Early Mesozoic Phytogeography and Climate

Alfred M. Ziegler, J. Michael Parrish, Yao Jiping, Eric D. Gyllenhaal, David B. Rowley, Judith Totman Parrish, Nie Shangyou, Andrew Bekker and Michael L. Hulver

Phil. Trans. R. Soc. Lond. B 1993 **341**, 297-305
doi: 10.1098/rstb.1993.0115

Early Mesozoic phytogeography and climate

ALFRED M. ZIEGLER[1], J. MICHAEL PARRISH[2], YAO JIPING[1],
ERIC D. GYLLENHAAL[3], DAVID B. ROWLEY[1],
JUDITH TOTMAN PARRISH[4], NIE SHANGYOU[1],
ANDREW BEKKER[1] AND MICHAEL L. HULVER[1]

[1]*Department of the Geophysical Sciences, University of Chicago, Chicago, Illinois 60637, U.S.A.*
[2]*Department of Biological Sciences, Northern Illinois University, Dekalb, Illinois 60115, U.S.A.*
[3]*Field Museum of Natural History, Chicago, Illinois 60605, U.S.A.*
[4]*Department of Geosciences, University of Arizona, Tucson, Arizona 85719, U.S.A.*

SUMMARY

Triassic and Jurassic floral lists from Eurasia have been subjected to an ordination study. A latitudinal gradient is revealed for each interval of each epoch which can be interpreted climatically as ranging through the dry subtropical to the warm and cool temperate biomes. Floras at the dry end of the spectrum may be identified by the dominance of microphyllous conifers and the regional association with evaporites. At the other extreme, the cool temperate floras are recognized by the abundance of deciduous ginkgophytes and broadleaved conifers. The highest diversity, centered at about 40° palaeolatitude, occurs in the intermediate warm temperate zone which may contain all of the above floral elements in association with numerous fern and cycad genera. The transitions between these biomes remained at relatively constant latitudes, from the late Triassic to the early Cretaceous, suggesting climate stasis over a long interval. Climate changes, perceived locally, appear to be the result of continental motion rather than true global change. During the early and middle Triassic, however, the biomes are less distinct, with floras interpreted as warm temperate extending to latitudes of up to 70° north.

1. INTRODUCTION

Various approaches to reconstructing early Mesozoic climates have been tried in recent years, including geochemical, sedimentological, palaeontological and mathematical. Stable isotope analysis of oxygen and carbon can be used to provide information on temperature and precipitation changes (Holser *et al.* 1989; Simms & Ruffell 1990), but these studies are limited to regions that have been unaffected by diagenesis. Climatically significant sediments and palaeosols give a broad view of the distribution and the seasonality of rainfall patterns (Parrish 1993; Hallam 1984), but specific information is limited to the few regions that have been subjected to careful sedimentological analysis. Fossil macro- and micro-floras have been examined in considerable detail (Dobruskina 1987; Vakhrameev 1991; Visscher & van der Zwan 1980), but rigorous statistical treatments are still uncommon. Finally, general circulation model studies are now available for at least the Pliensbachian and Kimmeridgian stages of the Jurassic (Chandler *et al.* 1992; Moore *et al.* 1992; Valdes & Sellwood 1992), but need to be tested more thoroughly with geological information. Thus, a diversity of information is available, but detailed maps of the whole earth must be completed before meaningful comparisons can be made of global change through the long interval of the early Mesozoic.

We believe that phytogeography provides the most direct and comprehensive way to reconstruct the various climatic patterns of past intervals. Fossil plants have many advantages: (i) unlike marine organisms, they occupy a realm that has a more pronounced climate signal; (ii) unlike animals, they are sedentary, which eliminates concerns about seasonal migrations; (iii) unlike isotopes, they are not subject to diagenetic alteration with time; and (iv) unlike computer model output, they represent 'ground truth'. In addition, plants are abundantly preserved in many regions of the world, and have been the subject of intense study, so that taxonomic lists from hundreds of areas may be quickly assembled from the literature.

Recently we completed phytogeographical studies of the Early and Late Permian (Ziegler 1990), and the Late Cretaceous (Horrell 1991), and the approaches we developed have been expanded in the present study. Instead of basing floral provinces on generic or geographic names, we assign each to a climatically defined biome following the scheme developed for the present day by Walter (1985). In this way we allow for comparisons through geologic time using a modern analogue. The biomes, as adapted for palaeoclimate purposes, comprise (1) the tropical everwet, (2) the tropical summerwet, (3) the subtropical desert, (4) the midlatitude winterwet, (5) the warm temperate, (6) the cool temperate, (7) the midlatitude desert, (8) the cold temperate, (9) the arctic, and (10) the glacial.

Phil. Trans. R. Soc. Lond. B (1993) **341,** 297–305
Printed in Great Britain

They were defined by Walter on the basis of seasonal aspects of temperature and precipitation gleaned from about 8000 meteorological stations worldwide. Their definition is rigorous but the categories are broad enough to encompass all the present and presumably all the past floral zones. Assignment of the floral assemblages to the appropriate biomes is based on the physiognomic adaptations of their constituents. The three high latitude biomes (8, 9 and 10) are not found in the late Cretaceous (Horrell 1991) probably because of the generally warm poles.

The study reported herein consists of a preliminary statistical analysis of northern paleohemisphere Eurasian floras of four Triassic and three Jurassic intervals. This geographic quadrant contains about two thirds of the described floral localities for these times. The palaeographic reconstructions are based on a new apparent polar wander path (APWP) (D. B. Rowley, unpublished results) determined from a reassessment of palaeomagnetic data (Van der Voo 1993). Our global APWP is derived from 20 Ma sliding window averages of each continent followed by weighting and averaging of these within a common frame of reference. Our goal is to assess whether floras defined rigorously can be traced through 200 Ma of earth history, and if so, whether their latitudinal ranges through time reveal anything about global change or perhaps global stasis. The biome approach allows us, in principle, to map the earth's terrestrial realm in terms of its constituent climates, and then to describe climate change in terms of variation in the proportions of each biome through time. For example, migration of the temperate biomes poleward would point toward global warming, and this is precisely the situation at the beginning of the Mesozoic. Also, a general absence of tropical rainforests during the Mesozoic (Horrell 1991; Ziegler *et al.* 1987, and reported herein) is of major importance in characterizing world climate and productivity.

