

# THE DISTRIBUTION OF LATE PALAEOZOIC FLORAS

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**ABSTRACT.** This paper deals with aspects of the distribution of terrestrial plants and palaeocontinents in the Late Palaeozoic. The quality of the palaeobotanical data is considered in relation to choice of time intervals, choice of taxonomic and floristic units, and subjectivity of the fossil record. The Early Carboniferous and a loosely defined Late Carboniferous/Early Permian are chosen as the most convenient time intervals for the presentation of data, while the genus is taken as the most appropriate taxon for this treatment. The world distribution of palaeofloristic units, defined in terms of selected genera, is then given for these two phases of the Late Palaeozoic period. The distribution patterns are considered in terms of offered reconstructions of continental positions and climate.

THIS paper aims to examine the significance of certain aspects of Late Palaeozoic land plant distribution in the context of palaeocontinent and pole positions which have been postulated mainly on geophysical evidence. Ideally, the fossil plant distribution data should be presented as objectively as possible, but there are many innate shortcomings in the available records, and in the possible ways in which they may be plotted. These are briefly considered below, and the plant distribution data are then presented for two phases of the Palaeozoic period, the Early Carboniferous, and a loosely defined 'Late Carboniferous/Early Permian' interval. These distribution patterns are then considered in relation to the offered continental reconstructions and to the possible related causal factors.

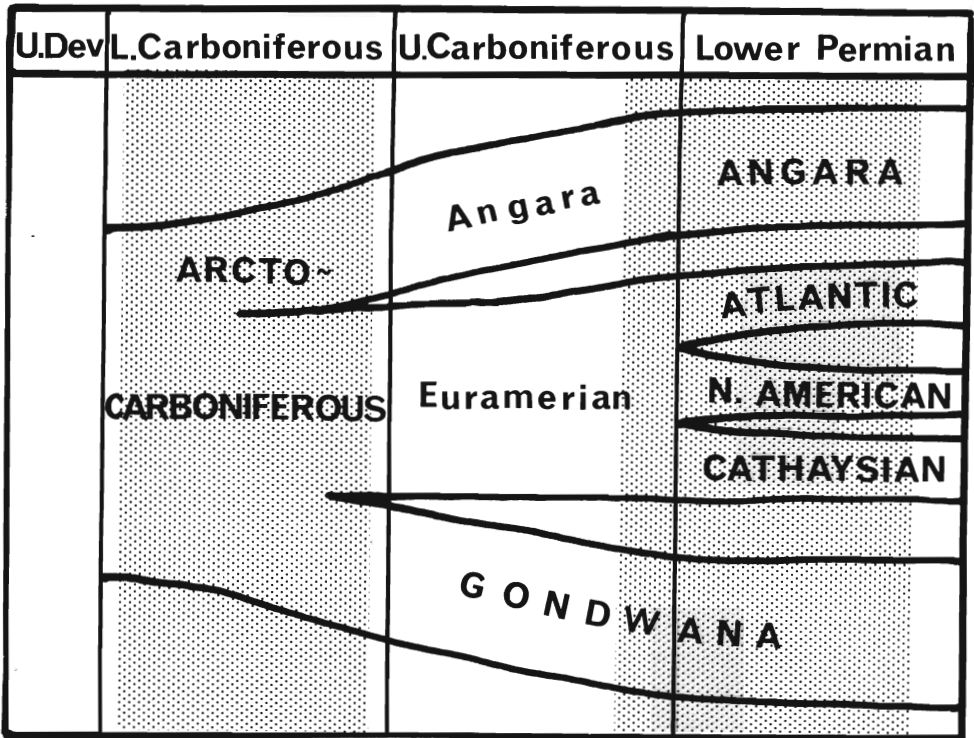
## QUALITY OF THE FOSSIL DATA

### *Choice of time units*

Any attempt to plot the distribution of a group of fossils on a palaeogeographic reconstruction presents a dilemma. The more precisely defined the time interval, the fewer the fossil occurrences which may acceptably be plotted, but the more significant the comparison between more or less synchronous sites. If the time interval is extended (or less reliably dated occurrences are included) the more data can be shown, but the weaker its collective significance. We have attempted a compromise in offering maps and other data based on two time intervals. The first is Early Carboniferous–Tournaisian, Viséan, and the Namurian A and B. The second is a broadly interpreted 'Late Carboniferous/Early Permian' interval—approximately equivalent to 'Upper Carboniferous', Asselian, and Sakmarian of Harland *et al.* (1967). These two intervals have been chosen partly because on the basis of previously published data (see, for example, Jongmans 1952, 1954a; Vakhrameev *et al.* 1970; Meyen 1972) the very cosmopolitan character of Devonian and Early Carboniferous floras gives way to pronouncedly regional floras by the Carboniferous/Permian transition. This general feature of world floras is portrayed in terms of subjectively defined phylogeographic

hierarchical units in a diagram based on the work of Meyen (text-fig. 1). The two intervals for which data are plotted here are indicated by the shading on this diagram.

Probably the greatest single weakness of the information presented here is the level of uncertainty in the age assignment of most of the floras dealt with. In general, the conditions under which land plant macrofossils come to be preserved are such that they occur in sections in which marine fossils are scarce or absent. This problem is most acute for the majority of Gondwana fossil plant records. Some indication of the order of uncertainty involved is illustrated by the different interpretations placed on the so-called '*Rhacopteris* flora' of the several Gondwana subcontinents. The Australian records of *Rhacopteris* were, until recent time, regarded as Lower Carboniferous in age, on the basis of the occurrence of that genus in Europe and North



TEXT-FIG. 1. A diagrammatic representation of the progressive differentiation of the major floristic provinces (phytochoria) from the Devonian to the Early Permian, greatly simplified from Meyen 1969a. The distance between units in the vertical dimension is a subjective measure of their biotic distance in terms of constituent taxa. Only the two higher levels of Meyen's hierarchy of floristic units are shown here—'kingdoms' (in capital letters) and 'areas' (in lower-case letters). Meyen's Arctocarboniferous kingdom approximates to the '*Lepidodendropsis* flora' of the present authors; however, the time at which the Gondwana flora becomes distinct from the floras of the northern continents is here shown somewhat later than was suggested by Meyen. The northern floras differentiate through the Late Carboniferous, constituting an Angara area and a Euramerian area, while the Gondwana flora is by then recognized as a distinct kingdom. By the end of the Early Permian the differentiation of the world floras constitutes five distinct kingdoms.

America (Jongmans 1952, Read and Mamay 1964, Rigby 1969). However, Campbell *et al.* (1969), in a revision of the biostratigraphy of the Australian Carboniferous and Permian, now regard the *Rhacopteris* of that subcontinent as having a Westphalian to Stephanian range, although the full palaeontological basis for this conclusion has not yet been published (but see, for example, Evans 1969). This and many other (usually less drastic) age reassignments have encouraged us to take rather broad time intervals for our two plots of plant distribution; and, in general, we have accepted the age assignment given to a flora by the author describing it.

### *Choice of floristic and taxonomic units*

Most attempts at Upper Palaeozoic palaeogeography have involved trying to recognize floristic provinces (generally tacitly assumed to more or less correspond to the major 'phytochoria' or floristic units which may be recognized in the extant flora). These palaeofloristic units have generally been defined very subjectively, either being regarded as characterized by a single genus (e.g. '*Glossopteris* flora' of many authors), by a group of characteristic genera (e.g. '*Lepidodendropsis-Rhacopteris-Triphyllopteris* flora' of Jongmans 1952), or by designation of a region within which the flora is uniquely, or at least typically, developed (e.g. 'Euramerian flora').

