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Phil. Trans. R. Soc. Lond. B 1993 **341**, 277-286
doi: 10.1098/rstb.1993.0113

Cretaceous phytogeography and climate signals

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SUMMARY

We address two aspects of Cretaceous plants and climate. Firstly, we briefly characterize Cretaceous global phytogeography and review some quantitative temperature estimates derived from plants. Secondly, by adopting a multivariate statistical approach to palaeophytogeographic mapping, we examine the effect of the rise in diversity and ecological radiation of angiosperms on the climate signal offered by non-angiosperms.

In the Cretaceous, plant productivity was concentrated at middle and high latitudes. Polar cool temperate rain forests in coastal areas, where winter temperatures were ameliorated by the proximity of the ocean, were conifer-dominated and deciduous. In more continental high latitudes, winter temperatures probably fell well below freezing, thermally depressing metabolic rates and allowing some plants to retain their leaves year round. However, this 'evergreenness' necessitated desiccation resistance in the form of reduced leaf size and thick cuticles. At mid latitudes, open canopy woodlands and forests were dominated by a mixture of microphyllous conifers, moderately xeromorphic ferns, cycadophytes, pteridosperms and sphenophytes. Late Cretaceous broadleaved coriaceous angiosperms were mostly subordinate shrubs and small trees. Large angiosperm trees were comparatively rare. Although the evidence is meagre, low latitude vegetation tended to be xeromorphic and only patchily forested. Tropical everwet vegetation was, if present at all, highly restricted and consequently not understood.

Non-angiosperms exhibit a weak, poorly differentiated phytogeographic pattern linked most strongly to the evaporation:precipitation ratio. This relationship is reflected in foliar physiognomy, and was established long before the Cretaceous. As the advent of the angiosperms did not significantly alter this relationship, it may be possible to calibrate the non-angiosperms of the Mesozoic using the physiognomic techniques developed for woody dicots.

Taxonomy independent of political and stratigraphic boundaries is essential in order to satisfactorily reconstruct palaeophytogeography and derivative climatic signals, as are non-selective reporting of floral composition and detailed descriptions of plant physiognomy. Without this basic information the full potential of the plant fossil record to reveal past climate and environmental change cannot be exploited.

1. PLANT PHYSIOGNOMY AND CLIMATE

To a large extent the morphology and anatomy of land plants is constrained by their immediate physical conditions. These constraints have operated throughout land plant evolution and have resulted in repeated morphologies under similar environmental conditions. These 'repeating polymorphic sets' (Meyen 1973) can be used qualitatively and quantitatively to determine past climates.

The facts that modern vegetation can be described and mapped without resorting to taxonomic lists (e.g. Holdridge 1947; Walter 1985; Box 1981; Olsen *et al.* 1983; Leemans 1989; Prentice 1990; Prentice *et al.* 1992), and that patterns of plant distributions have an observable (albeit complex) relationship with climate, show that the physiognomy of individual organs, whole plants, and vegetational units up to the scale of global biomes is strongly influenced by (and thus reflective of) climate. Adaptive relations between environmental factors and physiognomic character states have been shown to have a theoretical (Givnish 1979, 1986; Givnish & Vermeij 1976) and experimental (Parkhurst & Loucks 1972) basis, being observed in unrelated plants growing in similar environments irrespective of spatial or temporal separation.

While modern angiosperm-rich vegetation and the physiognomy of woody dicotyledonous angiosperms display quantifiable climatic signals (Wolfe 1979; Spicer 1990; Wing & Greenwood, this volume), non-angiosperms as yet provide only qualitative climatic data. Furthermore angiosperms could have influenced the relationship between ancient groups (e.g. conifers, cycadophytes, pteridosperms, ferns) and climate, thereby compounding the difficulties of interpreting and calibrating climatic signals derived from non-angiosperms.

The physiognomic approach to the interpretation of climatic signals has several advantages over the floristic or nearest living relative (NLR) techniques that have dominated previous palaeoclimatological interpretation. The fundamental assumption of the NLR approach is that climatic tolerances of living taxa can be extrapolated without modification to ancestral forms, implying evolutionary stasis. One example of the inappropriateness of this technique is seen in Mesozoic cycads, whose demonstrably wider morphological and anatomical range included deciduous and frost-tolerant forms. Thus, the presence of cycads at high Cretaceous latitudes does not imply polar 'subtropical' climates or significantly reduced obliquity (Spicer 1987). For the Mesozoic and earlier periods, a physiognomic approach to climate analysis is the only viable technique.

Several recent studies have mapped the distribution of fossil plant taxa to determine Mesozoic vegetational and climatic patterns (Ziegler 1990; Horrell 1991; Vakhrameev 1991; Saward 1992). The use of palaeobotanical genera for determining Mesozoic vegetational units or biomes is not an NLR approach because these taxa are not being compared directly with living forms. As with all fossils the name primarily denotes a morphotype that in many instances conveys the physiognomy of a particular organ.

Intuitively one might suspect that as the angiosperms radiated geographically and ecologically and new competitive régimes were established, climatic influences on the physiognomy and distribution of ferns and gymnosperms may have been fundamentally altered. Determining whether this was the case is a pre-requisite for developing and calibrating physiognomic relationships of extinct non-angiosperms to climate.

2. CRETACEOUS GLOBAL PHYTOGEOGRAPHY: A BRIEF OVERVIEW

The Cretaceous was a time of profound vegetational change due largely to the evolutionary and geographic radiation of the angiosperms. By the Albian angiosperms were present from pole to pole but were ecologically dominant only locally. Throughout the Late Cretaceous angiosperms progressively infiltrated the pre-existing vegetation, but gymnosperms, ferns and sphenophytes dominated land-plant biomass until the Tertiary. As the broad scale characteristics of Cretaceous phytogeography have been reviewed in several recent works (e.g. Spicer & Chapman 1990; Spicer & Corfield 1992; Dettmann *et al.* 1992; Francis & Frakes 1993), only a general account will be given here.