2. FLORAL DATA ASSEMBLY

Triassic and Jurassic floras are known from thousands of sites throughout Eurasia, and this vast stockpile of information is well organized and accessible in the literature owing to the efforts of Russian and Chinese palaeobotanists and geologists. Dobruskina in '*Triassic floras of Eurasia*' (1982; see also Dobruskina 1980) is a comprehensive source of floral lists, maps and interpretations, while Vakhrameev in '*Jurassic and Cretaceous floras and climates of the Earth*' (1991; and Vakhrameev *et al.* 1978) gives maps and interpretations, and references to lists. We have relied on these and some more recent primary literature sources for our lists, except for China where the Russian sources are weak. Comprehensive data on China is found in '*Regional stratigraphic data*', a series of volumes prepared in the late seventies and early eighties by the 'Stratigraphic group' of each privince. A new series, '*Regional geology*' (of each province), is now appearing, and we used the available volumes of this set in preference to the older ones. Unfortunately, these Chinese sources provide no indication of who identified the fossils, so quality may have been sacrificed for quantity in using these lists. To judge by the length and number of the lists, considerable effort must have gone in to the collection and identification process. Our plan is eventually to add lists to our database from other areas of the world, but the areas covered do include most of the available sites for the early Mesozoic.

Our goal in the present study is to introduce some rigor into phytogeography by subjecting all this data to a modern statistical treatment. Considerable care has gone into assembling the lists so that the climate signal will emerge. Inconsistent taxonomy from worker to worker or between countries can of course yield spurious results. This can be minimized by using only the most recent publications and by working at higher taxonomic levels, and it can be tested by looking for correlated political and floral boundaries. Geographic barriers, such as mountain ranges or seaways, are sometimes invoked to account for discontinuities. Again, the use of higher taxonomic levels avoids the problem of species level endemism, and the extensive but contiguous array of localities in Eurasia gives us confidence that free geographic interchange existed throughout the early Mesozoic. An exception might be the association of some Jurassic floras of Europe with islands, but the fossils give no hint of this. Drops in sea level at times might have allowed for occasional migrations to such sites. Still another source of variation in floral lists would be at the community level. Local physiographic gradients, such as mountain slopes, may mimic broader climate patterns. Fossil floras also commonly exhibit community succession. In order to reduce these effects, we have usually combined all the lists in a single formation and throughout an area. We have not, however, grouped lists across formation boundaries, however narrowly defined in the temporal sense the formation may be. There will always be an ecological bias in palaeobotanical studies toward the lowland depositional sites, and there is not much that can be done about this except to pay special attention to areas of active tectonism or volcanism where perched basins might have been preserved.

The temporal resolution of inland strata is notoriously poor, and rarely is better than the series level. In this study, the floras have been grouped in the Early and Middle Triassic, whereas we split the Late Triassic lists into the Carnian and Norian (plus Rhaetic) stages. The Late Triassic was longer than the Early and Middle combined, so this is appropriate. The Jurassic lists are simply grouped according to the Early, Middle and Late subdivisions of this period. This means that our time resolution is from 5 to 20 Ma, and that Milankovitch level cycles are completely out of reach. Yet most of the lists would be eliminated from the analysis if only the well correlated ones were used. The maps we present therefore show the time averaged effects of a potentially broad range of climate modes for each site. Our feeling is that the Milankovitch effect is disproportionately felt during glacial times when major ice advances are triggered by comparatively minor orbital variations. Climates of the Mesozoic, we would argue, showed more modest excursions and these are mainly observed at the boundaries between the desert and wetter zones such as in the Newark Series of eastern North America (Olsen 1986).

3. FLORAL DATA ANALYSIS

A statistical treatment of the early Mesozoic lists has been applied in this study so that objective comparisons between both the regions and the time intervals may be achieved. The method chosen is an ordination technique termed 'detrended correspondence analysis'. Gauch (1982) describes this method and states: 'The result of ordination is the arrangement of species and samples in a low-dimensional space such that similar entities are close by and dissimilar entities far apart.' The method has been widely used by plant ecologists, and is ideal for our purposes because natural gradations may be portrayed in two dimensional plots of either the localities or the taxa, and the patterns observed in each type can be visually and statistically compared. The computer program we used was developed by Hill (1979; see also Hill & Gauch 1980), and modified for IBM PC by Christopher Clampitt in 1985. In our study the genus level was employed as the basic unit, but the species diversity information for each genus was also entered. Our lists were trimmed to the 100 most common genera because of capacity limitations in the computer program, and mainly leaf genera of the vascular plants were used.

Ordination plots of the axis 1 and 2 scores for both localities and genera were generated for each of the seven time intervals. From the locality plots it was determined on inspection that the principal axis shows a general correlation with palaeo-latitude for each period. From the taxonomic plots a certain consistency through time in the order of genera and even higher taxonomic levels may be observed. To portray this, a series of plots correlating the axis 1 scores for adjacent intervals was prepared (figure 1). The level of correlation is variable with the tightest arrays seen in the Jurassic, and the loosest between the Middle and Late Triassic. The negative slope observed in this latter plot is an artifact of computation due to the fact that the low latitude end of the scale was to the left in the first two ordinations and to the right in all the rest. This method of correlating axis 1 scores was suggested to us by R. A. Spicer. In effect it is a test of consistency between intervals, and it provides an average of the successive intervals which are in a real sense replicates of one another. The spectrum produced is parallel to the climatic gradient and can be used as a measuring stick to relate particular floras to their respective climates.