For any attempt at analysing the significance of the distribution of fossil floras spatially, a prime consideration is that the taxa we are dealing with represent monophyletic groups. The occurrence of a fossil plant taxon on the fragments of a once continuous land mass constitutes a disjunct distribution, only if all its members can be regarded as having had a single centre of origin. In palaeobotanical work, the most appropriate level of taxon from this point of view is undoubtedly the genus. A genus of fossil plants, where its definition is based on a number of distinctive features, probably represents collectively the derivatives of a single breeding population. Families are in general less securely defined, at least in the case of compression fossils which make up a large part of the available records; and differences of opinion between authors as to their limits suggest that, in general, they are even more subjective in character than genera, and hence perhaps more likely to be polyphyletic. Species based on compression fossils are, on the other hand, more clearly defined, but are generally more limited in their spatial distribution, and to attempt to consider their occurrence in both time and space would have increased the scope of the present work beyond reasonable bounds.

This treatment is confined only to plant compression and impression fossils; two important categories of fossils, petrifications and spores, are not dealt with. The petrifications, although important and informative botanically, are of too sporadic occurrence to make a consistent contribution to the palaeogeographic picture. Further, there is of course a partial overlap of many genera based on petrifications with those based on compression fossils, and the presence and absence of those genera based solely on petrifications is clearly governed largely by the occurrence of conditions favouring their preservation, rather than their actual distribution as living organisms. The spore data are fast rivalling the macrofossil data in terms of the number and distribution of localities, but many problems are involved in the palaeogeography of spores. On presently available data there is a marked discrepancy

between the palynological palaeogeographic provinces in the Lower Carboniferous and those of the macrofossils (compare for example Jongmans 1952 and Sullivan 1967). A similar observation might be made for the Permian. It may be that the fossil spore record is reflecting features of the parent floras which are lost in the possibly more facies-controlled macrofossil record. But the generic concept in palynology is certainly in a state of greater instability than is the case with macrofossils. This, and the complexity of factors affecting long-distance spore transport, complicate any attempt to reconcile macrofossil and palynological records on a world-wide basis, and this is not attempted here.

### *Subjectivity of the record*

The records of genera used here in plotting floristic provinces inevitably include a considerable subjective element. It is the nature of palaeontology that as knowledge of material increases, particularly if from a wide range of localities, concepts of generic limits change. This makes any attempt to collate records from all over the world, involving data published over a considerable number of years, particularly vulnerable. Almost all the records accepted here for the genera *Lepidodendropsis* (Lower Carboniferous) and *Lycopodiopsis* (Permian of Gondwanaland) would have been reported as '*Lepidodendron*' fifty years ago. A striking example of the order of revision that may occur can be seen in Rigby (1969). While much of the data used here has been accepted uncritically from primary or secondary sources, we have in a few instances taken quite subjective decisions as to the acceptability of identification, where the necessary information to make such a decision was available.

It is perhaps appropriate to contrast the quality of Palaeozoic fossil plant records with those of extant genera of plants for which analysis of distribution has been attempted on a world-wide basis (e.g. the Coniferales, Sneath 1967). The generic concept in the conifers, and the definitions of genera have undergone relatively little change over the last fifty years, with the exception of some 'splitting' within the Cupressaceae and Taxodiaceae for example. The simple recording of presence or absence which may be involved in compiling data of this type has very different significance for the living conifers than for even the commonest Palaeozoic plant genera. Obviously, many different types of factors may be involved in an 'absence' record in the case of fossils. In a treatment of the type attempted by Sneath (1967) the 'absence' of the Southern Hemisphere genus *Podocarpus* from the present flora of north-west Europe is as reliable a statistic as the 'presence' of the genus *Pinus* in the same area. But the same level of certainty patently does not apply for most fossil plant records. The apparent absence of a genus of fossil plants from a particular area could result from at least four different circumstances: (1), that the genus never existed there; or (2), that it lived in the area, but never became preserved there as a fossil; or (3), that although it was at one time represented there by fossil material, this is either no longer accessible at surface exposure, or it has been totally removed by subsequent geological events; or (4), that the genus is represented by fossil material accessible at outcrop, but that this has never been found. The likelihood of any one of these four being the reason for absence in a particular instance will of course vary

from one area to another. The more thoroughly the area has been explored geologically, the greater the certainty with which we can attribute 'absence' to any given situation. But the palaeogeographical significance of the apparent absence in these several different circumstances depends on which of the four causes applies. For example, the lack of any acceptable record of *Glossopteris* in the Permian of north-west Europe is probably a statistically more significant observation than its absence to date on the African continent north of the equator. But it is difficult to specify the level of significance in any quantitative way.

In attempting to recognize palaeofloristic provinces we encounter a further intractable problem connected with the mental processes of the palaeobotanists involved, which may be called 'psychopalaeobotany'. This arises from the subjective nature of the limits of many fossil plant genera, which is met in its most acute form when the distribution of fossil plants is being considered. Inevitably, palaeobotanists are influenced by the knowledge of the known spatial limits of taxa in assigning any fossil material. That is to say, they are already using what is known of the past distribution of, say, a genus, before attributing a given specimen to it; so that there is some tendency for new records to conform to (and so seemingly confirm) the previously established pattern of distribution. Prior to Edwards's (1952) valuable revision of the Carbo-Permian lycopods of Gondwanaland, there were many records in the literature of Gondwana *Lepidodendron* species. Edwards, after examining many of these, assigned most of them to the genus *Lycopodiopsis sensu lato*, making the general observation that there are indeed no acceptable records of the genus *Lepidodendron* in Gondwanaland. Since this time, there has been a general tendency to attribute Carbo-Permian Gondwana lycopods to *Lycopodiopsis* (and other 'Gondwana genera') rather than to the 'northern genus' *Lepidodendron*, even possibly when the morphology alone did not offer an adequate basis for such attribution. Perhaps all palaeobotanists attempting to determine a group of fossil plants are to some extent influenced by preconceived ideas related to its geographic origin, as indeed are botanists dealing with living plants, in somewhat milder degree. It can only be remarked that once a hypothetical framework of palaeofloristic provinces is set up, this may marginally influence the attribution of fossil specimens, especially of fragmentary or poorly preserved material, and that this is a possible source of error in our interpretations of past plant distributions which is especially hard to eliminate.

In the treatment of plant distributions of the two Upper Palaeozoic time intervals given below, we initially considered the possibility of plotting the recorded distribution of a number of individual genera. In view of the numbers involved, this was abandoned, and we have resorted to plotting the distribution of palaeofloristic units which are defined in terms of 'characteristic genera', not all of which are present at every plotted locality for the association, but of which a significant proportion occur in any one instance.