(*a*) *High (above 66°) palaeolatitudes*

Late Early Cretaceous data from the Arctic Ocean margin indicate the existence of humid forests composed primarily of seasonally deciduous conifers (some of which were broad-leaved: e.g. *Podozamites*) and ginkgophytes (*Sphenobaiera*, *Ginkgo*, *Baiera*) with an understorey of ferns, sphenophytes, pteridosperms and cycadophytes (Smiley 1966, 1967, 1969*a,b*; Scott & Smiley 1979; Vakhrameev 1991). These polar cycadophytes, unlike relictual thermophyllic modern forms, were deciduous and frost resistant (Spicer & Chapman 1990). Although charcoalified layers in the extensive coals suggest frequent but minor burning (Lamberson, personal communication 1993) drought was rare as tree growth rings generally lack false rings that might indicate water stress (Parrish & Spicer 1988*a*). Large earlywood:latewood ratios suggest no obvious summer restrictions on photosynthesis but a rapid transition to winter dormancy, a pattern consistent with the present day polar light régime. Qualitative interpretation suggests a cool temperate thermal régime with a humid atmosphere. Rainfall was probably high and more-or-less evenly distributed, at least during the summer. With the obliquity similar to that of the Recent, the lack of insolation for several months of each year must have resulted in seasonal temperature variations, but winter temperatures may not have fallen much below freezing. There is no evidence for permafrost or deeply frozen soils.

The migration of angiosperms into the high Arctic in latest Albian times provides a means of obtaining quantitative air temperature estimates. Foliar physiognomic studies have long shown a relationship between the ratio of toothed to entire-margined woody dicotyledonous angiosperm leaves and mean annual temperature (MAT; Bailey & Sinnott 1915, 1916; Wolfe 1979) in vegetation that is not water limited. This relationship appears to have been established by the Cenomanian (Wolfe & Upchurch 1987). Leaf margin analysis yields a Cenomanian MAT of 10 ± 3°C on the coastal plain of northern Alaska (i.e. Cretaceous sea level at palaeolatitude 75°N; Spicer & Parrish 1990). This figure is identical to that obtained from overall vegetational physiognomy (Parrish & Spicer 1988*b*). The mean annual range of temperature is difficult to estimate but vegetational limits indicate a cold month mean no lower than −11°C (Parrish *et al.* 1987). Warm month means may have exceeded 25°C. Angiosperm foliar physiognomy suggests an increase in MAT to about 12–13°C for the same area in the Coniacian, before the pronounced cooling in the Campanian and Maastrichtian, when diversity decline and tree ring data suggest lower summer temperatures and significant drying. MATS fell to about 5 ± 3°C at 85°N (Spicer & Parrish 1990).

Circum-Antarctic Cretaceous vegetation has been characterized as a cool temperate podocarp and araucarian-dominated forest (Askin 1989, 1992; Drinnan & Crane 1990; Spicer 1990; Truswell 1990). The Early Cretaceous of the Antarctic region is perhaps best understood from the Otway and Gippsland Basins, south-eastern Australia (Douglas 1969, 1973; Douglas & Williams 1982; Dettmann *et al.* 1992). This area is not only important because of its high palaeolatitude (above 66°S throughout the Cretaceous and possibly as high as 85°S (Veevers & Ettriem 1988)) but also because it provides physiognomic data for the continental interior. Barremian vegetation was dominated by broad-leaved (*Elatocladus*) and microphyllous (*Brachyphyllum*) conifers. Pteridosperms (e.g. *Reinitzia*), *Taeniopteris*, microphyllous bennettitaleans, and the deciduous (Cantrill & Webb 1987) osmundaceous fern *Phyllopteroides* formed the understorey and ground cover. Aptian floras from the same region show *Ginkgo* as a canopy component and brachyphyll conifers more widespread than broad-leaved forms (Dettmann *et al.* 1992). The lacustrine Koonwarra flora in the south-eastern part of the Austro-Antarctic rift valley is diverse: its 57 known plant megafossil forms include the oldest presumed angiosperm flower (Drinnan & Chambers 1986; Taylor & Hickey 1990). The arrival of non-magnoliid angiosperms in latest Aptian-early Albian times coincides with the virtual disappearance of the bennettitaleans, taeniopterids and sphenopsids, but the mixture of broad-leaved and microphyllous conifers remained as canopy dominants with a fern understorey rich in the deciduous *Phyllopteroides*. Fossil trees from the margins of greater Antarctica exhibit the same strong seasonal signal as those from the Arctic throughout the Cretaceous (e.g. Jefferson 1982; Francis 1986; Chapman & Smellie 1992).

This canopy of broad and micro-leaved conifers with a fern understorey variously admixed with bennettitaleans, pteridosperms, and an increasing proportion of angiosperms, seems to persist in south-eastern Australia throughout the Cretaceous (Drinnan & Crane 1990). The high proportion of microphyllous conifers and cycadophytes (often with thick cuticles) co-existing with broad-leaved and thin-cuticled deciduous ferns, ginkgophytes and pteridosperms has been interpreted as mixed 'evergreen' (a persistent leaf load) and deciduous (periods of no leaf load) vegetation growing where winter temperatures dropped low enough to curtail respiration and render it energetically worthwhile for some plants to retain their leaves throughout the dark winters (Parrish *et al.* 1991). In contrast, microphyllous plants with thick cuticles are largely absent from Cenomanian coastal plain floras of New Zealand (Daniel *et al.* 1990) which, like those in the Arctic, would have experienced warmer winters moderated by maritime influence.

Vegetational considerations provide a rough estimate of 5–8°C MAT for the Albian of south-eastern Australia (Parrish *et al.* 1991), which is somewhat higher than those obtained by isotopic means from meltwaters sourced high on the rift valley margins (Gregory *et al.* 1989).