The polarity of the floral spectrum is evident in all the plots (figure 1) despite the looseness of fit of some. At one end are members of the Ginkgoales, including *Ginkgo*, *Baiera* and *Sphenobaiera*; the Leptostrobales, represented by *Czekanowskia* and *Phoenicopsis*; and certain conifers including *Podozamites*, *Pityophyllum* and *Desmiophyllum*. This association is clearly 'the principal core of the Siberian flora' as described from the Early and Middle Jurassic by Vakhrameev (1991, p. 10 & p. 246) and was assigned by him to the 'warm temperate seasonal climate', where the 'winter temperature might temporarily have declined below zero'. Vakhrameev gives no definite reasons for his assignment although he does quote some early oxygen isotope temperature estimates from surrounding epeiric seas. These indicate surprisingly warm conditions but would not however, if accurate, be necessarily relevant to the continental floras. Vakhrameev may also have relied on the fact that the only recent occurrence of any of these genera is *Ginkgo* in the warm temperate zone of south China. This site, however, is on the side of a mountain 1500 m high (Del Tredici *et al.* 1992) and pre-Pleistocene occurrences are limited to cooler latitudes (Tralau 1968). The trees of the Siberian flora are known to have been deciduous, and display well-defined annual growth rings according to Vakhrameev. Thus we assign this flora to the cool temperate deciduous biome 6. In addition, the flora is of relatively low diversity, and Cretaceous representatives of this group of genera are known to have grown in cool climates on the Alaskan North Slope (Spicer & Parrish 1986).

Our 'cool temperate' assignment implies cold winters and warm summers with a growing season of 4 to 8 months (Ziegler 1990). The growing season would start when average daily temperatures reached 10°C, and would continue if precipitation was maintained at 20 mm or more per month. As will be seen from the map patterns, even this assignment implies considerably warmer poles than today using our uniformitarian assumptions. We feel confident in excluding the cold temperate biome 8 from the early Mesozoic climate spectrum because of the presence at high latitudes of these deciduous plants. To judge by modern analogues, deciduous trees need a full month to generate foliage and they are outcompeted during shorter growing seasons by plants that do not have this limitation (Walter 1985, p. 189).

The opposite end of the floral spectrum (figure 1) is dominated by the microphyllous conifers, *Brachyphyllum*, *Pagiophyllum* and *Voltzia*. This association is limited to lower latitudes, and the proximity to evaporites, the xeromorphic adaptations and the consistently low diversities all point to a subtropical dry environment. The palaeo-latitudinal range is from 10° to 40°, forming the poleward limit of the evaporite belt during most intervals. We assign the evaporites to the subtropical desert biome 3 and the xerophytic floras tentatively to the winterwet biome 4 or more generally to the dry subtropical zone (Ziegler 1990).

The middle of the floral spectrum is occupied by high diversity assemblages containing ferns, cycads, and seed ferns as well as by the conifers and ginkgoes mentioned at the ends of the spectrum. An assignment to the warm temperate biome 5 was made by Krassilov (1981), with which we agree. Coal swamps are commonly found with these floras but also extend into biome 6.

4. PHYTOGEOGRAPHY AND CLIMATE

The ordination study shows that the floras of Eurasia were gradational during each of the Triassic and

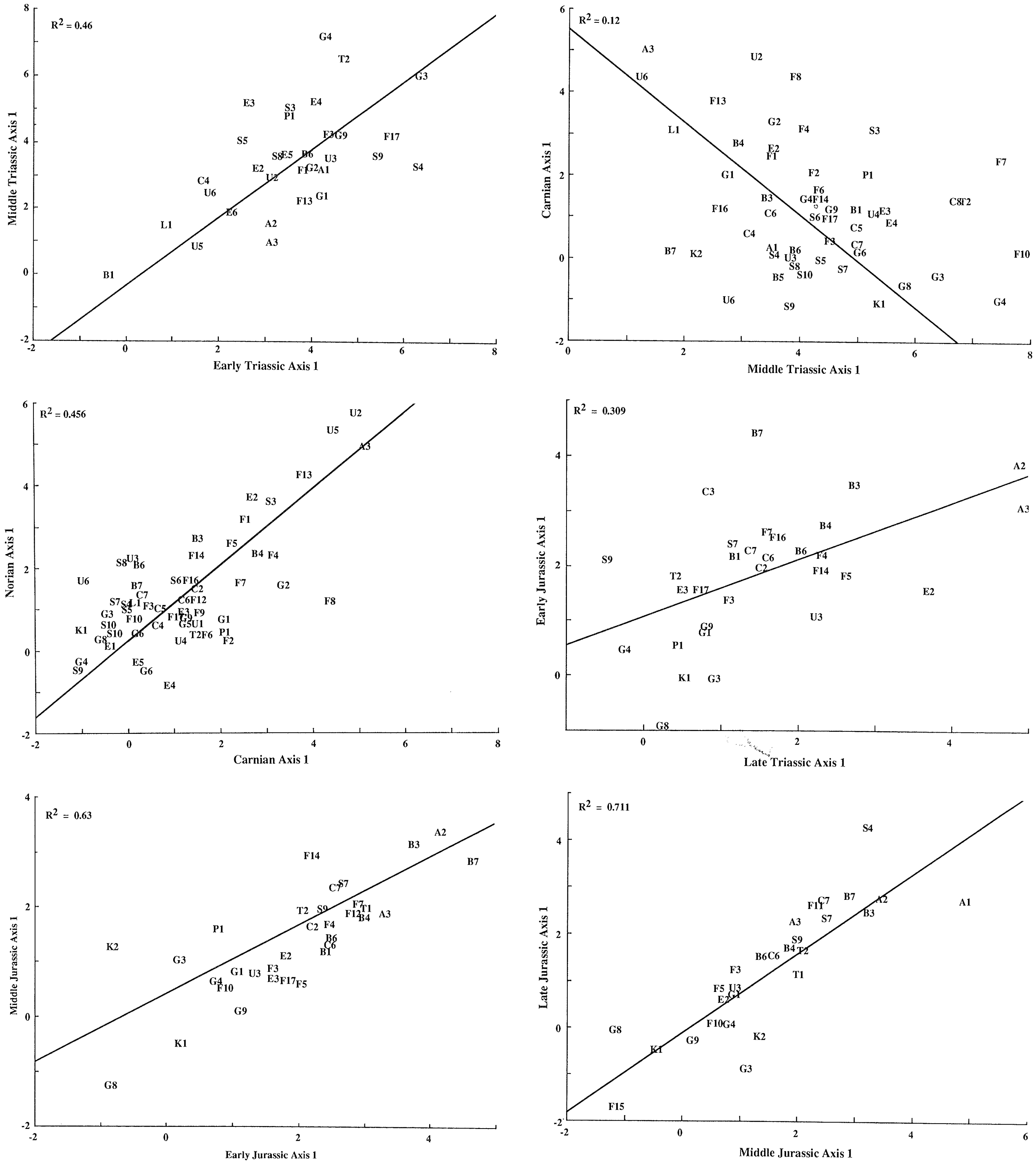

Figure 1. Correlation of the axis 1 generic scores for the adjacent time intervals as determined from the detrended correspondence analysis. The codes are given in the Appendix.