## LATE PALAEOZOIC FLORAS

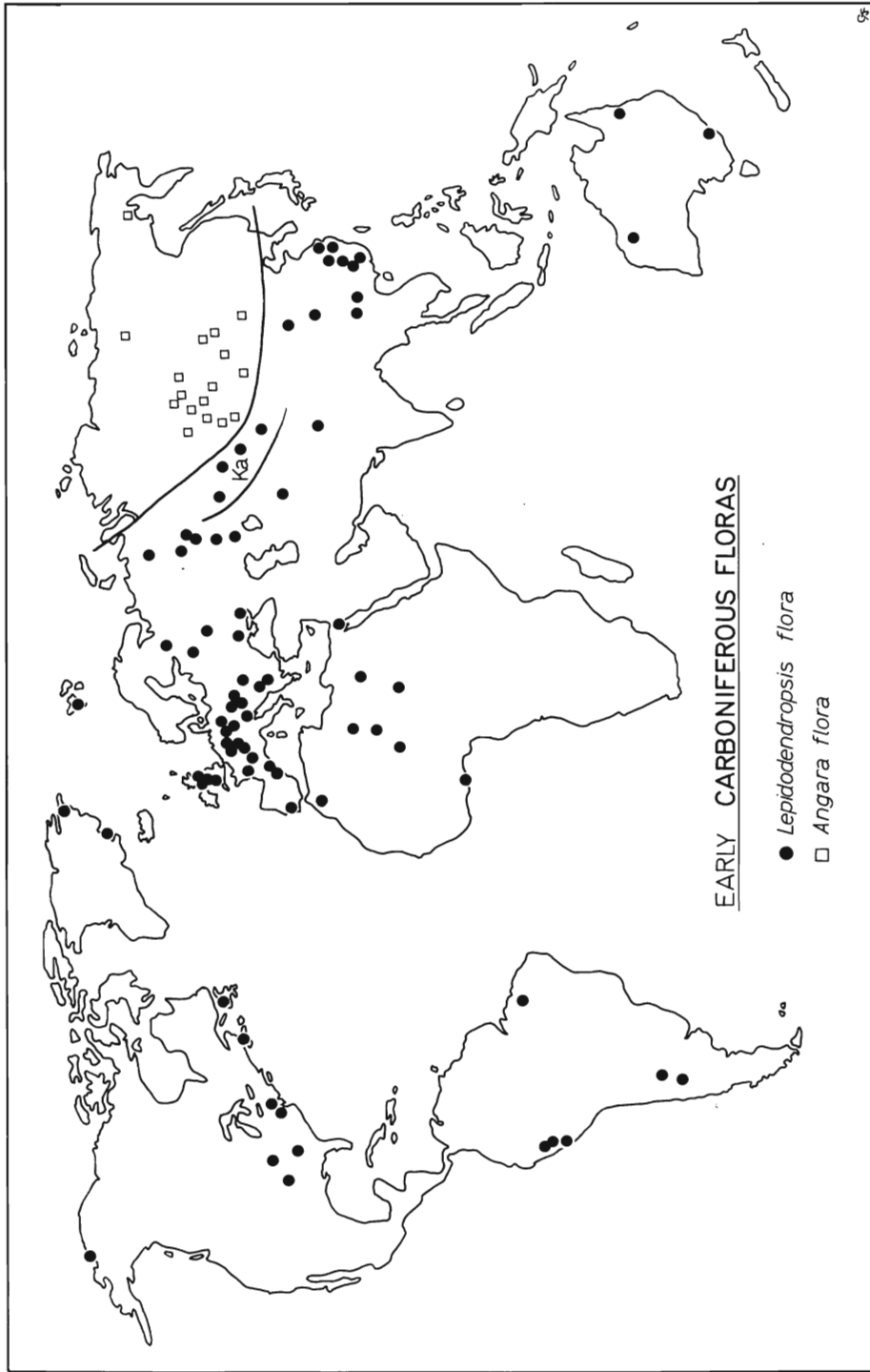
*Early Carboniferous floras* (text-figs. 2 and 3)

Jongmans (1952 et seq.) is particularly associated with the thesis that during the Early Carboniferous there was a cosmopolitan flora of world-wide extent (his '*Lepidodendropsis* flora' or '*Lepidodendropsis-Rhacopteris-Triphyllopteris* flora'). This concept has been challenged most seriously by Russian workers, who recognize a distinct Early Carboniferous Angara province (text-fig. 1) covering much of Siberia, and antecedent to the widely recognized Permian floristic unit covering much the same area (see Meyen 1969a, Vakhrameev *et al.* 1970, Chaloner and Meyen, in press). Meyen further suggests that the clear differentiation of a Gondwana floral province, so evident in the Permian, may be discerned by Early Carboniferous time (see text-fig. 1, based on Meyen 1969a). The difficulty of recognizing the time at which a distinctive Gondwana province may be recognized is aggravated by the difficulty of dating Gondwana fossil floras within the Late Devonian to Late Carboniferous interval. For this reason we follow Jongmans in recognizing a single Early Carboniferous floristic province outside Angaraland, but it is clear that all the Gondwana Early Carboniferous records warrant re-examination, particularly in terms of the extent to which their age can be assessed on grounds other than their floristic composition.

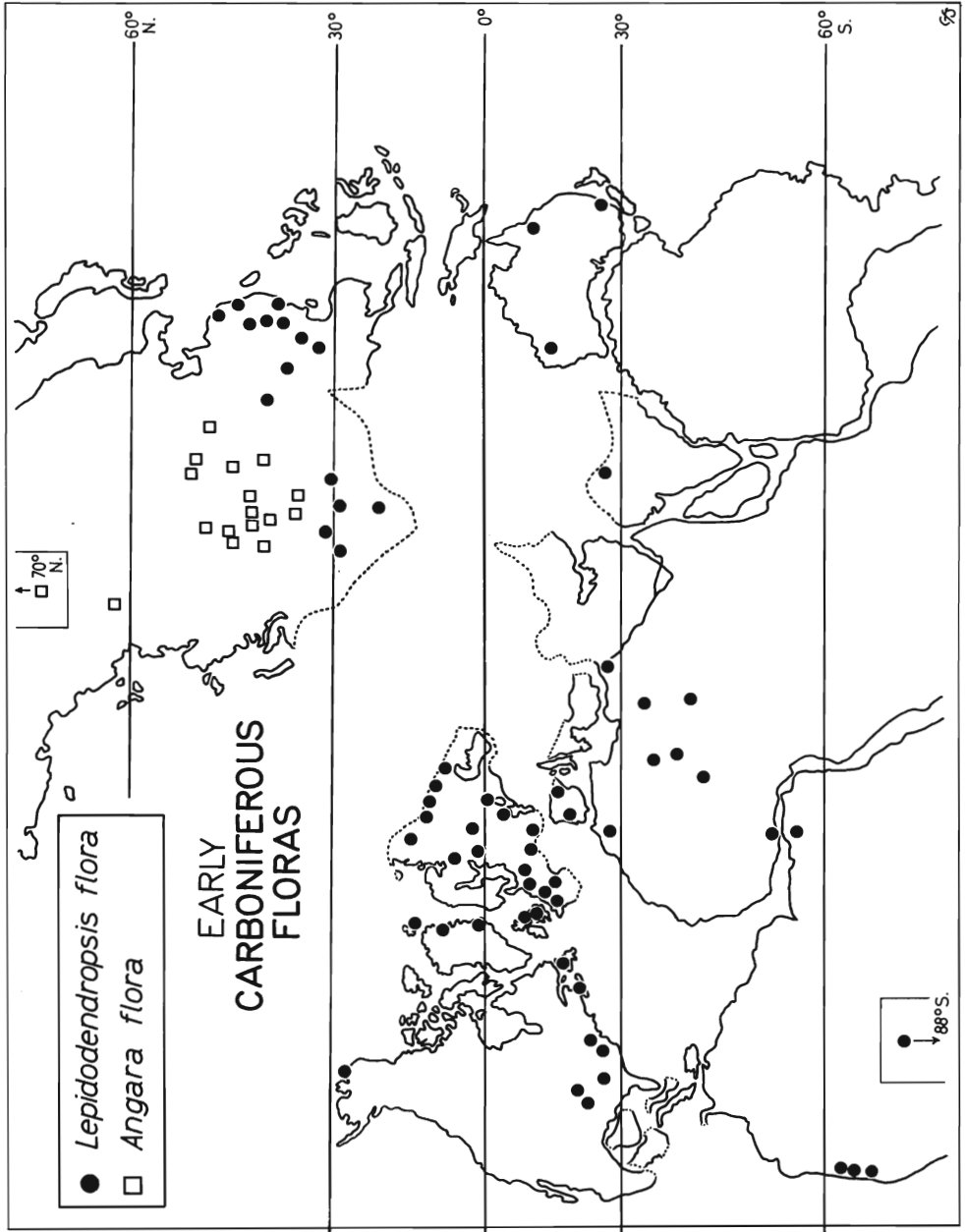
The cosmopolitan Early Carboniferous flora ('*Lepidodendropsis* flora' of text-figs. 2 and 3) is based on occurrences of floras with a predominant representation of the following genera: *Lepidodendropsis*, *Sublepidodendron*, *Stigmaria*\*, *Lepidodendron*\*, *Archaeosigillaria*\*, *Archaeocalamites*, *Sphenophyllum*\*, *Sphenopteris*\*, *Rhodeopteridium* (*Rhodea* of earlier authors), *Fryopsis* (*Cardiopteris* of earlier authors), *Cardiopteridium*, *Anisopteris* or *Rhacopteris*\*, *Adiantites*, and *Triphyllopteris* (genera marked \* also occur outside the Early Carboniferous time interval).

