ASPECTS CONCERNING THE IDENTIFICATION AND DISTRIBUTION OF LATE PALAEOZOIC PLANTS IN GONDWANALAND*

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ABSTRACT

The distribution of species of larger lycopsid and sphenopsid plants in the Late Devonian, Carboniferous and Permian show that the Gondwana Province was ecologically isolated from non-Gondwana regions during much of this time. Evidence provided by the distribution of ferns (generally lacking in the pre-Permian remains) and seed-plants (not present in the Devonian) support conclusions provided by lycopsid and sphenopsid plant remains. The terrestrial climate probably deteriorated gradually in the Carboniferous of Gondwanaland, but temperate climates probably replaced frigid climates fairly rapidly early in the Permian.

INTRODUCTION

The history in Australia of major vascular-plant groups is outlined for the Late Palaeozoic, and the manner by which the groups suggest palaeoclimates is summarised. Many problems in Gondwana palaeogeography and stratigraphy involving interpretations based on plant remains, particularly those from the Carboniferous, have resulted from the indiscriminate use of Euroamerican taxa. Much of this discussion is complementary to the detailed review of Indian palaeoclimates based on floral evidence during Gondwana time, given by LELE (1976) ; for Argentina by ARCHANGELSKY AND ARRONDO (1975) ; and for Brazil by RÖSLER (1976).

Each continental drift episode (see BRIDEN, 1969) has been associated with a period of floristic instability with concomitant floral evolution. Some of BRIDEN's drift episodes coincide with boundaries between major plant periods—first colonization of the land, to Palaeophyticum, to Mesophyticum, to Neophyticum. Major extinctions of invertebrate families closely follow the changes from one plant period to another, an interpretation based on data tabulated by PITRAT (1970).

The Gondwana floras during the Late Palaeozoic more often than not were isolated from other coeval floras (Carboniferous : see RIGBY, 1970. Permian : see HSÜ, 1976 ; MEYEN, 1971 ; RIGBY, 1972b ; SURANGE, 1971 ; and references they cite).

The following factors are assumed throughout the discussion :

(1) Some of the authors quoted are examples only of many references on the same topic.

(2) The data are related to the appropriate palaeogeographical maps given by SMITH *et al.*, (1973) but no reference is made to this paper in the text. I prefer a separate history for East and West Antarctica (RIGBY, 1972b) such as given by ELLIOT (1972). However, the maps prepared by SMITH *et al.*, (1973) have been used as disjunction or conjunction of Antarctica in no way affects the discussion here.

(3) The earth's ecliptic has been constant since the Devonian. DONN AND SHAW (1977) have shown that palaeoclimates can be explained through effects on atmospheric

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temperature influenced by the changing distribution of continents and sea throughout the passage of time, without major changes in the ecliptic.

(4) It cannot be stressed too strongly that many of the genera are form genera, so the use of the same generic name in two different areas or times in no way suggests any natural relationship unless the same species is involved.

LYCOPSIDA

The fossil remains of arborescent members of this group are difficult to classify in many cases, as neither anatomy, nor fructifications, nor leaf scar structure is retained, hence generic attribution is not possible. Most remains from Australia are in the knorria stage where all of the softer tissue surrounding the xyelm cylinder has been removed before preservation ; others are in the bergeria stage where only the epidermal layer has been lost. More space is devoted to a dsicussion of the arborescent lycopods as their record is continuous from the Devonian to the Triassic.

Leptophloeum australe (McCoy) Walton occurs in many parts of the Late Devonian of Australia, and is usually the only recognizable plant where it occurs, although *Cyclostigma* has been recorded from the same rock units at Goonoo Goonoo, New South Wales (Feistmantel, 1890), and has been reported, together with *Sublepidodendron*, from Queensland. *L. australe* also occurs in South Africa and possibly South America (Plumstead, 1967). *L. rhombicum* from North America and *L. australe* lie distributed in the tropics or warm temperate zone, although the Chinese occurrence of *L. rhombicum* appears to lie in a cold region. Some figured specimens of *L. rhombicum* from China (Chinese Palaeozoic Plants ; 1974 ; pl. 4, fig. 2) are indistinguishable from fossils of *L. australe* from Australia. The authors of this book include *L. australe* as a junior synonym of *L. rhombicum*.

