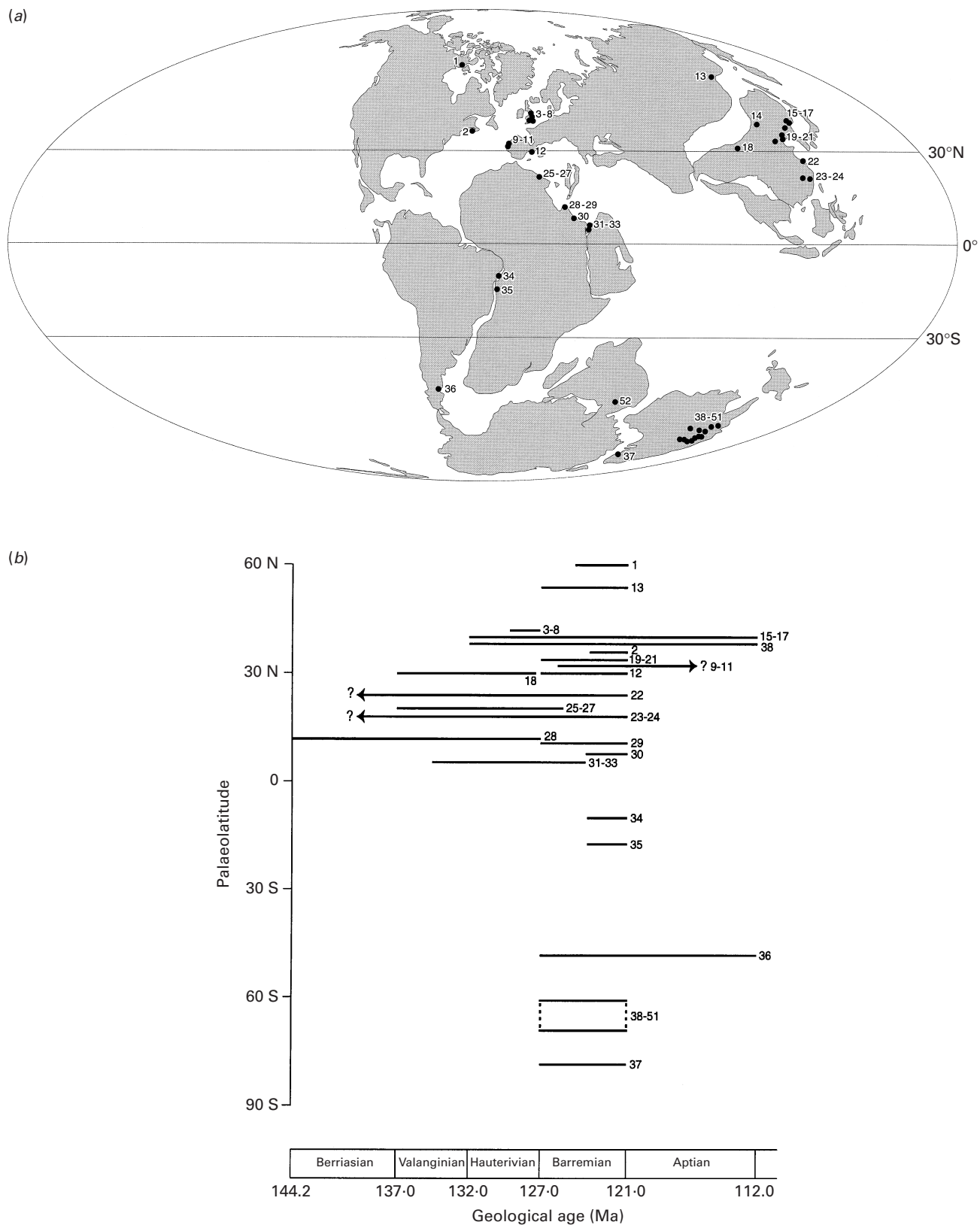
(a)

(b)

Fig. 1. (A) Global distribution of possible pre-Aptian Cretaceous (> 121 Ma) angiosperm occurrences, plotted onto a palaeogeographic map of age 135 Ma (Valanginian). Note that the oldest substantiated occurrences are located in northern Africa and the Levant. Localities: 1. Canada, Late Barremian (Burden & Hills, 1989); 2. Nova Scotia, Late

of Israel (Brenner, 1996) and Morocco (Gubeli, Hochuli & Wildi, 1984). A few occurrences of angiosperm pollen have been recorded from older (Berriasian) sediments in Libya (Thusu *et al.*, 1988) and China (Li & Liu, 1994), but the constraints on these dates are poor; in Libya these deposits could be as young as Hauterivian (Thusu *et al.*, 1988), while the Chinese sediments may be as young as Barremian (Li & Liu, 1994). Slightly younger (Hauterivian) palynomorphs are known from Morocco (Gubeli *et al.*, 1984), England (Hughes & McDougall, 1987, 1994), and possibly China (though the ages of the Chinese sediments are not well-constrained; Li & Liu, 1994). By the Barremian, angiosperms appear to have been widespread, and there are rich palynofloras from central Africa, Australia, Europe and China (see Fig. 1). Macrofloras are more poorly known. Several taxa have been described from late Hauterivian–Barremian strata (*Asiatofolium*, *Changzihella*, *Jixia*, *Shenkuoa*, *Regersia*- Sun *et al.*, 1993; *Archaefructus*, *Liaoxia*, *Eragrosites*, *Chaoyangia* - Sun *et al.*, 1998; Cao *et al.*, 1998; Duan, 1998) of China (including the lower part of the Yixian Formation – see comments above), from the Barremian of Russia (Vachrameev & Kotova, 1978), and from Barremian deposits in Portugal (*Anacostia*: Friis *et al.*, 1997).

The apparent North African–Levant distribution of the earliest angiosperms suggests that angiosperms may have originated in the Northern Gondwanan Palynological Province (Brenner, 1996). During the Early Cretaceous, this region lay between the palaeoequator and 25° North (Smith *et al.*, 1994). China may also have been an important area during the early radiation of angiosperms, but poorly resolved dating of these deposits, a situation that will hopefully improve in the future, prevents fuller discussion of the significance of the Chinese floras. Biogeographic evidence (see above) suggests that south-east Asia might have been a centre of angiosperm diversification, but the palaeobotanical record of this region is extremely poor at present, and little is known of early angiosperms in this area.

Angiosperms appear to have spread quickly into high-latitude areas during the Hauterivian–Barremian, but angiosperm remains from this time interval are extremely rare (Fig. 1). Angiosperm fossils become much more abundant during the Aptian–Albian stages, and it appears that the major poleward migration of angiosperms occurred at approximately 100 Ma, although differences in both diversity and abundance between low and high latitudes persisted for at least another 30 million years (Lidgard & Crane, 1988, 1990; Crane & Lidgard, 1989; Drinnan & Crane, 1990). By 70 Ma angiosperms dominated the diversity of the low-latitude palynofloras accounting for 60–80% of the pollen, whereas in the high latitudes, it accounted for between 30 and 50% of the total pollen (Crane, 1987). The remaining percentage of the flora in the high latitudes consisted of gymnosperms and pteridophytes. It is suggested that the apparent paucity of early angiosperms in these high-latitude environ-

Barremian (Doyle *et al.*, 1982); 3–8. England, various localities and horizons (Late Hauterivian–Barremian) (Hughes & McDougall, 1987, 1994; Hughes, Dewrey & Laing, 1979; Penny, 1989, 1992); 9–11. Portugal, various localities, Barremian–?Aptian (Friis *et al.*, 1997); 12. Spain, Barremian (Doubinger & Mas, 1981); 13. Russia, Barremian (Vachrameev & Kotova, 1978); 14–24. China, various localities and horizons (?Berriasian–Aptian) (Cao *et al.*, 1998; Duan, 1998; Gan & Zhang, 1985; Li & Liu, 1994; Sun *et al.*, 1993, 1998; Wang *et al.*, 1999); 25–27. Morocco, various horizons (Valanginian–Barremian) sampled in the same borehole (Gubeli *et al.*, 1984); 28–29. Libya, various horizons (Berriasian–Barremian) sampled in the same borehole (Thusu *et al.*, 1988); 30. Egypt, Late Barremian (Penny, 1989, 1992); 31–33. Israel, various localities and horizons (Late Valanginian–Barremian) (Brenner, 1974, 1996; Brenner & Bickoff, 1992; Conway, 1996); 34. Gabon, Late Barremian (Doyle *et al.*, 1977); 35. Congo, Late Barremian (Dejax, 1987 cited in Salard-Cheboldaeff, 1990); 36. Argentina, Barremian–Aptian (Archangelsky & Gamerro, 1967); 37. Australia, Barremian (Mitchell *et al.*, 1997); 38–51. Australia, Late Barremian (Burger, 1993); 52. India, ?Barremian–Aptian (Banerji, 2000). The wide age ranges given for some localities reflects current best estimates for the age of these deposits; it is likely that further work will allow more precise age estimates to be made. In addition, the upper boundaries of some of the geological units mentioned herein are considerably younger than the Barremian–Aptian boundary; these units have been included in this survey as their lower boundary is within the pre-Aptian Early Cretaceous, indicating that a substantial part of these units may have been deposited prior to the Aptian. Similar comments apply to the age-constraints on the dinosaur distribution data presented in Figs 3–5. (B) Graphical representation of the data presented on the palaeogeographic map in A. Solid horizontal lines represent the temporal ranges of primitive angiosperm taxa from specific localities. Numbers appended to each line correspond to the localities listed in A. Arrows and question marks at the termination of lines indicate uncertainty in the dating of the upper or lower boundaries of the strata in question. Note that the earliest occurrences of angiosperms all occur within 30° of the palaeoequator; angiosperms do not appear in higher latitudes until the Barremian.
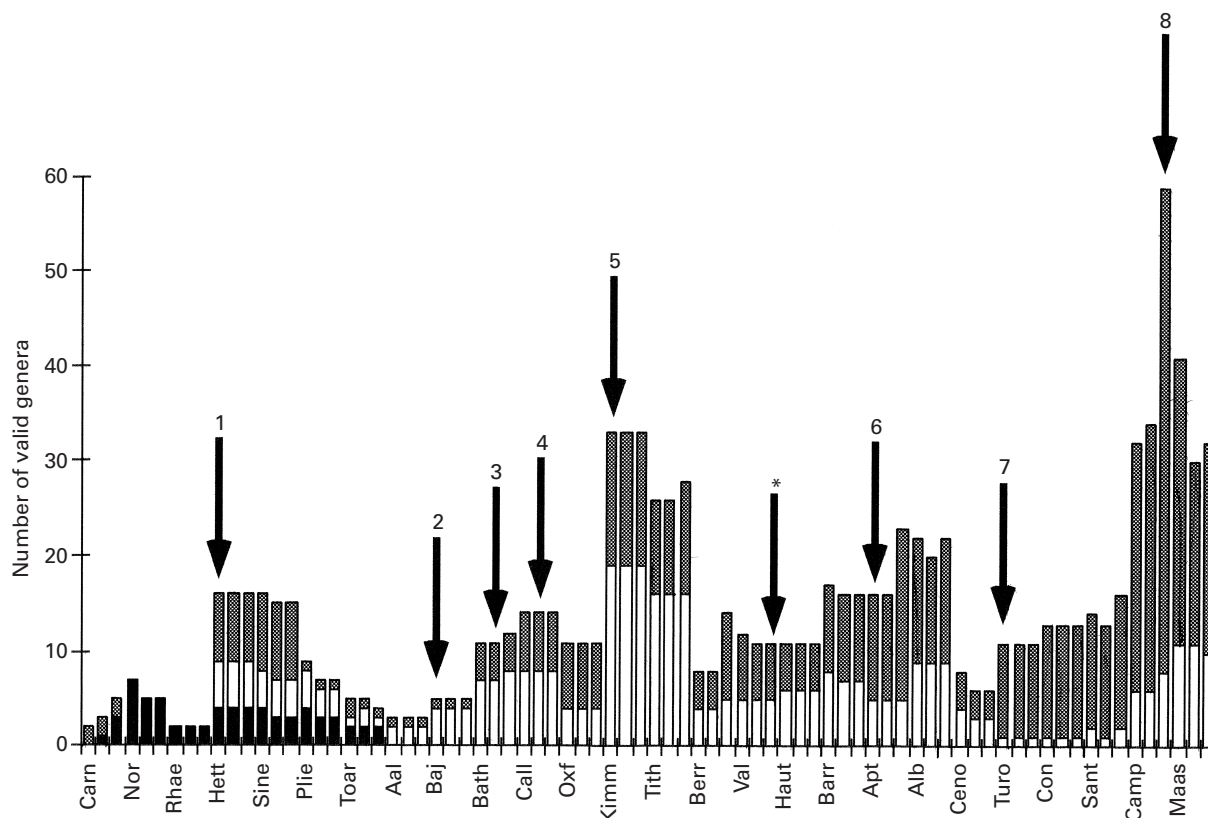
Fig. 2. Generic-level diversity of herbivorous dinosaurs through time (after Barrett, 1998). Unshaded areas represent sauropods, shaded areas represent prosauropods, and stippled areas represent ornithischians. The time of angiosperm origin is indicated by the asterisk. The numbered arrows indicate major events in the evolution of herbivorous dinosaurs. 1. Earliest-known occurrences of dinoturbated sediments; 2. Onset of the major stegosaur and sauropod radiations; 3. Earliest-known occurrences of hypsilophodontid ornithopods (?origin of pleurokinetic jaw mechanism); 4. Earliest-known occurrence of iguanodontid ornithopods (?origin of pleurokinetic jaw mechanism); 5. Acme of stegosaur and sauropod radiations; 6. Acme of iguanodontid radiation; 7. Onset of neoceratopian and hadrosaurid ornithopod radiations; 8. Acme of neoceratopian and hadrosaurid radiation. None of these events correlate with the origin of angiosperms. Abbreviations: Aal, Aalenian; Alb, Albian; Apt, Aptian; Baj, Bajocian; Barr, Barremian; Bath, Bathonian; Berr, Berriasian; Call, Callovian; Camp, Campanian; Carn, Carnian; Ceno, Cenomanian; Con, Coniacian; Haut, Hauterivian; Hett, Hettangian; Kimm, Kimmeridgian; Maas, Maastrichtian; Nor, Norian; Oxf, Oxfordian; Plie, Pliensbachian; Rhae, Rhaetian; Sant, Santonian; Sine, Sinemurian; Tith, Tithonian; Toar, Toarcian; Turo, Turonian; Val, Valanginian.

ments was due to limitations of light and temperature through a substantial part of the year. In these conditions conifer and fern vegetation would have offered few opportunities for the growth of 'weedy' angiosperms (Wing & Boucher, 1998).

Although the early angiosperms were originally an invasive element in the high-latitude regions, there is increasing evidence to suggest that these areas were centres of origination for later angiosperm groups. High-latitude environments, especially those in southern Gondwana, appear to have been centres of origination for species including *Nothofagus* (Dettmann *et al.*, 1990; Dettmann, 1992). *Nothofagus* is an important element in the present day temperate rainforests of the southern hemisphere and has a

fossil record that suggests it evolved in southern high latitudes at approximately 70 Ma (Hill & Scriven, 1995).

(2) Temporal and geographical distribution of Early Cretaceous dinosaurs and changes in dinosaur browsing behaviour

Assuming that angiosperms originated sometime during the Early Cretaceous (?Valanginian) in the palaeotropics (perhaps in northern Gondwana), we can now compare the timing of this event, and its location, with major events in the evolution of dinosaur herbivory. This approach examines the congruence between the floral and faunal records,

and thereby tests some of the major assumptions underlying hypotheses of dinosaur–angiosperm co-evolution.

Bakker's (1978, 1986) hypothesis predicts that: (i) there should be marked faunal turnover at the Jurassic/Cretaceous boundary, with an almost complete replacement of high-browsing sauropods by low-browsing ornithischians, principally ornithopods; (ii) that the radiation of low-browsing ornithischian dinosaurs should be coincident with the angiosperm radiation; and (iii) that low-browsing should be ecologically unimportant prior to the Early Cretaceous. This hypothesis also implies that other forms of dinosaur-mediated vegetational disturbance (such as sustained trampling) should be negligible prior to the advent of flowering plants. Finally, if the evolution of complex jaw mechanisms in herbivorous dinosaurs was linked to the origin or early radiation of angiosperms then there should be a strong temporal correlation between these two evolutionary events.

(a) Changes in dinosaur faunas through time

As demonstrated by Bakker (1978) sauropod diversity and abundance declined steeply at the Jurassic/Cretaceous boundary (Fig. 2). However, although the generic-level diversity of sauropods was greatly reduced, sauropods remained an important component of Early Cretaceous faunal diversity (McIntosh, 1992; Weishampel, 1992), with sauropods accounting for between 25 and 50 % of the total diversity of herbivorous dinosaurs at this time (Fig. 2).

Laurasian sauropods were greatly reduced in abundance during the Early Cretaceous, although they were still moderately diverse. For example, the Wealden Group (late Valanginian – early Aptian) of southern England has yielded the remains of several sauropod taxa (including brachiosaurids, a diplodocid and titanosaurids; see Upchurch, 1995), although each of these taxa is only represented by a few specimens (P. Upchurch, personal communication; P. M. Barrett, personal observations). This limited evidence, however, suggests that sauropods were well-established members of the Wealden fauna and not isolated curiosities, a conclusion supported by the presence of numerous sauropod footprints and trackways (Wright *et al.*, 1998). Recent discoveries in North America and Thailand have demonstrated that sauropods could be locally abundant in some Laurasian faunas (Kirkland *et al.*, 1997; Buffetaut & Suteethorn, 1998); indeed, in the Thai faunas

sauropods are the most abundant dinosaurs (Buffetaut & Suteethorn, 1998). Limited evidence from the People's Republic of China suggests that a diversity of sauropods also persisted in this region (Wiman, 1929; Dong, 1992).

From the Middle Jurassic onwards, sauropods were the dominant terrestrial herbivores in South America, and accounted for almost all of the generic-level diversity and biomass of herbivorous dinosaurs in this region (Bonaparte, 1986, 1996; McIntosh, 1992; Weishampel, 1992). Current evidence also indicates that sauropods were the most abundant members of Early Cretaceous dinosaur faunas in Africa (e.g. Jacobs *et al.*, 1993; Sereno *et al.*, 1994, 1999). A single fragmentary skeleton and a few isolated remains record the presence of sauropods in the Early Cretaceous of Australia (Molnar, 1980*b*). Early Cretaceous dinosaur faunas are currently unknown from India, Madagascar and Antarctica.

Low-browsing ornithischian dinosaurs were rare components of Early Cretaceous Gondwanan faunas (Bonaparte, 1986, 1996; Weishampel, 1992). The Early Cretaceous record from South America is particularly poor; a recent compendium of dinosaur localities (Weishampel, 1992) includes only two records of ornithischian body fossils from this region, although several ornithopod and ?thyreophoran trackways have also been documented. The African record is marginally better, although still poor, consisting of several ornithopod taxa from the late Aptian of Niger (Taquet, 1976; Galton & Taquet, 1982) and the Valanginian of South Africa (Cooper, 1985; de Klerk *et al.*, 1998), and a few indeterminate fragments. Australia has yielded the richest Early Cretaceous ornithischian faunas in Gondwana, including various ornithopods (Bartholomai & Molnar, 1981; Molnar & Galton, 1986; Rich & Vickers-Rich, 1989), a controversial record of a neoceratopian (Rich & Vickers-Rich, 1994), and the unusual ankylosaur *Minmi* (Molnar, 1980*a*).