(*b*) *Middle (66–40°) and low (below 40°) palaeolatitudes*

Vegetation below 40° palaeolatitude is predominantly xeric throughout the Cretaceous. Microphyllous conifers such as *Frenelopsis*, *Pseudofrenelopsis*, *Brachyphyllum*, *Cupressinocladus* and *Pagiophyllum* represent the extinct Cheirolepidiaceae which, on the basis of the distribution of megafossils and their characteristic pollen *Classopollis* (*Corallina* of some authors), was locally abundant even in saline coastal environments. Although Vakhrameev (1981) depicted *Classopollis* increasing towards the equator, the distribution of *Classopollis* retrieved from the Mesozoic Climates Project database (Price *et al.* 1991) is far more variable than his maps imply (figure 1). As the Cheirolepidiaceae probably occupied a wide range of habitats (Alvin 1982; Watson 1988), the *Classopollis* patchiness may reflect heterogeneity in moisture availability. Some members of the Cheirolepidiaceae, such as *Frenelopsis* and *Pseudofrenelopsis*, exhibit extreme xeromorphism, with highly reduced leaves, thick cuticles, specialized sunken stomata and even fimbriate margins adjacent to areas of thin cuticle which may have induced the nucleation and absorption of water from a humid atmosphere (Alvin *et al.* 1981; Spicer 1989). Other mid and low latitude plants also exhibit xeromorphic characters (e.g. many cycadophytes and the fern *Weichselia*: Alvin 1974) and are often preserved charcoalified, while others indicate warmth (e.g. the barrel shaped, manoxylic, and therefore presumably frost-sensitive, bennettite *Cycadeoidea*).

In Campanian and Maastrichtian times leaf margin analysis suggests a latitudinal temperature gradient of 0.3°C/1° latitude, and at mid latitudes (50°N) a mean annual range of 8°C is inferred. At 30°N the Cenomanian MAT is given as 23°C rising to 25°C in the Coniacian and Santonian before declining to a low of 22°C in mid Maastrichtian times (Wolfe & Upchurch 1987). Leaf size tended to be small at low middle latitudes and Wolfe & Upchurch (1987) suggested this may indicate moderate to low precipitation. Larger leaf sizes near 50°N and above 65°N in the Campanian indicate wetter régimes at these latitudes.

3. A MULTIVARIATE APPROACH TO UNDERSTANDING PHYTOGEOGRAPHIC PATTERNS AND CLIMATE SIGNALS IN NON-ANGIOSPERMS

Broad phytogeographic patterns can be easily determined by highly subjective means (e.g. Vakhrameev 1991) and they imply that non-angiosperm vegetation was controlled by, and therefore displays, climatic influences. However many Mesozoic phytogeographic maps are based on a few key taxa and the criteria for delimiting boundaries between biomes change as the taxa evolve. This results in vegetational unit boundaries that are arbitrary and the positioning of phytogeographic boundaries tends to be at a geographic resolution that is poor even by the demands of atmospheric general circulation models. Ideally, higher resolution objective methods of determining floristic patterns are required.

For many years Russian and Chinese geologists and palaeobotanists have collated palaeofloristic data in the form of comprehensive taxonomic lists from specified sites. The Chinese Provincial Stratigraphic Reports contain details of sedimentary sequences in over 400 geologic regions within China, with lists of plant fossil species given for each fossiliferous stratigraphic unit. The Russian taxon lists are of comparable quality. Central co-ordination ensured a taxonomic uniformity seldom matched in the West; Asian data therefore provide a framework for evaluating methods of palaeophytogeographic and climatic analysis (see also Ziegler *et al.*, this volume). Using multivariate statistical analysis these floral lists can be used to map phytogeography and, because at the generic level the taxonomy of fossil vegetative organs

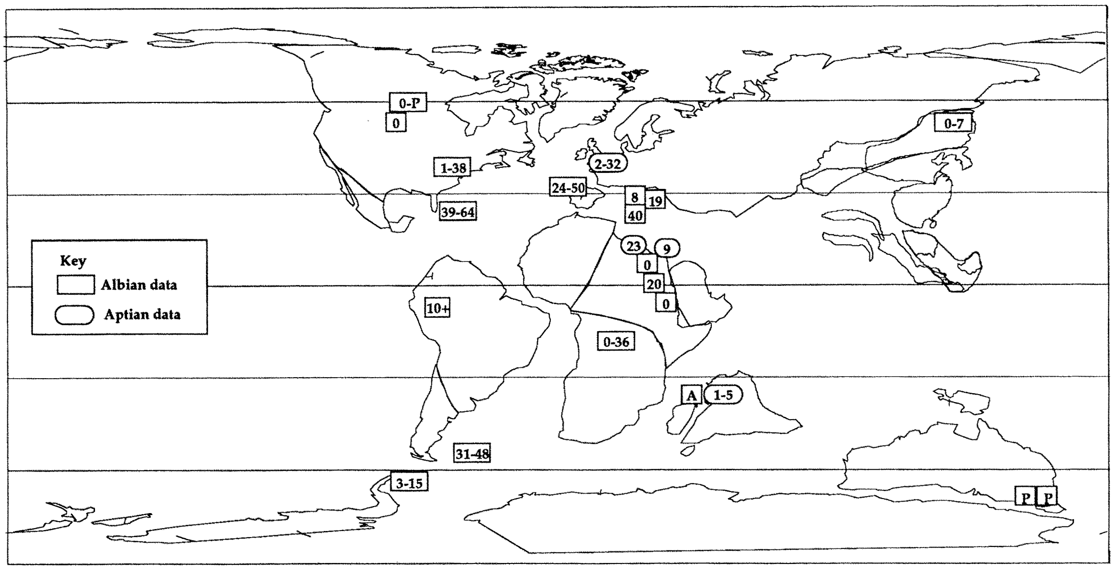

Figure 1. Aptian and Albian distribution of *Classopollis* and *Corallina* pollen derived from the Mesozoic Climatic Modelling Research Project Oracle Database. Figures are percentages. P = present, R = rare, A = abundant. Note the juxtaposition of high and low percentages, even at low latitudes. This probably reflects genuine variations in the distribution and abundance of the Cheirolepidiaceae.

reflects morphology and thus physiognomy, these patterns may be expected to have some correlation with climate. Analyses were carried out on data summed over relatively long time intervals (i.e. the Early and Late Cretaceous), due to limitations in stratigraphic correlation and dating.