Jurassic intervals considered, so that any subdivision made for mapping purposes is bound to be artificial. These broad-scale gradations are to be expected if climate is the controlling factor and this is why there are endless variations in the way that present day floras are mapped. The axis 1 plots (figure 1) provide a way to compare the adjacent intervals in a consistent way by a method termed here 'sequential correlation'. The biome boundaries were initially selected along axis 1 of the Middle Jurassic ordination in the following way. The deciduous ginkgoes and conifers were found to be at the left of the plot at values of less than 1.3, while the xerophytic conifers were to the right at values above 2.2. Accordingly the warm temperate biome 5 was defined to include the intermediate values, while biomes 6 and 4 were assigned to the lower and higher values respectively. The equivalent values for the adjacent Jurassic intervals were determined by simply projecting the selected Middle Jurassic values to the appropriate axis of the graph, assuming that the correlation line is a faithful representation of the equivalent floras from time to time.

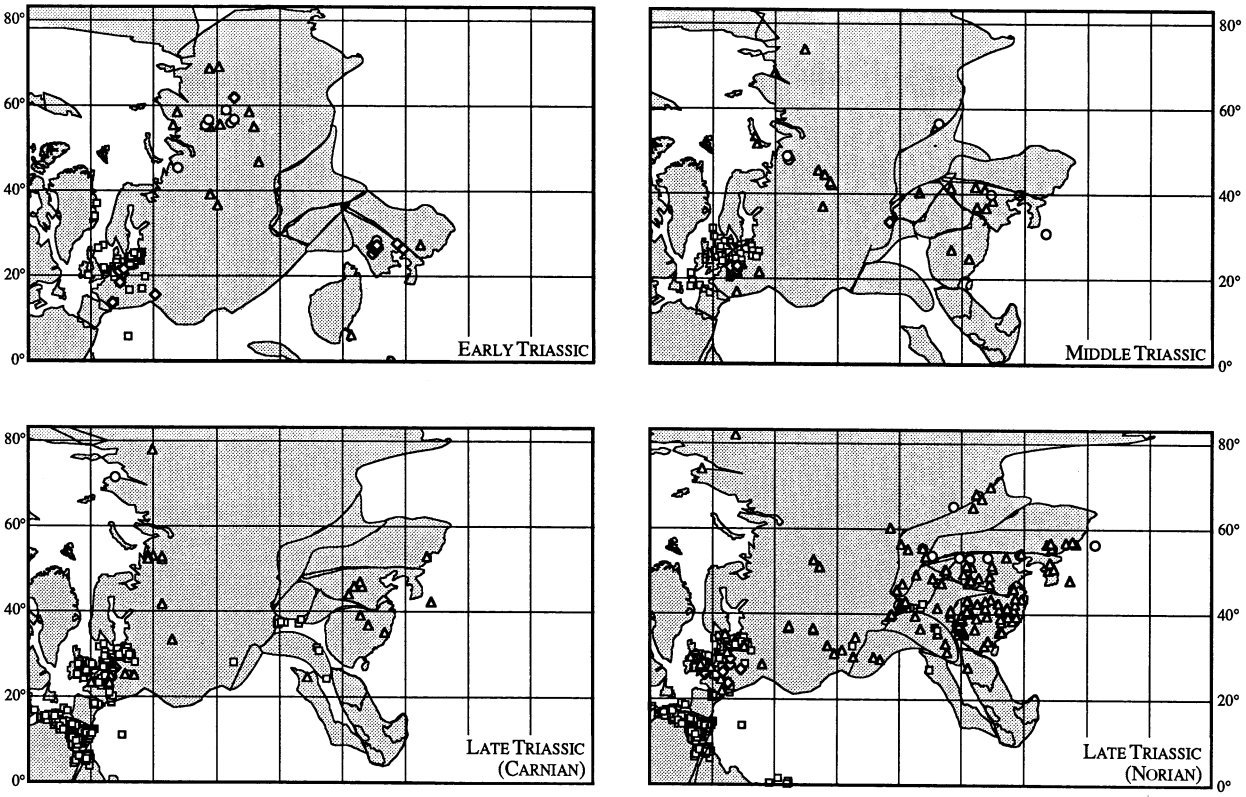

Figure 2. Triassic palaeogeographic maps showing the evaporite deposits (squares), dry subtropical floras (diamonds), warm temperate floras (triangles) and cool temperate floras (circles). The evaporite data is the same on both Carnian and Norian Stage maps. The localities on the Norian map include some floras that are rather imprecisely dated as simply 'Upper Triassic'. See figure 3 for a location map in present coordinates.

We began with the Jurassic because the correlations are tightest, but the values so determined were 'sequentially correlated' through the entire Jurassic and Triassic datasets. Accordingly, the boundaries selected are arbitrary but they should be consistent through the entire 100 Ma sequence.