The representation of this flora in any area depends, among other factors, on the intensity of geological or palaeobotanical exploration mentioned earlier. For example, all the genera just cited occur within the Early Carboniferous of north-west Europe, while a record of only two (*Lepidodendropsis* and *Archaeosigillaria*) is regarded as a basis for plotting an occurrence of the flora in West Africa (text-fig. 2). The rather isolated extension of the flora into Alaska is based on only three genera (*Lepidodendropsis*, *Fryopsis*, and *Adiantites*; see Mamay, quoted in Chaloner and Meyen, in press). Localities where this flora occurs have been plotted as '*Lepidodendropsis* flora' on the present-day world map as text-fig. 2, and on the pre-drift continents as postulated by Smith, Briden, and Drewry (this volume), as text-fig. 3. Because of the loss of high palaeolatitudes on the latter projection, occurrences of this flora on Gondwanaland are also shown on the reassembly of that continent given in text-fig. 6.

The Angara flora of the Early Carboniferous interval is characterized by the presence of *Lepidodendropsis*, *Sublepidodendron*, *Lophiodendron*, *Archaeocalamites*, *Chaccasopteris*, and *Angaropteridium* (see Chaloner and Meyen, in press, and references there cited). Of these six genera, it is noteworthy that three occur widely outside the Angara area. It may be noted that Vakhrameev *et al.* (1970) recognize a region between the typical Angara (Early Carboniferous) unit and the European



TEXT-FIG. 2. Early Carboniferous floras plotted on the present continent positions (the zenithal projection is based on that used in Chaloner and Meyen, in press). The ubiquitous *Lepidodendropsis* flora occurs on all continents except Antarctica, while the Angara flora may be recognized as a distinct floristic area in Siberia (see text-fig. 1); in the Kazakhstan province (Ka) there are elements of Angara type in floras otherwise similar to those of the Euramerican area. (Principal sources in plotting this map were Archangelsky 1965; Chaloner and Meyen, in press; Høeg *et al.* 1957; Jongmans 1954a; Mensah and Chaloner 1971; Rigby 1969; Vakhrameev *et al.* 1970; and further sources there cited.)



TEXT-FIG. 3. Early Carboniferous floras plotted on the pre-drift continent positions suggested by Smith, Briden, and Drewry (this volume). Occurrences off the top and bottom margins of the map are shown in boxes, together with the approximate palaeolatitude. Sources of this data are those indicated in the legend for text-fig. 2.



occurrences of the *Lepidodendropsis* flora, as a Kazakhstan area, having floristic affinity with both the Angara and *Lepidodendropsis* floras (shown as 'Ka' on text-fig. 2).

#### *Early Carboniferous continent positions*

If one accepts the *Lepidodendropsis* flora as a single floristic unit (and not, as it may be, a result of the lack of precision in our taxa) it would appear that the degree of floristic differentiation on a world basis is much less pronounced in the Early Carboniferous than at the close of that period. But the underlying palaeogeographical significance of this is problematical. The floristic picture seems to show little relationship to either palaeolatitude or to the continuity of land masses as a factor controlling plant migration. The *Lepidodendropsis* flora ranges over palaeolatitudes of 30° N. in Alaska, and over 45° N. in China to approximately 50° S. in West Africa, and the even more southerly Argentine floras (see text-fig. 6). The Early Carboniferous Angara flora which reaches into high palaeolatitudes (70° N. in Siberia) spans the same palaeolatitudes in its southerly extension as the Chinese occurrences of the *Lepidodendropsis* flora. The separation of these two floras on the eastern side of Eurasia at much the same latitude seems most likely to be related to a barrier in the form of an epicontinental sea during the Tournaisian and Visean (see figs. 1 and 2 in Vakhrameev *et al.* 1970). The 'outliers' of *Lepidodendropsis* flora on the Siberian plate, in central Asia, south (in palaeolatitude) of the Angara area occur in puzzling disjunction from the Ural and west European occurrences, as shown on the symposium pre-drift continents (text-fig. 3). The most southerly occurrence of this outlier, in the Hissar Range, includes a number of species in common with the European Early Carboniferous flora (such as *Archaeocalamites radiatus*, *Lepidodendron veltheimii*, and *Lepidodendron spetzbergensis* as well as *Lepidodendropsis*; Vakhrameev *et al.* 1970). The longitudinal gap between the Siberian plate and that of Europe of the symposium reconstruction gains no support from the fossil plant data, which could be more easily reconciled with their juxtapositions as represented in the Permian map (our text-fig. 5).

