MESozoic FLorAS

by P. D. W. BarNARD

Abstract. A review of Mesozoic floras and palaeofloristic zones based on macrofossil remains is presented and summarized in the form of four maps. The palaeofloristic region of the Mesozoic are discussed and plant distribution indicated in an attempt to demonstrate some latitudinal and or climatic zonation of the floras when plotted on the symposium maps. The results show the difficulties encountered and the need for further research.

In this brief survey of Mesozoic floras I have attempted by plotting the distribution of selected fern genera to test (a) the reconstruction of the continents and (b) the Russian palaeofloristic regions. I have assumed that throughout the Mesozoic there existed a sufficient temperature gradient between the equator and the poles to influence the distribution of plants. Some taxa would have been distributed in narrower belts around the equator than others. The vegetation of the higher latitudes would have comprised a more restricted group of taxa. I have restricted my study to macrofossil remains.

In attempting to prepare a palaeofloristic reconstruction the literature search needs careful delimitation. The three parameters to be considered are: (1) the size of the time interval; (2) the minimum size of a flora to be regarded as a significant sample; (3) the taxa and the standard of taxonomy. Ideally selection would be restricted to as small a time interval as possible (e.g. a stage); all floras with less than 20 species would be disregarded and only those taxa used which can be clearly distinguished. Owing to shortage of notice for the symposium my preliminary survey of the literature has been briefer with respect to the Trias and Cretaceous but more thorough in the Jurassic.

The Early Triassic

This map is based on fig. 16 of Dobruskina (1970). On it I have indicated the boundaries between the floras which Dobruskina regards as belonging to three main regions: Angara, Euramerican, and Gondwana. In Dobruskina these points are plotted on a conical projection Eurasia. I have transposed these to the reconstructed Triassic map with the omission of some points in Germany. I have added a series of points to South America, South Africa, and Australia to indicate the distribution of the Gondwana, Dicroidium flora. This has given the map a greater appearance of symmetry.

The majority of localities in Europe listed by Dobruskina contain very few species. This makes the correlation of these Early Triassic floras on the basis of the plants they contain extremely difficult. I believe therefore that at this time the deduction of palaeofloristic regions is more a matter of faith than an exercise based on fact. However, I concede that the European area may possibly be distinguished by the sphenopsid genus Schizoneura (S. paradoxa) in association with the conifer Voltzia (V. heterophylla). In the Angara region the situation is very similar with sparse

[Special Papers in Palaeontology No. 12, pp. 175-187]
TEXT-FIG. 1. Early Triassic, Angara, and Euramerican floristic regions after Dobruskina 1970 with some additions to the Gondwana region to show the distribution of *Dicroidium*. ○ = Angaran flora; ● = Euramerican flora; △ = *Dicroidium* flora; — — — = boundary between Angaran and Euramerican regions; - - - - = boundary to the Gondwanan floristic region.
floras with the possible exception of the Tunguska basin. Here a richer flora with the following: a pteridosperm 
*Lobatoferis*, a sphenopsid *Neokoretralphyllites*, and a pteridosperm *Tersiella*, combine with other genera (Radchenko 1960) to give the region a distinctive character. In Kazakhstan and central Asia the floras show some mixing of taxa from Europe and the Angara region.

The boundary between the Angara and Euramerican paleofloristic regions shown on the map lies between 50° N. and 65° N. The Euramerican region lies within a belt between approximately 15° N. and 55° N., and it can be deduced that this belt represented the Early Triassic equivalent of a subtropical to warm temperate flora. The belt of the Euramerican flora as here projected coincides very closely with the belt of Triassic evaporite deposits depicted by Lotze (1964, fig. 10) who suggested that evaporite deposits are indicative of past warm-arid climates. The Siberian Angara flora being cooler but possibly still a temperate flora even though it extended to within 10° of the Triassic pole.

There is a challenging hiatus on the map with no Early Triassic flora known to me from a broad zone between 15° N. and 30° S. Below 30° S. there flourished a rich Gondwana flora in which *Dicroidium* was a prominent genus existing from the Early Triassic through to the Carnian. This is another major weakness of this reconstruction; most of the floras represented by points on the southern half of the maps are not synchronous with those in the north. The *Dicroidium* flora spread over a wide belt around the Southern Hemisphere between 30° S. to well below 60° S. in Tasmania and the Antarctic continent. It contained some taxa which are also found in the Northern Hemisphere but also possessed a number of endemic taxa in addition to *Dicroidium*. Notable are some of the conifers (e.g. *Rissikia*) which Townrow (1967) regards as early podocarps. This southern flora lies to the south of the African Triassic evaporite deposits figured by Lotze and may have been a warm temperate flora. The high latitudes to which the Angara and the Gondwana flora extend may be an indication of the equability of the Triassic climate.

