MESOZOIC AND TERTIARY DISTRIBUTIONS, AND PROBLEMS OF LAND-PLANT EVOLUTION

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ABSTRACT. Some of the main problems of both gymnosperm and angiosperm distribution from the Mesozoic and Tertiary are re-examined using palaeolatitudes provided from the palaeomagnetic evidence. The general conclusions are most encouraging for palaeobotany in that pre-Eocene extinct plant fossils may be used with much greater confidence as climatic belt indicators.

THE new palaeolatitude information appears to have considerable impact on a number of selected evolutionary problems of fossil plants. It provides the opportunity to see whether this better palaeogeographic information will help to shift the centre of the apparent problem in each case so that scope for new approaches may become obvious.

It would be wrong, however, not to record first that in my opinion a great part of the difficulty in interpreting fossil plants and plant assemblages is due to the widespread and continued use by palaeobotanists of backwards-in-time (non-evolutionary) taxonomy and nomenclature. Although this is not the occasion to attack this self-defeating procedure, it seems likely that the need to end it will become clearer.

The topics discussed below are general, and the plots are neither exhaustive nor based on critical new fossil data.

FLORAL CHANGES AND CLIMATE

Although it has long seemed very likely that the northerly palaeolatitude of the British area had increased during the interval from Permian to Recent time, it was not previously possible to record any relatively accurate intermediate points. Although our Eocene flora (being close enough to the present) contained recognizable tropical and subtropical plants, it has not been clear that our Jurassic and Cretaceous floras were in fact more tropical. This could not have been determined from the many well-preserved plants, because either they belonged to extinct taxa or it was not possible to interpret their Mesozoic distributions (as in certain coniferophytes).

The palaeomagnetic information can now be used in reverse to allow definitions of Mid-Mesozoic climatic belts by their plants. The floras had already been recorded and classified geographically as in Asia (Vakhrameev *et al.* 1970) but with the continent in its present position thus necessitating complex explanations of land and sea distribution; now they can be seen (text-figs. 1, 2) to correspond fairly closely to palaeolatitudinal belts, presumably based on atmospheric circulation patterns not very different from the present ones.

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THE ECOLOGIC NICHE OF THE *CLASSOPOLLIS* PLANTS

These plants were presumably coniferophytes, and their affinity within the group is gradually being settled. The pollen grains are often abundant in Jurassic and Cretaceous rocks, and the reasons for their distributions are now becoming clearer.

Using the distributions given by Vakhrameev *et al.* (1970) and Reyre (1970), the plots (text-figs. 1, 2) indicate a general latitudinal control, which is emphasized by the rarity of these grains in the Arctic.

These conifers were undoubtedly important in tropical floras and judging by the frequent great abundance of the pollen in a good state of preservation, the plants must have been lowland dominants.

The well-known increase in abundance of *Classopollis* as palynologic facies are traced seaward in deltas (Hughes and Moody-Stuart 1967, Chaloner and Muir 1968, Batten 1973, and others), further indicates that the plants probably grew on the seaward margins of deltas, as mangrove plants do now. With only the very restricted distributions of Recent conifers in mind, it is difficult for botanists to envisage such a habitat for short-leaved coniferophytes; the Recent high altitude or high latitude distribution of conifers is of course entirely irrelevant.