In Laurasia, several clades of low-browsing dinosaurs (principally hypsilophodontid and iguanodontid ornithopods and nodosaurid ankylosaurs) diversified in the Early Cretaceous (Valanginian–Albian), but these radiations were limited in scope and produced a small number of genera (Fig. 2). Indeed, many Early Cretaceous dinosaur faunas are depauperate in comparison with those from the Late Jurassic and Late Cretaceous (see Fig. 2 and faunal lists in Weishampel, 1992). However, although Early Cretaceous Laurasian ornithischian faunas had a relatively low generic-level diversity, the taxa represented in these faunas could be extremely abun-
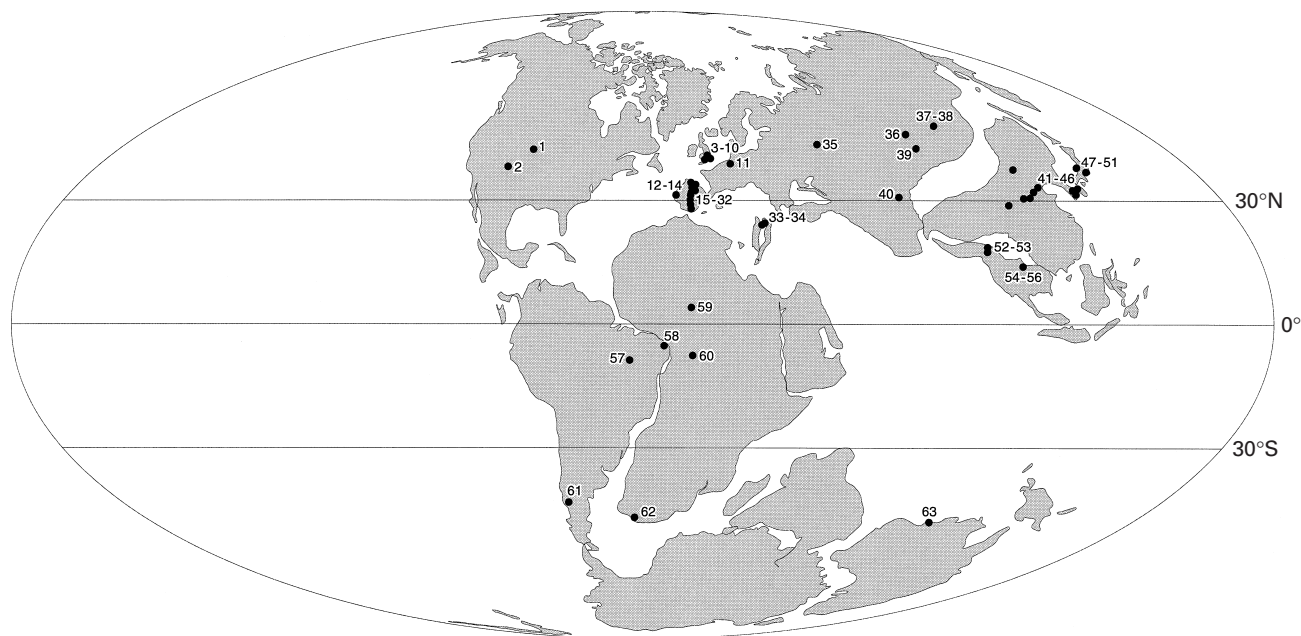
Fig. 3. Global distribution of pre-Aptian Cretaceous (> 121 Ma) sauropod occurrences, plotted onto a palaeogeographic map of age 135 Ma (Valanginian). Localities: 1. USA, Barremian; 2. USA, Berriasian–Hauterivian; 3–10. England, various localities and horizons (Berriasian–earliest Aptian); 11. France, Late Barremian; 12–14. Portugal, various localities and horizons (Berriasian–Middle Aptian); 15–32. Spain, various localities and horizons (Berriasian–Aptian); 33. Italy, Late Hauterivian–Early Barremian; 34. Croatia, Early Barremian; 35–38. Russia, various localities and horizons (Berriasian–Middle Aptian); 39. China, ?Valanginian–Albian; 40. Uzbekistan, Hauterivian–Barremian; 41–46. China, various localities and horizons (Berriasian–Albian); 47–48. South Korea, Berriasian–Hauterivian; 49–51. Japan, various localities and horizons (Berriasian–Hauterivian); 52–53. China, various localities and horizons (Berriasian–Albian); 54–56. Thailand, Hauterivian–Valanginian; 57–58. Brazil, pre-Aptian Early Cretaceous; 59. Niger, Hauterivian–Barremian; 60. Cameroon, Barremian–Aptian; 61. Argentina, Berriasian–Valanginian; 62. South Africa, Valanginian; 63. Australia, Berriasian–Hauterivian. Data from D. B. Weishampel, J. Le Loeuff, R. A. Coria, E. M. Gomani, X.-J. Zhao, X. Xu, P. M. Barrett and A. Sahni, in preparation).

dant. For example, the ornithopod dinosaur *Iguanodon* is known from thousands of specimens (Norman, 1980, 1986, 1987 *a, b*) which represent hundreds of individuals.

The global record of early Late Cretaceous (Cenomanian–Santonian) sauropods is extremely sparse, although this apparent rarity probably reflects poor sampling of this time interval. A number of often fragmentary specimens indicate that sauropods were present in South America, Africa, Europe, Central Asia and Australia at this time (Weishampel, 1992; Calvo & Salgado, 1995; Bonaparte, 1996), although our knowledge of these animals is extremely limited. The latest Cretaceous (Campanian–Maastrichtian) record is much richer, and dinosaur faunas in South America, Europe, India and Madagascar are dominated by titanosaurid sauropods, which are both diverse and abundant (e.g. Bonaparte, 1984, 1986, 1996; Dong, 1992; Le Loeuff, 1993; Jain & Bandyopadhyay, 1997; Sampson *et al.*, 1997; Curry & Forster, 1999).

Sauropod material has also been documented from the Campanian of New Zealand (Molnar & Wiffen, 1994). Only a single genus of sauropod was present in North America at this time (*Alamosaurus* – a titanosaurid), which is often regarded as an immigrant from South America (Bonaparte, 1984, 1986). The titanosaurid radiation accounts for most of the generic-level diversity of Late Cretaceous sauropods (McIntosh, 1992), and also constitutes around 25–35 % of the total generic-level diversity of non-North American herbivorous dinosaurs (P. M. Barrett, unpublished data). Most other sauropod lineages had become extinct by this time, but a radiation of nemegtosaurids took place in Mongolia (Upchurch, 1999), and there is additional evidence of other late-surviving diplodocoids from South America (Jacobs *et al.*, 1993).

Ornithischians continued to be rare components of Late Cretaceous Gondwanan faunas (Bonaparte, 1984, 1986). Fragmentary remains from India, mainland Africa, Madagascar, Australia and New
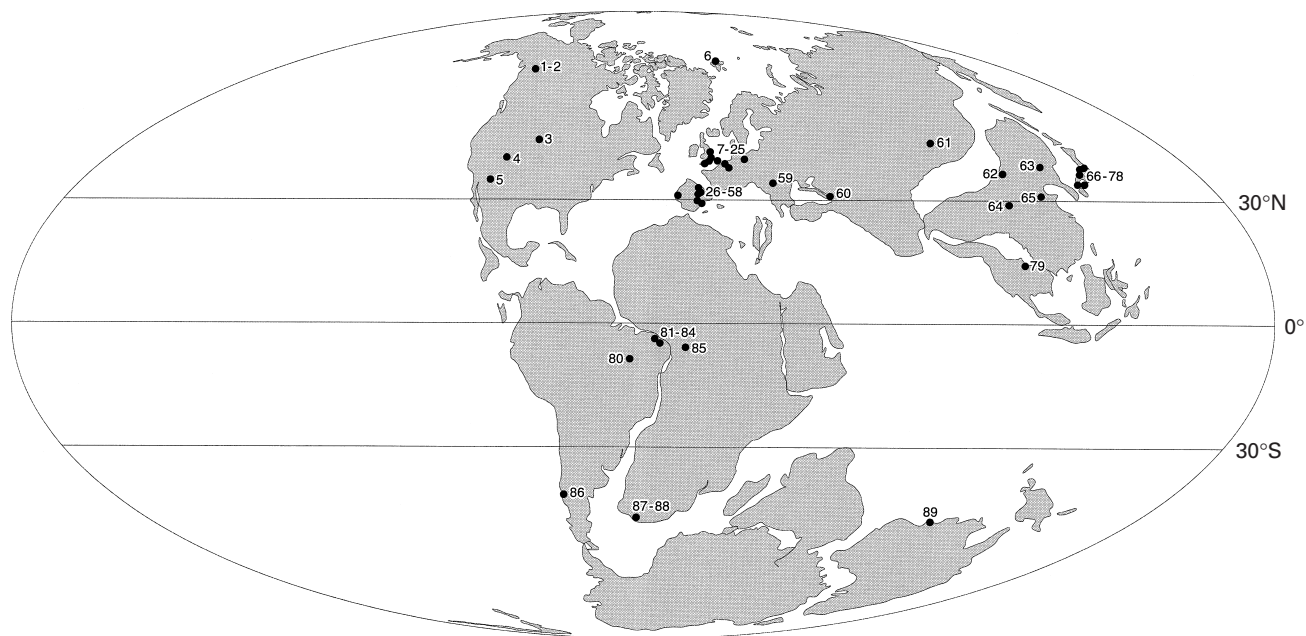
Fig. 4. Global distribution of pre-Aptian Cretaceous (> 121 Ma) ornithopod occurrences, plotted onto a palaeogeographic map of age 135 Ma (Valanginian). Localities: 1–2. Canada, Barremian–Aptian; 3. USA, Barremian; 4. USA, Berriasian–Hauterivian; 5. USA, Early Cretaceous; 6. Svalbard, Barremian; 7–19. England, various localities and horizons (Berriasian–earliest Aptian); 20. Belgium, Barremian–Aptian; 21–24. France, various localities and horizons (Hauterivian–Barremian); 25. Germany, Berriasian; 26–55. Spain, various localities and horizons (Berriasian–Aptian); 56–58. Portugal, various localities and horizons (Berriasian–Hauterivian); 59. Romania, Berriasian–Hauterivian; 60. Georgia, Berriasian–Hauterivian; 61. China, ?Valanginian–Albian; 62. Mongolia, Early Berriasian; 63–65. China, various localities and horizons (Early Cretaceous); 66–78. Japan, various localities and horizons (Berriasian–Aptian); 79. Thailand, Berriasian; 80–84. Brazil, various localities, all pre-Aptian Early Cretaceous; 85. Cameroon, Barremian-Aptian; 86. Chile, Hauterivian; 87–88. South Africa, various localities, all Valanginian; 89. Australia, Valanginian–Aptian. Data from D. B. Weishampel, J. Le Loeuff, R. A. Coria, E. M. Gomani, X.-J. Zhao, X. Xu, P. M. Barrett and A. Sahni, in preparation).

Zealand demonstrate the presence of ornithischians in these areas (Weishampel, 1992), but the material is not sufficiently well-preserved to permit detailed taxonomic assignments. Exploration of the Antarctic Peninsula has yielded partial skeletons of an ornithopod and a nodosaurid ankylosaur, and a single hadrosaur tooth (Hooker, Milner & Sequeira, 1991; Gasparini, Pereda-Suberbiola & Molnar, 1996). South American faunas are better-known, and contain rare hadrosaurid and iguanodontian ornithopods (Brett-Surman, 1979; Coria & Salgado, 1996), a dubious record of a ceratopid (Tapia, 1918), and fragmentary remains of armoured dinosaurs (Bonaparte, 1996; Salgado & Coria, 1996). These taxa are usually viewed as emigrees from North America, following the establishment of a Central/South American landbridge sometime during the Late Cretaceous (Bonaparte, 1984, 1986). Although the South American ornithischian fauna displays moderate familial-level diversity, generic-

level diversity and abundance are still very low in comparison with those of sauropods.

The evidence presented above demonstrates that faunal turnover at the Jurassic/Cretaceous boundary was a complex series of events that occurred over different time-scales in different regions. The decline in diversity of high-browsing sauropods was not a sudden event (*contra* Bakker, 1978), but transpired over a much longer period, and was limited to the northern continents. In Laurasia, the radiation of low-browsing ornithischians was coincident with sauropod decline; in Gondwana sauropods remained abundant and diverse, while ornithischians were rare. As a result, a dominant low-browsing regime was not established in the Early Cretaceous of Gondwana and some parts of Laurasia (south-east Asia), though low-browsing is likely to have been much more important over the remainder of Laurasia (principally Europe and North America) and Australia. Moreover, high-browsing sauropods
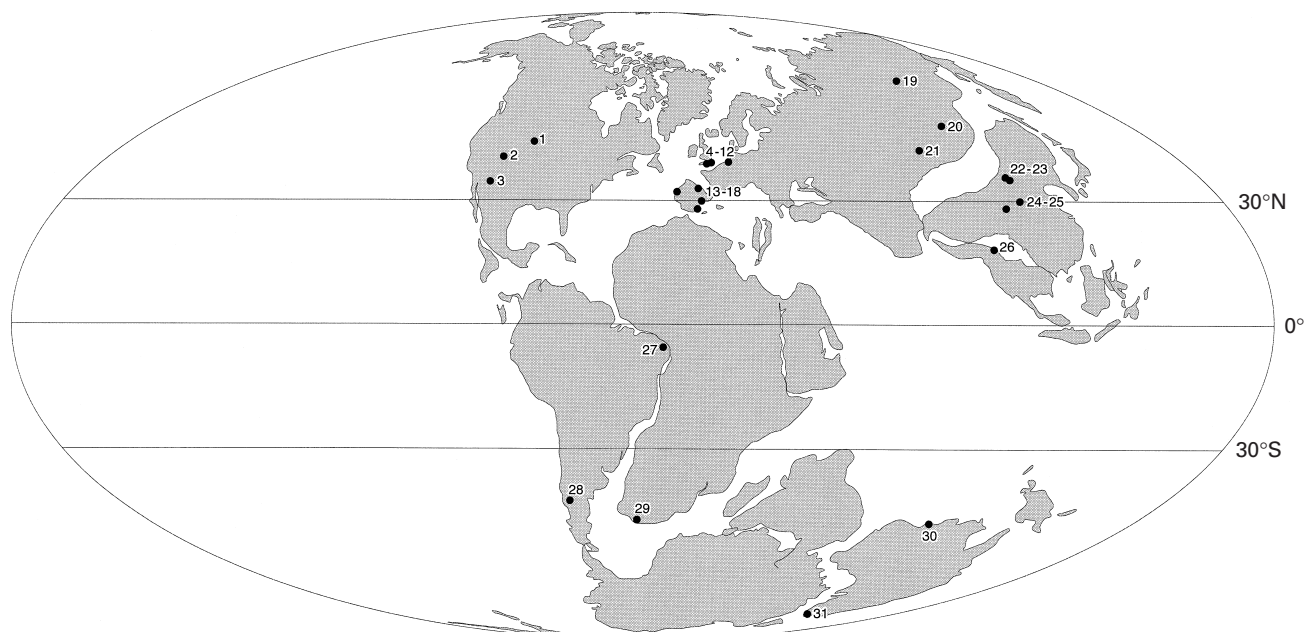
Fig. 5. Global distribution of pre-Aptian Cretaceous (> 121 Ma) thyreophoran (Ankylosauria + Stegosauria) occurrences, plotted onto a palaeogeographic map of age 135 Ma (Valanginian). Localities: 1–3. United States, various localities and horizons (?Berriasian–Barremian); 4–11. England, various localities and horizons (Berriasian–Early Aptian); 12. Germany, Berriasian; 13–17. Spain, various localities and horizons (Hauterivian–Albian); 18. Portugal, Early Berriasian; 19–20. Russia, various localities and horizons (Berriasian–middle Aptian); 21–26. China, various localities and horizons (Early Cretaceous); 27. Brazil, pre-Aptian Early Cretaceous; 28. Argentina, Berriasian–Valanginian; 29. South Africa, Valanginian; 30–31. Australia, various localities and horizons (Berriasian–Aptian). Data from D. B. Weishampel, J. Le Loeuff, R. A. Coria, E. M. Gomani, X.-J. Zhao, X. Xu, P. M. Barrnett and A. Sahni, in preparation).

continued to dominate Late Cretaceous Gondwanan faunas, while low-browsing ornithischians were inconspicuous in these regions. As a result, the faunal changes outlined by Bakker (1978, 1986) cannot be considered as global phenomena, but seem to have been confined to parts of Laurasia.

(b) Geographical overview of the distribution of Early Cretaceous dinosaurs

Recent years have witnessed several attempts to compile a database incorporating all known dinosaur localities (Weishampel & Weishampel, 1983; Weishampel, 1992; The most recent of these datasets (D. B. Weishampel, J. Le Loeuff, R. A. Coria, E. M. Gomani, X.-J. Zhao, X. Xu, P. M. Barrett and A. Sahni, in preparation) has been used to demonstrate the global distribution of herbivorous dinosaurs in the pre-Aptian Early Cretaceous (Figs 3–5).

Most Early Cretaceous dinosaur localities (approximately 55 % of the total; $N = 109$) are situated at palaeolatitudes higher than 30 °N and 30 °S, with

particularly high concentrations of sites in western Europe and northern China. Of those localities situated between 30 °N and 30 °S, the majority lie in a relatively narrow band between 25 and 30 °N and are concentrated in southern Iberia and southern China. Only a few Early Cretaceous dinosaur localities (around 11 % of the total number) lie within 20° of the palaeoequator. No herbivorous dinosaur-bearing horizons of this age are currently known from eastern Africa, northern South America, the Levant, Antarctica, India or Madagascar. Sereno et al. (1999) recently reported several pre-Aptian dinosaur localities in the Sahara Desert (Berriasian–Hauterivian in age); these sites were situated close to the palaeoequator. The faunas recovered from these localities are dominated by sauropods, with rare theropods. Ornithischians have not been recovered to date (Sereno et al., 1999).

There appear to be no major differences in distribution between the major clades of herbivorous dinosaurs during the pre-Aptian Early Cretaceous. Sauropods and ornithopods are often found at the same sites and are represented on almost all of the

major continental landmasses (with the exception of those regions mentioned above). Stegosaurs and ankylosaurs appear to be less widespread, and are mainly confined to the northern hemisphere (mostly above 30 °N), although some doubtful records (often footprints) appear to extend their distribution into South America and sub-Saharan Africa (Weishampel, 1992; D. B. Weishampel, J. Le Loeuff, R. A. Coria, E. M. Gomani, X.-J. Zhao, X. Xu, P. M. Barrett and A. Sahni, in preparation).