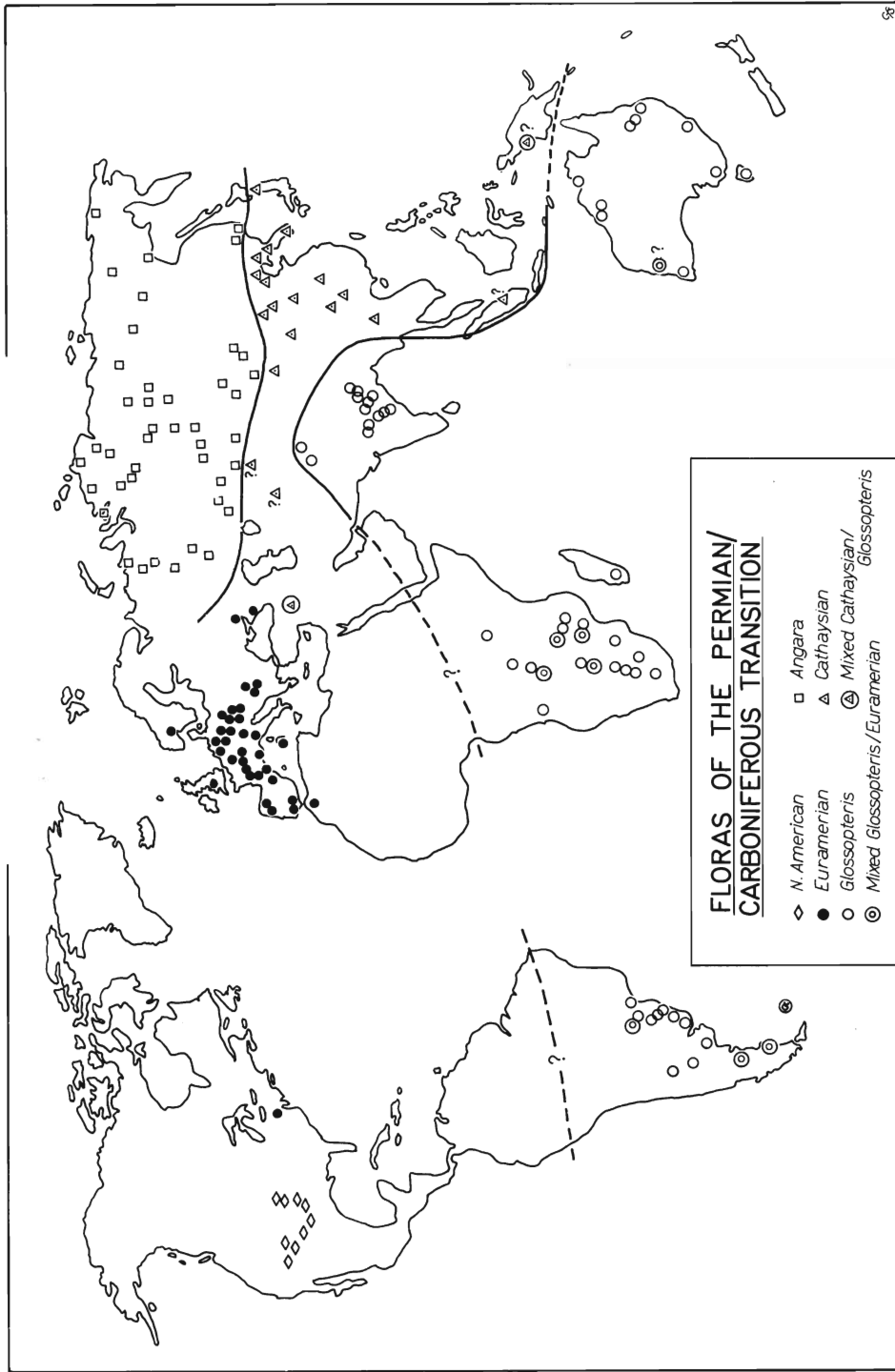
#### *Late Carboniferous/Early Permian floras* (text-figs. 4 and 5)

This interval is characterized by a regional differentiation of world floras which show a degree of divergence unrivalled in any other period of geological time, with the possible exception of the Late Tertiary and Recent. Four principal provinces may be delimited: the Euramerian, Angara, *Glossopteris* (or Gondwana), and Cathaysian floras (abbreviated as EU, AN, GL, and CA in Table 1); a further North American province (NA in Table 1) may be recognized, although it has been treated by some authors as being part of the Cathaysian province. This palaeofloristic differentiation of Late Palaeozoic floras has been recognized (although with changing concepts as to the limits of the units) for over forty years (Seward 1933; Jongmans 1952, 1954a; Gothan and Weyland 1964; Wagner 1962; Havlena 1962; and Chaloner and Meyen, in press). The general features of these floras and their composition have been dealt with by these authors. The principal genera forming the basis for the subjective

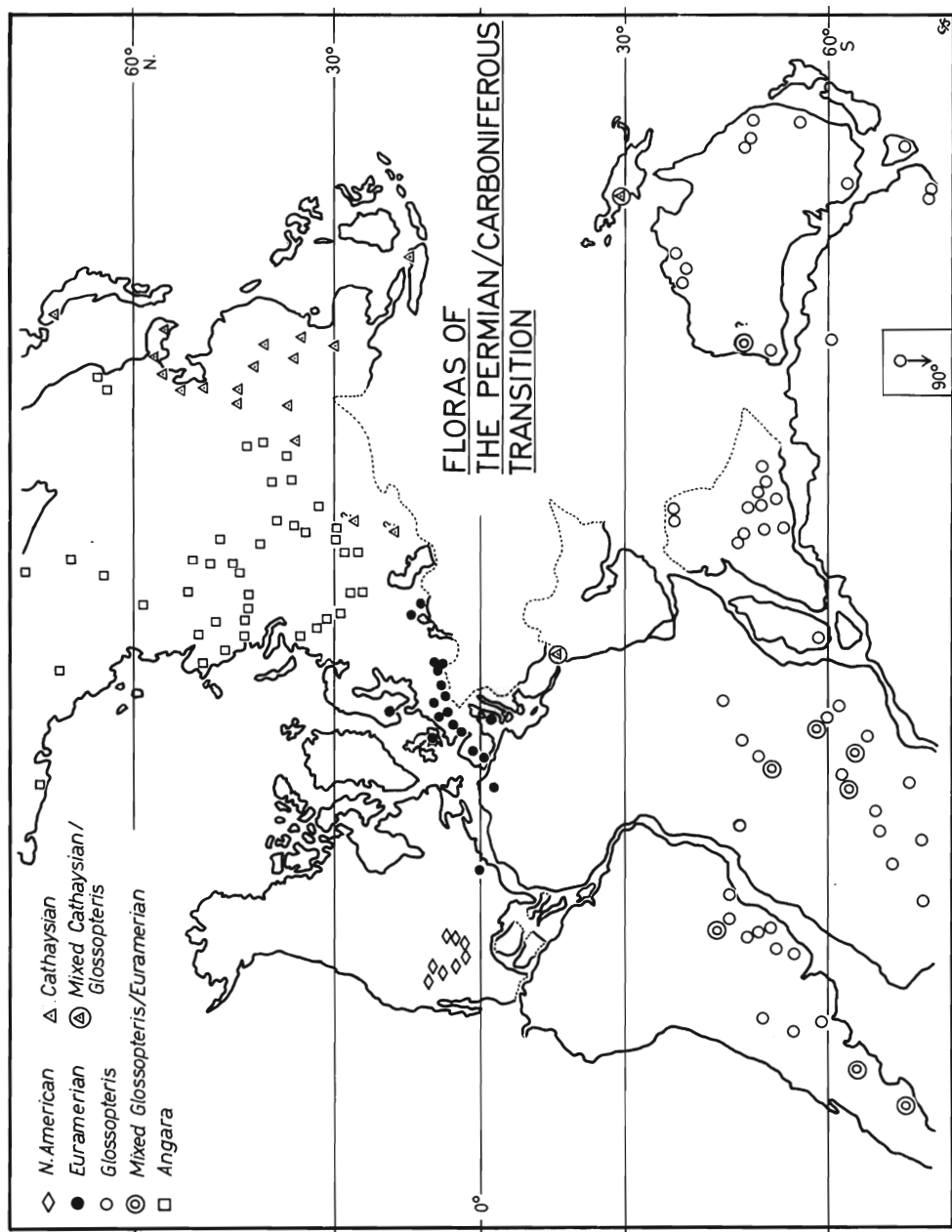
demarcation of these provinces are summarized in Table 1. The localities for which plant records are available are shown, allocated to their appropriate province, in text-fig. 4 on the present continent positions, and in text-fig. 5 on the symposium pre-drift reconstruction. Localities on a reassembled Gondwanaland are shown in text-fig. 6.

