# LATE PALAEOZOIC AND TRIASSIC FLORAS OF INDIA AND THEIR RELATION TO THE FLORAS OF NORTHERN AND SOUTHERN HEMISPHERES

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## ABSTRACT

The development, composition and phytogeographical distribution of the northern and southern hemisphere floras from the Carboniferous to the Triassic times is critically reviewed in the light of more recent knowledge and with particular reference to India and other Gondwana countries. The Lower Carboniferous floras of Gondwanaland, and especially of India, are much impoverished in contrast to the Euramerian Lepidodendropsis flora. It seems more reasonable that the southern flora evolved from pre-existing Devonian stocks on ice-free areas of Gondwanaland whereas the Glossopteris flora arose under the impact of Carbo-Permian glaciation. Most of the so-called Euramerian elements in the Glossopteris flora (e.g. ferns, lycopods) may well be of southern nativity. Several of them are now proved to be distinct; the remaining few, obviously, warrant critical study.

The Gondwana, Angara, Euramerian and Cathaysian floras and their respective palaeoenvironments had attained sharp geobotanical distinction in the Permian. Floral migration or contact between them across the Tethys is discussed. Particular attention is drawn to the phytogeographic significance of the Kashmir site (Gangamopteris beds) in the light of its geotectonic background and the recent findings of several extra-Gondwana (Cathaysian/Angara ?) plants. The Kashmir site is here referred to Vakhrameev's " Middle Asiatic floras of uncertain affinity " which also includes the Hazro locality of Turkey. The Middle Asiatic region needs extensive palaeobotanical exploration to understand the nature of the maritime (Tethyan) floras of the various Permian geobotanical provinces.

During the Triassic, the floral picture of the northern hemisphere became almost cosmopolitan following the withdrawl of previous physico-geographic barriers. The southern hemisphere (Gondwana) floras also tended to become more harmonious but their essential distinctiveness was still maintained by the characteristic prevalence of the Dicroidium flora.

## INTRODUCTION

BY the Late Palaeozoic, the vegetation of our globe was distinguishable mainly into four distinct geobotanical provinces. The largest of these was the Gondwana supercontinent in the southern hemisphere, comprising the present South America, South Africa, India, Australia and Antarctica. The Gondwanaland was bounded on its northern periphery by a girdling ocean — the Tethys, beyond which lay the three other geobotanical provinces of the northern hemisphere, viz., (1) Eurameria (covering Europe and North America), (2) Angara (covering the U.S.S.R. and Central Asia), (3) Cathaysia (covering China, Indochina, Korea, Japan, Laos and Indonesia). When these floral provinces are seen in the present context of the world map we come across two very striking facts which were pointed out by Sahni (1936) about 40 years ago (1) some countries with closely related floras lie on the opposite sides of the biggest oceans of the globe and (2) others with very distinct floras, for example the Gondwana province of India Australia and the Cathaysian province of China-Sumatra lie dovetailed with each other. This was probably one of the strongest palaeobotanical arguments that has given sustained support to the idea of Continental Drift. Unfortunately, however, the Drift theory failed to make impact for a long time because the very cause and mechanism of drift were not known. In the last decade this serious gap has largely been filled by the great advances in our knowledge of the geological, palaeomagnetic, and tectonic structure of the Earth and its ocean floors. We now know, for instance, how the opening of the North Atlantic caused the disjunction of the homogeneous Carbo-Permian floras of Europe from that of Eastern U.S.A. Similarly, in the southern hemisphere the supercontinent of Gondwanaland, with its unique succession of floras, eventually broke into fragments that were far flung from each other. India, especially, drifted much farther north of the equator and subsequently collided with the Asian block which resulted in the juxtaposition of the Glossopteris flora with those of Cathaysia and Angara. Scientists all over the world are now trying their best to evolve different models of continental-fits, especially of Gondwanaland compo-

nents in an attempt to explain the variety of data emerging from the study of earth sciences (Tarling & Runcorn, 1973). As we look back, we are amazed to see how this visionary concept of Wegener, which was only a little more than a simple jig-saw-fit, has taken about 45 years of profound thinking on the parts of geologists like Suess, du Toit, Blanford brothers and Palaeobotanists like Jongmans, Halle, Zalessky, Gothan, Seward, Sahni and many others to stand the tests of modern science.