(c) Advent of low-browsing behaviour

Late Jurassic dinosaur faunas cannot be characterised as predominantly high-browsing (*contra* Bakker, 1978, 1986). Although sauropods are usually considered to be high-browsing forms, analogous to giraffes (Coombs, 1975; Bakker, 1978), it is likely that they used their long necks for a variety of food gathering behaviours. For example, it has been suggested that the primary function of the long neck was to increase the horizontal feeding range of sauropods (Martin, 1987; Martin, Martin-Rolland & Frey, 1998; Stevens & Parrish, 1999), and this model (in part) seems to apply to several taxa (see below). Moreover, sauropod feeding mechanisms appear to have had a phylogenetic component, as different sauropod families possessed distinctive combinations of characters associated with food gathering and processing (Calvo, 1994; Barrett & Upchurch, 1995; Upchurch & Barrett, 2000).

Late Jurassic sauropods belonged to several different families, including the Diplodocidae, Dicraeosauridae, Camarasauridae, Brachiosauridae and Euhelopodidae (McIntosh, 1992; Upchurch, 1995, 1998; Wilson & Sereno, 1998). Diplodocid sauropods, such as *Diplodocus* and *Apatosaurus*, seem to have been specialised for browsing over a wide vertical range (Barrett & Upchurch 1994, 1995; Upchurch & Barrett, 2000); their long necks would have permitted them to browse up to 10 m above ground level, a figure that could have been exceeded by several metres if they were capable of rearing up onto their hindlimbs for short periods, as suggested by Bakker (1978). The forelimbs of diplodocids are short in comparison with the hindlimbs (with forelimb/hindlimb ratios of 0.7), and this has been interpreted as an adaptation to low-browsing (Upchurch & Barrett, 2000) as the anterior region of the thorax is carried closer to the ground. The necks also seem to be laterally flexible, permitting diplodocids to feed over a wide horizontal range (Stevens & Parrish, 1999; Upchurch & Barrett, 2000).

Dicraeosaurids seem to be specialist low-browsers (Upchurch & Barrett, 2000). *Dicraeosaurus* is a relatively small sauropod, with a maximum browsing height of 4 m. The neck appears to be very flexible laterally, but vertical movements of the neck appear to have been limited by the presence of very tall neural spines on the posterior cervical and anterior dorsal vertebrae. The forelimbs of *Dicraeosaurus* are even shorter than those of diplodocids, with forelimb/hindlimb ratios of 0.64.

Brachiosaurids and at least some euhelopodids were high-browsing forms, with greatly elongated necks that were laterally inflexible (Martin *et al.*, 1998; Upchurch & Barrett, 2000). *Brachiosaurus* was an extremely large animal and may have been able to browse at heights of up to 14 m; euhelopodids such as *Omeisaurus* could reach tree canopies up to 10 m above ground level. The forelimbs of *Brachiosaurus* were relatively longer than the hindlimbs, with a forelimb/hindlimb ratio of 1:1. This feature elevates the anterior part of the thorax and can be regarded as an adaptation to high-browsing (Upchurch & Barrett, 2000).

Camarasaurids were medium-level browsers, which lacked the extremely elongate necks and long forelimbs of brachiosaurids. The necks appear to have been laterally inflexible, and would have allowed camarasaurids to browse at heights of between 8 and 9 m (Martin *et al.*, 1998; Upchurch & Barrett, 2000).

This brief survey of sauropod food-gathering adaptations demonstrates that they cannot be stereotyped as high-browsing animals. Dicraeosaurids and diplodocids probably spent a significant proportion of time browsing on vegetation within the first 2 m of ground level. Even high-browsing sauropods such as brachiosaurids are likely to have browsed at lower levels from time-to-time, and sauropod juveniles would also have been low-browsers. Low-browsing forms like *Diplodocus* and *Apatosaurus* were extremely abundant in North American faunas, and in some localities were the most common dinosaurs (Dodson *et al.*, 1980). Similarly, *Dicraeosaurus* was an important component of East African faunas during the Late Jurassic (Russell *et al.*, 1980).

Although sauropods were the most abundant and diverse Late Jurassic dinosaurs, this observation often overshadows the importance of other dinosaur herbivores in these faunas. Stegosaurs, such as *Stegosaurus* and *Tuojiangosaurus*, reached the peak of their diversity during the Late Jurassic, and were abundant in North America, Africa, western Europe

and China (Galton, 1992). In many of these faunas, stegosaurs were the second most abundant dinosaur taxa and constituted an appreciable proportion of the total vertebrate biomass (Dodson *et al.*, 1980; Russell *et al.*, 1980; Galton, 1985*a*).

Bakker (1978) suggested that stegosaurs habitually reared up into a bipedal stance, using the tail as a prop, in order to reach into tree canopies up to 3 m above ground level; he therefore regarded stegosaurs as a component of the high-browsing fauna. Although it is possible that stegosaurs occasionally fed in this way, it is unlikely that they were habitual high-browsers. Elephants are also capable of rearing into a bipedal stance during feeding, but only do so rarely (Coe *et al.*, 1987). Moreover, the limb proportions, heavy build and weight-bearing manus of stegosaurs suggest that they were habitually quadrupedal (Coombs, 1978), and consequently exerted most of their browsing pressure on low-stature vegetation. The cervical series of *Stegosaurus* is arched downwards (Sereno, 1997), and a similar downward curvature of the neck is also seen in *Kentrosaurus* and several Chinese stegosaurs (Galton, 1992); this feature does not support the notion of high-browsing stegosaurs (Sereno, 1997), and may be interpreted as an adaptation for low-browsing.

Low-browsing ornithopods appear to be rare components of most Late Jurassic faunas, but some faunas demonstrate that they can be locally abundant. For example, around 150 individuals of the primitive iguanodontian *Dryosaurus* have been collected from the Middle Saurian Beds of Tendaguru (Russell *et al.*, 1980), and another primitive iguanodontian, *Camptosaurus*, is well represented in several quarries in the Morrison Formation of North America (Dodson *et al.*, 1980). Several genera of hypsilophodontids (*Drinker*, *Yandusaurus*) are also present in Late Jurassic faunas (Bakker *et al.*, 1990; He & Cai, 1984), but are extremely rare.

Finally, rare ankylosaur remains are known from the Late Jurassic of Europe (Galton, 1983), and recent discoveries in North America (*Mymoorapelta*, *Gargoyleosaurus*) have greatly augmented this record (Kirkland & Carpenter, 1994; Kirkland *et al.*, 1998; Carpenter, Miles & Cloward, 1998). Ankylosaurs are low-slung quadrupedal animals, and would have browsed within the first metre above ground level.

Middle Jurassic dinosaur faunas are poorly known in comparison with those from the Late Jurassic (Weishampel, 1992), but the limited evidence available suggests that they had similar faunal compositions. Sauropods were the most abundant members of these communities, but low-browsing

dinosaurs (especially stegosaurs) were also well represented. For example, the Lower Shaximiao Formation (Bathonian–Callovian) of Sichuan has yielded a fauna which includes several genera of euhelopodid sauropods, stegosaurs and small ornithopods (Dong, Zhou & Zhang, 1983). Of the sauropods present in this fauna, one genus (*Omeisaurus*) had an extremely elongate, laterally inflexible neck and was probably a specialist high-browser, while a second genus (*Shunosaurus*) had a much shorter, laterally flexible neck and may have browsed at low levels along with stegosaurs and ornithopods (Upchurch & Barrett, 2000). Middle Jurassic faunas from England are broadly similar in overall composition, and include the high-browsing sauropod *Cetiosaurus* (Upchurch & Barrett, 2000; P. Upchurch & J. Martin, in preparation) and low-browsing stegosaurs (Galton, 1985*a*), rare ornithopods (Galton, 1980) and rare ankylosaurs (Galton, 1983).

This survey of Late Jurassic dinosaur faunas demonstrates that browsing pressure on low-stature vegetation would have been much higher at this time than envisioned by Bakker (1978, 1986). Although some of the individual components of this low-browsing fauna were rare (small ornithopods, ankylosaurs), their combined presence, and the recognition that sauropods and stegosaurs could also be low-browsers, suggests that dinosaur herbivores were exerting considerable pressure on low-stature plants well before the Early Cretaceous, and that low-browsing may have been important as early as the Middle Jurassic.

(*d*) *Evolution of complex jaw mechanisms*

If the evolution of complex jaw mechanisms, such as pleurokinesis, was coupled with the origin or early radiation of angiosperms, we would expect to find a close temporal correlation between these events. Comparison of the faunal and floral records suggests that this is not the case.

Pleurokinesis is characteristic of all euornithopod dinosaurs (hypsilophodontids, basal iguanodontians, hadrosaurids), although it is best developed in the hadrosaurids (Norman, 1984; Weishampel, 1984*a*). If all hypsilophodontids were capable of pleurokinesis, as has been suggested, then the origin of the pleurokinetic mechanism extends back to at least the Middle Jurassic, as the earliest-known representatives of the Hypsilophodontidae are known from this time interval (Galton, 1980; He & Cai, 1984). Basal iguanodontians, with more elaborate pleurokinetic mechanisms, first appear in the Middle

Jurassic and are represented in Late Jurassic faunas by forms like *Camptosaurus*. The major radiation of pleurokinetic ornithopods occurs from the late Early Cretaceous onwards with increased levels of speciation among basal iguanodontians and the origin and radiation of the Hadrosauridae (Norman & Weishampel, 1992; Weishampel & Horner, 1992). The lack of temporal congruence between an Early Cretaceous (Valanginian) origin of angiosperms and major events in the evolution of pleurokinetic ornithopods suggests that these events cannot be linked.

In their analysis of Mesozoic evolutionary metrics, Weishampel & Norman (1989) identified a late Early Cretaceous peak in ornithischian diversification. This peak was attributed in large part to the radiation of pleurokinetic ornithopods and appeared to correlate with a period of increased rates of species origination in angiosperms. Weishampel & Norman (1989) interpreted this coincident pattern as possible evidence of dinosaur–angiosperm coevolution. In order to test Weishampel & Norman's (1989) hypothesis, Weishampel & Jianu (2000) re-assessed the former's evolutionary metric data. Weishampel & Jianu (2000) compared raw taxic estimates of diversity (calculated from counting numbers of fossil species present during a given stratigraphic interval), as utilised by Weishampel & Norman (1989), with diversity estimates that included both raw taxic data and diversity data from ornithischian 'ghost lineages'. Ghost lineages represent portions of the history of a clade for which there is no direct fossil evidence, but whose existence can be identified by calibrating the phylogeny of the clade against stratigraphy (Norell & Novacek, 1993). For example, the Early Cretaceous ornithischian *Echinodon* is a member of the monophyletic clade Heterodontosauridae (Sereno, 1991; Norman & Barrett, in press), which is otherwise represented by several Early Jurassic genera. Although heterodontosaurid specimens have not been recovered from any intervening Middle and Late Jurassic deposits to date, the phylogenetic and stratigraphic position of *Echinodon* indicates that representatives of the Heterodontosauridae must have been present throughout this interval, demonstrating that a substantial part of the history of this clade (approximately 55 million years) is not represented in the fossil record (Norman & Barrett, in press). Inclusion of ghost lineages in diversity estimates thus provides a more accurate census of taxa within a particular clade, providing that the phylogeny of the clade in question is well understood (Weishampel & Jianu, 2000). When the 'cryptic'

diversity revealed by consideration of the ghost lineages is included, the apparent peak in ornithischian diversity during the late Early Cretaceous disappears (Weishampel & Jianu, 2000). This change results from the addition of many ghost lineages during the basal Cretaceous and the early Late Cretaceous, whose presence is indicated by ornithischian phylogeny, but which have no fossil record.

Weishampel & Jianu (2000) also used a ghost lineage approach to analyse the diversity of ornithischian feeding mechanisms through time. They characterised various ornithischian jaw mechanisms on the basis of functional morphology [orthal slicer, transverse (i.e. pleurokinetic) grinder, etc.] and plotted the frequency of each of these distinctive functional complexes through time (see also Barrett, 1998). During the Early Cretaceous, the absolute (species level) and relative (as a proportion of all herbivorous dinosaur taxa) frequencies of the different ornithischian jaw mechanisms remained almost constant, indicating that there was no strong linkage between the evolution of pleurokinesis, or of any other jaw mechanisms, with the Early Cretaceous diversification of angiosperms (Weishampel & Jianu, 2000).

The evolution of other complex jaw mechanisms within the Dinosauria display poor temporal correlations with major events in angiosperm history. The advanced precision-shearing jaw mechanism of neoceratopians (Ostrom, 1964, 1966) did not become established until the early Late Cretaceous, and the propalinal jaw mechanism of psittacosaurids (Sereno, 1992; Barrett, 1998) appeared sometime in the late Early Cretaceous. Current evidence suggests that all of the major developments in sauropod jaw mechanics (including propaliny and well-developed shearing mechanisms) had appeared by the Late Jurassic, if not earlier (Calvo, 1994; Barrett & Upchurch, 1995; Upchurch & Barrett, 2000).

The foregoing demonstrates that there is currently no evidence to support the contention that the evolution of pleurokinesis, or of any other ornithischian jaw mechanism, is linked to either the origin or the Early Cretaceous diversification of angiosperms (see also Sereno, 1997; Weishampel & Jianu, 2000).

(e) 'Dinoturbation'

Herbivory is not the only form of environmental disturbance that animals can exert on plants. Trampling and other physical interference by mega-

fauna has been demonstrated to be one of the major factors affecting the structure and composition of modern vegetation (Owen-Smith, 1988). Consequently, it is reasonable to assume that extinct megafauna would also have had a significant physical impact on contemporaneous vegetation.

Palaeoichnologists and sedimentologists have recognised bedding planes that display evidence of extensive trampling by dinosaurs (e.g. Lockley, 1991). Such surfaces are covered with numerous dinosaur footprints, and the sediment shows intense disturbance and deformation. Mollusc shells and plant remains are often found several centimetres or more below the surface of these sedimentary units, having been pushed into this position by the force of dinosaurs trampling the surface; the term 'dinoturbation' has been coined to describe these intensively bioturbated sediments (Dodson *et al.*, 1980).

Dinoturbated sediments have been reported from many different regions, including North America, Europe, northern Africa and eastern Asia (Lockley, 1992). The earliest-known examples of dinoturbation are Early Jurassic in age, and dinoturbated sediments are relatively common within Late Mesozoic sedimentary basins. Current data seem to indicate that dinoturbation increased through the Early and Middle Jurassic, reaching its maximum during the Late Mesozoic (Lockley, 1992). Consequently, Mesozoic floras endured dinoturbation for a period of at least 55 Ma before the first appearance of angiosperms.

(*f*) Direct evidence of dinosaur–angiosperm interaction

Fossilised faeces (coprolites) and gut contents (enterolites or cololites) provide direct evidence of diet in extinct animals (Thulborn, 1991; Hunt, Chin & Lockley, 1994; Chin, 1998). These trace fossils often contain the undigested remnants of the animal's food; for example, herbivore coprolites would be expected to contain seeds, palynomorphs and fragments of stems, leaves and fruits. However, convincing enterolites are extremely rare (Currie, Koppelhus & Muhammad, 1995; Molnar & Clifford, 2000) and coprolites are rarely found in direct association with the animal that produced them (Thulborn, 1991; Hunt *et al.*, 1994; Chin, 1998).

To date, no coprolites that can be attributed to herbivorous dinosaurs have been recovered from Early Cretaceous deposits. An ankylosaur skeleton (referable to the genus *Minmi*) containing an enterolite has recently been reported from the Early Cretaceous (Albian) of Australia (Molnar & Clifford, 2000). The taphonomic and sedimentological context of the specimen suggest that a mass of triturated plant material in the ribcage represents genuine fossilised gut contents (Molnar & Clifford, 2000). The last meal of this individual seems to have consisted of various angiosperm fruits (Molnar & Clifford, 2000; R. E. Molnar, personal communication). This specimen demonstrates that angiosperms did form a part of the diet of some herbivorous dinosaurs in the late Early Cretaceous, although it does not provide any information on dinosaur diets at the time of angiosperm origin.

(3) Comparison of the floral and faunal records – summary

On the basis of current data, we reject the hypothesis that changes in dinosaur browsing behaviour led to the origin of angiosperms (see also Sereno, 1997). There appears to be no temporal correlation between the origin of angiosperms and any major event in the evolution of herbivorous dinosaurs (including the evolution of anatomical innovations associated with herbivory, first appearances of major clades and the onset of heavy dinoturbation). Moreover, the apparent absence of dinosaurs from the Northern Gondwana Palynological Province demonstrates that there is currently no known spatial coincidence between the distribution of the earliest angiosperms and herbivorous dinosaurs. Additionally, the ecology of early angiosperms suggests that they were neither sufficiently abundant nor widespread to have been a major component of dinosaur diets during the Early Cretaceous.

IV. DISCUSSION

(1) Potential for dinosaur–angiosperm coevolution in the late Early to Late Cretaceous

Although dinosaurs cannot be implicated in the origin of flowering plants, there is considerable potential for dinosaur–angiosperm coevolution in late Early Cretaceous and Late Cretaceous terrestrial ecosystems. The major radiations of hadrosaurid ornithopods, ceratopians and titanosaurid sauropods began during the early part of the Late Cretaceous (along with more limited radiations of pachycephalosaurs, ankylosaurs and nemegtosaurid sauropods) and generic-level diversity peaked during the Campanian and early Maastrichtian stages

(approximately 83–68 Ma) (see chapters in Weishampel *et al.*, 1992; Barrett, 1998; Weishampel & Jianu, 2000; Fig. 2). The speciation and extinction rates of herbivorous dinosaurs display several sharp increases during this period (Weishampel & Norman, 1989; Weishampel & Jianu, 2000) and the presence of large monospecific herds of herbivorous dinosaurs in the Late Cretaceous (such as in the hadrosaurid *Maiasaura* – see Weishampel and Horner, 1992) has been cited as possible evidence of an increase in total dinosaur biomass at this time (Tiffney, 1992). The apparent increase in biomass has been postulated to be the consequence of the greater productivity of angiosperms (which were assumed to have had a higher biomass during the Late Cretaceous and to have made up much of the diet of most low-browsing dinosaur herbivores) in comparison with the productivity of earlier gymnosperm and pteridophyte communities (Tiffney, 1992). However, no quantitative estimate of dinosaur biomass through time (particularly one that incorporates corrections for taphonomic and collection biases) is currently available and this suggestion remains untested at present. Moreover, this theory disregards the importance of the sauropod communities, which may have been predominantly high-browsing, that dominated much of the world outside of North America during the Late Cretaceous. Nevertheless, it is possible that the vegetational disturbance (due to both herbivory and dinoturbation) caused by dinosaurs contributed to the diversification of angiosperms during the latest stages of the Cretaceous (Campanian/Maastrichtian).

Rates of angiosperm diversification increased during the late Early Cretaceous and Late Cretaceous (Niklas *et al.*, 1983, 1985; Weishampel & Norman, 1989; Fig. 6) and angiosperms had achieved a global distribution by this time (see Fig. 1). Moreover, angiosperm biomass increased significantly during the Campanian and Maastrichtian (Wing & Sues *et al.*, 1992; Wing *et al.*, 1993; Lupia *et al.*, 1999). Indeed, given the temporal and spatial overlap between Late Cretaceous dinosaurs and angiosperms, the prevalence of herbivore–angiosperm interactions in modern ecosystems (e.g. Crawley, 1983; Werger *et al.*, 1989; Lindroth, 1989), and the presence of an array of mechanical defences in other Cretaceous seed plants (Weishampel, 1984*b*; Wing & Sues *et al.*, 1992) it would be extremely surprising if there were no examples of co-evolutionary interactions between dinosaurs and angiosperms at this time.