Some *Cyclostigma* are associated with *Leptophloeum australe*, and others with Carboniferous floras. Chaloner (1967) has limited cyclostigmas to the Frasnian and Famennian, whereas in Gondwanaland they extend as high as the Viséan (summarised in Rigby, 1970) where *C. aegyptiaca* occurs in the Clarke River Formation of Queensland. The species also occurs in Sinai within a typical Early Carboniferous flora (Jongmans, 1955) which Rigby (1970) has related to the pre-Gondwana Carboniferous flora rather than the Euroamerican Carboniferous floras.

Chaloner and Boureau (1967) include the Late Devonian *Protolepidodendron lineare* Walkom (1928) as a synonym within the genus *Archaeosigillaria*. Walkom says, it is quite distinct from *A. vanuxemi* (Goeppert) Kidston.

Other lycopod stems are known from the Early Carboniferous, most of them are decorticated and in the knorria stage. They are often called *Lepidodendron veltheimii* Sternberg in Australian literature. As far as I can see, they lack any evidence of parichnos and a ligule even when relatively undecorticated, although the better preserved *Lepidodendron osbornei* Walkom (1928) may have a ligule. Without more, better preserved material these stems are probably best identified as 'lycopod stem *incertae sedis*'. Walkom (1928) reported *L. osbornei*, *Ulodendron minus* Lindley & Hutton, and *Stigmaria ficoides* Brongniart from the same locality in the Early Carboniferous Wallaringa Formation, New South Wales. I am inclined to agree with Crookall (1964) who suggested that some specimens identified as *Ulodendron* are stems of other lycopods bearing ulodendroid scars ; hence Walkom's three species may all have belonged to the same plant (natural) species. Others have reported *Stigmaria ficoides* from elsewhere. The arrangement and structure of scars on these specimens suggets they are leaf, not root scars.

Stems have been identified as *Lepidodendron volkmannianum* Sternberg, but over the last ten years or so, these specimens have tended to be placed in *Sublepidodendron*, which may be correct. They also resemble mature stems of *Lepidodendropis*, where, by secondary elongation in leaf cushions, the appearance of a whorled arrangement of scars develop. *Lepidodendropsis* occurs in the Early Carboniferous tropics of Europe and North America, the Late Carboniferous temperate to tropical zone of Australia, South America and Sinai (20°—50°S) and the Wutung Series (latest Devonian) of China which appears to have been cool temperate and isolated by ocean from other occurrences. LEE (1964) questions whether the Chinese Late Devonian floras had any close relationship with coeval floras elsewhere.

WHITE (1959) reported a knorria stage stem from the Early Permian Harris Sandstone, Western Australia, as *Lycopodiopsis pedroanus* (Carruthers) Edwards basing her opinion on EDWARDS (1952) who had combined all Gondwana *Lycopodiopsis* and *Cyclodendron* into a single species. I think her figured specimen is generically indeterminate. EDWARDS drew attention to the habit of authors' accepting too readily various northern hemisphere Carboniferous genera for doubtful specimens or for specimens of clearly southern hemisphere affiliation. I have examined a few knorria stage specimens from Mt. Bannerman, Western Australia, from either the Poole Sandstone (Early Permian) or the Liveringa Formation (Late Permian). They are generically indeterminate, and appear to be the same as WHITE's specimen.