ORIGIN OF NORTHERN AND SOUTHERN HEMISPHERE CONIFERS

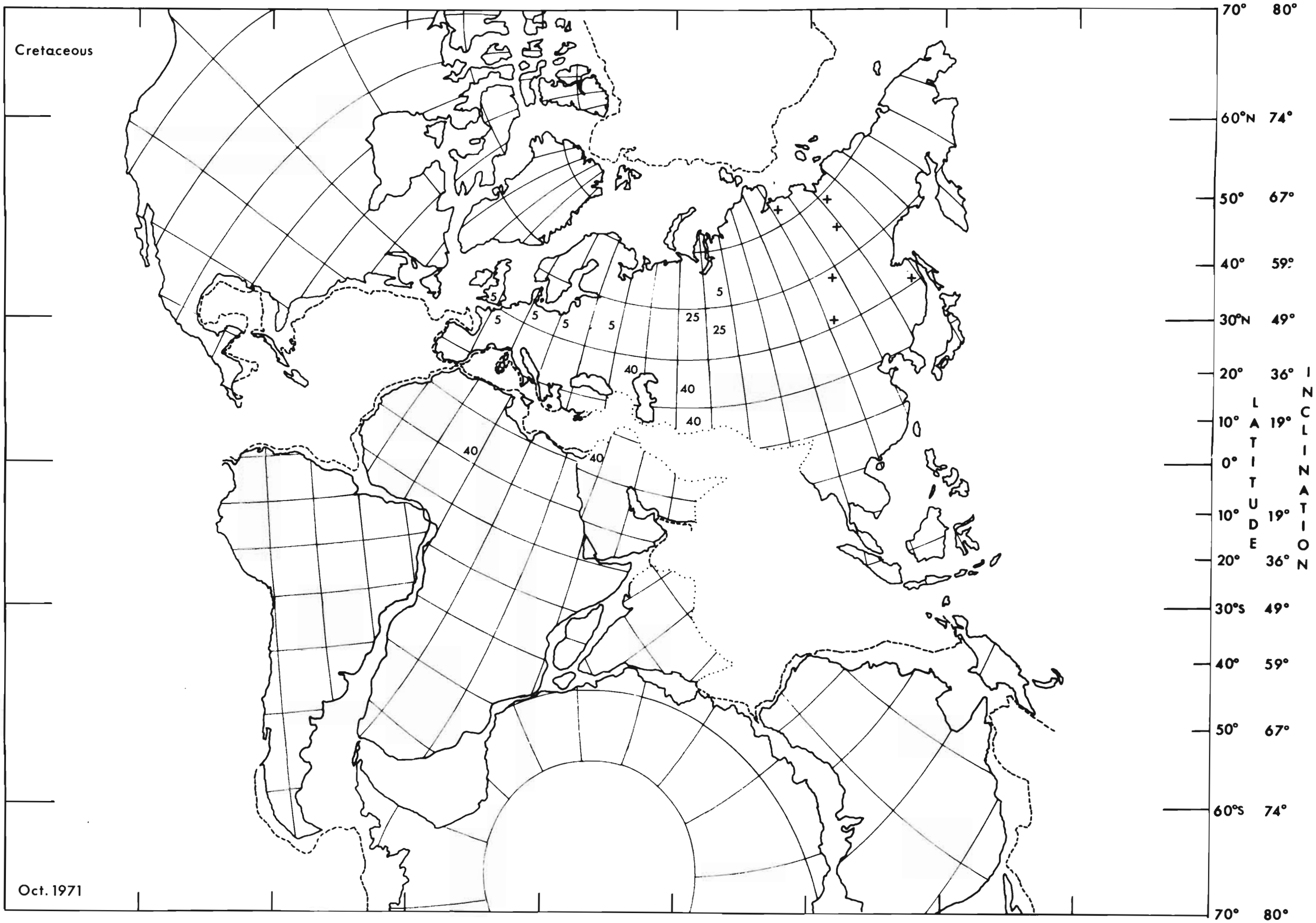
Florin (1940, p. 69) propounded the view that the well-known Southern Hemisphere conifer families Araucariaceae and Podocarpaceae arose independently from the *Cordaites* group in about Permian time and have thus been unconnected with the northern conifers throughout their history.

Since in the Mesozoic coniferophytes were tropical lowland plants, and since at least in Triassic and Jurassic times Pangaea was still in existence (text-fig. 1) astride the tropics, it would seem more likely that coniferophytes at this time were universal in suitable lattitudes. This is borne out by the actual plants of the Triassic and Jurassic in the two hemispheres which look relatively similar both in specimens and in the literature. *Classopollis* among other extinct fossils was present in both areas; and no conifer pollen that it is necessary to refer to an extant family (owing to concurrence of detail in *several* organs) was important in either. It seems likely that in pre-Cretaceous times the coniferophytes were a varied but universal group for which entirely neutral and independent nomenclature is appropriate.