Some direct evidence does document the possible occurrence of dinosaur–angiosperm interactions during the Late Cretaceous. Putative hadrosaur enterolites have been noted in the Late Cretaceous genera *Edmontosaurus* (Kräusel, 1922) and *Corythosaurus* (Currie *et al.*, 1995). A concretion found within a 'mummified' *Edmontosaurus* skeleton was shown to include leaves of the conifer *Cunninghamites* (Kräusel, 1922), while a similar mass found within the gastric region of a *Corythosaurus* skeleton contained short sections of wood, seeds and seed pods from both angiosperms and gymnosperms (Currie *et al.*, 1995). However, although these concretions might be enterolites, this identification cannot be established with certainty (Currie *et al.*, 1995). It is equally possible that these concretions were formed wholly or partially as *post mortem* sedimentary infills that entered the carcasses of these individuals prior to burial (Currie *et al.*, 1995).

Coprolites can be locally abundant in many Late Cretaceous terrestrial settings (e.g. Matley, 1941; Rodríguez de la Rosa, Cevallos-Ferriz & Silva-Pineda, 1998; Nambudiri & Binda, 1989). Several examples of possible dinosaur coprolites from the Cerro del Pueblo Formation (Campanian) of Mexico (Rodríguez de la Rosa *et al.*, 1998) and the Whitemud Formation (Maastrichtian) of Canada (Nambudiri & Binda, 1989) contain the remains of seeds, cuticles and fruits from monocotyledonous and dicotyledonous angiosperms. Although the Cerro del Pueblo coprolites cannot be attributed to herbivorous dinosaurs with confidence [as they are associated with a variety of vertebrate taxa – see Rodríguez de la Rosa *et al.* (1998)] a dinosaur origin can be considered likely as few of the other animals present in the assemblage appear to have been large herbivores (other reptiles in the assemblage include crocodiles and aquatic turtles). The biological origin of the coprolites from the Whitemud Formation has been questioned (K. Chin, personal communication). Moreover, a dinosaurian origin is difficult to support, as no dinosaur skeletal material has been recorded from this formation (Weishampel, 1992; D. B. Weishampel, J. Le Loeuff, R. A. Coria, E. M. Gomani, X.-J. Zhao, X. Xu, P. M. Barrett and A. Sahni, in preparation). The angiosperm molecular biomarker oleanane and its derivatives have been detected in coprolites from the Two Medicine Formation (Campanian) of Montana (Chin & Brassell, 1994). These coprolites have been referred to herbivorous dinosaurs (probably hadrosaurs) on the basis of their size, provenance, association with bone-beds of the hadrosaurid *Maiasaura* and their
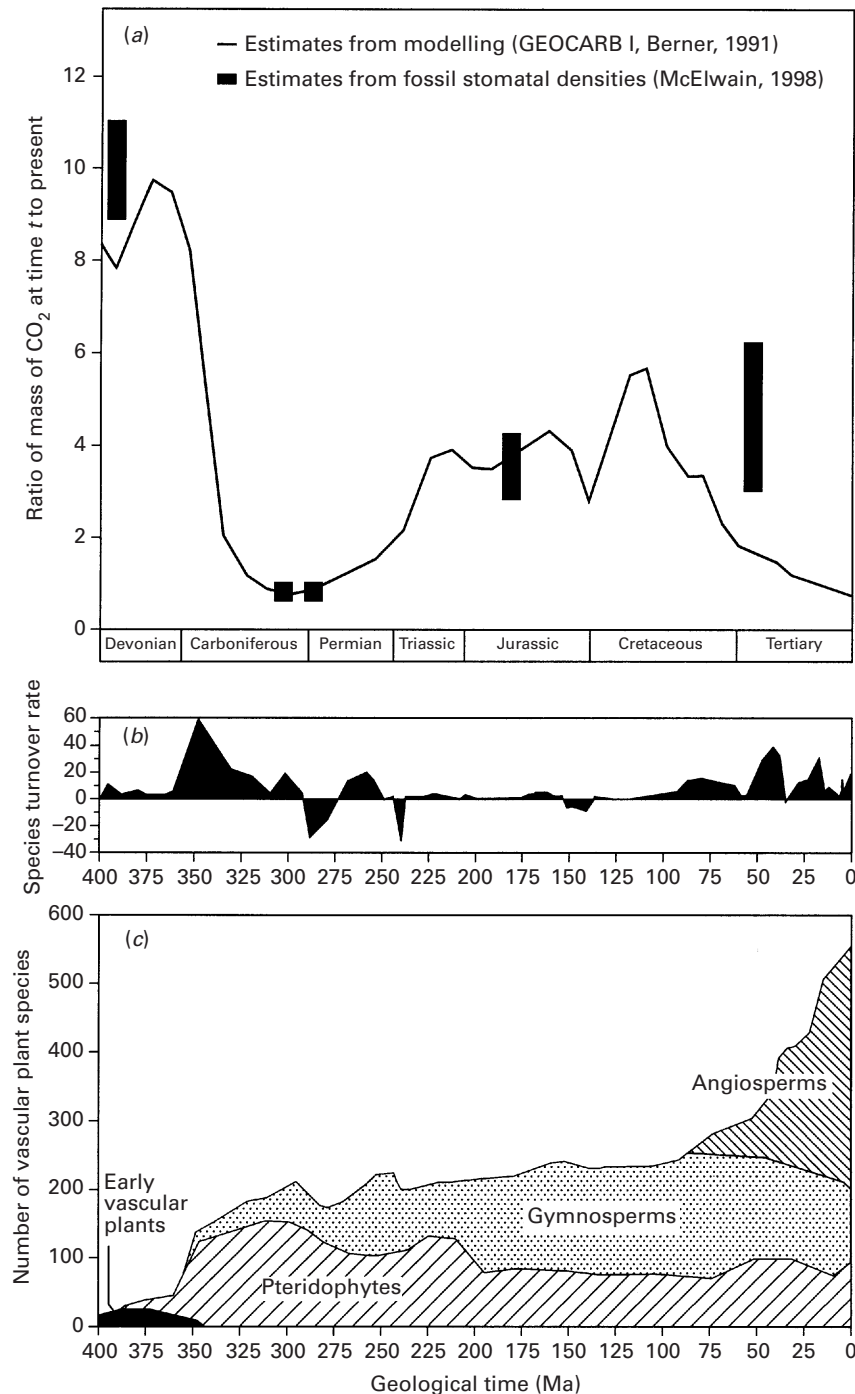
Fig. 6. (A) Estimated variations in atmospheric CO_2 during the past 400 million years (redrawn from Berner, 1991) shown alongside (B, C) major events in vascular plant evolution (rates of species turnover and changes in species-level diversity through time) over the same time scale (redrawn from Niklas *et al.*, 1983, 1985; Niklas, 1997). The CO_2 data used are taken from the GEOCARB I model rather than GEOCARB II since the latter model incorporates a predicted drawdown effect of atmospheric CO_2 due to increased rates of weathering associated with vascular plant evolution. Using GEOCARB II in hypotheses dealing with the effect of atmospheric CO_2 on plant evolution would, therefore, involve a certain amount of circularity. However, both models I and II agree in the general direction of the trends and these are further supported by independently derived results from carbon isotope analysis of palaeosols (Mora *et al.*, 1996) and of stomatal densities on fossil leaves (McElwain, 1998).

'block-like' morphology, which is similar to that seen in large, extant mammalian herbivores (Chin, 1990; K. Chin, personal communication). The absence of oleananes and other biomarkers from the sediments that encased these coprolites demonstrates that these were the diagenetic products of the original faecal mass, and not contaminants from the surrounding soil (Chin & Brassell, 1994). Other herbivorous dinosaur coprolites from the same localities contain fragments of conifer needles, seeds and wood, but no evidence of angiosperm tissues (Chin & Gill, 1996; K. Chin, personal communication). However, continuing investigation in this area is likely to yield interesting results.

Several lines of indirect evidence also suggest that dinosaurs might have been interacting with angiosperms during the Late Cretaceous. Large numbers of hadrosaur footprint casts have been reported on the roofs of several coal mines in the Blackhawk Formation (Campanian) of Utah, USA (Parker & Balsley, 1980; Balsley & Parker, 1983). These footprint assemblages are closely associated with the tree stumps of dicotyledonous palms and taxodiaceous conifers, which are preserved in life position (Parker & Balsley, 1980; Balsley & Parker, 1983). In several instances, the orientation of the footprint casts shows that the trackmakers were facing the trees in a posture that is consistent with them feeding on the tree foliage (Parker & Balsley, 1980; Balsley & Parker, 1983; Taggart & Cross, 1997).

Plants that are subject to intense browsing or grazing pressure by large vertebrate herbivores often possess a range of mechanical defences in order to deter would-be predators. These defences include spines, thorns, trichomes, silicaceous phytoliths, the deposition of large amounts of parenchyma, changes in growth form, basal meristems and the possession of sclerophyllous leaves (e.g. Crawley, 1983; Lindroth, 1989). The identification of these features in fossil angiosperms would provide at least circumstantial evidence of dinosaur–angiosperm interactions. However, Cretaceous angiosperms appear to lack many of these specialisations (Tiffney, 1992), suggesting that predation by large herbivores may not have been an important selective factor. Some Late Cretaceous angiosperm woods contain a high proportion of parenchyma (making up over 50% of the total tissue in one instance) and it is possible that this feature may represent an example of a mechanical defence against dinosaur herbivory (Wheeler & Lehman, 2000). However, parenchyma is also deposited in response to high levels of atmospheric CO_2; during the Cretaceous, levels of atmospheric CO_2 were much higher than they are today (Wheeler & Lehman, 2000; see discussion of atmospheric CO_2 levels in the Cretaceous below).

In modern ecosystems, animals play an important role in angiosperm seed dispersal (Janzen, 1983), and it is possible that dinosaurs might have fulfilled this role during the Cretaceous. Dinosaurs would have been capable of travelling great distances from the parent plant and would have provided the seeds with a large supply of nutrients (in the form of faeces) when the seeds were voided from the body. However, most Cretaceous angiosperm fruits are rather small (Crane *et al.*, 1995; Eriksson, Friis & Löfgren, 2000*a*; Eriksson *et al.*, 2000*b*) and are unlikely to have been particularly attractive to large herbivores (Wing & Tiffney, 1987*b*; although coprolites and enterolites do suggest that these were eaten by at least some herbivores – see above). It has been suggested that the small berry-like fruits of some late Early Cretaceous angiosperms were adapted for animal dispersal and it is possible that this potential food source would have been attractive to small herbivores (arboreal mammals, birds, pterosaurs, some small ornithischian dinosaurs) (Fleming & Lips, 1991; Eriksson, *et al.*, 2000*a, b*). However, the seeds of Cretaceous angiosperms were generally small and light, suggesting that they might have been dispersed abiotically (Tiffney, 1984). Janzen (1984) has suggested that small seeds can be dispersed biotically as a consequence of the accidental ingestion of the seeds by large herbivores bulk-feeding on the foliage of a plant ('whole plant as attractant' syndrome). If dinosaurs were dispersing angiosperm seeds in this way (Wing & Tiffney, 1987*b*) it could explain the absence of mechanical defences in these plants, as angiosperms would have been selected to attract large herbivores rather than to deter them (Tiffney, 1992).

Some circumstantial evidence for dinosaur–angiosperm coevolution has been provided by the recognition of two or three distinctive dinosaur assemblages in the late Campanian of western North America, each of which is associated with a particular floral province (Lehman, 1997). A northern '*Corythosaurus* fauna' (broadly characterised by the presence of centrosaurine ceratopids and lambeosaurine hadrosaurids) recovered from the Judith River and Two Medicine Formations of Montana, USA and Alberta, Canada can be distinguished from a southern '*Kritosaurus* fauna' (dominated by hadrosaurine hadrosaurs and chasmosaurine ceratopians) from the Kirkland, Fruitland and Ajuga Formations of New Mexico and Texas. This lati-

tudinal change in the composition of the large herbivore faunas is coincident with a floristic transition from the northern 'Aquillapollenites palynofloral province' to the southerly 'Normapolles palynofloral province' (Lehman, 1997). The Normapolles palynoflora and associated megafossils indicate the presence of open-canopy woodland with widely spaced trees that grew in a non-seasonal dry climate. By contrast, the Aquillapollenites palynoflora and megaflora represent a closed canopy forest that grew under more mesic conditions (Wolfe & Upchurch, 1987). Examination of fossil woods from these palynofloral provinces indicates that the northern Aquillapollenites province was dominated by taxodiacean conifers, while the southern Normapolles province was dominated by araucarian conifers and dicotyledonous trees (e.g. Horrell, 1991). It is possible that the different vegetational structure and composition of these northern and southern provinces might have controlled the composition of the herbivorous dinosaur fauna; however, this suggestion must remain tentative until a more extensive palaeobotanical census of this region has been carried out and until the food preferences of individual dinosaur taxa are known more precisely. Moreover, other factors, such as mean annual temperature, temperature ranges and humidity levels, may have had a strong effect on dinosaur provincialism in Late Cretaceous North America (Lehman, 1997).

Other studies on Late Cretaceous (Campanian–Maastrichtian) North American dinosaur biogeography have suggested that specific dinosaur assemblages were strongly linked to particular palaeoenvironments; in particular, large ceratopids seem to have had a preference for low-lying, humid coastal areas, while sauropods, ankylosaurs and pachycephalosaurs inhabited drier inland regions, such as alluvial plains (Lehman, 1987; Brinkman, Ryan & Eberth, 1998). This faunal provincialism might reflect the influence of the presumably different floral communities that dominated these palaeoenvironments, although this hypothesis remains to be tested.

Wing & Sues et al. (1992) suggested that a temporal comparison of the floral and faunal events that occurred during the late Early and Late Cretaceous in North and South America could act as a test for hypotheses of dinosaur–angiosperm coevolution. The dominant herbivores in North America at this time were low-browsing ceratopian and hadrosaurian ornithischians; in South America high-browsing titanosaurian sauropods were the most important large herbivores. If low-browsing was an important ecological factor driving the angiosperm radiation, the absence of an intense low-browsing regime in the late Early and Late Cretaceous of South America should result in significantly different floras from those seen in coeval North American deposits. Specifically, angiosperms should be much rarer components of South American Cretaceous floras (Wing & Sues et al., 1992). There are several problems with the faunal and ecological generalisations of (Wing & Sues et al., 1992), however. Most important of these are uncertainties relating to titanosaur neck function and feeding habits. At present, little is known regarding the functional morphology of the titanosaur postcranial skeleton and the possibility that titanosaurs employed a variety of low- and high-browsing strategies (as seen in some other sauropods; Barrett & Upchurch, 1995; Upchurch & Barrett, 2000; Stevens & Parrish, 1999) cannot be discounted. However, the relatively long forelimbs (forelimb/hindlimb ratio of 0.83 in Opisthocoelicaudia) and laterally inflexible necks of at least some titanosaurs (Upchurch & Barrett, 2000) argue against obligate low-browsing. Consideration of neck length and shoulder height suggests maximum browsing heights of around 6–8 m (Upchurch & Barrett, 2000), a distance that might have been augmented by the apparent ability of some titanosaurs to rear into a bipedal stance (Wilson & Carrano, 1999). In addition, the test proposed by (Wing & Sues et al., 1992) overlooks several minor faunistic factors, including the presence of rare high-browsing(?) animals in North America (the titanosaurid Alamosaurus) and of rare low-browsing taxa in South America (principally hadrosaurs) during the Late Cretaceous. Nevertheless, the overall taxonomic and ecological differences between North and South American dinosaur communities suggest that a comparison of the angiosperm fossil records in these regions should provide some insights into dinosaur–angiosperm interactions.

Earliest Cretaceous (Berriasian–Barremian) floras from Argentina are dominated by ferns and araucarian and podocarpacean conifers (Archangelsky, 1963, 1966; Traverso, 1966); angiosperm palynomorphs and megafossils were absent during this interval and did not make their first appearance until the early Aptian (Archangelsky & Gamerro, 1967; Romero & Archangelsky, 1986; S. Archangelsky, personal communication). Other areas of South America have been less extensively studied, but there are reports of angiosperm pollen from pre-Aptian strata in Brazil and other regions of north-western

South America (Romero, 1993; S. Archangelsky, personal communication). Angiosperms were diverse in southern South America by the Late Cretaceous and were represented by small arborescent forms (mainly palms) and shrubs, although large angiosperm trees did not appear until the latest Cretaceous (Maastrichtian) and Tertiary (Berry, 1937; Romero, 1978, 1992, 1993; Romero & Arguijo, 1981; Ancibor, 1995). The earliest North American angiosperms are represented by palynomorphs from late Barremian deposits in Canada (Burden & Hills, 1989; Doyle, Jardiné & Doerenkamp, 1982); consequently, there was no significant lag between the first occurrence of angiosperms in North and South America. Moreover, angiosperms increased in both abundance and diversity on both continents in the latter part of the Cretaceous (Wing & Boucher, 1998; Romero & Arguijo, 1981; Romero, 1993). The slightly later occurrence of large angiosperm trees in South America than in North America (where the first large angiosperm trees appear in the Campanian; Wing & Sues *et al.*, 1992) may be of some interest. However, the relatively short lag between these two events may be explicable by taphonomic or sampling biases, as the Late Cretaceous angiosperm flora of South America is poorly known at present. On the basis of current evidence, real or perceived differences in dinosaur browsing behaviour are unlikely to have played a major role in the early radiation of angiosperms in either region.

Similar comments apply to India, as titanosaurs were the most abundant large-bodied herbivores in this region also (von Huene & Matley, 1933; Jain & Bandyopadhyay, 1997). Ornithischians were extremely rare elements of the fauna (Weishampel, 1992; D. B. Weishampel, J. Le Loeuff, R. A. Coria, E. M. Gomani, X.-J. Zhao, X. Xu, P. M. Barrett and A. Sahni, in preparation). Early Cretaceous floras consisted almost entirely of bennettitaleans and various conifers (Tiwari & Tripathi, 1995; Rajanikanth, 1996; Srivastava *et al.*, 1999); the first appearance of angiosperm palynomorphs occurs during the Aptian (Tiwari & Tripathi, 1995) and rare angiosperm megafossils have been reported from the ?Barremian–Aptian Rajmahal Formation (Banerji, 2000). Monocotyledonous and dicotyledonous angiosperms were present in Late Cretaceous floras and were represented by shrubs and small trees; they occur in association with the conifers *Brachyphyllum* and *Araucarites* (Mohabey, Udhoji & Verma, 1993; Tandon *et al.*, 1995). The slightly later occurrence of the first angiosperms in India and southern South America relative to the first occurrences in Europe and North America can be interpreted solely as a consequence of the poleward migration of angiosperms (Lidgard & Crane, 1988, 1990; Crane & Lidgard, 1989; Drinnan & Crane, 1990): it does not support the hypothesis that differences in the Cretaceous dinosaur faunas between these areas led to divergent patterns in their vegetational histories.