Some specimens figured by WHITE AND CONDON (1959) from the basal Lyons Group (Earliest Permian) are in the knorria stage. Their anatomical section does not show sufficient diagnostic characters for determination ; they do not resemble any of the *Lepidodendron* sections figured, e.g., by LEMOIGNE (1965), but show some resemblance to Lower Gondwana lycopods with known anatomy such as *Lycopodiopsis derbyi* (RAO, 1940) and *Eligodendron branisae* Archangelsky & de La Sota (1966). There is no difference between the surface of the knorria specimens and similar specimens of *Lycopodiopsis derbyi* (e.g. MAACK, 1947 ; pl. 86, fig. 25), but they are not similar to specimens of *Cyclodendron leslii* (Seward) Kräusel (e.g. KRÄSUEL, 1961 ; pl. 39, fig. 40) where the circular nature of the scar seems always to be retained. *Lepidodendropsis* and other Late Palaeozoic lycopods may have a similar knorria stage. The Early Mesozoic genus *Pleuromeia* has a different arrangement of scars with a phyllotaxy more resmebling mature stems of *Lepidodendropsis*, but with laterally broadened cushions having a central strand and two fine lateral strands (NEUBURG, 1960). *Pleuromeia* is most unlikely to have given rise to any of the knorria specimens from Western Australia, this will be discussed further below. RIGBY (1966) recorded *Cyclodendron leslii* from the Early Permian Irwin River Coal Measures of Western Australia. In the Permian, *Cyclodendron* occurs in quadrats 1, 8-12 (Fig. 1), *Lycopodiopsis* land *Eligodendron* in quadrats 1 and 8 only. The stratigraphically lower part of these distributions are in cooler climates possibly similar to the Late Devonian climate of China. FULFARO (1972) has recorded *Lycopodiopsis* sp. from the Botucatu Sandstone (Permo-Triassic) of Brazil where a warm to hot climate is thought to have prevailed, based on the presence of red beds (also see RÖSLER, 1976).

Pleuromeia has been reported from the Triassic of both eastern and Western Australia (BRUNNSCHWEILER, 1954 ; RETALLACK, 1975). RETALLACK's figured specimens (1975, figs. 8-10) lack the leaf scar ornamentation given by NEUBURG (1960) as typical of the genus. Circular leaf scars figured by RETALLACK more closely resemble scars of *Cyclodendron* as figured by KRÄUSEL (1928, e.g. pl. 1, fig. 8). I suggest the so-called *Pleuromeia* described by RETALLACK is some imperfectly known, as yet unnamed, arborescent lycopod probably decended from *Cyclodendron*. *Pleuromeia* is restricted to northern Europe and Siberia