A genus which is of considerable interest in any discussion of Triassic floras is *Lepidopteris* which is first recorded from the Upper Permian of England and Germany and ranges through to the Rhaetian. Its absence from the Lower and Middle Trias in Europe is probably an indication of the inadequacy of the samples obtained from the beds of this age in this area. A possible alternative explanation being some change in climate, such as greater aridity. During this time *Lepidopteris* was widespread in Gondwana, occurring in Argentina, Natal, and Australia as a component of the *Dicroidium* flora. The genus then reappears in Europe during the Upper Trias. Dobruskina (1970, fig. 15) shows its distribution from the Pechora basin in the north to Anlung, Kweichow province of China in the east. The genus thus ranges from over 60° S. on the reconstructed Triassic map to nearly 60° N. It is, however, unrecorded from the zone 30° N. to 40° S. and it is not yet known from North America. How and in which direction this genus migrated across the equator is unknown. It does, however, indicate the very wide distribution of at least one Triassic plant taxon. Townrow (1960) has commented on the anatomy of the *Lepidopteris* leaf deduced from cuticle studies, showing that both the European and Gondwana leaves are essentially similar. He further compared *Lepidopteris* with a number of living temperate zone dicotyledonous waterside herbs.
MIDDLE MESOZOIC FLORA

By the end of the Middle Triassic a new flora was developing throughout the world, and I shall refer to this succession of assemblages as the Middle Mesozoic Flora to distinguish it from those of the Early Trias and others of the Late Cretaceous after the appearance of the Angiosperms. This epoch is typified by ferns of the Dipteridaceae and Matoniaceae; Pteridosperms sensu lato, e.g. Pachypteris and Ctenozamites groups together with the Caytoniales; Bennettitales and Nilssoniales; Ginkgoales and Czekanowskiales; and conifers with small leaves, e.g. organ genera Brachyphyllum and Pagiophyllum together with Classopolis pollen.

The Rhaeto-Liassic

Most of the localities where the components of this flora first appear are shown on text-fig. 2. In North America the Dipteridaceae and Bennettitales first appear in the Chinle Formation (Carnian and Norian) of the south-western United States. The Dipteridaceae in the Barreal beds (Carnian) of San Juan province, Argentina, and also in the La Tenera flora of Chile which also contains Dicroidium and is about the same age. In South Africa the Dipteridaceae are found in the Molteno beds of Basutoland (Carnian) and in Australia in the Ipswich series (Carnian) of Queensland. In Europe the Dipteridaceae together with the Bennettitales are known from the Carnian of Lunz in Austria and Neue Welt in Switzerland. In eastern Asia this flora is first recorded from Tonkin in Vietnam (called Rhaetic, possibly Norian) and the Carnian of Japan.

However, by the Rhaetian it was widely established in a broad belt from c. 50° N. (text-fig. 2) to 60° S. I have plotted the distribution of the genus Dictyophyllum of the Dipteridaceae as an indicator for the region occupied by this flora in Rhaetian and Early Liassic (Hettangian and Sinemurian) times.

I have indicated (text-fig. 2) the boundary line drawn by Vakhrameev (1964, fig. 1, and 1966, text-fig. 1) between the Eurasian floristic region and the Siberian region. It may be noted that Dictyophyllum is recorded from the Bogeslovska basin in the eastern Urals and in southern Primorie both of which occur within the Siberian province. The most northerly of the Siberian flora, that from the Vilyue depression

TEXT-FIG. 2. Rhaetic and Lower Lias floras (Lepidopteris and Thaumatopteris zones) showing the distribution of Dictyophyllum. North America: 1, Mexico; 2, Honduras. South America: 3, Chile (La Tenera, Carnian); 4, Argentina (Mendoza); 5, Argentina (Neuquén); 6, Argentina (Chubut). 7, Greenland (Scoresby Sound). Europe: 8, France, Normandy; 9, Vendée et Sèvres; 10, Sweden, Scania; 11, Germany, Franconia; 12, Poland; 13, Hungary; 14, Rumania; 15, Donetz basin. 16, Armenia. Iran: 17, Elburz Mountains. Urals: 18, Bogoslovska basin; 19, Chelyabinsk basin; 20, Turgai, Tobol basin. Central Asia: 21, Chagyl (Tuarky); 22, Ferghana, Kok-Yangak; 23, Sonkul; 24, Issyk-kul; 25, Alakol; 26, Kenderlyk. Siberia: 27, Chelym-Yenisei basin; 28, Kansk basin; 29, Vilyue depression; 30, Southern Primorie. Japan: 31, Yamagushi (Carnian). China: 32, West Huphe; 33, Szechuan; 34, Hunan. Vietnam: 35, Tonkin (?Norian). Africa: 36, Basutoland (Carnian). Australia: 37, Queensland, Ipswich (Carnian).