In Cretaceous time on the other hand (text-fig. 2) the Middle Atlantic had opened, and eastern Tethys had not closed except apparently for some proximity of islands in the Indonesian area. The fossil evidence shows that some characters of the extant Pinaceae and other families had appeared in the Early Cretaceous in the Northern Hemisphere, perhaps indicating separation.

It seems more likely, however, that the genuine separation of Northern and Southern conifers dated from Mid-Cretaceous time when angiosperms began to fill the equatorial lowlands providing a substantial biologic barrier.

During the Tertiary era, the Northern Hemisphere conifers lost most of their hitherto major *Sequoia* and *Taxodium* elements and are now dominated by the Pinaceae particularly in the present cool temperate regions. This was probably due



TEXT-FIG. 2. Cretaceous map with percentage occurrences of *Classopollis* pollen grains (Early Cretaceous) for Eurasia. Information from Vakhrameev *et al.* (1970) and other sources. + = single grains observed.

to the combined effect of climatic cooling towards the Pleistocene, and to increasing angiosperm competition in all more favoured habitats.

In the Southern Hemisphere, Araucariaceae and Podocarpaceae are closer morphologically to some of the universal Mid-Mesozoic types, but were isolated from Cretaceous times. Interestingly in the Far East is the northerly relict (China and 'Indochina'), or redistribution, of the Podocarpaceae as an exception to the general pattern, with the Cretaceous map (text-fig. 2) suggesting that relict is the correct interpretation.

ORIGIN AND RADIATION OF ANGIOSPERMOUS PLANTS

Almost every major region of the globe has been postulated at some time as the place of origin, and then rejected for lack of evidence; the main difficulty, however, may well be the lack of adequately fine stratigraphic correlation to detect a migration from an area of origin.

Without prejudging the question of possible polyphyletic origin, the most likely places on general grounds are the tropical lowlands and these can now be examined with the aid of the Cretaceous palaeolatitude map (text-fig. 2). This can perhaps be done most profitably by checking the theory of poleward migration (Axelrod 1959); the original theory was based on megafossils only, and was never very well supported in detail by latitudes assumed to be palaeolatitudes, or by the then quoted stratigraphic time-correlations (Axelrod 1959, text-figs. 1–3). Axelrod incidentally postulated an upland origin but it is not necessary here to consider this detail further (Hughes 1972 (in press)).

Text-fig. 3 shows the critical data from Axelrod's figures replotted by Cretaceous palaeolatitude. In those cases in which the percentage figure is shown in brackets, the age and percentage are taken from Axelrod; in other cases, the following changes have been made in accordance with references cited or with my reassessment:

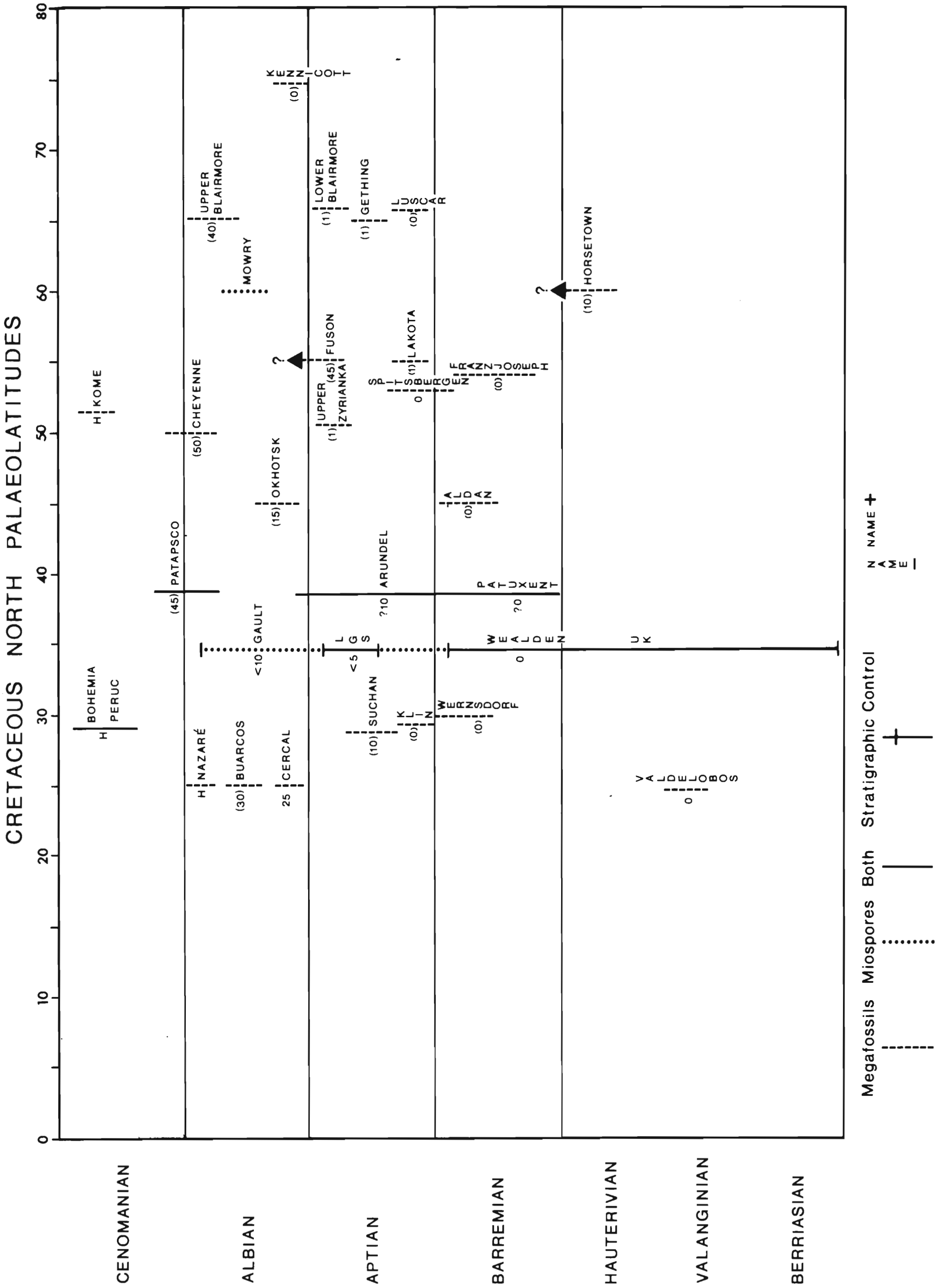
Lower Potomac floras (Patuxent–Arundel Formations): The best estimate of age is Barremian to Early Albian (see Doyle 1969); the matrix of the original angiosperm leaf specimens from Frederiksburg is apparently palynologically consistent with other Patuxent samples, but the time-scale position of the samples is not known within the range and there is no genuine lithologic mapping of the formations from current outcrops, let alone from those no longer available (Frederiksburg).

Lower Greensand (Britain): The fossil wood localities are of Mid to Late Aptian age. The whole succession from Barremian to Early Albian age contains *Clavatipollenites*, but *Tricolpites*, etc., are confined to the Albian (Kemp 1968).

Portugal: The Valle de Lobos flora does not contain confirmed angiosperm megafossils. The Cercal and later floras are thought to be of Albian and later ages (Teixeira 1948, Groot and Groot 1962).

Greenland (Kome, etc.): These floras have been taken out of consideration as they are not of Early Cretaceous age (Koch 1964).

It is clear that an oblique line could be drawn (on text-fig. 3) from Early Aptian in low latitudes to Late Aptian in the highest latitudes in the sense of Axelrod's



TEXT-FIG. 3. Replotting on palaeolatitudes, and reassessment in some cases, of data from Mid-Cretaceous plant assemblages originally provided by Axelrod (1959).

theory and his (1959) presentation. The stratigraphic control is, however, not very strong and the necessary changes of correlation or of taxonomy to make the line horizontal (of equal age) are not great. There are two anomalous cases: (1) the Fuson flora of Wyoming with a very high angiosperm percentage for the Aptian, and (2) the Lower Horsetown of Northern California which does not fit and demands closer scrutiny than when it was placed in an apparent latitude of 38° N. by Axelrod.