Only leaf or leafy shoot genera (see Spicer & Thomas (1986) for papers on the peculiarities of palaeobotanical systematics) were analysed as they display the strongest physiognomic relationship to climate. Synonymies were identified using the Plant Fossil Record database (Holmes *et al.* 1991) and genera were merged or rejected as appropriate. No angiosperms were included in the databases because existing generic names are often erroneous, of local usage, or artificial and without physiognomic significance (e.g. *Dicotylophyllum*). Data matrices for generic presence or absence and genera weighted by species

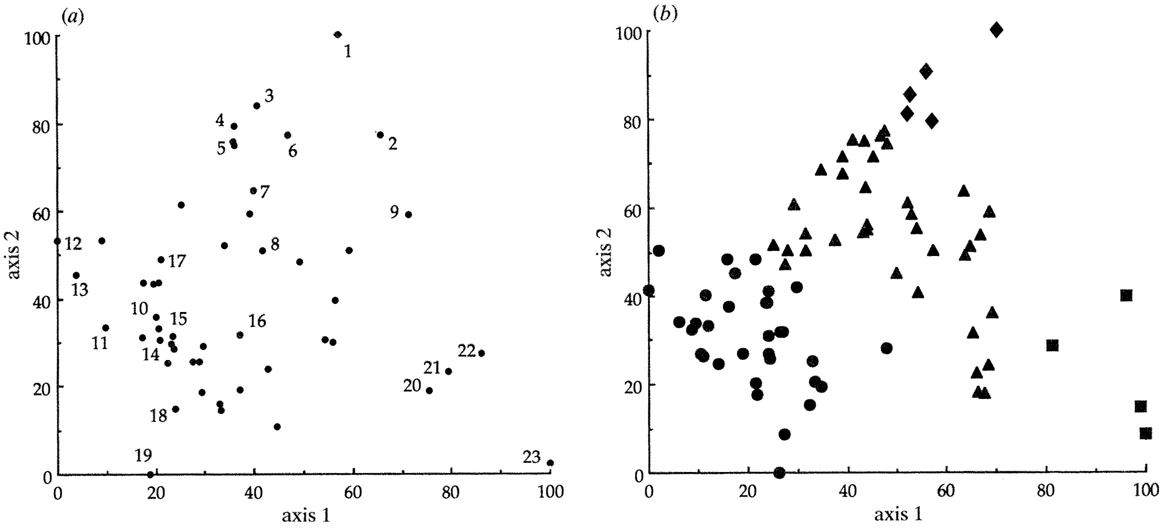

Figure 2. (*a*) Correspondence analysis (CA) of Early Cretaceous plant genera. Data for this and subsequent CAs derived from: Baikovskaya (1956); Guo (1980, 1981); Iwai *et al.* (1975); Kimura (1987); Kirichkova & Budantsev (1967); Krassilov (1982); Lee (1988); Samylina (1963, 1964, 1967); Vakhrameev (1958); Vakhrameev *et al.* (1978); reports of the Stratigraphic Groups of South China, Fujian, Gansu, Heilongjiang, Jiangsu, Jiangxi, Jilin, Liaoning, Nei Mongol, Ningxia, Qinghai, Shaanxi, Shandong, Xinjiang, Xizang, Yunnan and Zeijiang. For clarity, only key genera are shown: 1, *Frenelopsis*; 2, *Nageopsis*; 3, *Pagiophyllum*; 4, *Elatides*; 5, *Brachyphyllum*; 6, *Otozamites*; 7, *Anomozamites*; 8, *Zamites* ; 9, *Zamiophyllum*; 10, *Ginkgo*; 11, *Dicksonia*; 12, *Baierella*; 13, *Baiera*; 14, *Czekanowskia*; 15, *Sphenobaiera*; 16, *Nilssonia*; 17, *Podozamites*; 18, *Asplenium*; 19, *Dennstaedtia*; 20, *Gleichenia*; 21, *Klukia*; 22, *Ptilophyllum*; 23, *Weichselia*. (*b*) CA site plot for the Early Cretaceous of Asia. Circles = sites rich in broad-leaved deciduous genera; triangles = sites rich in intermediate genera; diamonds = sites rich in xeromorphic genera; squares = sites rich in *Weichselia*.

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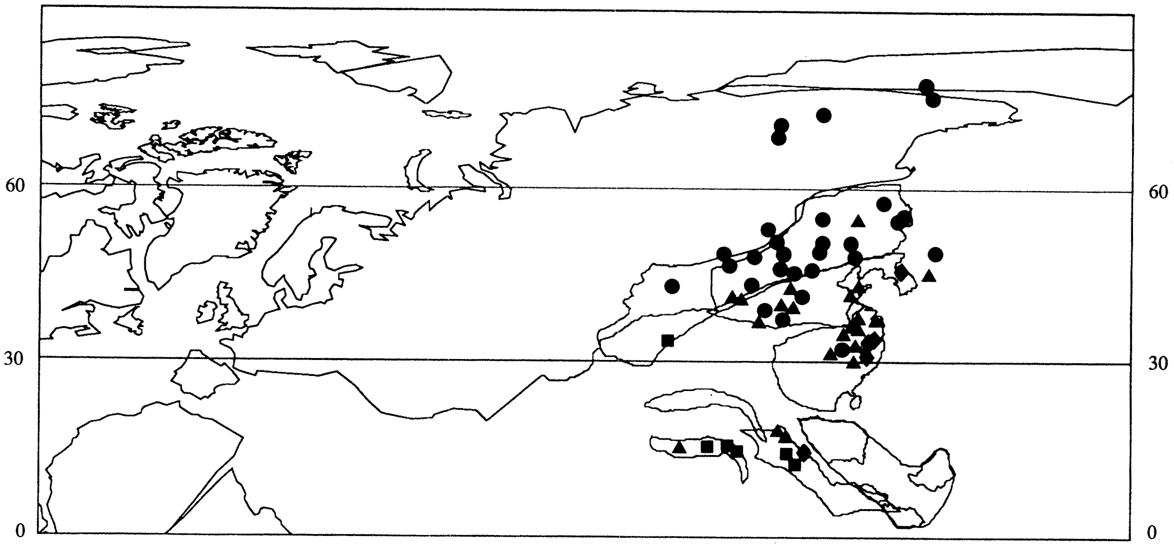