The palaeo-phytogeographic maps (figures 2–3) show the three biomes selected above in relation to paleo-latitude and their contemporary evaporite deposits (Paleogeographic Atlas Project lithofacies database). The major palaeo-continents are shown on the maps and localities that occur peripherally to these elements are included although there is uncertainty about their exact relationships. In some areas there is an overlap of the biomes as defined, which could be due to short or long term climate change within these long intervals. In some cases, points will be plotted on top of each other, and these represent different formations deposited within the same epoch. In the following paragraphs, the maps will be discussed in chronological order, and the patterns compared with published maps. Particular attention will be given to the distinction between local and worldwide change. Local changes can occur when a continent moves latitudinally but the net worldwide change is insignificant. We feel this distinction is very important and point out that there is much confusion about this in the literature.

The Lower Triassic biome map (figure 2*a*) shows that the subtropical dry floras of Europe group together with those of North China, a relationship that has been noticed by a number of workers (Wang 1985; Dobruskina 1987; Mader 1990). This pattern is a holdover from the late Permian and, taken together, the evaporites and floras indicate very dry conditions at latitudes of 10° to 30°. The warm temperate biome 5 as we define it extends to paleolatitudes of 70° in Siberia, while the cool- and cold temperate biomes 6 and 8 are believed to have existed there in the late Permian (Ziegler 1990). 'Evidently the barriers that formerly divided the phytochoria were breached and the climatic conditions became more uniform on a global scale' (Meyen 1987, p. 313). Some of the highest latitude floras contain the arborescent lycopod, *Pleuromeia*, which seems to have achieved a world-wide distribution at this time in coastal and lacustrine situations (Dobruskina 1987). A climate devoid of hard frosts is implied for coastal settings. Oxygen isotope measurements of Tethyan sequences provide support for the idea of warmer climates in the early Triassic (Holser *et al.* 1989). An interesting outlier of biome 5 occurs at 5° from the equator of Hainan Island. This may be a holdover of the *Gigantopteris* flora of the Permian (Yao 1978) which has been widely interpreted as representing the tropical rainforest biome 1 (Ziegler 1990). With the northward motion toward the subtropics, conditions for hygrophytic plants of the South China microcontinent must have become very tenuous. Tropical coal swamps seem to have disappeared in the early Triassic, except for an equatorial setting on the Qiangtang Block (Deng *et al.* 1980), consistent with the develop-

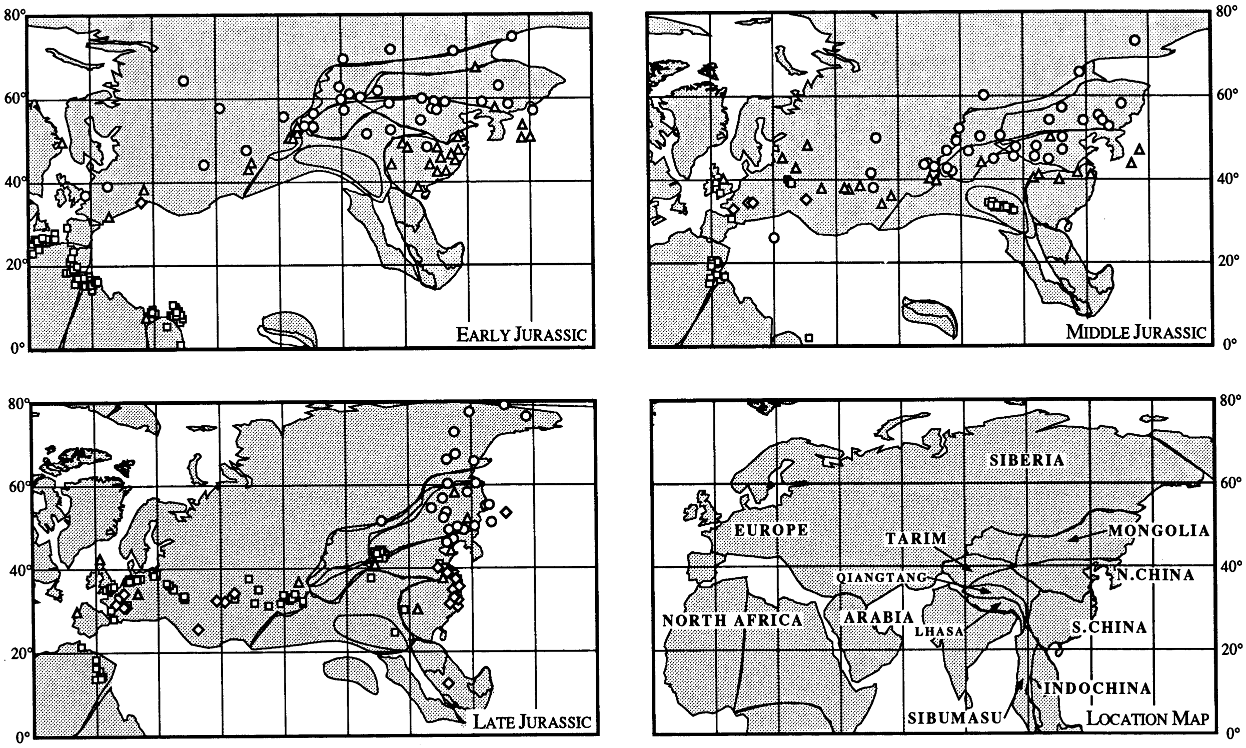

Figure 3. Jurassic palaeogeographic maps showing the evaporite deposits (squares), dry subtropical floras (diamonds), warm temperate floras (triangles) and cool temperate floras (circles). The lower right map shows the outline of the paleocontinental margins on a present day base map. Some areas that contain Triassic and Jurassic floras, like Japan, are not shown because their relationships during those times are poorly constrained. The localities are included on the palaeogeographic maps for the sake of completeness, but with the caveat that their original positions are very uncertain.

ment of the Pangean monsoons (Parrish 1993). The cool temperate biome 6 is found mainly in central Siberia associated with one of the most extensive outpourings of flood basalts in the geologic record (1 million square kilometres and 3.5 km thick, according to Daragan-Sushchov (1989)). Recently obtained dates indicate that they are of earliest Triassic age (Campbell *et al.* 1992) but the claim that they were emplaced in just 600 000 years cannot be true because related tuffs occur throughout adjacent Lower and Middle Triassic marine sequences (Kazakov *et al.* 1983). In any case, a considerable topographic edifice resulted from both volcanism and underplating, the remnant of which is still an impressive feature. Our cool temperate floras were probably related to this upland setting. Temperate latitude swamps disappeared about the beginning of the Triassic in both hemispheres, in association with the near extinction of the cordaitids in the Northern Hemisphere and the glossopterids in the Southern Hemisphere. Drying and warming of the climate have both been invoked as a mechanism, but it is difficult to believe that the physical environment could have been eliminated completely. The explanation may be related to the extinction of the swamp adapted plants.