• = Floras containing Dictyophyllum; ○ = floras with no Dictyophyllum; ♂ = floras older than the Rhaetic containing Dictyophyllum; — — — = boundary between the Siberian and Eurasian floristic regions after V. A. Vakhrameev 1964; ······· = northern and southern limits to the distribution of Dictyophyllum; — — — = southern boundary to the Eurasian region and northern boundary to the Gondwana region.
contains only 10 species, too few to draw conclusions. The other Siberian floras shown (nos. 19, 20, and 25–28) contain more species but the Dipteridaceae, Matoniaceae, and Marattiaceae are very rare as are the cycadophytes and short-leaved conifers. These floras have a preponderance of cladophlebid ferns, Ginkgoales, Czekanowskiales, and long-leaved conifers, Elatacladus, Pityophyllum, and Podozamites. The difference in the composition of the floras is striking and does appear to reflect some environmental cause and not simply a latitudinal effect; it may be due to some effect of the continental mass on the climate. It might be possible to detect some latitudinal effect on the Jurassic floras from the Southern Hemisphere, in Argentina and especially the Australian–New Zealand regions, if these were better known.

I have omitted (text-fig. 2) a number of floras included by Vakhrameev (1964) either because I regard them as belonging to the Upper Lias or because they contained too few species to be regarded as useful samples. A table in which a number of Middle Asian Jurassic floras are correlated is given in Assereto et al. (1968). Those floras of Middle Asia which remain are essentially similar to those of Europe and China (Vakhrameev’s east Asian province). I have failed to recognize any separate floristic provinces within the broad Eurasian region because my analysis has been based at the generic level; a more detailed analysis at the specific level would reveal differences but I am uncertain how these should be interpreted.

The southern floras which contain Dictyophyllum differ considerably from those of the Northern Hemisphere. They contain very few if any species in common with Eurasia and must be regarded as constituting a separate Gondwana floristic region.

The considerable spread of the Middle Mesozoic flora at this time as shown by the distribution of Dictyophyllum, to between 50°–60° on either side of the equator is consistent with the argument that the Jurassic world had a warm and highly equable climate. Colbert (1964) mentions the occurrence of dinosaurs in Liassic times in southern England and south-western North America both c. 30° N. on the symposium map and in central India which is c. 30° S. I mention this because the 30° latitudes on the map pass through the most concentrated regions for the occurrence of Dictyophyllum in the Northern Hemisphere. Axelrod and Bailey (1968) mention that the climate of the Cameron Highlands (Malaya) in which Dipteris and Matonia occur today has an equability of 70% and a mean annual temperature of 65°F. They also calculated that Cretaceous dinosaur country would have had a high equability and a mean annual temperature range between 51°–81°F. Colbert (1964) also records the existence of ichthyosaur remains in the Lias of Greenland. I therefore suppose that a sub-tropical to warm temperate climate existed over these regions of the globe and that it is not yet possible to recognize genuine changes due to the effect of latitude.

The Mid Jurassic

What I have already said regarding the plotting of points on the Early Jurassic map (text-fig. 2) also applies to the map of the Middle Jurassic (text-fig. 3). This spans the three stages, Aalenian, Bajocian, Bathonian, and probably also includes some Callovian floras. On this map I have indicated the distribution of Sagenopteris
(Caytoniales) as an indicator of the spread of the Middle-Mesozoic flora at this period. It occurs within the belt 40° N. to 50° S. a somewhat narrower belt than that indicated by Dictyophyllum at the beginning of the Jurassic. I have also shown the distribution of the schizeaceous fern Klukia which has a more restricted distribution around the western end of the Tethyan sea, from Western Europe to Central Asia and from 5° S. to 35° N. It thus delimits a European–Central Asian floristic region which corresponds to a combination of Vakhrameev’s (1964) European and Central Asian provinces. I have indicated the boundary to Vakhrameev’s Siberian region which includes the remaining Asiatic localities.