Figure 3. Phytogeographic map of Asia for the Early Cretaceous based on the analyses shown in figure 2*a*,*b*. Symbols as in figure 2*b*.

abundance were constructed. Matrices were analysed using correspondence analysis (CA). This is a particularly robust exploratory ordination technique that provides the same scaling of character and sample plots (providing ready comparison) and can accommodate 'fuzzy' data matrices where some information is missing (Hill 1973, 1979). Exploratory analysis of Early Cretaceous Chinese data matrices (Spicer *et al.* 1988) demonstrated the ability of this technique to display not only phytogeographic patterns but also to detect anomalies produced by tectonic displacement of terrains. In the current analyses presence-absence and species abundance data gave similar results and only the presence-absence results are presented here.

The genus and site plots of the CA analyses for the Early Cretaceous of Asia are shown in figure 2*a*,*b*. Axes 1 and 2 represent the greatest variation in the data matrix but even then they account for only 17% of the total, indicating that the pattern is weak. In figure 2*a*, axis 1 demonstrates a clear separation of the more xeromorphic ferns *Weichselia*, *Klukia* and *Gleichenia* from the deciduous ginkgophytes *Baierella* and *Baiera*. *Frenelopsis*, *Pagiophyllum*, *Nageopsis*, *Elatides*, *Brachyphyllum* and *Otozamites*, all of which have some xeromorphic characteristics, are displayed high on axis 2. Broad-leaved deciduous taxa (e.g. *Ginkgo*, *Nilssonia*, *Podozamites*, *Czekanowskia*, *Sphenobaiera*) cluster in the lower left quadrant of the plot. Genera typical of seasonal, cool, damp vegetation have low scores on both axes whereas genera of drier possibly warmer areas have high scores on both axes. However, the separation of *Weichselia* from *Frenelopsis* suggests that these taxa rarely co-occur.

There are no clear discontinuities in the comple-

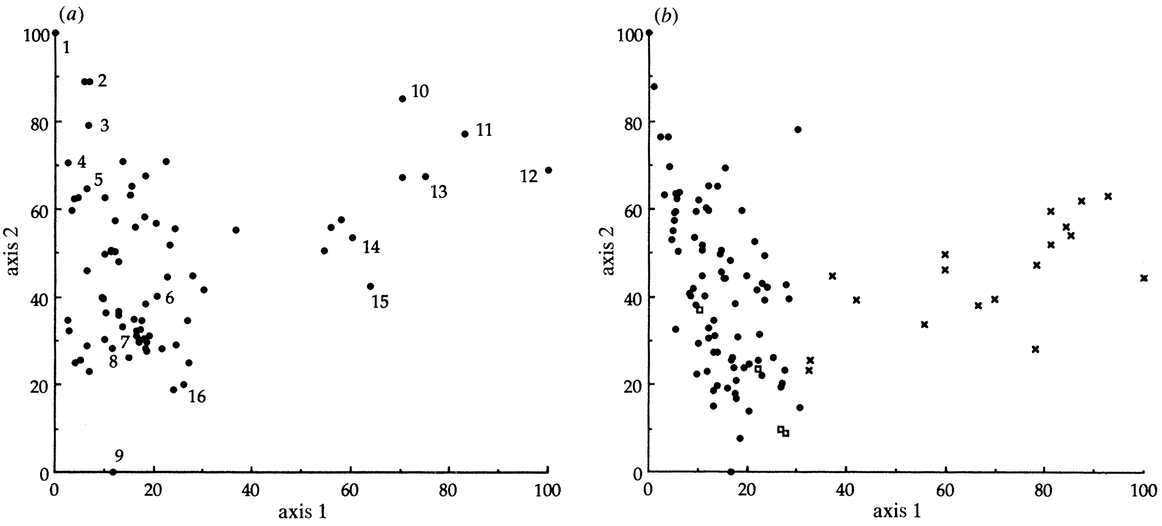

Figure 4. (*a*) CA genus plot for the Early Cretaceous of Asia and the Late Cretaceous of China and Russia. 1, *Frenelopsis*; 2, *Nageiopsis*; 3, *Zamites*; 4, *Pagiophyllum*; 5, *Brachyphyllum*; 6, *Nilssonia*; 7, *Ginkgo*; 8, *Baiera*; 9, *Mohria*; 10, *Pinus*; 11, *Agathis*; 12, *Glyptostrobus*; 13, *Sequoia*; 14, *Thuja*; 15, *Cephalotaxopsis*; 16, *Dennstaedtia*. (*b*) CA site plot for the Early Cretaceous of Asia and the Late Cretaceous of China and Russia. The Russian sites plot high on axis 1 due to the inclusion of 'modern' genera. Closed circles = Early Cretaceous sites of Asia; open squares = Late Cretaceous sites of China; crosses = Late Cretaceous sites of Russia.