Although some direct evidence demonstrates that angiosperm–dinosaur interactions did occur during the late Early and Late Cretaceous, such evidence is rare. Angiosperms almost certainly formed a part of dinosaur diets during the Late Cretaceous, but enterolites, coprolites and estimates of plant biomass suggest that other plants, such as conifers, were perhaps the major constituents of dinosaur fodder (Taggart & Cross, 1997). If this were the case, the potential for 'tight' angiosperm–dinosaur coevolution would have been severely limited. It is possible that some form of diffuse coevolution (mediated by dinoturbation, unselective bulk feeding by large dinosaurs) did occur, but support for this hypothesis remains circumstantial. Many of the lines of indirect evidence forwarded in support of diffuse coevolutionary scenarios require further testing. Much more direct information on dinosaur diets and angiosperm physiognomy and distribution is needed before any coevolutionary hypotheses can be either accepted or refuted completely.

(2) Other potential Cretaceous animal–angiosperm interactions

Although current evidence suggests that the influence of dinosaur herbivores on angiosperm diversity and abundance was minimal, it is possible that other herbivores had a much more significant impact on the angiosperm radiation. Direct evidence (fossilised gut contents, coprolites) of insect predation on Cretaceous angiosperms is sparse (Labandeira, 1998), but herbivory can be inferred from fossil feeding traces such as leaf mines (Labandeira *et al.*, 1994) and other damage to leaves caused by feeding (e.g. Scott, Stephenson & Chaloner, 1992; Labandeira, 1998; Wilf *et al.*, 2000). Studies on the functional morphology of insect mouthparts can also offer important information (Labandeira, 1997). However, comparison of the times of appearance of innovations in insect feeding systems with the timing of the angiosperm radiation suggests that there is not a strong relationship between the evolution of angiosperms and insect herbivory (Labandeira, 1997). Moreover, analysis of insect familial-level

diversity through time suggests that no marked increase in insect diversity coincided with either the time of angiosperm origin or the onset of angiosperm diversification (Labandeira & Sepkoski, 1993).

Nevertheless, insect pollinators are thought to have played a key role in the taxonomic and ecological diversification of angiosperms (Crepet & Friis, 1987; Crepet, 1996). Late Early and early Late Cretaceous angiosperms possess many features that demonstrate the possession of established pollination syndromes, each of which is characterised by an array of floral features that indicate a high level of pollinator specificity (Crepet, 1996). The establishment of these pollination syndromes is coincident with the origin and diversification of many anthophilous insect clades, notably lepidopterans, various hymenopterans (bees, pollen wasps) and dipterans (Grimaldi, 1999). Consequently, many authors currently accept that coevolutionary interactions between early angiosperms and insects were of major ecological and evolutionary importance (Crepet & Friis, 1987; Stewart & Rothwell, 1993; Crepet, 1996; Grimaldi, 1999; but see Hughes, 1994 for a radically different point of view). Insect herbivory (aphids, beetles) on angiosperms also seems to have been important by the Late Cretaceous (e.g. Farrell, 1998; von Dohlen & Moran, 2000; Wilf *et al.*, 2000). Insect pollination is thought to have been derived from pollinivory by insects with chewing mouthparts, and it has been suggested that various key angiosperm characteristics, such as closed carpels, appeared in order to protect the ovules from predation (e.g. Crepet & Friis, 1987).

Multituberculates were small, possibly arboreal mammals with specialised orthal slicing and palinal jaw actions (Krause, 1982; Jenkins & Krause, 1983). They were abundant during the Late Cretaceous and Early Tertiary and are generally thought to have been herbivorous (granivorous and frugivorous), although omnivory is also a possibility (Krause, 1982). The radiation of multituberculates during the Late Cretaceous (Campanian–Maastrichtian) was coincident with increasing angiosperm diversity and abundance and with increasing diaspore sizes (Tiffney, 1984); it has been suggested that these mammals played a role in angiosperm seed dispersal (Wing & Tiffney, 1987b; Weishampel & Norman, 1989; Collinson & Hooker, 1991). Some authors have argued that mammal–angiosperm interactions were established even earlier in the Cretaceous, perhaps as early as the Barremian (Eriksson *et al.*, 2000a, b). Granivorous and frugivorous birds have also been implicated in the Late

Cretaceous increases in angiosperm diversity and abundance (Wing & Tiffney, 1987b; Collinson & Hooker, 1991).

Mammal-angiosperm and insect-angiosperm interactions may have been widespread during the late Early and Late Cretaceous, but their impact on angiosperm macroevolution is difficult to assess, as direct evidence of these interactions is extremely rare. Data from insect and mammalian coprolites and fossil gut contents may help to identify specific angiosperm-insect associations, providing a basis for the more explicit formulation of coevolutionary hypotheses, and would also allow testing of mammalian dietary inferences that are currently based on functional morphology. The evidence for bird-angiosperm interactions during the Late Cretaceous is extremely poor at present, due to the lack of a well-supported phylogeny for crown-group birds, the poor fossil record of birds in Late Cretaceous terrestrial settings and the lack of dietary information for many of the relevant taxa. Detailed examination of the data used to support models of insect/mammal/bird–angiosperm coevolution is beyond the scope of the present review, but such an undertaking could provide fertile ground for future research.

(3) An alternative hypothesis to account for the initial radiation of angiosperms

Long-term carbon cycling modelling indicates that levels of atmospheric CO_2 have fluctuated greatly during the past 600 million years. Estimations suggest, for example, that approximately 420 million years ago, atmospheric concentrations were up to 15 times higher than at present (Berner, 1991, 1997, 1998). Although many of the variables used to construct the long-term carbon cycle model are difficult, if not impossible, to measure with any great accuracy (including for example, past geological and biological factors such as changes in seafloor spreading rates, changing elevation, area and position of the continents, weathering rates, and estimates of global degassing through volcanic activity), other independent lines of evidence also support the broad trends of the model. These include a measure of past levels of atmospheric CO_2 through the analysis of stomatal densities on fossil leaves (e.g. McElwain, 1998) and carbon isotopic analysis of paleosols (e.g. Mora, Driese & Colarusso, 1996; Retallack, 1997).

If estimated values for atmospheric CO_2 through the Phanerozoic are compared with the broad-scale evolutionary changes documented in the plant fossil

record it would appear that the emergence of the major plant groups occurred at times of increasing atmospheric CO_2 (Fig. 6). In addition, there appears to be a positive correlation between increasing levels of atmospheric CO_2 and increasing rates of species turnover (Fig. 6).

Why should high atmospheric CO_2 levels drive plant evolution? One possible explanation for the observed correlation is that the warming associated with elevated CO_2 would have increased the land area available for colonisation, due, for example, to the melting of extensive continental ice sheets (Otto-Bliesner & Upchurch, 1997); the resulting new habitats would provide many opportunities for rapid local evolutionary events. There is little evidence, however, for centres of origination in the high latitudes (where the majority of continental ice sheets are located) in the geological record (but see discussion on *Nothofagus*, above).

Another consideration might be the physiological effect that elevated atmospheric CO_2 levels would have had on plants. The direct effects of elevated atmospheric CO_2 on present-day ecosystems are well documented and include increased water use efficiency (dry matter production per unit water lost) and increased integrated nutrient use efficiency (tissue C/N ratio) (Woodward, 1992). The extent and activity of symbiotic associations with mycorrhizal fungi and N_2-fixing bacteria also increase with elevated levels of CO_2. Although these effects can be partially offset by increases in temperature, given the enormous historical increases in CO_2, it is most likely that the effects of CO_2 would have been greater than those of temperature (Bennett & Willis, 2000). Thus, increased CO_2 would increase the ability of plants to colonise drier and/or more nutrient-poor sites, increasing the range of niches available for plant growth, and thus increasing the opportunities for the emergence of novel plant forms. Moreover, if plant groups extant at the times of high CO_2 were less able to exploit the opportunities provided by increased CO_2 than novel plant forms (Beerling & Woodward, 1997), then the latter would be able to expand. This is consistent with the evidence from the plant fossil record; few major plant taxa become extinct at times of increasing atmospheric CO_2, but existing groups tabefy to some extent, and newly appeared groups display an increase in diversity (Niklas *et al.*, 1983, 1985; Willis & Bennett, 1995; Niklas, 1997).

It is not only the colonisation of new habitats which could increase speciation, however, but increased levels of atmospheric CO_2 could also have direct physiological influence on plants in their current habitats. For example, Phillips & Gentry (1994) observed an increase in the rate of turnover of plant generations over the past 40 years, which they attribute to the recent increase in atmospheric CO_2 (see also Phillips & Shiel, 1997). If turnover rates increase then so too will the probability of genetic mutations becoming fixed in a population and thus the rate of speciation.

A combination of direct and indirect effects of CO_2 on plant growth and survival may well have been a major contributory factor to the emergence of major plant groups and increased species turnover at times of high atmospheric CO_2. Changes in atmospheric CO_2 levels are global, not local; thus with increasing atmospheric CO_2, the opportunities for plant migration are minimal [compared to migration during, for example, glacial-interglacial cycles (Bennett, 1997)], increasing the evolutionary and selective pressures on plants. In terms of abiotic stress (*sensu* DiMichele, Phillips & Olmstead, 1987), increasing levels of atmospheric CO_2 will provide a level of stress which exceeds dispersal capacity and from which plant populations cannot escape; evolution to cope with the changing environment may have been the only option for plants in a world of increased CO_2.

Geological evidence from continental flood-basalts, continental drift rates, sea-floor spreading rates and orogenic events, indicates that periods of global plate spreading and subduction may have been episodic with relatively short periods of activity separated by long periods of inactivity. These short periods of activity are termed 'pulsation tectonics' (Sheridan, 1987, 1997; Huggett, 1997). The proposed mechanisms behind the pulsation tectonics model are described elsewhere (for a review see Sheridan, 1987). Of interest here is the timing and environmental impact of these 'pulses'. Five periods of increased tectonic activity (measured from sea-floor spreading rates) have been recognised in the geological record: between approximately 460 and 430 Ma, 375 and 350 Ma, 300 and 260 Ma, 170 and 160 Ma, and 120 and 80 Ma. Associated with these pulses were increased seafloor spreading rates, volcanism and eustatic sea level rises (Arthur, Dean & Schlanger, 1985; Berner, 1991; Larson, 1991*b*; Sheridan, 1987, 1997). In addition to the physical changes in size, shape and position of the continents, it has been suggested that pulses of faster global plate spreading were associated with significant changes in atmospheric gas concentrations; it has been linked to increases in atmospheric CO_2 levels in particular

(Sheridan, 1987, 1997). At least two processes associated with plate spreading are thought to be responsible for large increases in atmospheric CO_2 levels; the eruption of mantle superplumes and increased volcanic activity.

The most recent tectonic pulse is thought to have occurred between 120 and 80 Ma at the time of the final break-up of Pangea, and the formation of the South Atlantic Ocean margins, the Indian Ocean margins (east of Madagascar and between Australia and Antarctica) and the northern Atlantic Ocean margins between Europe, Canada and Greenland. To date, evidence has been found for at least one superplume, relating to periods of faster global plate spreading between 120 and 80 Ma (Larson, 1991a, b). The Early to mid-Cretaceous increase in atmospheric CO_2 concentrations predicted by Sheridan's (1987, 1997) model also correlates well with the pulse of atmospheric CO_2 predicted by Berner's (1991) geochemical model and palaeobotanical data. The resulting climatic effects of this increased concentration of atmospheric CO_2 would include an increase in global temperatures (Caldeira & Rampino, 1991) and humidity leading to both increased evaporation and moisture-holding capacity of the atmosphere.

This pulse and the correlated increase in atmospheric CO_2 coincides with the initial radiation of the angiosperms (although it post-dates the origin of angiosperms by around 15 Ma) and with increased rates of species turnover. By contrast, times of relative tectonic stability correspond to times of relative stasis in the plant fossil record. Pulses of fast plate spreading have shorter durations than intervals of slow spreading; similarly, periods of stasis in the plant record (i.e. periods with low species turnover rates) are the norm interspersed with periods of rapid species turnover.

V. CONCLUSIONS

(1) Several phylogenetic analyses predict the occurrence of pre-Cretaceous angiosperms, but evaluation of the palaeobotanical and palynological record does not sustain this contention. Pre-Cretaceous angiosperm fossils are unknown at present, and palaeobotanical data currently support a palaeo-tropical origin for angiosperms (in the Northern Gondwana Palynological Province) sometime during the Early Cretaceous (?Valanginian). This view is congruent with phylogenetic evidence that nests angiosperms within a paraphyletic Gnetales.

(2) Angiosperms were rare elements of Early Cretaceous floras and did not comprise a significant proportion of standing plant biomass until the Late Cretaceous. Consequently, it is unlikely that angiosperms formed a major constituent of dinosaur diets until the latest Cretaceous.

(3) No major event in the evolution of herbivorous dinosaurs can be correlated with the origin of angiosperms. Anatomical innovations in dinosaur chewing mechanisms (pleurokinesis, precision-shearing) either preceded or post-dated angiosperm origins. The onset of ecological factors, such as dinoturbation and low-browsing, occurred during the Early and Middle Jurassic, while the major radiations of low-browsing ornithischian dinosaurs occurred during the late Early and Late Cretaceous. Changes in dinosaur browsing behaviour at the Jurassic – Cretaceous boundary may not have been as marked as suggested previously. Moreover, current evidence suggests that there was no spatial overlap between the earliest angiosperms and the major clades of herbivorous dinosaurs. Consequently, hypotheses that implicate herbivorous dinosaurs in the origin of angiosperms are rejected.

(4) Direct evidence of dinosaur–angiosperm interactions is extremely rare. Circumstantial evidence, such as the coincident radiation of angiosperms with those of hadrosaurian and ceratopian dinosaurs and the association of different dinosaur communities with specific palaeoenvironments, is suggestive of the diffuse coevolution of dinosaurs and angiosperms, but is not conclusive. Additional information on dinosaur diet (from coprolites/enterolites), specific dinosaur–angiosperm associations and angiosperm physiognomy and anatomy will permit more detailed studies of potential coevolutionary interactions.

(5) The mid – Late Cretaceous radiations of anthophilous insects and granivorous and frugivorous multituberculate mammals may have had a more significant impact on angiosperm diversification (through the evolution of specialised pollination syndromes, fruits etc.) than large, bulk-feeding herbivorous dinosaurs. However, the apparent lack of mechanical defences in Cretaceous angiosperms may be due to selection for seed dispersal by bulk-feeding dinosaurs ('whole plant as attractant' syndrome). Although this would represent an important example of diffuse coevolution between these disparate lineages, this hypothesis is difficult to test as other dispersal syndromes (e.g. wind pollination) would select for very similar seed and fruit characteristics. Dinosaur–angiosperm co-

evolution in the Late Cretaceous cannot be ruled out, or strongly supported, on the basis of current evidence.

(6) Elevated levels of atmospheric CO_2 might have facilitated the early stages of the angiosperm radiation by allowing improved water efficiency, increased integrated nutrient use efficiency and by reducing the time between successive generations. Elevated atmospheric CO_2 levels may be related to a pulse of global tectonic activity; if this were the case, the diversification of angiosperms could be the direct result of a major geological event. However, this hypothesis should remain tentative until the geological phenomena and physiological mechanisms that may be involved are understood in more detail. Moreover, other edaphic and biotic factors (such as changes in global climate, plant-plant competition, animal-plant interactions) are likely to have had a profound influence on angiosperm diversification. Disentangling the effects of this gamut of potential macroevolutionary agents on the evolution of Cretaceous terrestrial ecosystems is likely to provide fertile ground for future research.

VI. ACKNOWLEDGEMENTS

VIII. REFERENCES

ANCIBOR, E. (1995). Palmeras fosiles del Cretacico tardio de la Patagonia, Argentina (Bajo de Santa Rosa, Rio Negro). *Ameghiniana* **32**, 287–299.

ARCHANGELSKY, S. (1963). A new Mesozoic flora from Tíco, Santa Cruz Province, Argentina. *Bulletin of the British Museum (Natural History) Geology* **8**, 47–92 + 12 pls.

ARCHANGELSKY, S. (1966). New gymnosperms from the Tíco flora, Santa Cruz Province, Argentina. *Bulletin of the British Museum (Natural History) Geology* **13**, 261–295 + 8 pls.

ARCHANGELSKY, S. & GAMERRO, J. C. (1967). Spore and pollen types of the Lower Cretaceous in Patagonia (Argentina). *Review of Palaeobotany and Palynology* **1**, 211–217.

ARTHUR, M. A., DEAN, W. E. & SCHLANGER, S. O. (1985). Variations in the global carbon cycle during the Cretaceous related to climate, volcanism and changes in atmospheric CO_2. *Geophysical Monograph Series* **32**, 503–529.

BAKKER, R. T. (1978). Dinosaur feeding behaviour and the origin of flowering plants. *Nature* **274**, 661–663.

BAKKER, R. T. (1986). *The Dinosaur Heresies*. Longman Scientific & Technical.

BAKKER, R. T., GALTON, P. M., SIEGWARTH, J. & FILLA, J. (1990). A new latest Jurassic vertebrate fauna, from the highest levels of the Morrison Formation at Como Bluff, Wyoming. Part IV. The dinosaurs: a new *Othnielia*-like hypsilophodontid. *Hunteria* **2**, 8–13.

BALSLEY, J. K. & PARKER, L. R. (1983). *Cretaceous wave-dominated delta, barrier islands, and submarine fan depositional systems: Book Cliff, east-central Utah*. American Association of Petroleum Geologists Field Guide.

BANERJI, J. (2000). Occurrence of angiosperm remains in an Early Cretaceous intertrappean bed, Rajmahal Basin, India. *Cretaceous Research* **21**, 781–784.

BARRETT, P. M. (1998). *Herbivory in the non-avian Dinosauria*. Unpublished Ph.D. dissertation, University of Cambridge.

BARRETT, P. M. (2000). Evolutionary consequences of dating the Yixian Formation. *Trends in Ecology and Evolution* **15**, 99–103.

BARRETT, P. M. (in press). Tooth wear and possible jaw action of *Scelidosaurus harrisonii* Owen and a review of feeding mechanisms in other thyreophoran dinosaurs. In *The Armored Dinosaurs* (ed. K. Carpenter). Bloomington: Indiana University Press.

BARRETT, P. M. & UPCHURCH, P. (1994). Feeding mechanisms in *Diplodocus*. *Gaia* **10**, 195–203.

BARRETT, P. M. & UPCHURCH, P. (1995). Sauropod feeding mechanisms: their bearing on palaeoecology. In *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers* (eds. A-L. Sun & Y-Q. Wang), pp. 107–110. Beijing: China Ocean Press.

BARTHOLOMAI, A. & MOLNAR, R. E. (1981). *Muttaburrasaurus*, a new iguanodontid (Ornithischia: Ornithopoda) dinosaur from the Lower Cretaceous of Queensland. *Memoirs of the Queensland Museum* **20**, 319–349.

BEERLING, D. J. & WOODWARD, F. I. (1997). Changes in land plant function over the Phanerozoic: reconstructions based on the fossil record. *Botanical Journal of the Linnean Society* **124**, 137–153.

BEHRENSMEYER, A. K., DAMUTH, J. D., DIMICHELE, W. A., POTTS, R., SUES, H-D. & WING, S. L. (1992). *Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Plants and Animals*. Chicago: University of Chicago Press.