TABLE 1. Genera which may be regarded on a subjective basis as characterizing each of the five palaeofloristic provinces shown in text-figs. 4 and 5. This list shows the general aspect of the several floras in an expedient way, and no critical taxonomic judgement is intended in the lumping of certain genera for the purpose of this list (e.g. *Neuropteris/Odontopteris*; *Lycopodiopsis/Cyclodendron*) nor in the segregation of others (e.g. *Cordaites* and *Noeggerathiopsis*). The genera shown for each province either occur in a high proportion of the localities or are locally abundant; but certain of these characteristic genera have also been reported in isolated instances outside the areas for which they are listed; for example, the records of *Sphenophyllum*, *Annularia*, and *Pecopteris* in the 'mixed' floras in Gondwanaland (see p. 284). *EU* = Euramerian; *NA* = North American; *AN* = Angara; *CA* = Cathaysian; *GL* = *Glossopteris* (Gondwana).

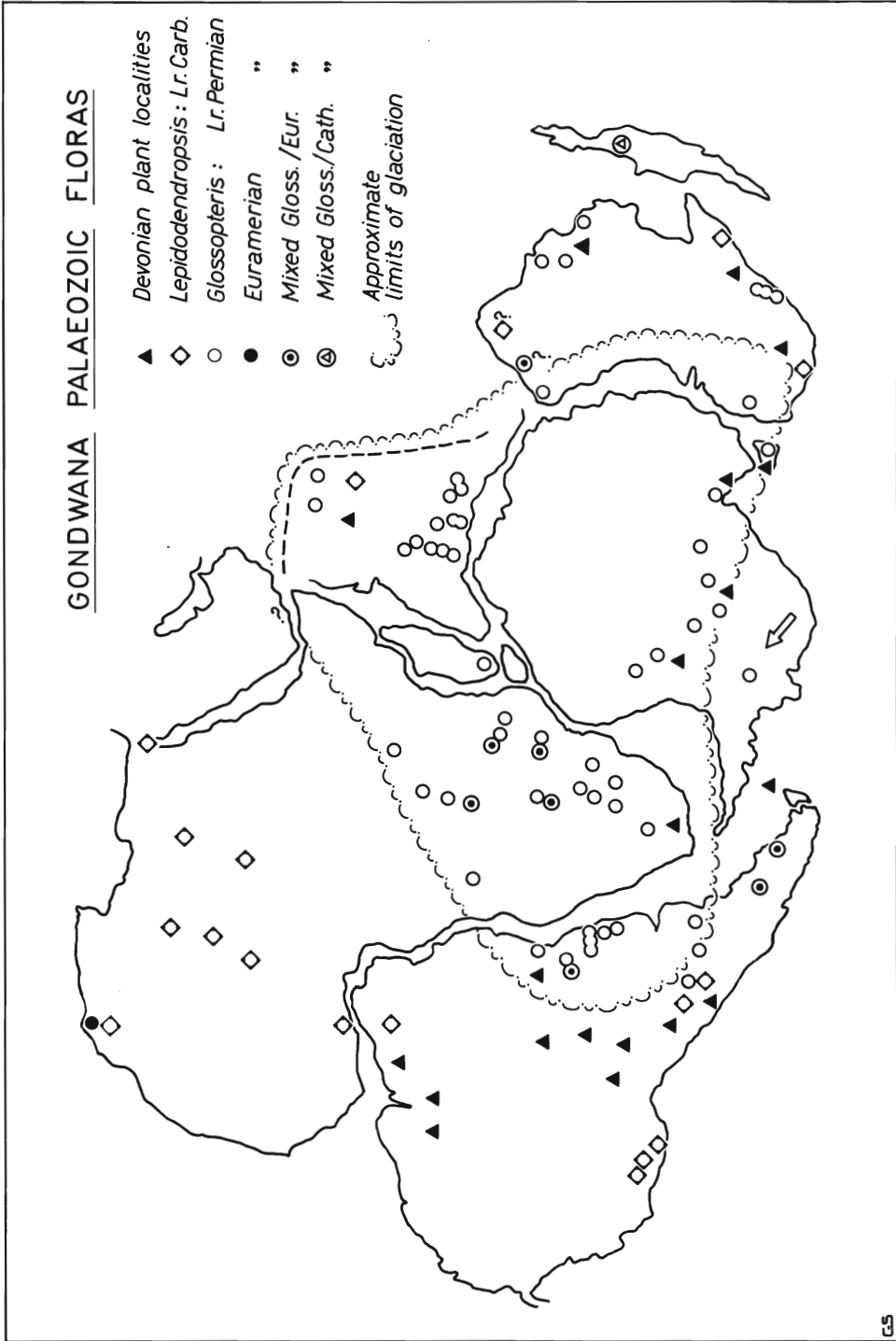
	<i>EU</i>	<i>AN</i>	<i>NA</i>	<i>CA</i>	<i>GL</i>
1. Alethopteris	×				
2. Calamites	×				
3. Sigillaria	×				
4. Cordaites	×	×		×	
5. Pecopteris	×	×		×	
6. Callipteris	×	×	×		
7. Neuropteris/Odontopteris	×	×			
8. Sphenophyllum	×	×	×	×	
9. Annularia	×	×			
10. Walchia	×	×	×		
11. Taeniopteris	×		×	×	
12. Intia		×			
13. Tschernovia		×			
14. Annulina		×			
15. Viatcheslavia		×			
16. Angaridium		×			
17. Paragondwanidium		×			
18. Ruffloria		×			
19. Vojnovskya		×			
20. Supaia			×		
21. Glenopteris			×		
22. Russellites			×		
23. Gigantopteris			×	×	
24. Protoblechnum			×	×	
25. Tingia				×	
26. Lobatannularia				×	
27. Gondwanidium					×
28. Noeggerathiopsis					×
29. Gangamopteris					×
30. Glossopteris					×
31. Trizygia					×
32. Lycopodiopsis/Cyclodendron					×
33. Schizoneura					×



TEXT-FIG. 4. Latest Carboniferous/Early Permian floras plotted on the present continent positions (the zenithal projection is based on that used in Chaloner and Meyen, in press). Occurrences of floras assigned to five major phytogeographic units ('kingdom', cf. legend to text-fig. 1) are shown here. Only major sites or centres of close groups of localities are shown for the European area. Boundaries between the several floristic provinces are shown as a continuous line where fairly clearly defined, and a broken line where arbitrary or highly speculative. Although only a single occurrence of the Euramerican flora (of the Dunkard group in the Appalachian basin) is shown in North America, similar Early Permian floras with *Calopteris* occur within the eastern part of the area later occupied by the 'North American flora' shown here. The two occurrences of the Cathaysian flora to the east of the Caspian Sea, marked with queries, are problematical both floristically and in terms of age. (Principal sources in plotting this map were Archangelsky 1965; Chaloner and Meyen, in press; de Jersey 1968; Du Toit 1954; Ghosh and Sasry 1967; Høeg and Bose 1960; Kon no 1966; Lacey and Huard Moine 1966; Lacey and Kulkarni 1969; Lacey and Smith 1972; Plumstead 1963, 1967a, b; Rigby 1966, 1972; Surange 1965; Vakhrameev *et al.* 1970; Wagner 1962; and references there cited).