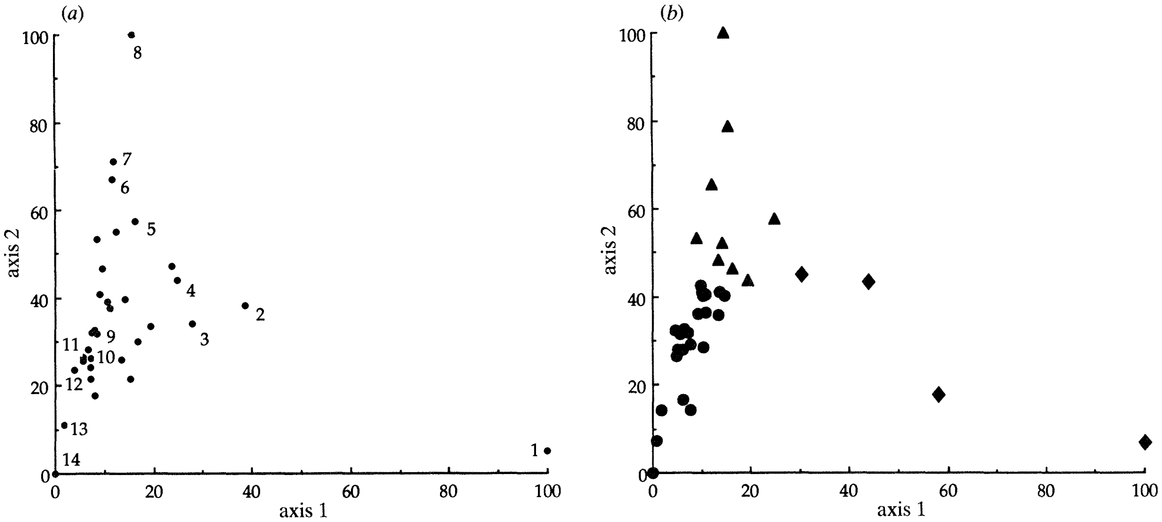

Figure 5. (*a*) CA genus plot for the Late Cretaceous of Asia using only genera common to the Early Cretaceous. The xeromorphic conifers plot to the right and the broad-leaved deciduous genera to the left. 1, *Frenelopsis*; 2, *Ruffordia*; 3, *Pagiophyllum*; 4, *Brachyphyllum*; 5, *Otozamites*; 6, *Ctenis*; 7, *Pterophyllum*; 8, *Sphenolepis*; 9, *Nilssonia*; 10, *Sphenobaiera*; 11, *Ginkgo*; 12, *Podozamites*; 13, *Asplenium*; 14, *Cephalotaxopsis*. (*b*) CA site plot for the Late Cretaceous of Asia using only genera common to the Early Cretaceous. Circles = sites rich in broad-leaved deciduous genera; triangles = sites rich in intermediate genera; diamonds = sites rich in xeromorphic genera.

mentary site plot (figure 2*b*). This suggests there were no distinct divisions in the original vegetation that would enable biomes to be clearly delineated. However, using the trends identified in the genus plot, sites were grouped for mapping purposes; their distribution is displayed on a Berriasian palaeogeographic reconstruction in figure 3. Sites rich in broad-leaved, seasonally deciduous genera tend to plot at higher latitudes. Similarly defined sites in the continental interior plot in the most southerly positions. This continentality effect is weak, however. *Weichselia*-rich sites are restricted to the Tethys margins and in China are only known from the Lhasa Block, which may not have been attached to mainland Asia in the Early Cretaceous. The sites rich in xeromorphic conifers of the Cheirolepidiaceae are restricted to low latitudes along the south-eastern coast of Asia.

Figure 4*a,b* shows the genus and site plots for the Early Cretaceous of Asia, to which have been added Late Cretaceous data from Russia and China. Angiosperms were excluded from the ordination. However, should they have had a disrupting effect on the relationship between non-angiosperms and climate, this should be reflected in the breakdown of the trends apparent in the Early Cretaceous plots.

Figure 4*b* shows a strong separation on axis 1 of Late Cretaceous Russian sites from the remainder. The Late Cretaceous Chinese sites plot with those of the Early Cretaceous of Asia. Axis 2 spreads this Chinese Late Cretaceous–Asian Early Cretaceous

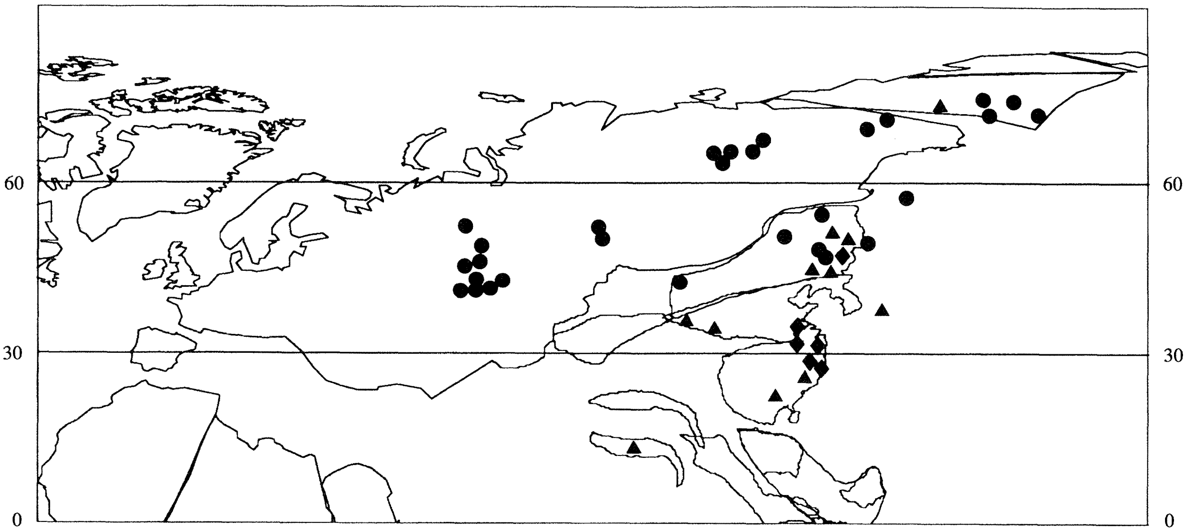

Figure 6. Late Cretaceous phytogeographic map of Asia based on figure 5*a,b*. Note the similarity to figure 3. Symbols as in figure 5*b*.