BEHRENSMEYER, A. K., HOOK, R. W., BADGLEY, C. E., BOY, J. A., CHAPMAN, R. E., DODSON, P., GASTALDO, R. A., GRAHAM, R. W., MARTIN, L. D., OLSEN, P. E., SPICER, R. A., TAGGART, R. E. & WILSON, M. V. H. (1992). Paleoenvironmental contexts and taphonomic modes. In *Terrestrial*

Ecosystems through Time: Evolutionary Paleoecology of Plants and Animals (eds. A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H-D. Sues & S. L. Wing), pp. 15–136. Chicago: University of Chicago Press.

BENNETT, K. D. (1997). *Evolution and Ecology: the Pace of Life.* Cambridge: Cambridge University Press.

BENNETT, K. D. & WILLIS, K. J. (2000). Effect of global atmospheric carbon dioxide on glacial-interglacial vegetation change. *Global Ecology and Biogeography* **9**, 355–361.

BENTON, M. J. (1983). Dinosaur success in the Triassic: a non-competitive ecological model. *Quarterly Review of Biology* **58**, 29–55.

BENTON, M. J., WILLS, M. A. & HITCHIN, R. (2000). Quality of the fossil record through time. *Nature* **403**, 534–537.

BERNER, R. A. (1991). A model for atmospheric CO_2 over Phanerozoic time. *American Journal of Science* **291**, 339–376.

BERNER, R. A. (1997). The rise of plants and their effect on weathering and atmospheric CO_2. *Science* **276**, 544–546.

BERNER, R. A. (1998). The carbon cycle and CO_2 over Phanerozoic time: the role of land plants. *Philosophical Transactions of the Royal Society, Series B* **353**, 75–82.

BERRY, E. W. (1937). An Upper Cretaceous flora from Patagonia. *Johns Hopkins University Studies in Geology* **12**, 11–31+pls. I–V.

BONAPARTE, J. F. (1984). Late Cretaceous faunal interchange of terrestrial vertebrates between the Americas. In *Third Symposium on Mesozoic Terrestrial Ecosystems, Short Papers* (eds. W-E. Reif & F. Westphal), pp. 19–24. Tübingen: Attempto Verlag.

BONAPARTE, J. F. (1986). History of the terrestrial Cretaceous vertebrates of Gondwana. In *IV Congreso Argentino de Paleontologica y Stratigraphica. Actas 2*, pp. 63–95. Mendoza.

BONAPARTE, J. F. (1996). *Dinosaurios de America del Sur.* Buenos Aries: Museo Argentino de Ciencias Naturales.

BOWE, L. M., COAT, G. & DE PAMPHILIS, C. W. (2000). Phylogeny of seed plants based on all three genomic compartments: Extant gymnosperms are monophyletic and Gnetales' closest relatives are conifers. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 4092–4097.

BREMER, K. (2000). Early Cretaceous lineages of monocot flowering plants. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 4707–4711.

BRENNER, G. J. (1974). Palynostratigraphy of the Lower Cretaceous Gevar'am and Talme Yafe Formations in Gevar'am 2 well. *Bulletin of the Geological Survey of Israel* **59**, 1–27.

BRENNER, G. J. (1976). Middle Cretaceous floral provinces and early migrations of angiosperms. In *Origin and Early Evolution of Angiosperms* (ed. C. B. Beck), pp. 23–47. New York: Columbia University Press.

BRENNER, G. J. (1996). Evidence for the earliest stage of angiosperm pollen evolution: a paleoequatorial section from Israel. In *Flowering Plant Origin, Evolution and Phylogeny* (ed. D. W. Taylor & L. J. Hickey), pp. 91–115. New York: Chapman & Hall.

BRENNER, G. J. & BICKOFF, I. S. (1992). Palynology and age of the Lower Cretaceous basal Kurnub Group from the Coastal Plain to the northern Negev of Israel. *Palynology* **16**, 137–185.

BRETT-SURMAN, M. K. (1979). Phylogeny and palaeobiogeography of hadrosaurian dinosaurs. *Nature* **277**, 560–562.

BRIGGS, J. C. (1995). *Global Biogeography.* Amsterdam: Elsevier.

BRINKMAN, D. B., RYAN, M. J. & EBERTH, D. A. (1998). The paleogeographic and stratigraphic distribution of ceratopsids (Ornithischia) in the Upper Judith River Group of western Canada. *Palaios* **13**, 160–169.

BUFFETAUT, E. & SUTEETHORN, V. (1998). Early Cretaceous dinosaurs from Thailand and their bearing on the early evolution and biogeographical history of some groups of Cretaceous dinosaurs. *New Mexico Museum of Natural History and Science. Bulletin* **14**, 205–210.

BURDEN, E. T. & HILLS, L. V. (1989). Illustrated key to the genera of Lower Cretaceous terrestrial palynomorphs (excluding megaspores) of western Canada. *American Association of Stratigraphic Palynologists, Contributions Series* **21**, 147pp.

BURGER, D. (1993). Early and middle Cretaceous angiosperm pollen grains from Australia. *Review of Palaeobotany and Palynology* **78**, 183–234.

CALDEIRA, K. & RAMPINO, M. R. (1991). The mid-Cretaceous superplume, carbon dioxide and global warming. *Geophysical Research Letters* **18**, 987–990.

CALVO, J. O. (1994). Jaw mechanics in sauropod dinosaurs. *Gaia* **10**, 183–194.

CALVO, J. O. & SALGADO, L. (1995). *Rebbachisaurus tessonei* sp. nov. A new Sauropoda from the Albian–Cenomanian of Argentina; new evidence on the origin of the Diplodocidae. *Gaia* **11**, 13–33.

CAO, Z-Y., WU, S-Q., ZHANG, P-A. & LI, J. (1998). Discovery of fossil monocotyledons from Yixian Formation, western Liaoning. *Chinese Science Bulletin* **43**, 230–233.

CARPENTER, K., MILES, C. & CLOWARD, K. (1998). Skull of a Jurassic ankylosaur (Dinosauria). *Nature* **393**, 782–783.

CHAW, S-M., PARKINSON, C. L., CHENG, Y., VINCENT, T. M. & PALMER, J. D. (2000). Seed plant phylogeny inferred from all three plant genomes: monophyly of extant gymnosperms and origin of Gnetales from conifers. *Proceedings of the National Academy of Sciences of the United States of America* **97**, 4086–4091.

CHIAPPE, L. M., JI, S-A., JI, Q. & NORELL, M. A. (1999). Anatomy and systematics of the Confuciusornithidae (Theropoda: Aves) from the Late Mesozoic of North-eastern China. *Bulletin of the American Museum of Natural History* **242**, 1–89.

CHIN, K. (1990). [Abstract] Possible herbivorous dinosaur coprolites from the Two Medicine Formation (Late Cretaceous) of Montana. *Journal of Vertebrate Paleontology* **10** (3 – supplement), 17A–18A.

CHIN, K. (1998). On the elusive trail of fossil dung. *National Forum* **78**, 36–41.

CHIN, K. & BRASSELL, S. C. (1994). [Abstract] Characterization of biomarkers preserved in permineralized coprolites: molecular evidence of ancient diets. *Abstracts with Programs – Geological Society of America* **27**(7), 297.

CHIN, K. & GILL, B. D. (1996). Dinosaurs, dung beetles and conifers: participants in a Cretaceous food web. *Palaios* **11**, 280–285.

COE, M. J., DILCHER, D. L., FARLOW, J. O., JARZEN, D. M. & RUSSELL D. A. (1987). Dinosaurs and land plants. In *The Origin of Angiosperms and their Biological Consequences* (eds. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 225–258. Cambridge: Cambridge University Press.

COLBERT, E. H. (1993). Feeding strategies and metabolism in elephants and sauropod dinosaurs. *American Journal of Science* **293A**, 1–19.

COLLINSON, M. E. & HOOKER, J. J. (1991). Fossil evidence of interactions between plants and plant-eating mammals. *Philosophical Transactions of the Royal Society of London, Series B* **333**, 197–208.

CONWAY, B. H. (1996). A palynological investigation across the Jurassic–Cretaceous boundary on the south-east flanks of Mount Hermon, Israel. *Cretaceous Research* **17**, 197–214.

COOMBS, W. P. JR. (1975). Sauropod habits and habitats. *Palaeogeography, Palaeoclimatology, Palaeoecology* **17**, 1–33.

COOMBS, W. P. JR. (1978). Theoretical aspects of cursorial adaptation in dinosaurs. *Quarterly Review of Biology* **53**, 393–418.

COOPER, M. R. (1985). A revision of the ornithischian dinosaur *Kangnasaurus coetzeei* Haughton, with a classification of the Ornithischia. *Annals of the South African Museum* **95**(8), 281–317.

CORIA, R. A. & SALGADO, L. (1996). A basal iguanodontian (Ornithischia: Ornithopoda) from the Late Cretaceous of South America. *Journal of Vertebrate Paleontology* **16**, 445–457.

CORNET, B. (1989). The reproductive morphology and biology of *Sanmiguelia lewisii*, and its bearing on angiosperm evolution in the Late Triassic. *Evolutionary Trends in Plants* **3**, 25–51.

COUGHENOR, M. B. (1985). Graminoid responses to grazing by large herbivores: adaptations, exaptations, and interacting processes. *Annals of the Missouri Botanical Garden* **72**, 852–863.

CRANE, P. R. (1985). Phylogenetic analysis of seed plants and the origin of angiosperms. *Annals of the Missouri Botanical Gardens* **72**, 716–793.

CRANE, P. R. (1987). Vegetational consequences of the angiosperm diversification. In *The Origin of Angiosperms and their Biological Consequences* (eds. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 105–144. Cambridge: Cambridge University Press.

CRANE, P. R., DONOGHUE, M. J., DOYLE, J. A. & FRIIS, E. M. (1989). Angiosperm origins. *Nature* **342**, 131.

CRANE, P. R., FRIIS, E. M. & PEDERSEN, K. R. (1995). The origin and early diversification of angiosperms. *Nature* **374**, 27–33.

CRANE, P. R. & LIDGARD, S. (1989). Angiosperm diversification and paleolatitudinal gradients in Cretaceous floristic diversity. *Science* **246**, 675–678.

CRAWLEY, M. J. (1983). *Herbivory: The Dynamics of Animal–Plant Interactions*. Oxford: Blackwell Scientific Publications.

CREPET, W. L. (1996). Timing in the evolution of derived floral characters: Upper Cretaceous (Turonian) taxa with tricolpate and tricolpate-derived pollen. *Review of Palaeobotany and Palynology* **90**, 339–359.

CREPET, W. L. & FRIIS, E. M. (1987). The evolution of insect pollination in angiosperms. In *The Origin of Angiosperms and their Biological Consequences* (eds. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 181–201. Cambridge: Cambridge University Press.

CROMPTON, A. W. & ATTRIDGE, J. (1986). Masticatory apparatus of the larger herbivores during Late Triassic and Early Jurassic time. In *The Beginning of the Age of the Dinosaurs* (ed. K. Padian), pp. 223–236. Cambridge: Cambridge University Press.

CURRIE, P. J., KOPPELHUS, E. B. & MUHAMMAD, A. F. (1995). "Stomach" contents of a hadrosaur from the Dinosaur Park Formation (Campanian, Upper Cretaceous) of Alberta, Canada. In *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota, Short Papers* (eds. A-L. Sun & Y-Q. Wang), pp. 111–114. Beijing: China Ocean Press.

CURRY, K. A. & FORSTER, C. A. (1999). [Abstract] New sauropods from Madagascar: a glimpse into titanosaur cranial morphology and evolution. *Journal of Vertebrate Paleontology* **19**(3 – suppl.), 40A–41A.

DETTMANN, M. E. (1992). Structure and floristics of Cretaceous vegetation of southern Gondwana; implications for angiosperm biogeography. In *Organisation Internationale de Paléobotanique, IVème conférence: Résumés des communications* (eds. D. Pons & J. Broutin), p. 47. Villeneuve d'Asca: Organisation Française de Paléobotanique.

DETTMANN, M. E., POCKNALL, D. T., ROMERO, E. J. & ZAMALOA, M. DE C. (1990). *Nothofagidites* Erdtman ex Potonié, 1960: a catalogue of species with notes on the paleogeographic distribution of *Nothofagus* B1 (southern beech). *New Zealand Geological Survey Paleontological Bulletin* **60**, 1–79.

DILCHER, D. L. & CRANE, P. R. (1984). *Archaeanthus*: an early angiosperm from the Cenomanian of the Western Interior of North America. *Annals of the Missouri Botanical Garden* **71**, 351–383.

DIMICHELE, W. A., PHILLIPS, T. L. & OLMSTEAD, R. G. (1987). Opportunistic evolution: abiotic environmental stress and the fossil record of plants. *Review of Palaeobotany and Palynology* **50**, 151–178.

DODSON, P., BEHRENSMEYER, A. K., BAKKER, R. T. & MCINTOSH, J. S. (1980). Taphonomy and paleoecology of the Upper Jurassic Morrison Formation. *Paleobiology* **6**, 208–232.

VON DOHLEN, C. D. & MORAN, N. A. (2000). Molecular data support a rapid radiation of aphids in the Cretaceous and multiple origins of host alternation. *Biological Journal of the Linnean Society of London* **71**, 689–717.

DONG, Z-M. (1992). *The Dinosaurian Faunas of China*. Berlin: Springer-Verlag.

DONG, Z-M., ZHOU, S. & ZHANG, Y. (1983). Dinosaur remains of Sichuan Basin. *Palaeontologia Sinica, Series C* **23**, 1–145 (in Chinese with English abstract).

DOUBINGER, J. & MAS, J. R. (1981). Une microflore du Barrémien dans la Province de Valencia, Espagne. *Cretaceous Research* **2**, 51–64.

DOYLE, J. A. (1998*a*). Molecules, morphology, fossils, and the relationship of angiosperms and Gnetales. *Molecular Phylogenetics and Evolution* **9**, 448–462.

DOYLE, J. A. (1998*b*). Phylogeny of vascular plants. *Annual Review of Ecology and Systematics* **29**, 567–599.

DOYLE, J. A., BIENS, P., DOERENKAMP, A. & JARDINÉ, S. (1977). Angiosperm pollen from the pre-Albian Lower Cretaceous of equatorial Africa. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* **1**, 451–473.

DOYLE, J. A. & DONOGHUE, M. J. (1993). Phylogenies and angiosperm diversification. *Paleobiology* **19**, 141–167.

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

DOYLE, J. A., JARDINÉ, S. & DOERENKAMP, A. (1982). *Afropollis*, a new genus of early angiosperm pollen, with notes on the Cretaceous palynostratigraphy and palaeoenvironments of northern Gondwana. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* **6**, 39–117.

DRINNAN, A. N. & CRANE, P. R. (1990). Cretaceous paleobotany and its bearing on the biogeography of austral angiosperms. In *Antarctic Paleobiology: its Role in the Reconstruction of Gondwana* (eds. T. N. Taylor & E. L. Taylor), pp. 192–219. New York: Springer-Verlag.

DRINNAN, A. N., CRANE, P. R. & HOOT, S. B. (1994). Patterns of floral evolution in the early diversification of non-magnoliid

dicotyledons (eudicots). *Plant Systematics and Evolution, Supplement* **8**, 93–122.

Duan, S-Y. (1998). The oldest angiosperm – a tricarpous female reproductive fossil from western Liaoning Province, NE China. *Science in China (Series D)* **41**, 14–20.

Eberth, D. A., Russell, D. A., Braman, D. R. & Deino, A. L. (1993). The age of the dinosaur-bearing beds at Tebch, Inner Mongolia, People's Republic of China. *Canadian Journal of Earth Sciences* **30**, 2101–2106.

Endress, P. K. (1987). The early evolution of the angiosperm flower. *Trends in Ecology and Evolution* **2**, 300–304.

Eriksson, O., Friis, E. M. & Löfgren, P. (2000*a*). Seed size, fruit size and dispersal systems in angiosperms from the Early Cretaceous to the Late Tertiary. *American Naturalist* **156**, 47–58.

Eriksson, O., Friis, E. M., Pedersen, K. R. & Crane, P. R. (2000*b*). Seed size and dispersal systems of Early Cretaceous angiosperms from Famalicão, Portugal. *International Journal of Plant Science* **161**, 319–329.

Fara, E. & Benton, M. J. (2000). The fossil record of Cretaceous tetrapods. *Palaios* **15**, 161–165.

Farlow, J. O. (1987). Speculations about the diet and digestive physiology of herbivorous dinosaurs. *Paleobiology* **13**, 60–72.

Farlow, J. O., Dodson, P. & Chinsamy, A. (1995). Dinosaur biology. *Annual Review of Ecology and Systematics* **26**, 445–471.

Farrell, B. D. (1998). 'Inordinate fondness' explained: why are there so many beetles? *Science* **281**, 555–559.

Felsenstein, J. (1978). Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Zoology* **27**, 401–410.

Fleming, T. H. & Lips, K. R. (1991). Angiosperm endozoochory: were pterosaurs Cretaceous seed dispersers? *American Naturalist* **138**, 1058–1065.

Foote, M. & Sepkoski, J. J. (1999). Absolute measures of completeness of the fossil record. *Nature* **398**, 415–417.

Friis, E. M., Crane, P. R. & Pedersen, K. R. (1997). *Anacostia*, a new basal angiosperm from the Early Cretaceous of North America and Portugal with trichotomocolpate/monocolpate pollen. *Grana* **36**, 225–244.

Friis, E. M. & Crepet, W. L. (1987). Time of appearance of floral features. In *The Origin of Angiosperms and their Biological Consequences* (eds. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 145–179. Cambridge: Cambridge University Press.

Friis, E. M., Pedersen, K. R. & Crane, P. R. (1999). Early angiosperm diversification: the diversity of pollen associated with angiosperm reproductive structures in Early Cretaceous floras from Portugal. *Annals of the Missouri Botanical Garden* **86**, 259–296.

Galton, P. M. (1973). The cheeks of ornithischian dinosaurs. *Lethaia* **6**, 67–89.

Galton, P. M. (1980). European Jurassic ornithopod dinosaurs of the families Hypsilophodontidae and Camptosauridae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **160**, 73–95.

Galton, P. M. (1983). Armoured dinosaurs (Ornithischia: Ankylosauria) from the Middle and Upper Jurassic of Europe. *Palaeontographica Abteilung A* **182**, 1–25.

Galton, P. M. (1985*a*). British plated dinosaurs (Ornithischia, Stegosauridae). *Journal of Vertebrate Paleontology* **5**, 211–254.

Galton, P. M. (1985*b*). Diet of prosauropods from the Late Triassic and Early Jurassic. *Lethaia* **18**, 105–123.

Galton, P. M. (1986). Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs. In *The Beginning of the Age of the Dinosaurs* (ed. K. Padian), pp. 203–221. Cambridge: Cambridge University Press.

Galton, P. M. (1992). Stegosauria. In *The Dinosauria* (paperback edition) (eds. D. B. Weishampel, P. Dodson & H. Osmólska), pp. 435–455. Berkeley: University of California Press.

Galton, P. M. & Taquet, P. (1982). *Valdosaurus*, a hypsilophodontid dinosaur from the Lower Cretaceous of Europe and Africa. *Geobios* **15**, 147–159.