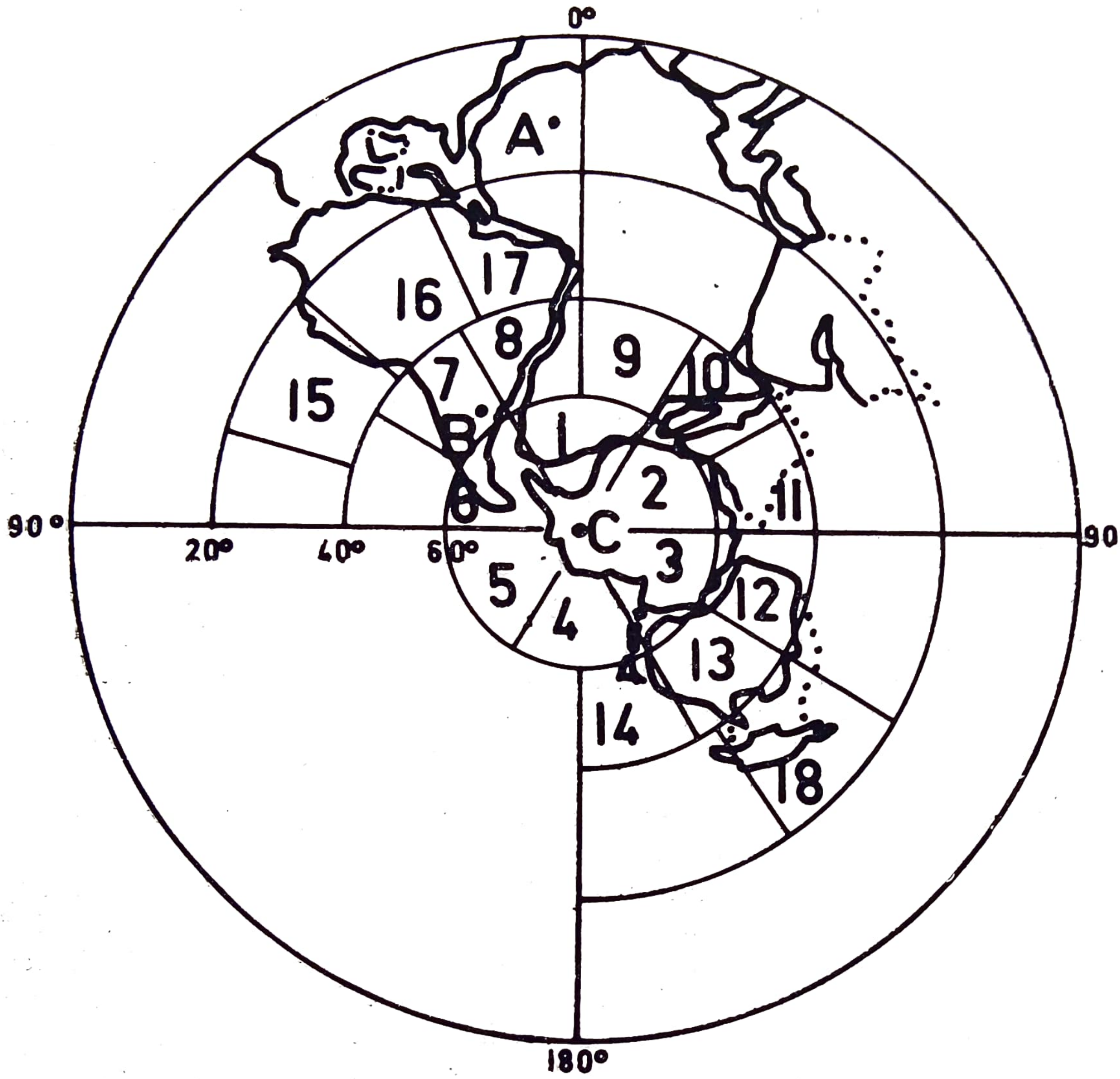

Fig. 1. Plant quadrats superimposed on the Permian reconstruction of SMITH *et al.*, (1973). Polar positions designated by letters : A—Mid Palaeozoic, B—Early Carboniferous, C—Late Carboniferous and Permian.

between palaeolatitudes 30°-60°N, whereas the Australian localities have the same palaeolatitudes south, this supports parallelism of development, not generic identity. MEYEN (1971) had discussed parallelism in development, or homoplasy, between Gondwana and Angara plant morphological types during the Palaeozoic. *Cyclostrobus* has been figured from the Narrabeen Group (Early Triassic) of the New South Wales (HELBY & MARTIN, 1965). CHALONER AND BOUREAU (1967) indicate that *Cyclostrobus* is not the strobilus of *Pleuromeia* by classifying it as *incertae sedis*, and *Pleuromeia* in the family Pleuromeiaceae. LEJAL (1969) has concluded that aerenchymatous tissue is reduced in some lycopod genera as an adaption to a dry atmosphere, e.g. the families Sublepidodendraceae, Archaeosigillariaceae, as opposed to lycopods that grow in a marshy or humid climate, where the tissue is well developed as in the Lepidodendraceae. Lycopods with parichnos seem to be entirely absent from Australia and elsewhere in Gondwanaland except in Patagonia where *Lepidodendron patagonicum* Archangelsky, and cf. *Lepidophlois laricinus* Sternberg have been found (ARCHANGELSKY, 1960). Evidence for the presence of parichnos is not entirely convincing, based on the figured specimens, although they do resemble some from Europe figured by WEISS (1907).

The general absence of lycopods with parichnos supports the idea that the climate in Gondwanaland during the part of the Late Palaeozoic when Late Palaeophytic lycopods were becoming established was generally neither humid nor tropical. It must be borne in mind, though, that if lycopods with parichnos had been present in Gondwanaland, then the dry-cold of the glacial episode would have exterminated them. They could not reappear except by migration from Laurasia (the northern hemisphere continent formed by Europe and North America), regardless of how favourable to them the climate became in post-glacial time.

SPHENOPSIDA

In Australia, during the Carboniferous, sphenopsids do not form any significant part of the fossil record until the Late Carboniferous in New South Wales and a few localities elsewhere, when stems of *Calamites peruvianus* Gothan are fairly common. A few specimens of foliage are known but they need revision after more specimens have been found.

Sphenopsids form a significant part of the Permian flora.

Phyllotheca australis Brongniart may or may not be synonymous with *P. indica* Bunbury. If it is, then *P. australis* is distributed in quadrats 8, 11-14, all in the cool temperate zone. *Raniganjia bengalensis* (Feistmantel) Rigby (in some places reported as *Umbellaphyllites ivini* (Walkom) Rigby) and *R. etheridgei* (Arber) Pant & Nautiyal are distributed in the same quadrats, and also quadrat 1. *Lelstotheca robusta* (Feistmantel) Maheshwari is more restricted (quadrats 8, 11, 13, 14).