Palaeobotanical knowledge of the past floras has also considerably grown during the last decade or so. We are now in a better position to visualise the development, composition and distribution of the floras in the Late Palaeozoic and Triassic times in the two hemispheres. The present article reviews these floras with particular reference to India.

## CARBONIFEROUS FLORAS

### India and Gondwanaland

The only records of Carboniferous plants from India are confined to the extra-Peninsular region of the Spiti area (Himachal Pradesh), occurring in fresh water intercalations in the marine sequence of the PO Series. The plants were first discovered by Hayden in 1904 and later Gothan and Sahni, and Hϕeg *et al.*, revised or added more plants. The meagre flora contains — ?*Astrophyllites* sp., *Adiantites* sp., *Rhacopteris* cf. *circularis*, *R. inaequilatera*, *R. ovata*, *Rhodea*, *Sphenopteridium* spp. A, B, and *Sphenopteris* sp. (Surange, 1966; Maithy, 1974d).

The paucity of plants and their unfavourable state of preservation has handicapped the certainty of their identification. As fragmentary leaves of fern/pteridosperms complex, they appear to be indistinguishable from the several carboniferous artificial taxa of the northern hemisphere which constitute the Rhacopteris flora (= Lepidodendropsis/Triphyllopteris flora or = Lepidodendropsis flora) of the Arcot-Carboniferous province. The Indian Carboniferous flora is neither substantial nor typical enough; it lacks certain characteristic elements like *Triphyllopteris* and *Lepidodendropsis* and the great complex of coeniopterid ferns (Surange, 1966). However, better records than India are provided by other Gondwana components (Table 1).

The South American flora of Peru, Mendoza, San Juan and La Rioza, (Archangelsky, 1970 & references cited therein) contains some typical plants including lycopods like *Lepidodendropsis*, *Archaeosigillaria*, *Palaeostigma* and fern-like plants such as *Triphyllopteris*, *Rhacopteris* (7 spp.) and *Adiantites* (6 spp.). The Australian records are also richer in *Rhacopteris* (5 spp.) with some new elements like *Austroclepsis* — a coenopterid fern. In Africa, where glaciation is evidenced right in the Carboniferous we hardly find any remains of Lepidodendropsis flora. On the contrary, in the Middle Carboniferous of S. Africa there appeared quite distinct plants of Glossopteroid aspect having smaller leaves that were devoid of vein anastomosis. These are referred by Plumstead (1967) to the Protoglossopteridae.

As far as the Upper Carboniferous is concerned, there is no evidence of plants from India and very meagre knowledge exists regarding other Gondwana components. At this time the Gondwana continent was under the profound influence of glaciation.

### Northern Hemisphere

The main Arcto-Carboniferous province of the northern hemisphere stretched far and wide from North America through Europe to as far east as China. The homogeneous vegetation of the Lepidodendropsis flora (= Rhacopteris flora) (Chaloner & Meyen, 1973; Chaloner & Lacey, 1973) which prevailed over this extensive area was dominated in the Lower Carboniferous by Lycopsids (*Lepidodendropsis*, *Lepidodendron*, *Bothrodendron*, *Archaeosigillaria*, *Stigmaria* etc.), *Sphenopsids* (*Archaeocalamites*, *Sphenophyllum*) along with a substantial proportion of Fern/Pteridosperm complex (*Rhacopteris*, *Anisopteris*, *Adiantites*, *Rhodeopteridium*, *Sphenopteridium*, *Sphenopteris*, *Cardiopteridium*, *Triphyllopteris*). The flora further elaborated in the Upper Carboniferous, thriving as a dense coal-swamp vegetation under warm humid climate. Similar influence prevailed largely in Cathaysia also, but some peculiar plants (*Tingia*, *Konchophyllum*) appeared there to