The Middle Triassic biome map (figure 2*b*) shows continued dry conditions in Europe (Mader 1990) while both north and south China have moved into latitudes favorable for biome 5, with some biome 6 floras mixed in. Evidence from the upland areas of central Siberia is lacking where one might expect cooler conditions. As with the preceding interval, warm temperate floras extend above 70° in northeast Siberia near the Lena Delta, and it is here, in the late Middle Triassic, that the first northern hemisphere coal swamps reappear after the end of the Permian (Kazakov *et al.* 1983). The timing is the same for the southern hemisphere reappearance of coal swamps in Argentina and Chile (Stipanicic 1983) and Antarctica (Taylor & Taylor 1990). Equatorial settings have not yielded macrofloras but, ‘the concept of an essentially arid nature of a wide equatorial climatic belt during Triassic times finds palynological support’ (Visscher & van der Zwan 1980). This microfloral study shows that ‘. . . high latitude hygrophytic floras, characterized by pteridophytes and cycadophytes are separated by a xerophytic equatorial flora, characterized by conifers’.

The early Upper Triassic, Carnian Stage map (figure 2*c*) shows even fewer cool temperate floras than earlier intervals, while most of the rather scattered sites that do exist fall within the warm temperate biome. An apparent mixture of environments in Europe has been the subject of a study by Visscher & van der Zwan (1980) who concluded, ‘in Europe, occurrences of hygrophytic palynofloras and coals within an arid climatic zone can be explained by the water-supply of extensive river-systems’. A mixture of wet- and dry-climate indicators also characterizes the Upper Triassic Chinle Formation in the western United States. Dubiel *et al.* (1991) have attributed this to the abundant but highly seasonal rainfall of the Pangean monsoon.

The late Upper Triassic, Norian Stage map (figure

2*d*) has excellent coverage in mid-latitudes because the Indosinian collisional events created many continental basins. Floras interpreted to be warm temperate seem to be everywhere and they dominate in the 30° to 50° latitudinal range. They are mixed with dry subtropical floras to the south in Europe and with cool temperate floras to the north in North China and Siberia. The Chinese refer to this cool temperate flora as the *Danaeopsis–Bernoullia* Flora, and to the warm temperate flora as the *Dictyophyllum–Clathropteris* Flora. All of these are fern genera, and the latter two continue into the Jurassic. Meyen (1987, p. 316) commented that the climatic zonality was not pronounced and overstated the case somewhat by saying that 'It is probable that a frostless climate prevailed all over the Earth'. It should be noted that the Norian is a long interval, so some of the overlapping of the floras is doubtless due to time-averaging of continental motions beneath climate zones.

The Lower Jurassic biome map (figure 3*a*) shows a more pronounced zonation than the Triassic maps with a transition from warm to cool temperate conditions centred about 45°N. The evaporites are mainly confined to the North Africa portion of Pangea which had moved northward into the subtropical belt. The one dry climate flora on the map is from the Alps, and so its original position is uncertain. Other maps of this and later intervals are included in Vakhrameev (1991, p. 252) and Krassilov (1981, p. 213) and show similar patterns. A general circulation model study is available for the early Jurassic (Chandler *et al.* 1992), which is based on the assumption that the atmospheric composition was the same as today's. Maximum seasonal temperature ranges of 45°C were generated over the higher latitude portions of the continents, which is not consistent with the floral data. Raising the carbon dioxide composition in the model might yield a better result (Kutzbach & Ziegler, this volume). By contrast, Parrish (1992) suggested that the global climate might have become slightly cooler in the Jurassic, permitting the wet season of the monsoon to be better expressed.

The Middle Jurassic biome map (figure 3*b*) is very similar to the preceding one but the general northward motion of the continents was replaced by a clockwise southern motion, with the Chinese elements moving south more rapidly than Europe. The biome boundaries maintained approximately the same latitudes, while the continent moved beneath. Krassilov (1981, p. 214) thought that the '. . . warm temperate ecotone moved progressively poleward', while Meyen (1987, p. 313) interpreted this as '. . . a strong warming which is reflected in the shifting towards the north of the boundaries . . . ', and Hallam (1984, p. 195) states that '. . . this arid zone spread northwards to embrace much of southern Eurasia'. These motions are relative to the land area only and not to paleolatitude, and therefore have no direct implications for global change.

The Late Jurassic biome map (figure 3*c*) illustrates the continuation of the changes from earlier times. By this time, much of Europe and southern Asia had moved southward and this may account for the development of evaporite deposits throughout southern Eurasia. Alternatively, this could represent the breakdown of the northern Pangean Monsoon and the consequent decrease of moisture to these latitudes (Parrish 1992). Two separate general circulation model studies are available for the late Jurassic (Moore *et al.* 1992; Valdes & Sellwood 1992) which give reasonable accounts of the geologically preserved information and the floral study presented here. Detailed comparisons can be made when the factors critical in controlling the floral biomes are isolated in the model studies (Kutzbach & Ziegler, this volume).

5. CONCLUSIONS

The subject of global change may be approached by mapping the distribution of climatically related biomes on the surface of the earth during successive time intervals, and then determining any changes in the latitude or area of the biomes through time. Clear distinctions should be drawn between worldwide changes and local changes that are due to latitudinal motions of continents beneath climate zones.

The method of establishing biome equivalences through time by sequentially correlating the axis 1 scores of the ordination plots of the detrended correspondence analysis seems to be a promising technique in paleoclimate studies. However, the present study is preliminary, and will be strengthened with the addition of more locality data from Eurasia and the rest of the world, and with the comparison of the map patterns with other aspects of the floras such as diversity and physiognomic adaptations. We feel that the basic patterns are real, but adjustment of the boundaries will doubtless be necessary.