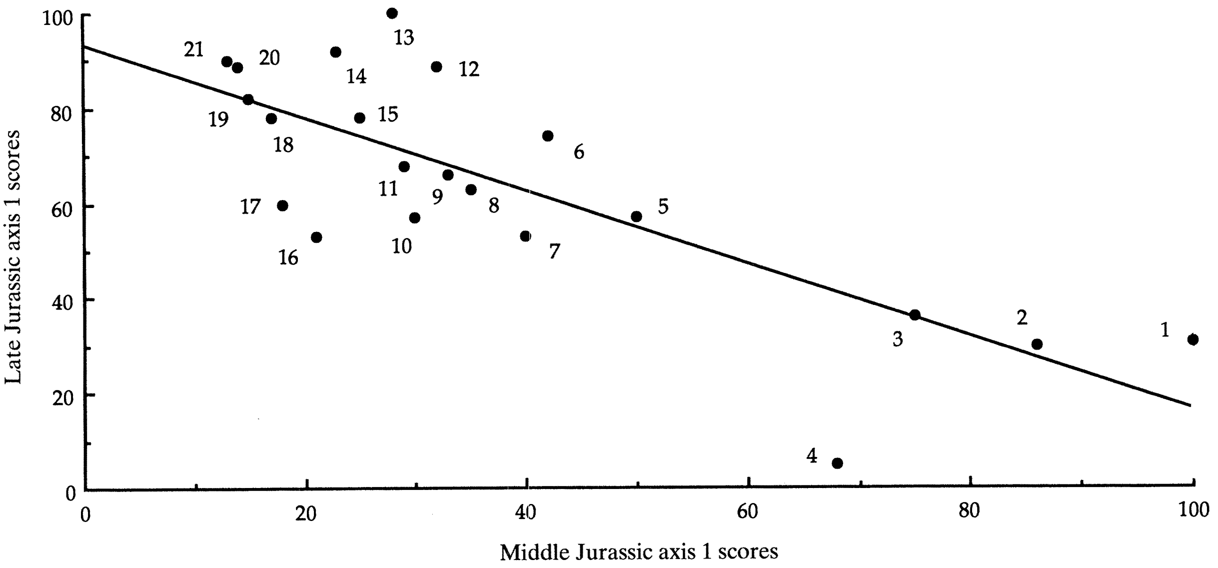

Figure 7. Axis 1 scores for CA presence–absence data for the Middle and Late Jurassic. The same trends of xeromorphic genera on the right and broad-leaved deciduous genera on the left is maintained into the Late Cretaceous (figures 2*a* and 5*a*), showing the long term ordering of genera and the maintenance of the pattern even after the rise of the angiosperms. 1, *Pagiophyllum*; 2, *Brachyphyllum*; 3, *Otozamites*; 4, *Ptilophyllum*; 5, *Sphenopteris*; 6, *Desmiophyllum*; 7, *Zamites*; 8, *Podozamites*; 9, *Pterophyllum*; 10, *Nilssonia*; 11, *Sphenobaiera*; 12, *Baiera*; 13, *Ctenis*; 14, *Ginkgo*; 15, *Coniopteris*; 16, *Cladophlebis*; 17, *Elatocladus*; 18, *Phoenicopsis*; 19, *Taeniopteris*; 20, *Czekanowskia*; 21, *Pityophyllum*.

swarm along a trend which, by examination of the genus plot (figure 4*a*), is similar to that seen in figure 2*a*. Sites rich in xeromorphic conifers occur towards the top left of the plot and those rich in broad-leaved deciduous taxa nearer the bottom left. The genus plot also explains why the Russian Late Cretaceous sites are segregated on axis 1; they are all characterized by extant conifer genera which are not recorded in either the Early Cretaceous sites or those of the Late Cretaceous of China. Possible explanations for this pattern include: (i) the Russian sites may genuinely record the initial evolution of these genera; (ii) it may indicate migration of these genera into Asia; or (iii) it could be the artifactual product of 'provincial taxonomy' (cf. Ziegler *et al.*, this volume).

When the data matrix is restricted to the Late Cretaceous, axis 1 of the genus plot (figure 5*a*) again shows a strong ordering from xeromorphic genera on the right to mesophytic and broad-leaved deciduous genera on the left. Axis 2 spreads the latter group along a trend from broad-leaved deciduous to more intermediate or mesophytic forms. The site plot (figure 5*b*) naturally reflects this pattern; when plotted on a Santonian palaeogeographic map (figure 6), these trends reflect similar phytogeographic patterns to those seen in the Early Cretaceous. They imply that the distribution of evaporation:precipitation ratios remained more-or-less constant in Asia throughout the Cretaceous. More importantly, however, these ordinations, together with similar analyses of Chinese presence–absence data from the Middle and Late Jurassic (figure 7), demonstrate that the relationship between non-angiosperm phytogeography, physiognomy, and climate remained stable throughout the late Mesozoic (see also Ziegler *et al.*, this volume). As the evolution of the angiosperms does not appear to disturb this relationship, the way is open to calibrate extinct non-angiosperm physiognomy against the quantitative signal obtained from the angiosperms.

We thank A. M. Ziegler and M. Hulver for the supply of palaeogeographic reconstructions and use of bibliographic material at the Chicago Paleogeographic Atlas Project, R. Brown for drafting assistance and R. Bateman for helpful comments. This is a product of the NERC-funded Mesozoic Climates Modelling Project (GR3/7939).