**TABLE 1 — DISTRIBUTION OF SOME IMPORTANT ELEMENTS OF THE CARBONIFEROUS FLORA IN GONDWANALAND AND NORTHERN HEMISPHERE. I (INDIA), A (AUSTRALIA), S. Af. (SOUTH AFRICA), S. Am. (SOUTH AMERICA), An. (ANTARCTICA), Em. (EURAMERIA), C (CATHAYSIA), Ag. (ANGARA)**

| GENERA | I | A | S. Af. | S. Am. | An. | Em. | C | Ag. |
|---|---|---|---|---|---|---|---|---|
| Lepidodendropsis | | | + | + | | + | + | + |
| Archaeocalamites | | + | + | | | + | + | + |
| Rhacopteris (Anisopteris) | + | + | + | + | | + | | |
| Adiantites | + | + | | + | | + | | |
| Lepidodendron | | + | + | | | + | | |
| Triphyllopteris | | | | + | | + | + | |
| Archaeosigillaria | | | + | + | | + | | |
| Rhodiopteridium | + | | | | | + | | |
| Fryopsis (Cardiopteris) | | + | | | | + | | |
| Sphenopteris | + | | + | | | + | | |
| Sphenopteridium | + | | | | | + | | |
| Sphenophyllum | | | | + | | + | | |
| Protolepidodendron | | | + | | | + | | |
| Cyclostigma | | | | + | | + | | |
| Sigillaria | | ? | | | | + | | |
| Stigmaria | | ? | | | | + | | |
| Austroclepsis | | + | | | | | | |
| Cardiopteridium | | | | | | + | + | + |
| Sublepidodendron | | | | | | + | | + |
| Bothrodendron | | | | | | + | | |
| Lepidostrobus | | | | | | + | | |
| Tingia | | | | | | | + | |
| Konchophyllum | | | | | | | + | |
| Caenodendron | | | | | | | | + |
| Cardioneura | | | | | | | | + |
| Angaropteridium | | | | | | | | + |
| Lophiodendron | | | | | | | | + |
| Tomiodendron | | | | | | | | + |
| Chacassopteris | | | | | | | | + |
| Eskadalia | | | | | | | | + |
| Angarophloios | | | | | | | | + |
| Angarodendron | | | | | | | | + |

herald the differentiation of the Cathaysian province which attained distinction in the Permian (Table 1). In the Angara area, situated between Europe and China, floral differentiation had apparently begun in the Lower Carboniferous by the appearance of peculiar Lycopsids (*Tomeodendron, Lophiodendron*) and Fern/Pteridosperms (*Chacassopteris, Angaropteridium*). *Lepidodendron, Lepidostrobus* and *Stigmaria* were strikingly absent (Chaloner & Meyen, 1973). By the Upper Carboniferous, the Angara became quite distinct from Euramerica and Cathaysia by the further proliferation of quite different Lycopsids, Sphenopsids, Fern/Pteridosperms and Cordaitales which thrived in a temperate climate.

We can clearly see, therefore, that the whole Carboniferous flora in the northern hemisphere areas, inspite of some differentiation, was by and large dominated by Lycopsids, Sphenopsids, Fern/Pteridosperms and Cordaitales, all of which showed a rising trend during the Carboniferous. In sharp contrast, a majority of these plant groups were either missing from the southern, Gondwanalands (e.g. India, S. Africa) or were scantily represented (e.g. Lycopsids in S. America) in the Lower Carboniferous and rather rapidly dwindled out in the Upper Carboniferous as a sad preface to the Carbo-Permian glaciation.

Comparisons of the Lower Carboniferous Gondwana plants with those of the northern

Lepidodendropsis flora have unfortunately to be based on some Lycopsids and largely on the Fern/Pteridosperm foliage of a very generalized type that are placed under form genera. The real affinities of the southern Lycopsids and Fern/Pteridosperm foliage will thus remain open to question (Plumstead, 1969, 1973a; Surange, 1966) until adequate material is discovered for their sterile and fertile parts. Such scrutiny has been possible at least in the case of the Permian Gondwana Lycopsids and ferns and all of them have been found to be distinct from the contemporary Euramerian plants. It is thus quite logical to assume that the Carboniferous antecedents of Gondwana Lycopsids and fern-like plants could also be different in some way (Surange, 1966, p. 164) from the Euramerian. In the Angara, similar results have been reached through critical analysis of the lower Carboniferous Lycopsids which were some time ago referred to Euramerian taxa (Chaloner & Meyen, 1973). We may therefore bear some caution in our minds even as we have to presently accommodate the southern Lower Carboniferous flora within the Arcto-Carboniferous realm.