Gan, Z-B. & Zhang, C-Y. (1985). Early Cretaceous palynology in northern Hebei. *Acta Palaeontologica Sinica* **24**, 558–567 (in Chinese with English summary).

Gandolfo, M. A., Nixon, K. C., Crepet, W. L., Stevenson, D. W. & Friis, E. M. (1998). Oldest known fossils of monocotyledons. *Nature* **394**, 532–533.

Gasparini, Z., Pereda-Suberbiola, X. & Molnar, R. E. (1996). New data on the ankylosaurian dinosaur from the Late Cretaceous of the Antarctic Peninsula. *Memoirs of the Queensland Museum* **39**, 583–594.

Grimaldi, D. (1999). The co-radiations of pollinating insects and angiosperms in the Cretaceous. *Annals of the Missouri Botanical Garden* **86**, 373–406.

Gubeli, A. A., Hochuli, P. A. & Wildi, W. (1984). Lower Cretaceous turbiditic sediments from the Rif chain (northern Marocco) – palynology, stratigraphy and palaeogeographic setting. *Geologische Rundschau* **73**, 1081–1114.

Hamby, R. K. & Zimmer, E. A. (1992). Ribosomal RNA as a phylogenetic tool in plant systematics. In *Molecular Systematics of Plants* (eds. P. S. Soltis, D. E. Soltis & J. J. Doyle), pp. 50–91. New York: Chapman & Hall.

He, X-L. & Cai, K-J. (1984). *The Middle Jurassic Dinosaurian Fauna from Dashanpu, Zigong, Sichuan. Volume I. The Ornithopod Dinosaurs*. Sichuan Scientific and Tecnological [*sic*] Publishing House. (In Chinese with English summary).

Herendeen, P. S. (1991). Charcoalified angiosperm wood from the Cretaceous of eastern North America and Europe. *Review of Palaeobotany and Palynology* **70**, 225–239.

Herrera, C. M. (1985). Determinants of plant–animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. *Oikos* **44**, 132–141.

Hickey, L. J. & Doyle, J. A. (1977). Early Cretaceous fossil evidence for angiosperm evolution. *Botanical Review* **43**, 3–104.

Hickey, L. J. & Taylor, D. W. (1996). Origin of the angiosperm flower. In *Flowering Plant Origin, Evolution and Phylogeny* (eds. D. W. Taylor & L. J. Hickey), pp. 176–213. New York: Chapman & Hall.

Hill, R. S. & Scriven, L. J. (1995). The angiosperm-dominated woody vegetation of Antarctica – a review. *Review of Palaeobotany and Palynology* **86**, 175–198.

Hooker, J. J., Milner, A. C. & Sequeira, S. E. K. (1991). An ornithopod dinosaur from the Late Cretaceous of west Antarctica. *Antarctic Science* **3**(3), 331–332.

Horrell, M. A. (1991). Phytogeography and paleoclimatic interpretation of the Maestrichtian. *Palaeogeography, Palaeoclimatology, Palaeoecology* **86**, 87–138.

von Huene, F. & Matley, C. A. (1933). The Cretaceous Saurischia and Ornithischia of the central provinces of India. *Palaeontologia Indica* **21**, 1–74.

Huggett, R. J. (1997). *Environmental Change: the Evolving Ecosphere*. London: Routledge.

Hughes, N. F. (1973). Mesozoic and Tertiary distributions, and problems of land-plant evolution. *Special Papers in Palaeontology* **12**, 189–198.

Hughes, N. F. (1976). *The Palaeobiology of Angiosperm Origins*. Cambridge: Cambridge University Press.

Hughes, N. F. (1994). *The Enigma of Angiosperm Origins*. Cambridge: Cambridge University Press.

Hughes, N. F., Dewrey, G. E. & Laing, J. F. (1979). Barremian earliest angiosperm pollen. *Palaeontology* **22**, 513–535.

Hughes, N. F. & McDougall, A. B. (1987). Records of angiospermid pollen entry into the English Early Cretaceous succession. *Review of Palaeobotany and Palynology* **50**, 255–272.

Hughes, N. F. & McDougall, A. B. (1994). Search for antecedents of Early Cretaceous monosulcate columellate pollen. *Review of Palaeobotany and Palynology* **83**, 175–183.

Hunt, A. P., Chin, K. & Lockley, M. G. (1994). The palaeobiology of vertebrate coprolites. In *The Palaeobiology of Trace Fossils* (ed. S. K. Donovan), pp. 221–240. John Wiley & Sons.

Jacobs, L. L., Winkler, D. A., Downs, W. R. & Gomani, E. M. (1993). New material of an Early Cretaceous titanosaurid sauropod dinosaur from Malawi. *Palaeontology* **36**, 523–534.

Jain, S. L. & Bandyopadhyay, S. (1997). New titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of central India. *Journal of Vertebrate Paleontology* **17**, 114–136.

Janzen, D. H. (1983). Dispersal of seeds in vertebrate guts. In *Coevolution* (eds. D. J. Futuyma & M. Slatkin), pp. 232–262. Sunderland: Sinauer.

Janzen, D. H. (1984). Dispersal of small seeds by big herbivores: foliage is the fruit. *American Naturalist* **123**, 338–353.

Jarman, P. J. (1974). The social organisation of antelope in relation to their ecology. *Behaviour* **58**, 215–267.

Jenkins, F. A., Jnr. & Krause, D. W. (1983). Adaptations for climbing in North American multituberculates (Mammalia). *Science* **220**, 712–715.

Kenrick, P. (1999). The family tree flowers. *Nature* **402**, 358–359.

King, G. M. (1990). Dicynodonts and the end-Permian event. *Palaeontologia Africana* **27**, 31–39.

King, G. M. (1996). *Reptiles and Herbivory*. London: Chapman & Hall.

Kirkland, J. I., Britt, B., Burge, D. L., Carpenter, K., Cifelli, R., Decourten, F., Eaton, J., Hasiotis, S. & Lawton, T. (1997). Lower to Middle Cretaceous dinosaur faunas of the central Colorado Plateau: a key to understanding 35 million years of tectonics, sedimentology, evolution and biogeography. *Brigham Young University Geology Studies* **42**, 69–103.

Kirkland, J. I. & Carpenter, K. (1994). North America's first pre-Cretaceous ankylosaur (Dinosauria) from the Upper Jurassic Morrison Formation of Western Colorado. *Brigham Young University Geology Studies* **40**, 25–42.

Kirkland, J. I., Carpenter, K., Hunt, A. P. & Sheetz, R. D. (1998). Ankylosaur (Dinosauria) specimens from the Upper Jurassic Morrison Formation. *Modern Geology* **23**, 145–177.

de Klerk, W. J., Forster, C. A., Ross, C. F., Sampson, S. D. & Chinsamy, A. (1998). A review of recent dinosaur and other vertebrate discoveries in the Early Cretaceous Kirkwood Formation in the Algoa Basin, Eastern Cape, South Africa. *Journal of African Earth Sciences* **27A**, 55.

Krassilov, V. A. (1981). Changes of Mesozoic vegetation and the extinction of dinosaurs. *Palaeogeography, Palaeoclimatology, Palaeoecology* **34**, 207–224.

Krause, D. W. (1982). Jaw movement, dental function ad diet

in the Paleocene multituberculate *Ptilodus*. *Paleobiology* **8**, 265–281.

Kräusel, R. (1922). Die Nahrung von *Trachodon*. *Paläontologische Zeitschrift* **4**, 80.

Labandeira, C. C. (1997). Insect mouthparts: Ascertaining the paleobiology of insect feeding strategies. *Annual Reviews of Ecology and Systematics* **28**, 153–193.

Labandeira, C. C. (1998). The role of insects in Late Jurassic to Middle Cretaceous ecosystems. *Bulletin of the New Mexico Museum of Natural History and Science* **14**, 105–124.

Labandeira, C. C., Dilcher, D. L., Davis, D. R. & Wagner, D. L. (1994). Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of coevolution. *Proceedings of the National Academy of Sciences of the United States of America* **91**, 12278–12282.

Labandeira, C. C. & Sepkoski, J. J., Jnr. (1993). Insect diversity in the Fossil Record. *Science* **261**, 310–315.

Larson, R. L. (1991a). Geological consequences of superplumes. *Geology* **19**, 967–970.

Larson, R. L. (1991b). Latest pulse of Earth: evidence for a mid-Cretaceous superplume. *Geology* **19**, 547–550.

Lehman, T. M. (1987). Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western Interior of North America. *Palaeogeography, Palaeoclimatology, Palaeoecology* **60**, 189–217.

Lehman, T. M. (1997). Late Campanian dinosaur biogeography in the Western Interior of North America. In *Dinofest International: Proceedings of a Symposium held at Arizona State University* (eds. D. L. Wolberg, E. Stump & G. Rosenberg), pp. 223–240. Philadelphia: Academy of Natural Sciences.

Le Loeuff, J. (1993). European titanosaurids. *Revue de Paléobiologie, Volume spéciale* **7**, 105–117.

Li, W-B. & Liu, Z-S. (1994). The Cretaceous palynofloras and their bearing on stratigraphic correlation in China. *Cretaceous Research* **15**, 333–365.

Li, W-H., Gouy, M., Wolfe, K. H. & Sharp, P. M. (1989). Angiosperm origins. *Nature* **342**, 131–132.

Lidgard, S. & Crane, P. R. (1988). Quantitative analyses of the early angiosperm radiation. *Nature* **331**, 344–346.

Lidgard, S. & Crane, P. R. (1990). Angiosperm diversification and Cretaceous floristic trends: a comparison of palynofloras and leaf macrofloras. *Paleobiology* **16**, 77–93.

Lindroth, R. L. (1989). Mammalian herbivore–plant interactions. In *Plant–animal interactions* (ed. W. G. Abrahamson), pp. 163–206. New York: McGraw-Hill Book Company.

Lockley, M. G. (1991). *Tracking Dinosaurs: a New Look at an Ancient World*. Cambridge: Cambridge University Press.

Lockley, M. G. (1992). La dinoturbacion y el fenomeno de la alteracion del sedimento por pisadas de vertebrados en ambientes antiguos. In *Los Dinosaurios y su entorno biotico: Actas del segundo curso de paleontologia en Cuenca* (ed. J. L. Sanz & A. D. Buscalioni). pp. 270–296. Instituto 'Juan de Valdes' Excmo, Ayuntamiento de Cuenca.

Luo, Z. (1999). A refugium for relicts. *Nature* **400**, 24–25.

Lupia, R., Lidgard, S. & Crane, P. R. (1999). Comparing palynological abundance and diversity: implications for biotic replacement during the Cretaceous angiosperm radiation. *Paleobiology* **25**, 305–340.

Magallon, S., Crane, P. R. & Herendeen, P. S. (1999). Phylogenetic pattern, diversity, and diversification of eudicots. *Annals of the Missouri Botanical Garden* **86**, 297–372.

MARTIN, J. (1987). Mobility and feeding of *Cetiosaurus* (Saur-ischia, Sauropoda) – why the long neck? In *Fourth Symposium on Mesozoic Terrestrial Ecosystems. Short Papers* (eds. P. M. Currie & E. H. Koster). *Occasional Papers of the Tyrell Museum of Palaeontology* **3**, 150–155.

MARTIN, J., MARTIN-ROLLAND, V. & FREY, E. (1998). Not cranes or masts, but beams: the biomechanics of sauropod necks. *Oryctos* **1**, 113–120.

MARTIN, W., GIERL, A. & SAEDLER, H. (1989). Molecular evidence for pre-Cretaceous angiosperm origins. *Nature* **339**, 46–48.

MATLEY, C. A. (1941). The coprolites of Pijdura, central provinces. *Records of the Geological Survey of India* **74**, 535–547.

McELWAIN, J. C. (1998). Do fossil plants signal paleo-atmospheric CO_2 concentration in the geological past? *Philosophical Transactions of the Royal Society*, Series B **353**, 83–96.

McINTOSH, J. S. (1992). Sauropoda. In *The Dinosauria* (paper-back edition) (eds. D. B. Weishampel, P. Dodson & H. Osmólska), pp. 345–401. Berkeley: University of California Press.

MITCHELL, M. M., DUDDY, I. R. & O'SULLIVAN, P. B. (1997). Reappraisal of the age and origin of the Casterton Formation, western Otway Basin, Victoria. *Australian Journal of Earth Sciences* **44**, 819–830.

MOHABEY, D. M., UDHOJI, S. G. & VERMA, K. K. (1993). Palaeontological and sedimentological observations on non-marine Lameta Formation (Upper Cretaceous) of Maharashtra, India: their palaeoecological and palaeo-environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology* **105**, 83–94.

MOLNAR, R. E. (1980 a). An ankylosaur (Ornithischia: Reptilia) from the Lower Cretaceous of southern Queensland. *Memoirs of the Queensland Museum* **20**, 77–87.

MOLNAR, R. E. (1980 b). Australian Late Mesozoic tetrapods: some implications. *Mémoires de la Société Géologique de la France* **139**, 131–143.

MOLNAR, R. E. & CLIFFORD, H. T. (2000). Gut contents of a small ankylosaur. *Journal of Vertebrate Palaeontology* **20**, 194–196.

MOLNAR, R. E. & GALTON, P. M. (1986). Hypsilophodontid dinosaurs from Lightning Ridge, New South Wales, Australia. *Geobios* **19**, 231–239.

MOLNAR, R. E. & WIFFEN, J. (1994). A Late Cretaceous polar dinosaur fauna from New Zealand. *Cretaceous Research* **15**, 689–706.

MORA, C. I., DRIESE, S. G. & COLARUSSO, L. A. (1996). Middle to Late Paleozoic atmospheric CO_2 levels from soil carbonate and organic matter. *Science* **271**, 1105–1107.

NAMBUDIRI, E. M. V. & BINDA, P. L. (1989). Dicotyledonous fruits associated with coprolites from the Upper Cretaceous (Maastrichtian) Whitemud Formation, southern Saskat-chewan, Canada. *Review of Palaeobotany and Palynology* **59**, 57–66.

NIKLAS, K. J. (1997). *The Evolutionary Biology of Plants*. Chicago: University of Chicago Press.

NIKLAS, K. J., TIFFNEY, B. H. & KNOLL, A. H. (1983). Patterns in vascular land plant diversification. *Nature* **303**, 614–616.

NIKLAS, K. J., TIFFNEY, B. H. & KNOLL, A. H. (1985). Patterns in vascular land plant diversification: an analysis at the species level. In *Phanerozoic Diversity Patterns: Profiles in Macroevolution* (ed. J. W. Valentine), pp. 97–128. Princeton &

San Francisco: Princeton University Press & American Association for the Advancement of Science.

NIXON, K. C., CREPET, W. L., STEVENSON, D. & FRIIS, E. M. (1994). A reevaluation of seed plant phylogeny. *Annals of the Missouri Botanical Garden* **81**, 484–533.

NORMAN, D. B. (1980). On the ornithischian dinosaur *Iguanodon bernissartensis* of Bernissart (Belgium). *Institut Royal des Sciences Naturelles de Belgique. Mémoire* **178**, 1–104.

NORMAN, D. B. (1984). On the cranial morphology and evolution of ornithopod dinosaurs. *Symposia of the Zoological Society of London* **52**, 521–547.

NORMAN, D. B. (1986). On the anatomy of *Iguanodon atherfieldensis* (Ornithischia: Ornithopoda). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique: Sciences de la Terre* **56**, 281–372.

NORMAN, D. B. (1987 a). On a mass-accumulation of vertebrates from the Lower Cretaceous of Nehden (Sauerland), West Germany. *Proceedings of the Royal Society of London*, Series B **230**, 215–255.

NORMAN, D. B. (1987 b). On the history of the discovery of fossils at Bernissart in Belgium. *Archives of Natural History* **14**, 59–75.

NORMAN, D. B. & BARRETT, P. M. (in press). Ornithischian dinosaurs from the basal Cretaceous (Berriasian) of England. *Special Papers in Palaeontology*.

NORMAN, D. B. & WEISHAMPEL, D. B. (1985). Ornithopod feed-ing mechanisms: their bearing on the evolution of herbivory. *American Naturalist* **126**, 151–164.

NORMAN, D. B. & WEISHAMPEL, D. B. (1991). Feeding mech-anisms in some small herbivorous dinosaurs: processes and patterns. In *Biomechanics in Evolution* (eds. J. M. V. Rayner & R. J. Wootton), pp. 161–181. Cambridge: Cambridge Uni-versity Press.

NORMAN, D. B. & WEISHAMPEL, D. B. (1992). Iguanodontidae and related ornithopods. In *The Dinosauria* (paperback edition) (eds. D. B. Weishampel, P. Dodson & H. Osmólska), pp. 510–533. Berkeley: University of California Press.

NORELL, M. A. & NOVACEK, M. J. (1993). Congruence between suprapositional and phylogenetic patterns: comparing cla-distic patterns with the fossil record. *Cladistics* **8**, 319–337.

NOVAS, F. A. & MOLNAR, R. E. (eds.) (1996). Proceedings of the Gondwanan Dinosaur Symposium. *Memoirs of the Queensland Museum* **39** (3), 489–731.

OSTROM, J. H. (1961). Cranial morphology of the hadrosaurian dinosaurs of North America. *Bulletin of the American Museum of Natural History* **122**, 39–186.

OSTROM, J. H. (1964). A functional analysis of jaw mechanics in the dinosaur *Triceratops*. *Postilla* **88**, 1–35.

OSTROM, J. H. (1966). Functional morphology and evolution of the ceratopsian dinosaurs. *Evolution* **20**, 290–308.

OTTO-BLIESNER, B. L. & UPCHURCH, G. R. (1997). Vegetation-induced warming of high latitude regions during the late Cretaceous. *Nature* **385**, 804–807.

OWEN-SMITH, R. N. (1988). *Megaherbivores: the Influence of Very Large Body Size on Ecology*. Cambridge: Cambridge University Press.

PARKER, L. R. & BALSLEY, J. K. (1980). [Abstract] Fluvial, coastal and delta plain plant communities, dinosaur footprint casts, prevailing winds, and climate during the Upper Cretaceous in Utah. *Abstracts with Programmes, Geological Society of America (Rocky Mountain Section), 33rd Annual Meeting* **12**(6), 300.

PENNY, J. H. J. (1989). New Early Cretaceous forms of the angiosperm pollen genus *Afropollis* from England and Egypt. *Review of Palaeobotany and Palynology* **58**, 289–299.

PENNY, J. H. J. (1992). The relevance of the Early Cretaceous angiosperm palynology of Egypt to biostratigraphy and reconstruction of angiosperm palaeolatitudinal migrations. *Cretaceous Research* **13**, 369–378.

PHILLIPS, O. & SHIEL, D. (1997). Forest turnover, diversity and CO_2. *Trends in Ecology and Evolution* **12**, 404.

PHILLIPS, O. L. & GENTRY, A. H. (1994). Increasing turnover through time in tropical forests. *Science* **263**, 954–958.

POLE, M. (1999). Latest Albian–earliest Cenomanian monocotyledonous leaves from Australia. *Botanical Journal of the Linnean Society of London* **129**, 177–186.