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Discussion

E. A. Jarzembowski (*P.R.I.S., University of Reading, U.K.*). Not only is there a need for accurate taxonomy in plant-based climate reconstruction as indicated by Dr Spicer, but also an awareness of taphonomy and animal interaction. Vascular plants and tree rings have been discussed, but has any allowance been made for the effect of sap-sucking hemipterous insects which were widespread in the Cretaceous? For example, recent cicadas (xylem-feeders) can sufficiently drain a tree to affect the width of growth rings (Raven 1983).

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Raven, J.A. 1983 Phytophages of xylem and phloem: a comparison of animal and plant sap-feeders. *Adv. ecol. Res.* **13**, 135–234.

R. A. Spicer. Dr Jarzembowski quite rightly stresses the importance of understanding taphonomic effects and processes in determining any climate signal from plant fossil material. In this instance the evidence for widespread insect activity either as pathogens or post-mortem degraders is minimal. One of the most notable characteristics of the Cretaceous high latitude floras is the low level of foliar damage ascribable to insects. This is evident from field evidence as well as museum material and is not the result of collection bias. To our knowledge only one insect fossil has been recovered from the Late Cretaceous of northern Alaska and that is an undescribed wing some 2 cm long from an iron-rich claystone nodule of Coniacian age. There is no evidence of insect borings in the wood and the lack of false rings (sometimes attributable to extreme insect defoliation), reaction tissue, etc., combined with the low level of foliar damage, argues strongly against the ubiquitous ring signatures being due to insect activity. Low latitude plant material is less well known but xeromorphic characters may have deterred sap sucking insects and again the evidence of foliar damage is at such a level that widespread ring signatures across several taxa are unlikely not to carry a strong climatic signal.

D. Cantrill (*British Antarctic Survey, Cambridge, U.K.*). Dr Spicer illustrated an example of the physiogonomic differences between Cretaceous floras from New Zealand (coastal) and southeastern Australia (continental interior) and put forward that these differences indicate much cooler inland conditions. While the argument about the physiognomic differences is cogent, the stratigraphic framework of these floras indicates a slightly different picture. The New Zealand flora is Albian to Cenomanian in age. However, the Australian flora ranges from Neocomian to Albian. The forms that he illustrated as indicating a cold signature are all derived from the base of the Victorian succession and are thus not directly comparable to the New Zealand flora as they are not the same age. If one looks at the stratigraphic change in the Victorian flora with time it is found that the small leaved *Ptilophyllum* and deciduous *Elatocladus* conifers occur in the base of the sequence (Neocomian). The middle part of the sequence contains deciduous *Ginkgoites*, whereas the Albian has many broad leaved conifers and indications of warmer climate. Thus the differences between the Victorian (Australia) and the Albian–Cenomanian New Zealand floras are not what Dr Spicer has suggested, and therefore the climatic differences in temperature between the coastal and continental interior sites are not as great.

In reply to the points I raised regarding the comparability of the New Zealand floras with the Victorian Cretaceous forms, Dr Spicer suggested that oxygen isotope work indicated mean annual temperatures of 0°C to possibly 6–7°C. He suggested that the water source of the precipitated carbonates was from high altitude along the rift margins, the assumption here being that this water reflected rain water. What he failed to point out was that the data are derived from concretions that were formed prior to compaction of the sediments. Traditionally, temperatures based on oxygen isotopes are derived from organisms that are believed to be growing in equilibrium with the water they are living in. The oxygen isotope data Dr Spicer refers to is based on pre-compaction carbonate and siderite concretions occurring in labile volcanogenic sediments. I would suggest that we do not know enough about diagenetic and palaeoweathering processes to understand what these results are telling us and whether they can be related to palaeotemperature conditions. Certainly they seem to be strongly at variance with the information we are getting from the plant fossils.

R. A. Spicer. The points raised by Dr Cantrill are good ones and allow us to expand on a necessarily brief account. The age difference between the Australian and New Zealand floras does not detract from the point we were making regarding the interpretation of physiognomic characteristics in relation to mean annual temperature ranges or the shifts in phenology in relation to winter temperatures. In fact the increase in leaf size and frequency of deciduousness with decreasing age is exactly what would be expected as the rift valley widened and the continental effect was destroyed by the strengthening maritime influence. As the winter temperatures rose and the mean annual temperature range decreased, the frequency of deciduousness, thin cuticles, and broad-leaved forms within the floras would, we suggest, have risen as a consequence of the switch in phenological strategies to minimize higher winter respiration. Thus although the New Zealand and Australian floras are not exactly coeval, physiognomic comparisons are useful.

Temperature trends from marine oxygen isotope data suggest a surface water cooling during the Aptian–Cenomanian interval (Spicer & Corfield 1992) but comparable data from high latitudes are lacking. If this cooling was experienced in the Australia–New Zealand area the temperature changes implied by the plants (especially winter warming) could not be explained by secular temperature trends and the most likely explanation for temporal and spatial shifts in physiognomy would be relative degrees of continentality.

In respect of the oxygen isotopes we were accepting at face value the temperatures given by Gregory *et al.* (1989). They determined mean annual temperatures between −2° and +5°C which are markedly lower than the 5–8°C obtained from vegetational considerations (Parrish *et al.* 1991). Gregory *et al.* (1989) examined non-marine carbonate concretions where vital effects may not have been significant unless the concretions were algal or bacterial products. We cannot comment on whether vital effects were involved or not and have to trust the expertise of Gregory *et al.* More problematic than vital effects is the influence of diagenetic factors which, of course, do not affect significantly climatic data obtained from plant fossil physiognomy. As far as we know the possible role of diagenesis in affecting the isotope ratios has yet to be determined for this material. If the temperature estimates reflect reality they could be interpreted as reflecting the influence of melt water from snow fields high on the rift valley shoulders; an interpretation offered by Gregory and colleagues.