The floras of the early Mesozoic fall into three main climatically related biomes, the dry subtropical, the warm temperate and the cool temperate, a zonation which is basically the same arrived at by Krassilov (1981, p. 212). However, Vakhrameev (1991, p. 246) assigned these three floras to the tropical (equatorial), the subtropical, and the temperate (moderate)-warm. This scale is too warm throughout, and gives the impression that the poles were very warm indeed. Even so, our maps show warm temperate floras above 70° in the Triassic and occasionally as high as 60° in the Jurassic, with no hint of the cold temperate, arctic or glacial climates that exist at these latitudes today. The tropical zone gives few hints of the rainforest biome so prominent today, and we agree with Visscher and van der Zwan (1980) that this environment was too stressful for plant life. This could have been due to greater latitudinal excursions of the intertropical convergence zone rendering this broad region seasonally arid (Ziegler *et al.* 1987), or to possibly higher temperatures which resulted in higher evaporation. The biome zonation seems to be much better defined in the Jurassic than the Triassic. This we interpret to correlate to slightly higher temperature gradients in the Jurassic and to decreasing strength of the Pangean monsoon through that interval (Parrish & Peterson 1988).

We thank R. A. Spicer for advice and help concerning statistical approaches and physiognomic interpretations in fossil plant studies. The Paleogeographic Atlas Project receives support from the following companies: Amoco, BHP Minerals, Conoco, Elf Aquitaine, Marathon, Mobil, Shell, Total, and Unocal. Financing for our work in China is provided by NSF grant EAR 9206523 to D. B. Rowley.

REFERENCES

Campbell, I.H., Czamanske, G.K., Fedorenko, V.A., Hill, R.I. & Stepanov, V. 1992 Synchronism of the Siberian Traps and the Permian-Triassic boundary. *Science, Wash.* **258**, 1760–1763.

Chandler, M.A., Rind, D. & Ruedy, R. 1992 Pangaean climate during the Early Jurassic: GCM simulations and the sedimentary record of paleoclimate. *Geol. Soc. Am. Bull.* **194**, 543–559.

Daragan-Sushchov, Y.I. 1989 Development patterns of the early Triassic lakes of the Tunguska syneclise. *Int. Geol. Rev.* **31**, 1007–1017.

Del Tredici, P., Ling, H. & Yang, G. 1992 The Ginkgos of Tian Mu Shan. *Conservation Biol.* **6**, 202–209.

Deng, W.M., Liu, G.J., Wen, S.X., Jiang, Z.T. & Zhang, Z.F. 1980 A general geological survey in Qiangtang Plateau, Northern Xizang (Tibet). *Scientia geol. sin.* **2**, 142–155.

Dobruskina, I.A. 1980 Stratigraphic position of Triassic plant-bearing beds of Eurasia. *Akademia Nauk Trans.* **346**, 124 pp.

Dobruskina, I.A. 1982 Triassic floras of Eurasia. *Academia Nauk Trans.* 196 pp.

Dobruskina, I.A. 1987 Phytogeography of Eurasia during the early Triassic. *Palaeogeogr. Palaeoclim. Palaeoecol.* **58**, 75–86.

Dubiel, R.F., Parrish, J.T., Parrish, J.M. & Good, S.C. 1991 The Pangean megamonsoon–evidence from the Upper Triassic Chinle Formation, Colorado Plateau. *Palaios* **6**, 347–370.

Gauch, H.G. 1982 *Multivariate analysis in community ecology.* (298 pages.) Cambridge University Press.

Hallam, A. 1984 Continental humid and arid zones during the Jurassic and Cretaceous. *Palaeogeogr. Palaeoclim. Palaeoecol.* **47**, 195–223.

Hill, M.O. 1979 DECORANA, A Fortran program for detrended correspondence analysis and reciprocal averaging, Ithaca, New York, Privately published.

Hill, M.O. & Gauch, H.G. 1980 Detrended Correspondence Analysis: An improved ordination technique. *Vegetatio* **42**, 47–58.

Holser, W.T., Schonlaub, H.P., Attrep, M. *et al.* 1989 A unique geochemical record at the Permian/Triassic boundary. *Nature, Lond.* **337**, 39–44.

Horrell, M.A. 1991 Phytogeography and paleoclimatic interpretation of the Maestrichtian. *Palaeogeogr. Palaeoclim. Palaeoecol.* **86**, 87–138.

Kazakov, A.M., Dagis, A.S. & Kurushin, N.I. 1983 Paleogeography of the Triassic of the north of middle Siberia. *Petroleum Geol.* **20**, 333–338.

Krassilov, V.A. 1981 Changes of Mesozoic vegetation and the extinction of dinosaurs. *Palaeogeogr. Palaeoclim. Palaeoecol.* **34**, 207–224.

Mader, D. 1990 *Palaeoecology of the flora in Buntsandstein and Keuper in the Triassic of Middle Europe.* (1582 pages.) Stuttgart & New York: Gustav Fischer Verlag.

Meyen, S.V. 1987 *Fundamentals of palaeobotany.* (432 pages.) London & New York: Chapman and Hall.

Moore, G.T., Hayashida, D.N., Ross, C.A. & Jacobson, S.R. 1992 Paldeoclimate of the Kimmeridgian/Tithonian (Late Jurassic) world: I. Results using a general circulation model. *Palaeogeogr. Palaeoclim. Palaeoecol.* **93**, 113–150.

Olsen, P.E. 1986 A 40-million-year lake record of early Mesozoic orbital climatic forcing. *Science, Wash.* **234**, 842–848.

Parrish, J.T. 1992 Jurassic climate and oceanography of the Circum-Pacific region. In *The Jurassic of the Circum-Pacific region* (ed. G. E. G. Westermann), pp. 365–379. Oxford University Press.

Parrish, J.T. 1993 Climate of the supercontinent Pangea. *J. Geol.* **101**, 217–235.