Schizoneura gondwanensis Feistmantel is much more widely distributed, occurring throughout most of Gondwanaland.

Trizygia is known only from the Mount Mulligan Coal Measures (Late Permian) of Queensland, and from West Irian (quadrats 13, 18) in the Australian region, but it is distributed widely elsewhere in Gondwanaland. Cathaysian species also occur in the temperate zone (40°—60°N). *Sphenophyllum* occurs only in the Irwin River Coal Measures, Western Australia, but is absent in eastern Australia. Elsewhere it occurs quite generally throughout the Late Palaeozoic world, except in New Guinea and Antarctica.

Stems of all the Gondwana sphenopsids are identical, any differences are accounted for by differences in growth stages. All are included in *Paracalamites australis* Rigby.

ASAMA (1968) suggests, from his observations of Cathaysian sphenopsids, that evolutionary variation is assisted by annual temperature changes providing that the mean winter temperature remains above 5°C. The mean winter temperatures in much of the early Permian of Gondwanaland may have been very close to 5°C, considering the lack of generic variation found in Gondwanaland.

FERNS AND FERN-LIKE FOLIAGE

Ferns and fern-like foliage are not as common in the Late Palaeozoic of Gondwanaland as in other places. Trunks of the zygopterid fern *Austroclepsis australis* (Osborne) Sahni occur in Early Carboniferous strata of New South Wales at a locality that may be presumed to have lain in the tropical region, before the Early Carboniferous Drift Episode.

Sporangia occur on only one species, *Neomariopteris lobifolia* (Morris) Maithy from the Permian. This species also has a fern-like cuticle, but it does not resemble any typical pteridospermous cuticle (RIGBY, 1975). If *N. polymorpha* (Feistmantel) Maithy is a synonym, then the species is distributed throughout most of Gondwanaland.

Permian fern trunks are rare. They are known only from Queensland (*Palaeosmunda*) and the Parana Basin, South America (*Tietea* and *Osmundacaulis*—HERBST, 1973). Tree ferns are restricted to warmer climates at present, hence the localities where they occur in the Permian probably lay in a similar climatic region.

The Permian species, sometimes known as *Alethopteris lindleyana* (Royle) Schimper, and at other times as *Cladophlebis roylei* Arber, is almost certainly based on fern, not pteridosperm fronds. I prefer not including the species in *Cladophlebis* which is a form genus for sterile fronds of the Osmundaceae, Schizeaceae, or Dicksoniaceae. *Alethopteris* is used for fern-like fronds with decurrent pinnules, so is also inappropriate. *Pecopteris* is used for both fern and pteridosperm fronds with more or less parallel sided or slightly curved pinnules having a midrib and branched or unbranched secondary veins. From the latter set of characters I now agree that ROYLE (1833) more correctly attributed the species to *Pecopteris*. However, his epithet *lindleyana* was preoccupied when he proposed the species. ARBER's proposed replacement epithet is available, making the name *Pecopteris roylei*, which has yet to be validated.

Other fern-like foliage may belong to ferns or to pteridosperms, as neither sporangia nor seeds are known.

Earliest Australian occurrences are in the pre-Gondwana (middle to late Carboniferous) Flora of New South Wales and Queensland where *Cyclopteris*-like fronds of *Bergiopteris insignis* Kurtz (as understood by ARCHANGELSKY, 1977), *Adiantites paracasica* Gothan and *Pseudorhacopteris obovata* (McCoy) Rigby occur (RIGBY, 1970 ; 1973). I think these plants show parallelism of development with some extra-Gondwana plants, e.g. between *Pseudorhacopteris* and *Rhacopteris*, and probably descended from some common Early Carboniferous or Late Devonian ancestor. In Peru, we see an impoverished flora of North American lycopods some species of *Lepidodendropsis*, growing along side species with fern-like foliage of local, endemic, pre-Gondwana species and genera (RIGBY, 1970).