The European–Central Asian floristic region (here characterized by the limits of the distribution of Klukia) also contains a number of fern taxa rarely encountered in the Siberian region, e.g. Marattia (Marattiopsis) and Phlebopteris. The rare pteridosperms Ctenozamites and Pachypteris lanceolata are also confined to this region. The Bennettitalean genera Otozamites and Ptilophyllum are represented by numerous species as are the cycads by Nilssonia and allied genera. As in the Early Lias it is the absence of many taxa found in the European–Central Asian region which is the striking feature of the Siberian floras. There are very few taxa exclusive to the Siberian region; the fern Raphaelia diamedes is regarded by Vakhrameev (1964) as distinctive of this region, but it does also occur in Central Asia. The line separating the Siberian region as drawn by Vakhrameev (1964) is somewhat oblique. However, I think it is sufficiently close to the 40° parallel to support the idea that the difference between the two phytogeographic regions could have been due to a stronger temperature and climatic gradient between the equator and the poles at this time.

The floras of western North America which are probably of Middle Jurassic age have unfortunately not been critically examined in recent decades. They are said to contain Sagenopteris and those from Oaxaca, Mexico, contain numerous species of Otozamites (Wieland 1914, Delevoryas 1966). The Oroville flora from California, Fontaine (in Ward 1900), contains a Marattia (called Angiopteridium californicum). These floras have the appearance of those from the European–Central Asian region without, however, the presence of the genus Klukia. They must for the time being be regarded as a separate western American province of the Northern Hemisphere European–Central Asian floristic region.

The floras from the Southern Hemisphere, 30°–50° S., contain a number of genera found in the Northern Hemisphere. The distribution of Sagenopteris is shown in Argentina, Graham Land, and India and the fern genera Marattia and Phlebopteris are also known from Gondwana. The Bennettitalean genus Otozamites is represented by a number of species in Argentina and India. Ptilophyllum with a number of species in India also occurs in Argentina. Nilssonia is rare and there are fewer cycads in the Gondwana floras as compared with those of Europe and Central Asia. Leaves of the Taeniopteris spatulata type are relatively abundant in the Gondwana floras of this time. In India they have been associated with the distinctive Pentoxylon, the fruits of which have been recorded from India and also from New Zealand which is off the Symposium Mercator map. I suspect that if the floras of Western Australia and the Cape York peninsula were fully described and then compared with revision of those from New South Wales, Victoria, and New Zealand it might be
possible to detect some differences due to the effect of latitude in the Southern Hemisphere.

There is little that can be deduced directly from either Sagenopteris or Klukia regarding the temperature in climatic regions under which they grew. In the Early Jurassic Sagenopteris grew within the Dictyophyllum belt and I suppose that the climate within the belt 40° N. to 50° S. was similar and of a tropical to sub-tropical type. The evaporite belt drawn by Lotze (1964, fig. 11) corresponds closely to the Northern Hemisphere Sagenopteris, Klukia belt. The Jurassic terrestrial tetrapod faunas of Colbert (1964, fig. 8) also fall broadly within the Sagenopteris belt. This evidence further supports any argument for a warm equable climate.

The Early Cretaceous

The map (text-fig. 4) includes floras attributed to the Neocomian plus some containing Weichselia but attributed to the Aptian/Albian. I have indicated the distribution of the matonaceous fern Weichselia as it has been widely recorded and appears to lie in a belt about 30° wide on either side of the Early Cretaceous equator. The Middle Mesozoic flora of this time was spread in a much wider belt from about 50° N. to 60° S. Other ferns such as Gleichenia, Nathorstia, Onychopsis, and Ruffordia give a better indication of the northern and southern limits of this broader floristic zone.

The line across Europe and Asia indicating the northern limit of Weichselia coincides well with the boundary of Vakhrameev's (1964) Siberian region. All the floras to the south of this line constitute a broad Eurasian–North American floristic region. To the north lies the Siberian–Canadian floristic region. In some contrast to the preceding Siberian floras, those from the Early Cretaceous contain an abundance of species belonging to a wide range of taxa. In the Siberian region, the fern genera Cladophlebis and Coniopteris are represented by a number of species; the Bennettitales which have been poorly represented in this region prior to the Late Jurassic are now present in the form of those genera with simple and simply dissected leaves (Nilssonopteris, Anomozamites, Pterophyllum). The true cycads also increase; the floras now contain a number of species of Nilssonia and allied genera. There are numerous species of Ginkgoales and the Czekanowskiales are now endemic to this region.