QUI, Y-L., LEE, J., BERNASCONI-QUADRONI, F., SOLTIS, D. E., SOLTIS, P. S., ZANIS, M., ZIMMER, E. A., CHEN, Z., SAVOLAINEN, V. & CHASE, M. W. (1999). The earliest angiosperms: evidence from mitochondrial, plastid and nuclear genomes. *Nature* **402**, 404–406.

RAJANIKANTH, A. (1996). Diversification and evolution of Early Cretaceous East Coast flora of India. *Palaeobotanist* **45**, 369–377.

RAUP, D. M. (1979). Biases in the fossil record of species and genera. *Bulletin of the Carnegie Museum of Natural History* **13**, 85–91.

RAYNER, R. J. (1992). *Phyllotheca*: the pastures of the Late Permian. *Palaeogeography, Palaeoclimatology, Palaeoecology* **92**, 31–40.

REGAL, P. J. (1977). Ecology and evolution of flowering plant dominance. *Science* **196**, 622–629.

RETALLACK, G. J. (1997). Early forest soils and their role in Devonian global change. *Science* **276**, 583–585.

RICH, T. H. & VICKERS-RICH, P. (1989). Polar dinosaurs and biotas of the Early Cretaceous of south-eastern Australia. *National Geographic Research* **5**, 15–53.

RICH, T. H. & VICKERS-RICH, P. (1994). Neoceratopsians and ornithomimosaurs: dinosaurs of Gondwana origin? *National Geographic Research* **10**(1), 129–131.

RODRÍGUEZ DE LA ROSA, R. A., CEVALLOS-FERRIZ, S. R. S. & SILVA-PINEDA, A. (1998). Palaeobiological implications of Campanian coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology* **142**, 231–254.

ROMERO, E. J. (1978). Paleoecologia y paleofitogeografia de las tafofloras del Cenofitico de Argentina y areas vecinas. *Ameghiniana* **15**, 209–227.

ROMERO, E. J. (1992). [Abstract] Angiosperm morphotypes of leaves in Chubut Group, Cretaceous, Argentina. *Organisation Internationale de Paléobotanique, IVème conférence: Résumés des communications* (eds. D. Pons & J. Broutin), p. 137. Villeneuve d'Asca: Organisation Française de Paléobotanique.

ROMERO, E. J. (1993). South American paleofloras. In *Biological Relationships between Africa and South America* (ed. P. Goldblatt), pp. 62–85. New Haven: Yale University Press.

ROMERO, E. J. & ARCHANGELSKY, S. (1986). Early Cretaceous angiosperm leaves from southern South America. *Science* **234**, 1580–1582.

ROMERO, E. J. & ARGUIJO, M. H. (1981). Analisis bioestratigrafico de las tafofloras del Cretácico Superior de Austrosudamerica. *Cuencas sedimentarias del Jurásico y Cretácico de América del Sur, Volume 2* (ed. Comité Sudamericano del Jurásico y Cretácico), pp. 393–406. Buenos Aires: Comité Sudamericano del Jurásico y Cretácico.

RUSSELL, D. A., BÉLAND, P. & MCINTOSH, J. S. (1980). Paleoecology of the dinosaurs of Tendaguru (Tanzania). *Mémoires de la Société Géologique de la France* **139**, 169–175.

SALARD-CHEBOLDAEFF, M. (1990). Inter-tropical African palynostratigraphy from Cretaceous to Late Quaternary times. *Journal of African Earth Sciences* **11**, 1–24.

SALGADO, L. & CORIA, R. A. (1996). First evidence of an ankylosaur (Dinosauria, Ornithischia) in South America. *Ameghiniana* **33**, 367–371.

SAMPSON, S. D., KRAUSE, D. W. & FORSTER, C. A. (1997). Madagascar's buried treasure. *Natural History* **1997**(3), 24–27.

SCHUSTER, R. M. (1972). Continental movements, 'Wallace's line' and Indomalayan-Australasian dispersal of land plants: some eclectic concepts. *Botanical Reviews* **38**, 3–86.

SCHUSTER, R. M. (1976). Plate tectonics and its bearing on the geographical origin and dispersal of angiosperms. In *Origin and Early Evolution of Angiosperms* (ed. C. B. Beck), pp. 48–138. New York: Columbia University Press.

SCOTT, A. C., STEPHENSON, J. & CHALONER, W. G. (1992). Interaction and coevolution of plants and arthropods during the Palaeozoic and Mesozoic. *Philosophical Transactions of the Royal Society of London, Series B* **335**, 129–165.

SCOTT, R. A., BARGHOORN, E. S. & LEOPOLD, E. B. (1960). How old are the angiosperms? *American Journal of Science* **258A**, 284–299.

SERENO, P. C. (1991). *Lesothosaurus*, 'fabrosaurids', and the early evolution of Ornithischia. *Journal of Vertebrate Paleontology* **11**, 168–197.

SERENO, P. C. (1992). Psittacosauridae. In *The Dinosauria* (paperback edition) (eds. D. B. Weishampel, P. Dodson & H. Osmólska), pp. 579–592. Berkeley: University of California Press.

SERENO, P. C. (1997). The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Science* **25**, 435–489.

SERENO, P. C., BECK, A. L., DUTHEIL, D. B., LARSSON, H. C. E., LYON, G. H., MOUSSA, B., SADLEIR, R. W., SIDOR, C. A., VARRICCHIO, D. J., WILSON, G. P. & WILSON, J. A. (1999). Cretaceous sauropods from the Sahara and the uneven rate of skeletal evolution among dinosaurs. *Science* **286**, 1342–1347.

SERENO, P. C., WILSON, J. A., LARSSON, H. C. E., DUTHEIL, D. B. & SUES, H-D. (1994). Early Cretaceous dinosaurs from the Sahara. *Science* **266**, 267–271.

SHERIDAN, R. E. (1987). Pulsation tectonics as the control of long-term stratigraphic cycles. *Paleoceanography* **2**, 97–118.

SHERIDAN, R. E. (1997). Pulsation tectonics as a control on the dispersal and assembly of supercontinents. *Journal of Geodynamics* **23**, 173–196.

SMITH, A. G., SMITH, D. G. & FUNNELL, B. M. (1994). *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge: Cambridge University Press.

SOLTIS, P. S., SOLTIS, D. E. & CHASE, M. W. (1999). Angiosperm phylogeny inferred from multiple genes as a tool for comparative biology. *Nature* **402**, 402–404.

SRIVASTAVA, A. K., BANUBAKODE, P. D., KALE, V. M., PATIL, G. V. & MANIK, S. R. (1999). Lower Cretaceous plant fossils from Bairam-Belkher area, District Amravati, Maharashtra and District Betul, Madhya Pradesh and their significance in stratigraphy. *Palaeobotanist* **48**, 39–48.

STEBBINS, G. L. (1981). Coevolution of grasses and herbivores. *Annals of the Missouri Botanical Garden* **68**, 75–86.

STEFANOVIC, S., JAGER, M., DEUTSCH, J., BROUTIN, J. & MASSELOT, M. (1998). Phylogenetic relationships of conifers inferred from partial 28S rRNA gene sequences. *American Journal of Botany* **85**, 688–697.

STEVENS, K. A. & PARRISH, J. M. (1999). Neck posture and

feeding habits of two Jurassic sauropod dinosaurs. *Science* **284**, 798–800.

STEWART, W. N. & ROTHWELL, G. W. (1993). *Paleobotany and the Evolution of Plants* (2nd edition). Cambridge: Cambridge University Press.

SUN, G., DILCHER, D. L., ZHENG, S-L. & ZHOU, Z. (1998). In search of the first flower: a Jurassic angiosperm, *Archaefructus*, from north-east China. *Science* **282**, 1692–1695.

SUN, G., GUO, S-X., ZHENG, S-L., PIAO, T-Y. & SUN, X-K. (1993). First discovery of the earliest angiospermous megafossils in the world. *Science in China (Series B)* **36**, 249–256.

SWAIN, T. (1976). Angiosperm – reptile coevolution. In *Morphology and Biology of Reptiles* (eds. A. d'A. Bellairs & C. B. Cox), pp. 107–122. London: Academic Press.

SWISHER, C. C. III., WANG, Y-Q., WANG, X-L., XU, X. & WANG, Y. (1999). Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature* **400**, 58–61.

TAGGART, R. E. & CROSS, A. T. (1997). The relationship between land plant diversity and productivity and patterns of dinosaur herbivory. In *Dinofest International: Proceedings of a Symposium held at Arizona State University* (eds. D. L. Wolberg, E. Stump & G. Rosenberg), pp. 403–416. Philadelphia: Academy of Natural Sciences.

TAKHTAJAN, A. (1969). *Flowering Plants – Origin and Dispersal*. Edinburgh: Oliver & Boyd.

TANDON, S. K., SOOD, A., ANDREWS, J. E. & DENNIS, P. F. (1995). Palaeoenvironments of the dinosaur-bearing Lameta Beds (Maastrichtian), Narmada Valley, Central India. *Palaeogeography, Palaeoclimatology, Palaeoecology* **117**, 153–184.

TAPIA, A. (1918). Una mandibula de dinosaurio procedente de Patagonia. *Physis* **4**, 369–370.

TAQUET, P. (1976). *Géologie et Paléontologie du Gisement de Gadoufaoua (Aptien du Niger)*. Paris: Cahiers de Paléontologie, C.N.R.S.

TAYLOR, D. W. & HICKEY, L. J. (1990). An Aptian plant with attached leaves and flowers: implications for angiosperm origin. *Science* **247**, 702–703.

TAYLOR, D. W. & HICKEY, L. J. (1996). Evidence for and implications of an herbaceous origin for angiosperms. In *Flowering Plant Origin, Evolution and Phylogeny* (eds. D. W. Taylor & L. J. Hickey), pp. 232–266. New York: Chapman & Hall.

THULBORN, R. A. (1991). Morphology, preservation and palaeobiological significance of dinosaur coprolites. *Palaeogeography, Palaeoclimatology, Palaeoecology* **83**, 341–366.

THUSU, B., VAN DER EEM, J. G. L. A., EL-MEHDAWI, A. & BU-ARGOUB, F. (1988). Jurassic – Early Cretaceous palynostratigraphy in north-east Libya. In *Subsurface Palynology of Northeast Libya*, (eds. A. El-Arnauti, B. Owens & B. Thusu), pp. 171–213. Benghazi: Garyounis University Publications.

TIFFNEY, B. H. (1984). Seed size, dispersal syndromes, and the rise of angiosperms: evidence and hypothesis. *Annals of the Missouri Botanical Garden* **71**, 551–576.

TIFFNEY, B. H. (1992). The role of vertebrate herbivory in the evolution of land plants. *Palaeobotanist* **41**, 87–97.

TIWARI, R. S. & TRIPATHI, A. (1995). Palynological assemblages and absolute age relationship of Intertrappean beds in the Rajmahal Basin, India. *Cretaceous Research* **16**, 53–72.

TOMIDA, Y., RICH, T. H. & VICKERS-RICH, P. (eds.) (1999). *Proceedings of the Second Gondwana Dinosaur Symposium*. National Science Museum Monographs **15**, 1–296.

TRAVERSE, A. (1988). *Paleopalynology*. Boston: Unwin Hyman.

TRAVERSO, N. E. (1966). *Brachyphyllum tigrense*, nueva conifera de la Formacion Baquero, Cretacico de Santa Cruz. *Ameghiniana* **4**, 189–194.

UPCHURCH, P. (1995). The evolutionary history of the sauropod dinosaurs. *Philosophical Transactions of the Royal Society of London, Series B* **349**, 365–390.

UPCHURCH, P. (1998). The phylogenetic relationships of sauropod dinosaurs. *Zoological Journal of the Linnean Society of London* **124**, 43–103.

UPCHURCH, P. (1999). The phylogenetic relationships of the Nemegtosauridae (Saurischia, Sauropoda). *Journal of Vertebrate Paleontology* **19**, 106–125.

UPCHURCH, P. & BARRETT, P. M. (2000). The evolution of sauropod feeding mechanisms. In *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record* (ed. H-D. Sues), pp. 79–122. Cambridge: Cambridge University Press.

UPCHURCH, P. & MARTIN, J. (in prep.). The anatomy and taxonomy of *Cetiosaurus* (Saurischia, Sauropoda) from the Middle Jurassic of England.

VACHRAMEEV, V. A. & KOTOVA, I. Z. (1978). Ancient angiosperms and accompanying plants from the Lower Cretaceous of Transbaikalia. *Paleontological Journal* **11**, 487–495.

WANG, X-F., XUE, D. & YUAN, S. (1999). Early Cretaceous microfloras in the Ejina Basin of West Inner Mongolia. *Acta Micropalaeontologica Sinica* **16**, 76–81 (in Chinese with English summary).

WEAVER, J. C. (1983). The improbable endotherm: the energetics of the sauropod dinosaur *Brachiosaurus*. *Paleobiology* **9**, 173–182.

WEISHAMPEL, D. B. (1984a). Evolution of jaw mechanisms in ornithopod dinosaurs. *Advances in Anatomy, Embryology and Cell Biology* **87**, 1–110.

WEISHAMPEL, D. B. (1984b). Interactions between Mesozoic plants and vertebrates: fructifications and seed predation. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* **167**, 224–250.

WEISHAMPEL, D. B. (1992). Dinosaurian distribution. In *The Dinosauria* (paperback edition) (eds. D. B. Weishampel, P. Dodson & H. Osmólska), pp. 63–139. Berkeley: University of California Press.

WEISHAMPEL, D. B., DODSON, P. & OSMÓLSKA, H. (eds.) (1992). *The Dinosauria* (paperback edition). Berkeley: University of California Press.

WEISHAMPEL, D. B. & HORNER, J. R. (1992). Hadrosauridae. In *The Dinosauria* (paperback edition) (eds. D. B. Weishampel, P. Dodson & H. Osmólska), pp. 534–561. Berkeley: University of California Press.

WEISHAMPEL, D. B. & JIANU, C-M. (2000). Plant-eaters and ghost lineages: dinosaurian herbivory revisited. In *Evolution of Herbivory in Terrestrial Vertebrates: Perspectives from the Fossil Record* (ed. H-D. Sues), pp. 123–143. Cambridge: Cambridge University Press.

WEISHAMPEL, D. B., LE LOEUFF, J., CORIA, R. A., GOMANI, E. M., ZHAO, X.-J., XU, X., BARRETT, P. M. & SAHNI, A. (in prep.). Dinosaur distribution. In *The Dinosauria (Second Edition)*. Berkeley: University of California Press.

WEISHAMPEL, D. B. & NORMAN, D. B. (1989). Vertebrate herbivory in the Mesozoic; jaws, plants and evolutionary metrics. *Special Papers of the Geological Society of America* **238**, 87–100.

WEISHAMPEL, D. B. & WEISHAMPEL, J. B. (1983). Annotated localities of ornithopod dinosaurs: Implications for Mesozoic paleobiogeography. *Mosasaur* **1**, 43–88.

WERGER, M. J. A., VAN DER AART, P. J. M., DURING, H. J. & VERHOEVEN, J. T. A. (eds.) (1989). *Plant Form and Vegetation Structure: Adaptation, Plasticity and Relation to Herbivory*. The Hague: SPB Academic Publishing.

WHEELER, E. A. & BAAS, P. (1993). The potentials and limitations of dicotyledonous wood anatomy for climatic reconstructions. *Paleobiology* **19**, 487–498.

WHEELER, E. A. & LEHMAN, T. M. (2000). Late Cretaceous woody dicots from the Aguja and Javelina Formations, Big Bend National Park, Texas, USA. *IAWA Journal* **21**, 83–120.

WILF, P., LABANDEIRA, C. C., KRESS, W. J., STAINES, C. L., WINDSOR, D. M., ALLEN, A. L. & JOHNSON, K. R. (2000). Timing the radiations of leaf beetles: hispines on gingers from the latest Cretaceous to Recent. *Science* **289**, 291–294.

WILLIS, K. J. & BENNETT, K. B. (1995). Mass extinction, punctuated equilibrium and the fossil plant record. *Trends in Ecology and Evolution* **10**, 308–309.

WILSON, J. A. & CARRANO, M. T. (1999). Titanosaurs and the origin of 'wide-gauge' trackways: a biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* **25**, 252–267.

WILSON, J. & SERENO, P. C. (1998). Early evolution and higher-level phylogeny of the sauropod dinosaurs. *Memoirs of the Society of Vertebrate Paleontology* **5**, 1–68.

WIMAN, C. (1929). Die Kreide-dinosaurier aus Shantung. *Palaeontologia Sinica (Series C)* **6**(1), 1–67.

WING, S. L. & BOUCHER, L. D. (1998). Ecological aspects of the Cretaceous flowering plant radiation. *Annual Reviews of Earth and Planetary Sciences* **26**, 379–421.

WING, S. L., HICKEY, L. J. & SWISHER, C. C. III. (1993). Implications of an exceptional fossil flora for Late Cretaceous vegetation. *Nature* **363**, 342–344.

WING, S. L., SUES, H-D., TIFFNEY, B. H., STUCKY, R. K., WEISHAMPEL, D. B., SPICER, R. A., JABLONSKI, D., BADGLEY., C. E., WILSON, M. V. H. & KOVACH, W. L. (1992). Mesozoic and Early Cenozoic terrestrial ecosystems. In *Terrestrial Ecosystems through Time: Evolutionary Paleoecology of Plants and Animals* (eds. A. K. Behrensmeyer, J. D. Damuth, W. A. DiMichele, R. Potts, H-D. Sues & S. L. Wing), pp. 327–416. Chicago: University of Chicago Press.

WING, S. L. & TIFFNEY, B. H. (1987a). Interactions of angiosperms and herbivorous tetrapods through time. In *The Origin of Angiosperms and their Biological Consequences* (eds. E. M. Friis, W. G. Chaloner & P. R. Crane), pp. 203–224. Cambridge: Cambridge University Press.

WING, S. L. & TIFFNEY, B. H. (1987b). The reciprocal interaction of angiosperm evolution and tetrapod herbivory. *Review of Palaeobotany and Palynology* **50**, 179–210.

WOLFE, J. A. & UPCHURCH, G. R., JR. (1987). North American non-marine climates and vegetation during the Late Cretaceous. *Palaeogeography, Palaeoclimatology, Palaeoecology* **61**, 33–77.

WOODWARD, F. I. (1992). A review of the effects of climate on vegetation: ranges, competition and composition. In *Global Warming and Biological Diversity* (eds. R. L. Peters & T. E. Lovejoy), pp. 105–123. New Haven: Yale University Press.

WRIGHT, J. L., BARRETT, P. M., LOCKLEY, M. G. & COOK, E. (1998). A review of the Early Cretaceous terrestrial vertebrate track-bearing strata of England and Spain. *New Mexico Museum of Natural History and Science. Bulletin* **14**, 143–153.

XU, X. & WANG, X-L. (1998). New psittacosaur (Ornithischia, Ceratopsia) occurrence from the Yixian Formation of Liaoning, China and its stratigraphical significance. *Vertebrata PalAsiatica* **36**, 147–158 (in Chinese with English summary).

ZAVADA, M. S. & MENTIS, M. T. (1992). Plant–animal interaction: the effect of Permian megaherbivores on the glossopterid flora. *American Midland Naturalist* **127**, 1–12.