MENSAH AND CHALONER (1971) reported *Lepidodendropsis* and *Archaeosigillaria* from the Early Carboniferous of Ghana where they probably grew before drift influenced the southward migratory path of the plants. The *Rhacopteris ovata* reported by BOUREAU (1954) from Niger belongs in *Rhacopteris*, not the pre-Gondwana *Pseudorhacopteris*. Both these floras are Laurasian rather than pre-Gondwana, thus supporting the view that west Africa lay on a migration route.

The Carboniferous-Permian transitional species, *Botrychiopsis plantiana* (Carruthers) Archangelsky & Arrondo, may be either a pteridosperm or a fern frond. Many specimens are known, but none are fertile. This is good, but not perfect evidence that the species belonged to a pteridosperm. As the species is closely associated with glacial horizons, it was probably a cold or cool climate form (found in quadrats 7, 8, 11-13 of fig. 1). Otherwise, Australia does not seem to have any undoubted pinnatifid pteridosperm fronds in the Permian. HOLMES (1977) notes that the Permian frond, *Dunedoonia reticulata*, from New South Wales, is bennettitalean-like, but it is also similar to many Carboniferous pteridosperm fronds. It is not possible to comment on this interesting plant until more specimens are found.

GYMNOSPERMS

Possible pteridosperms with pinnatifid fronds have already been mentioned. *Glossopteris* and *Gangamopteris* are by far the most common elements of the Lower Gondwana Flora. Their ancestors are unknown. They are considered to be leaves of pteridospermous trees (WHITE, 1908) that were deciduous (PLUMSTEAD, 1958). Some may have been cycadaceous as implied by RIGBY (1969, fig. 1, no. 16). The fructifications were dioecious, as no male and female frutifications have been found attached to the same plant. So far, the female genera *Dictyopteridium*, *Isodictyopteridium*, *Plumsteadia*, *Senotheca* (see RIGBY,1978) and *Austroglossa* (HOLMES, 1974), and the male genus *Eretmonia* (HOLMES, 1974) have been reported in Australia. *Mooia* has also been found.

No other microsporangiate fructifications have been proved to occur in Australia, although *Lidgettonia* has been reported (WHITE, 1964) as associated with the glossopterids. Other fructification genera occur elsewhere in Gondwanaland. The glossopterids had a coniferous habit with long and short shoots (RIGBY, 1967), and grew on trees (PLUMSTEAD, 1958) with gymnospermous wood lacking resin canals, as in the extant family Araucariaceae. The roots, *Vertebraria*, have a segmented appearance which has been explained by SCHOPF (1965). The most detailed review to date of the Glossopterid plant's morphology has been given by PANT AND SINGH (1974). Classification of these plants is not entirely satisfactory as they appear to be much more like the cordaitaleans than to most of the pteridosperms. I introduced the family Arberiaceae (RIGBY, 1972a) for some female fructifications as a prelude to sorting out some problems of glossopteris classification. *Arberia*, the type genus, has not been found attached. With deciduous leaves and well-marked growth rings in the wood, a temperate climate probably similar to contemporary middle latitudes, is suggested by the glossopterids.

Nephropsis-like scales are undoubtedly gymnospermous, but so far, only WALKOM (1928) has given any indication of their association on shoots, and LACEY *et al.* (1975) have figured an attached group of scales on the cross section of a shoot. Isolated scales are very common at many localities. I think they do not belong to the same plant that bore leaves of *Glossopteris* or *Gangamopteris* but to some other gymnosperm.

LELE (1976) showed that variations in the succession of Permian floras in India were climatically controlled. The cool temperate *Gangamopteris* floral phase of the Talchir Series was dominated by leaves lacking a midrib : *Gangamopteris*, *Rubidgea*, *Euryphyllum* and *Noeggerathiopsis ;* whereas the following, warm temperate *Glossopteris* floral phase was dominated by leaves with a strong midrib : *Glossopteris*, *Rhadbotaenia* and *Palaeovittaria.* He noted a tendency within certain genera to have long, narrow meshes during the colder regime and to have broad meshes, often netted, during the warmer regimes. Frail ferns appeared during colder periods whereas robust ferns delayed their appearance until warmer times. His data used for deducing Indian palaeoclimatology was based on analysis of large collections of plants from many localities. No other country has such extensive data on which to draw.