Parrish, J.T. & Peterson, F. 1988 Wind directions predicted from global circulation models of the western United States–a comparison. *Sedimen. Geol.* **56**, 261–282.

Simms, M.J. & Ruffell, A.H. 1990 Climatic and biotic change in the late Triassic. *J. geol. Soc. Lond.* **147**, 321–327.

Spicer, R.A. & Parrish, J.T. 1986 Paleobotanical evidence for cool north polar climates in middle Cretaceous (Albian–Cenomanian) time. *Geology* **14**, 703–706.

Stipanicic, P.N. 1983 The Triassic of Argentina and Chile. In *The Phanerozoic geology of the World*, vol. 2 (The Mesozoic, B) (ed. M. Moullade & A. E. M. Nairn), pp. 181–199. Amsterdam: Elsevier.

Taylor, E.L. & Taylor, T.N. 1989 Structurally preserved Permian and Triassic floras from Antarctica. In *Antarctic paleobiology* (ed. T. N. Taylor & E. L. Taylor), pp. 149–163. New York: Springer-Verlag.

Tralau, H. 1968 Evolutionary changes in the genus Ginkgo. *Lethaia* **1**, 63–101.

Vakhrameev, V.A. 1991 *Jurassic and Cretaceous floras and climates of the Earth.* (318 pages.) Cambridge University Press.

Vakhrameev, V.A., Dobruskina, I.A., Meyen, S.V. & Zaklinskaja, E.D. 1978 *Palaozoische und Mesozoische Floren Eurasiens und die Phytogeographie dieser Zeit.* (269 pages.) Jena: Gustav Fischer Verlag.

Van der Voo, R. 1993 Paleomagnetism of the Atlantic, Tethys and Iapetus Oceans. (411 pages.) Cambridge University Press.

Valdes, P.J. & Sellwood, B.W. 1992 A Palaeoclimate model for the Kimmeridgian. *Palaeogeogr. Palaeoclim. Palaeoecol.* **95**, 47–72.

Visscher, H. & van der Zwan, C.J. 1980 Palynology of the circum-Mediterranean Triassic: phytogeographical and palaeoclimatological implications. *Geol. Runds.* **70**, 625–634.

Walter, H. 1985 *Vegetation of the Earth.* (318 pages.) Berlin: Springer-Verlag.

Wang, Z.Q. 1985 Palaeovegetation and plate tectonics: Palaeophytogeography of North China during Permian and Triassic times. *Palaeogeogr. Palaeoclim. Palaeoecol.* **49**, 25–45.

Yao, Z.Q. 1978 On the age of "Gigantopteris Coal Series" and Gigantopteris-flora in south China, *Acta palaeont. sin.* **17**, 81–89.

Ziegler, A.M. 1990 Phytogeographic patterns and continental configurations during the Permian Period. In *Palaeozoic palaeogeography and biogeography* (ed. W. S. McKerrow & C. R. Scotese) (*Geol. Soc. Mem.* **12**), pp. 363–379.

Ziegler, A.M., Raymond, A.L., Gierlowski, T.C., Horrell, M.A., Rowley, D.B. & Lottes, A.L. 1987 Coal, climate and terrestrial productivity: the present and early Cretaceous compared, In *Coal and coal-bearing strata: recent advances* (ed. A. C. Scott) (*Geol. Soc. Spec. Pub.* **32**), pp. 25–49.

APPENDIX

Phylogenetic Assignments and Key for Genera Included in Figures 1–6

Lycophyta

L1	*Pleuromeia*
L2	*Selaginellites*

Sphenophyta

E1	*Annulariopsis*
E2	*Equisitites*
E3	*Neocalamites*
E4	*Paracalamites*
E5	*Phyllotheca*
E6	*Schizoneura*

Pteridophyta

F1	*Asterotheca*
F2	*Bernoullia*
F3	*Cladophlebis*
F4	*Clathropteris*
F5	*Coniopteris*
F6	*Danaeopsis*
F7	*Dictyophyllum*
F8	*Gleichenites*
F9	*Goeppertella*
F10	*Hausmannia*
F11	*Klukia*
F12	*Marattiopsis*
F13	*Pecopteris*
F14	*Phlebopteris*
F15	*Raphaelia*
F16	*Thamnopteris*
F17	*Todites*

Pteridospermophyta

S1	*Dicroidium*
S2	*Hyrcanopteris*
S3	*Lepidopteris*
S4	*Pachypteris*
S5	*Peltaspermum*
S6	*Ptilozamites*
S7	*Sagenopteris*
S8	*Scytophyllum*
S9	*Sphenopteris*
S10	*Thinnfeldia*

Cycadophyta: Cycadales

C1	*Anthrophyopsis*
C2	*Ctenis*
C3	*Ctenozamites*
C4	*Cycadocarpidium*
C5	*Doratophyllum*
C6	*Nilssonia*
C7	*Pseudoctenis*
C8	*Sinoctenis*

Cycadophyta: Bennettitales

B1	*Anomozamites*
B2	*Drepanozamites*
B3	*Otozamites*
B4	*Pterophyllum*
B5	*Spenozamites*
B6	*Taeniopteris*
B7	*Zamites*

Ginkgophyta, s.l.

G1	*Baiera*
G2	*Chiropteris*
G3	*Czekanowskia*
G4	*Ginkgo*
G5	*Ginkgoites*
G6	*Glossophyllum*
G7	*Leptostrobus*
G8	*Phoenicopsis*
G9	*Spenobaiera*

Coniferophyta: Ulmanniaceae

U1	*Ferganiella*
U2	*Glyptolepis*
U3	*Podozamites*
U4	*Swedenborgia*
U5	*Voltzia*
U6	*Yuccites*

Coniferophyta: Podocarpaceae

P1	*Desmiophyllum*

Coniferophyta: Cheirolepidiaceae

A1	*Araucarites*
A2	*Brachyphyllum*
A3	*Pagiophyllum*

Coniferophyta: Pinaceae

K1	*Pityophyllum*
K2	*Schizolepis*

Coniferophyta: Taxodiaceae

T1	*Elatides*
T2	*Elatocladus*