My reading of Crowley (1951) for the Fuson, and of Murphy (1956) for the Horsetown, is that in both cases the stratigraphic age is not well controlled and the beds could be much younger.

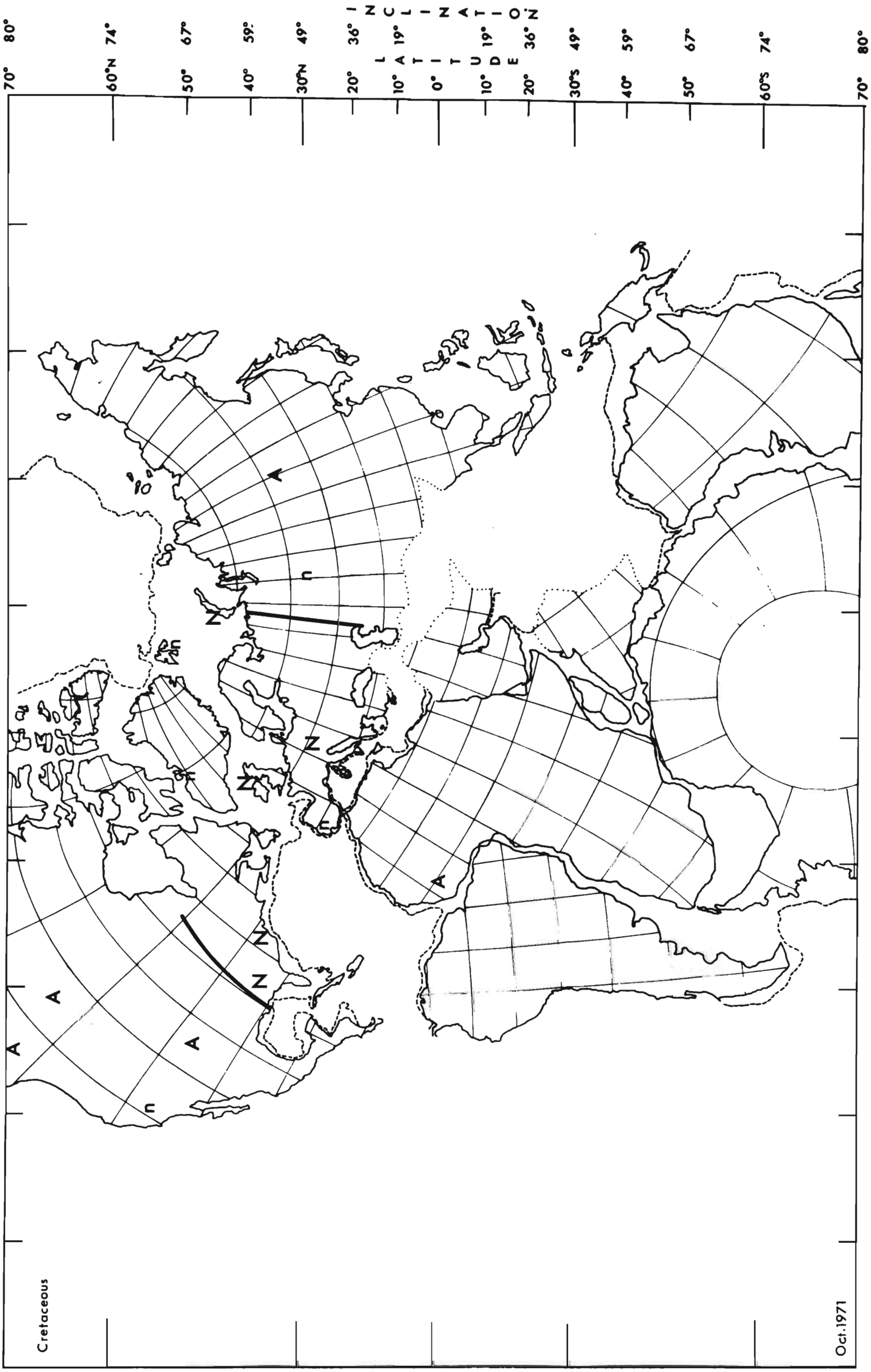
There is an unfortunate dearth of published evidence in latitudes below 25°, which could perhaps eventually come from West Africa and Venezuela; an exception is the Albian–Cenomanian flora of Peru (Brenner 1968) in palaeolatitude 10° S. with about 10% angiosperm pollen; Cretaceous rocks of this age in Central and Eastern 'Tethys' are mostly marine carbonates. The small amount of other Southern Hemisphere evidence so far available cannot be critical because of weaker time-correlation.