I think the treatment of KOVACS—ENDRODY (1977) of including *Gangamopteris* as a junior synonym in *Glossopteris* does nothing to assist taxonomy nor to aid stratigraphical, palaeo-climatological and other interpretations. She does not attempt to define her concept of *Glossopteris*, which will be very difficult, and would make the genus so all-embracing that it would become virtually meaningless in palaeotaxonomy, such as the term "broad-leafed angiosperm". Besides, some of her taxonomy is unacceptable, particularly the junior homonym "*Glossopteris major* (Fstm.) Kovacs" on p. 25, which she gives as a recombination for *Gangamopteris major* Feistmantel. PANT AND SINGH (1971) have pointed out that such a merger of genera is inappropriate at the present state of our knowledge, and I agree.

Cordaitaleans are well represented in the Permian, but there is lack of uniformity between investigators in the application of generic names. MEYEN (1963) considered *Noeggerathiopsis* to be a synonym of *Cordaites* with most or all leaves falling into Dana's species *spatulata* which has priority over *hislopii.* The late Devonian *Cordaites australis* McCoy does not appear to be related to the Permian cordaitaleans.

The Ginkgoaceae, Vojnovskyaceae and the Cycadales have not yet been reported in Australia. *?Pseudoctenis* sp., a genus of unknown affinities and previously known only from the Late Permian of India (quadrats 11, 12), is the only possibly cycad-like foliage known in Australia, unless some of the Glossopterids are cycadaceous.

Coniferales are rare, only the species *|Valkomiella australis* (Fesitmantel) Florin, from the Late Permian of New South Wales occurs in Australia. The genus also occurs in India and southern Africa (Quadrats 9, 11, 14) within the palaeolatitudes 40° and 60° S.

Angiosperms are completely unknown in the Late Palaeozoic as I have already noted (RIGBY, 1969), based on evidence from the fossil record.

INTERPRETATIONS

During the past there has been a tendency to identify fossil plants uncritically by using the closest, suitable-looking Laurasian specific or generic name, particularly from the Carboniferous, or to try and name specimens that are too poorly preserved for diagnostic characters to be recognized. Sometimes when floral lists with inappropriate or uncritical names have been utilized by geologists in stratigraphy, misleading conclusions have been reached.

Generic and specific differentiation was occurring in Gondwanaland before isolation from the north occurred, probably influenced by the Early Carboniferous Drift Episode when the pole shifted from B to C (Fig. 1) over a period of about 30 million years. From the meagre evidence available, migration probably involved passage from north to south through Peru. Another migration route may have passed through Egypt, but there must have been rapid internal migration within Gondwanaland as the floras of eastern Australia, South America, India and Egypt are remarkably similar during the Late Carboniferous, and subtly distinct from coeval floras elsewhere. They more closely resemble Early Carboniferous floras of Laurasia. The changing climate induced by polar shift provided the necessary hybridizing momentum to give rise to specific and generic differentiation with some ferns and seed plants, and to exterminate others. On the other hand, apparently only the lycopods that had the ability to withstand the changing environment without themselves changing, managed to survive.

One can see that frost heaving in aerenchyma would be catastrophically destructive. This feature and the Gondwana Carboniferous climate probably accounts for the lack of tropical-loving lycopods with aerenchyma tissue in Gondwanaland. Sometime during the early to middle part of Carboniferous time, lepidodendroids without aerenchyma, in particular *Lepidodendropsis,* entered Gondwanaland from the north. Localized genera arose during the Permian. Endemic arborescent lycopods continued into Early Triassic, then disappeared from the record.

Both herbaceous and arborescent sphenopsids became common at the beginning of the Permian, suggesting an improving climate.

In Australia tree ferns existed only during the Early Carboniferous, and locally in the Permian. This suggests a Late Carboniferous climatic deterioration, with at least seasonally cool weather continuing during much of the Permian.

Gymnosperms were never common except for endemic glossopterids which were very successful during the Permian, and the cordaites. Habit of the glossopterids suggests a seasonal temperate climate.

Australia's palaeoclimate was :

Late Devonian—Early Carboniferous ; tropical, or warm temperate.
Late Carboniferous ; temperate, definitely non-tropical.
Carboniferous—Permian boundary ; cool, as conditions were adverse to plant growth, and both glacial and periglacial sediments occur.
Permian ; temperate, becoming hotter.

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