TEXT-FIG. 5. Latest Carboniferous/Early Permian floras plotted on the pre-drift positions of continents suggested by Smith, Briden, and Drewry (this volume) for the Permian. On this reconstruction of continent positions, the North American flora and the Euramerican flora both fall within 20° of the palaeo-equator, while the Angara flora and the Cathaysian flora (in Siberia and Japan, for example, extend beyond 70° north palaeolatitude. Localities for the *Glossopteris* flora extend from approximately 40° south palaeolatitude to a position close to the approximate Permian pole position. Sources of data are as referenced for text-fig. 4.



TEXT-FIG. 6. Gondwanaland, reconstructed on the model proposed by Smith and Hallam (1970) with the South pole based on the Permian continent positions suggested by Smith, Briden, and Drewry (this volume). Principal localities for Devonian, Early Carboniferous, and Late Carboniferous/Early Permian (*Glossopteris*, Euramerian, and 'mixed' floras) are shown. The maximum extent of the Carbo-Permian glaciation approximately coincides with the subsequent spread of the *Glossopteris* flora. While a number of Devonian plant localities occur within the (subsequent) extent of the *Glossopteris* flora, the Early Carboniferous localities are either outside (or only just within the peripheral zone of) the area of the *Glossopteris* occurrences; this is discussed further in the text.

*Late Carboniferous/Early Permian continent positions*

The floristic provinces of this time interval show a number of features which are of immediate relevance to continental drift and to contemporaneous pole positions. The disjunction of the Late Carboniferous/Early Permian Euramerian flora, caused by the opening of the North Atlantic (text-fig. 4), has long been noted. The close similarity of the much more extensive Westphalian floras of the coalfields of the eastern half of the U.S.A. and those of Europe, which are not dealt with here, represent one of the best documented pieces of evidence of this disjunction. The even more striking separation of the fragments of the Gondwana (*Glossopteris*) flora is probably the most impressive of all the palaeontological consequences of the break-up of Gondwanaland; it was of course cited by Du Toit (1937) as supporting evidence for the drift hypothesis, before most geologists were prepared to accept that mechanism to account for it. The consequential juxtaposition of the *Glossopteris*, Cathaysian, and Angara floras produced by the northward movement of India against the Asian plate has been noted by many authors (e.g. Halle 1937; for more recent treatment, see Kon'no 1966 and Meyen 1969*b*).

Several critical areas of contact between the major floristic provinces (or the occurrence of floras of 'mixed composition') need special comment. On the Gondwana continent, there are no less than seven occurrences of so-called northern genera (i.e. genera which occur abundantly also in the Euramerian area), associated with otherwise typical *Glossopteris* floras (see, for example, Archangelsky and Arrondo 1969, Lacey and Smith 1972, and references there cited). *Sphenophyllum*, *Annularia*, and *Pecopteris* are genera which are commonly cited as being otherwise characteristic of northern floras. If it is accepted that these three genera, occurring mainly in South America and South Africa, are indeed congeneric with their northern counterparts, and are not, as some authors have suggested, the result of homoplasy, then the question is raised to what extent these northern elements in the 'mixed' floras should be seen as migrants from the Euramerian land mass, and hence indicators of migration routes (see, for example, Just 1952). Meyen (1972) appears to allow the presence of a 'few Euramerian-Cathaysiatic plants (ferns and sphenophylls)' as having penetrated from time to time as infrequent migrants into the Gondwana (*Glossopteris*) flora of South America and South Africa. The geographical gap, even pre-drift, between typical northern Late Carboniferous/Early Permian floras and these localities for 'mixed' floras is very considerable (text-figs. 4 and 5). However, it may not be necessary to invoke very long-distance migrations. All three genera are sufficiently broadly defined that their Gondwana representatives may have been directly derived from Early Carboniferous antecedents in the Southern Hemisphere rather than as Late Carboniferous/Early Permian migrants from the far north. Early Carboniferous floras are available in both South America and South Africa, peripheral to the area later occupied by the *Glossopteris* flora (text-fig. 6).

It must in any case be acknowledged that these three 'mixed' genera include homosporous species for which the necessary propagules (spores) could be readily carried across oceans by wind currents. In this attribute they differ, of course, from the several gymnospermous members of these floras (including among others *Taeniopteris*, *Cordaites*, *Callipteris*, *Walchia*, and, apparently, *Glossopteris*) which

would have required the movement of much less readily transportable seeds in order to effect migration. All spore-bearing fossil plants could have migrated over such vast distances that their occurrence offers a very poor basis for postulating land migration routes. Even where in living plants we know something of their reproductive biology, the reconstruction of a history of migration must be very speculative; with all fossil plants, whether reproduced by spores or seeds, deductions based on their supposed mobility are highly insecure. In the context of past geological time, the sporadic occurrence of individual land plant genera can rarely be cited as convincing evidence of contact or even juxtaposition between land masses.

There may be some significance in the fact that all the Gondwana localities for Early Permian 'mixed' Euramerian/*Glossopteris* floras occur in eastern South America and South Africa, near to or not far *within* the limits of glaciation (with one doubtful record from Western Australia and none at all in India and Antarctica) and also not very far from localities for potential source material of Early Carboniferous (*Lepidodendropsis* flora) age, lying in a peripheral position generally *outside* the limits of glaciation in South America and South Africa. This distribution seems to bear so little relation to proximity to the Early Permian Euramerian or other northern floras that other factors must be invoked; but the disposition of these 'mixed' floras with respect to the Permian pole position makes a simple latitudinal (climatic) control seem equally implausible. We discuss this problem further in our concluding summary section on floras, continents, and climate.

An entirely different problem is presented by the two mixed Gondwana/Cathaysian floras occurring in Hazro, Turkey, and in New Guinea. The flora represented at each of these localities is mainly of Cathaysian character, with the genus *Glossopteris* represented either by leaf fragments, or pieces of its axis, *Vertebraria*. Edwards (1955) has justifiably questioned whether leaf fragments of *Glossopteris* type are ever adequate on their own (without the supporting evidence of their very characteristic fructifications) as record of the genus, especially in localities far isolated from the principal area of the Gondwana flora. Disconcertingly *Glossopteris*-like leaves have been reported from far outside Gondwanaland (for example in Poland, see Bochenski 1957) which must be discounted on grounds other than merely the leaf shape and venation. Equally, it is known that a number of gymnosperm groups, not closely related to *Glossopteris*, show very *Glossopteris*-like venation in the leaves or leaflets (Alvin and Chaloner 1971). It is obviously desirable that records of *Glossopteris* based solely on leaf fragments, occurring away from its typical associates, should be examined critically for supporting evidence of fructifications.