LATE CRETACEOUS PALYNOLOGY

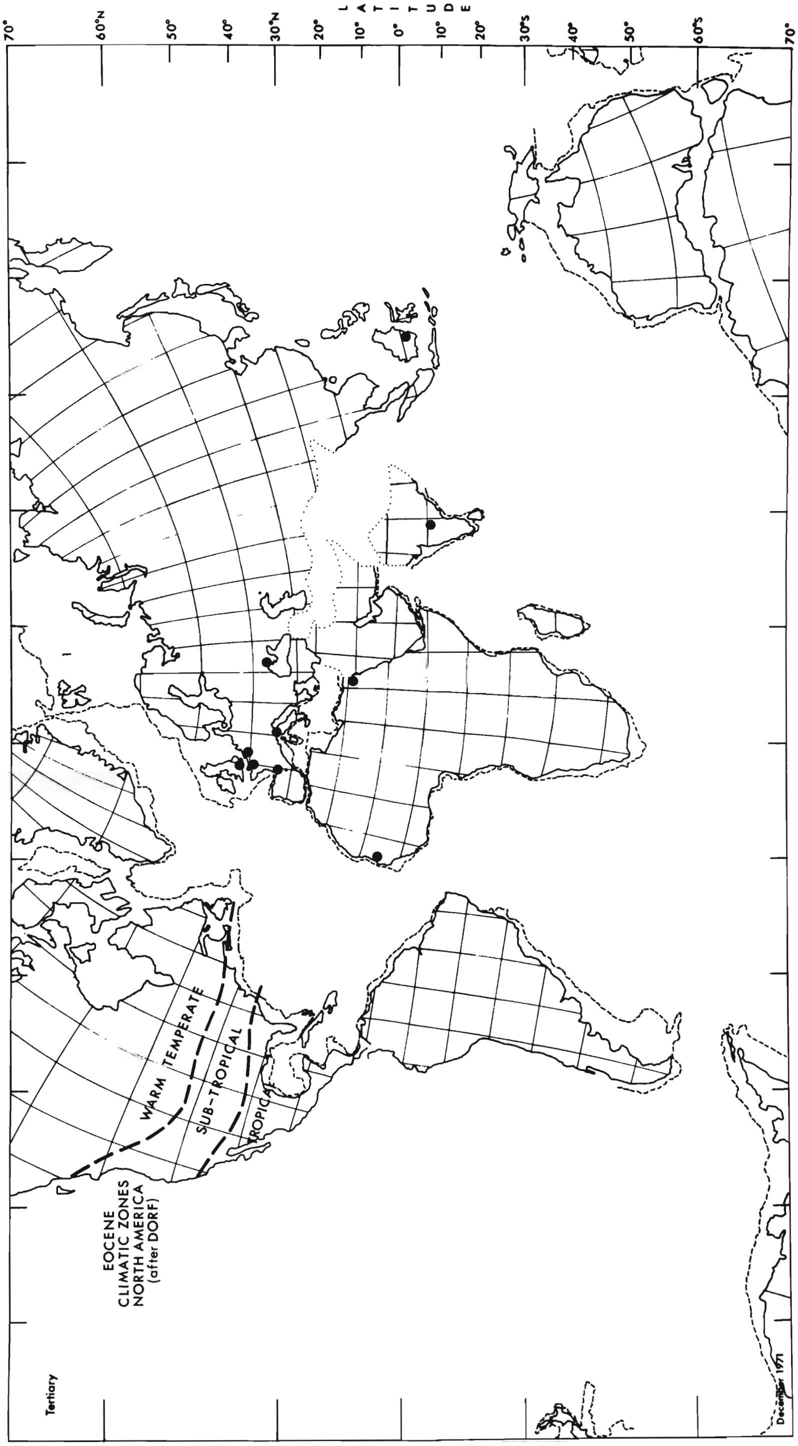
As shown by Goczan *et al.* (1967) and by others, the geographic restriction of the large extinct Normapolles group of angiosperm pollen to eastern North America, Europe, and western Siberia is still unexplained although the area is more compact with the North Atlantic 'closed' (text-fig. 4). Replotting emphasizes that the separation at the eastern boundary of the area is both in longitude and also within a continental area, and thus something more of a challenge. The approximately complementary distribution (in the Senonian) of the *Aquilapollenites* flora of east Siberia and western North America (see also Muller 1970, fig. 4) was fairly obviously restricted by seas from invading the Southern Hemisphere. The Palaeogene *Buttinia* distribution (Germeraad *et al.* 1968) in West Africa and northern South America appears to be entirely explained by a recently 'closed' South Atlantic.