○ = Floras containing Klukia; ○ = floras containing Sagenopteris; ○ = other floras, see text; — — boundary between the Siberian and European–Central Asian floristic regions after V. A. Vakhrameev 1964; — — — northern and southern limits to the distribution of Sagenopteris; ••••• = boundary to the European–Central Asian region.
The Early Cretaceous floras of British Columbia are very similar in their composition to those from Siberia.

The Eurasian–North American floristic region is represented by somewhat limited floras. These usually contain a wider variety of fern genera than those of the Siberian–Canadian region. They also usually contain the Bennettitalean genera *Otozamites* and *Zamites* and a reduced number of species of true cycads, *Nilssonia* and allied genera. This region can be divided into three provinces, a North American, a European–Central Asian, and an East Asian or Western Pacific province. These broad provinces are based on analyses at the specific level.

The *Weichselia* containing floras from Peru, Africa, and India, are, with the exception of those from India, poorly known and with few species. The Indian floras contain the pteridosperms *Pachypterus* and *Cycadopteris* and a number of Bennettitalean species belonging to the genus *Ptilophyllum*. It would probably be possible to recognize a Gondwana province and include all these floras in the Eurasian–North American floristic region for the time being.

To the south of the *Weichselia* belt we have Early Cretaceous floras in Argentina, South Africa (from the Sundays River in the Uitenhage area), and Australia. The Early Cretaceous flora from the Argentine is distinctive in containing the Bennettitalean genera *Dictyozaamites*, *Otozamites*, and *Zamites* but the species are specifically distinct from those north of the equator. The ferns too are different and there are a number of unique conifers including the podocarps *Apterocladus* and *Trisacoctadus*, and *Tomaxella* (Cheireolepidaeae). Although the remaining floras are too poorly known to comment on, it is possible to recognize a southern Gondwana floristic province to include all the area below about 30° S.

In attempting any deduction regarding the climate in the Early Cretaceous, *Weichselia* may be compared with the living *Matonia* from the Cameron Highlands in Malaya (Axelrod and Bailey 1968). If this comparison is accepted then there would appear to have been a steady decrease in the width of the tropical to subtropical belt from the Lias onwards. Yet despite this the cycad genus *Nilssonia* has been establishing itself outside the supposed warm belt in the Siberian region. There is no good fit here with either the Cretaceous evaporite belt drawn by Lotze (1964, fig. 5) or the broad belt of Cretaceous terrestrial tetrapod faunas shown by Colbert (1964, fig. 10).

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● = Floras containing *Weichselia*; ○ = other floras, see text; — — = boundary between the Siberian and Eurasian floristic regions after V. A. Vakhrameev 1964; — — = northern and southern limits to the distribution of *Weichselia*. 
LATE CRETACEOUS FLORAS

The early angiosperms (Aptian and Albian) appear over a wide belt in the Northern Hemisphere at localities within both the Siberian–Canadian region and the Eurasian–North American region (Samylna 1968). In the Southern Hemisphere the earliest occurrences are in the Stix River coalfield of Queensland, Cenomanian, and in Argentina from the Cerro Guido, probably Campanian in age.

In the Upper Cretaceous angiosperms gradually dominate the floras numerically and the fern and gymnosperm taxa characteristic of the Middle Mesozoic flora gradually disappear. There are fewer floras known from the Upper Cretaceous than earlier in the Mesozoic and the sample size is usually small. Vakhrameev (1970, ch. 8) recognized four floristic zones in Eurasia from west to east: European, Ural, Eastern Siberian, and Pacific provinces. The Pacific province has produced numerically large floras which appear unique in containing a number of Mesozoic gymnosperms which exist alongside the angiosperms until the end of the Cretaceous. Vakhrameev (1970, figs. 41 and 42) shows the north eastward migration of Nilssonia to the Pacific province to between 30° and 60° N.

CONCLUSION

This study has indicated the presence of a broad equatorial floristic belt and two polar floristic regions in Siberia and southern Gondwana throughout most of the Mesozoic. The climate over much of the globe has been deduced to be warm and equable for much of the time from 60° N. to 60° S. The maps may be slightly distorted in respect to northern America and Australia but the floristic evidence from both these regions is not well enough known to form the basis of any good argument. The presence of floras from Siberia in the Early Triassic, New Zealand in the Jurassic, and Alaska in the Cretaceous, all from latitudes of about 70° or more on the symposium maps, does, if their position is accepted, pose the problem of continuous darkness in the winter months. In the Middle Jurassic the separation of southern Iran by the Tethyan sea from the north and its union with Arabia may be questioned on the basis of the typical northern flora known from the Kerman coalfield.

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P. D. W. BARNARD
Department of Botany
The University
Reading, Berks.