The mixed Cathaysian/Gondwana flora at Hazro, eastern Turkey (Wagner 1962), is included on the maps of text-figs. 4 and 5 on account of its great phytogeographical interest, although Wagner favours a Middle or Upper Permian age for the flora. Its apparent combination of Cathaysian and Gondwana elements is the more remarkable on account of its isolation from both the nearest Gondwana record of *Glossopteris* (at Entebbe over 2000 miles to the south) and the nearest Cathaysian flora, an even greater distance to the east. The lack of any intermediate localities linking the Hazro flora and the main area of the Cathaysian flora in China is increased by the recent work of Dobruskina (1970) on the Madygen flora, which has hitherto formed the basis for one of the westernmost outposts of the Cathaysian flora (shown

on text-fig. 4 as a locality to the east of the Caspian Sea). This author interprets the whole of the plant-bearing formation of the Madygen suite as being of Triassic age, rather than Permian as had previously been supposed. It should be noted that Vakhrameev *et al.* (1970) regard all the Middle Asiatic floras (shown with queries in text-figs. 4 and 5) forming this western extension of the Cathaysian province as of 'uncertain phytogeographic affinity'. Clearly any new information on these critical localities near the meeting-point of the Angara, Cathaysian, and Gondwana floras (and particularly evidence from other fossil groups as to their age) will be of the greatest interest.

The Cathaysian/*Glossopteris* flora in New Guinea (Jongmans 1940, Kon'no 1966), unlike the Hazro situation, is complicated by the uncertain field relations between the Cathaysian and *Glossopteris* elements. However, even if as Kon'no believes, the *Glossopteris* flora overlies the Cathaysian flora there, the presence of both floras in the western half of New Guinea is a highly significant feature of the Late Permian palaeogeographic picture. It remains, with Hazro, as one of the most enigmatic occurrences forming a seemingly very disjunct outlier of the Cathaysian flora. In this context, the Djambi flora of Sumatra described by Jongmans (1937) as of Cathaysian affinity is of especial significance in linking Sumatra floristically with Cathaysia. It is certainly more conformable with the siting of Indonesia offered by the symposium reconstruction, rather than a position between India and Australia recently advocated by Ridd (1971).

#### FLORAS, CONTINENTS, AND CLIMATE

The distribution of Upper Palaeozoic floras reviewed above raises a series of questions concerning the interrelationship between them, the past positions of continents and palaeoclimate, which may now be briefly reviewed.

Despite the uncertainties arising from the problems considered earlier in this article, the following general picture seems clear. Devonian floras were surprisingly cosmopolitan (Rigby and Schopf 1969). Through the early part of the Carboniferous period there is also general uniformity of world floras. Although both the evidence for age and the composition of those of Gondwanaland are most in need of further study, they seem to resemble northern Early Carboniferous floras more closely than those of later Carboniferous age. The later Carboniferous (mainly Westphalian) flora of eastern U.S.A. and Europe, east to the Donetz Basin (and, less securely, east to China), seems to have no counterpart in Gondwanaland. It is tempting to link this with the Gondwana glaciation, and to attribute it to a general partial synchronicity of the Westphalian floras with that glaciation. The segregation of the four or five palaeofloristic provinces of the Late Carboniferous/Early Permian, following the Gondwana glaciation, must surely be causally linked with it. The accentuated climatic zonation apparently associated with the development of the Gondwana ice cap, and the opening up of new habitats on the retreat of the ice, doubtless both contributed to this situation.

The absence of any indication of an Early Carboniferous *Lepidodendropsis* (or Euramerian) type of flora within those parts of a reassembled Gondwanaland which were affected by glaciation (except India, see below), the relationship of the Gond-



wana *Glossopteris* flora itself to the spread of glacial conditions, and the occurrence in a few areas of the 'mixed' Euramerian/*Glossopteris* flora already discussed (text-fig. 6) may all be related to the effect of glacial conditions. Occurrences of representatives of the cosmopolitan Devonian flora are known from *pre-glacial* situations in South America, South Africa, India, Antarctica, and Australia. Presumably from such source material the succeeding Early Carboniferous *Lepidodendropsis* flora evolved in those parts of western South America, northern Africa, and eastern Australia which were not affected by glaciation. But it was prevented from doing so in eastern South America, South Africa, peninsular India, Antarctica, and parts of southern and eastern Australia by the onset of glaciation. In these latter areas evolution from Devonian stocks presumably proceeded along different lines, probably through the *Proto-Glossopteris* stage envisaged by Plumstead (1967b) in Carboniferous time, to the typical *Glossopteris*-*Gangamopteris* floras of the Early Permian. Recent work by Crowell and Frakes (1972) supports the earlier contention by King (1958) that glaciation began in Early Carboniferous time in South America and South Africa, but was later in India, Antarctica, and Australia, where it is presumed to have commenced in Late Carboniferous or even Early Permian time. This may explain, on the one hand, the occurrence of an Early Carboniferous *Rhacopteris* type flora in northern India *within* the area of subsequent glaciation but *before its onset*, and, on the other hand, the appearance of 'mixed' Late Carboniferous/Early Permian Euramerian/*Glossopteris* floras at some localities in South America and South Africa, brought about by the migration of Euramerian genera inwards from peripheral Early Carboniferous stocks and outwards of *Glossopteris* flora after the retreat of the ice in those areas. The general coincidence of the distribution of ice sheets and of the ensuing *Glossopteris* localities may simply reflect the fact that *Glossopteris*, as a genus adapted to relatively temperate conditions, spread over the high latitude areas previously covered by ice. The modern distribution of, say, the conifers *Picea* and *Abies* (Li 1953) approximates in a similar way in North America and Europe to the maximum spread of the Pleistocene glaciation. The relationship of the four more northerly provinces to a latitude-controlled climatic zonation is less clear. Many authors suggest a general correspondence of the Euramerian, Cathaysian, and North American provinces with an equatorial climatic belt, while the Angara flora represents a north temperate zone corresponding with that dominated by *Glossopteris* in Gondwanaland (see, for example, Edwards 1955, Wagner 1962). This appears very plausible on the basis of present-day continent positions, allowing for a northerly displacement of the equator through eastern U.S.A. and Europe. But such an explanation cannot be so easily reconciled with the symposium reconstruction (text-fig. 5). Here the junction between the Cathaysian province and that of Angaraland passes from central Asia, rising in a (palaeo-) north-easterly direction between the Angara flora of eastern Siberia and the Cathaysian flora of Korea and Japan. The only simple climatic phenomenon which might be invoked to explain this situation is the possibility that the oceanic effect of the Pacific favoured the more northerly extent of the Cathaysian flora along the Pacific margin of Asia.

Probably the most remarkable of all the climatic implications of Late Palaeozoic plant distribution is the existence of remains of *Glossopteris* within a few degrees of the Permian South pole (arrow in text-fig. 6). If the earth's axis has substantially

maintained its present orientation in space, this means that an apparently arborescent plant with relatively large leaves was able to survive under polar conditions, including several winter months of total darkness. The absence of polar ice caps and the redistribution of land and sea alone seem insufficient to account for climatic conditions at the centre of Gondwanaland so drastically different from those prevailing in Antarctica today.

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