BRITISH EARLY TERTIARY FLORAS

The Eocene London Clay flora, which is firmly believed to have been tropical, now appears to have been living at about 35° N., implying general high temperatures for the period and a wide tropical belt. The supposedly (also) Eocene temperate flora of Mull (Hebrides) only 400 miles to the north, has always presented a problem. Simpson (1961), reporting on the pollen, attempted to show that the Mull deposits were of much later date, thus removing the problem. There is, however, now a strong suspicion that the Mull deposits were much earlier than Eocene, a view recently strengthened by the identification there of *Aquilapollenites* by Martin (1968); this unusual pollen genus is principally of Late Cretaceous age with only a few species in the Palaeocene. Barghoorn (1951), in interpreting American Tertiary floras, postulated a climatic maximum for the Eocene with more temperate representation in approximately the same areas in the Maestrichtian and Palaeocene, which would have fitted the Mull flora. The positive evidence for this was never strong because it was at (or beyond) the limit of palaeoecologic extrapolation from the present day.



TEXT-FIG. 4. Cretaceous map with distribution of Normapolles and of *Aquilapollenites* (Late Cretaceous). Information from Tschudy (1970) and earlier sources.



TEXT-FIG. 5. Eocene map, with the data of Edwards (1936) replotted.

If as now seems more likely the climatic maximum was in the Maestrichtian (before the failure of Chalk coccolith production), the temperature nature of this early Mull flora must be attributed to its close proximity to the rapidly opening North Atlantic Ocean, rather than to palaeolatitude.

MALAYSIAN AFFINITY OF LONDON CLAY FLORA

Edwards (1936) plotted the occurrence along Tethys of Eocene floras with some resemblances to that of the London Clay. It was generally believed that this flora migrated eastward during the Tertiary and became established in Recent Malaysia. Recent palynologic work however in North Borneo (Muller 1968) has confirmed the presence of a similar flora there in the Eocene.

Migration of a complete flora, especially in longitude, has always seemed highly improbable. It appears to be much more likely that the Eocene tropical floras were established fairly uniformly along Tethys from Britain to Borneo (text-fig. 5), and that subsequently general cooling of climate through the Tertiary towards the Pleistocene has confined these floras to the southern part of the continent of Eurasia.

GENERAL CONCLUSION

It will now be possible to establish directly which extinct Mesozoic plants belonged to tropical, subtropical, temperate, or polar climatic belts. Coming at a time when palaeobotany has been strongly reinforced by palynology, the subject is now relieved of the burden of trying unsuccessfully to interpret these floras from the ecologic details relating to their extant but largely irrelevant (to this problem) successors.

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