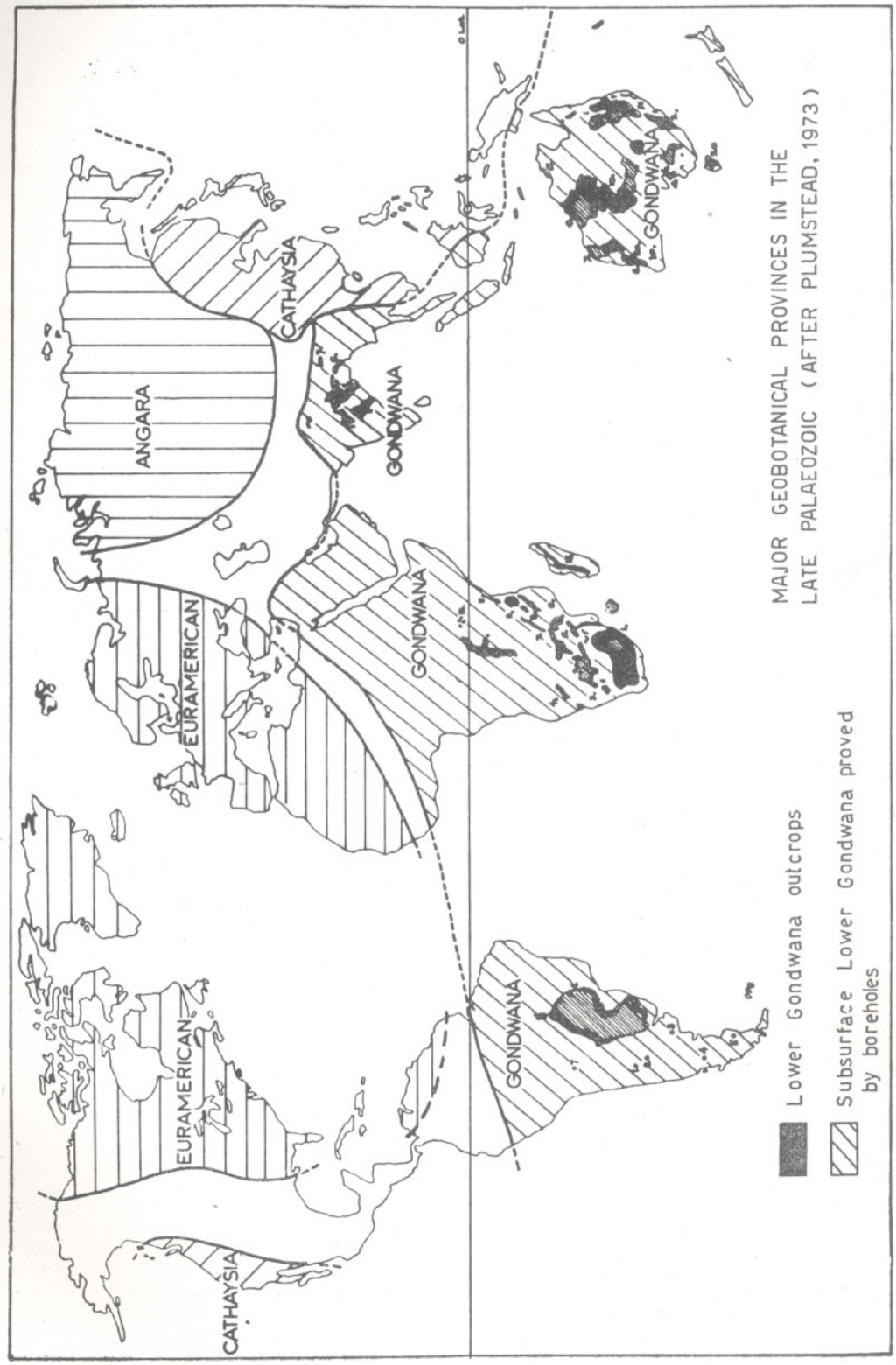
## PERMIAN FLORAS

The transition from the Carboniferous to the Permian marks an extraordinary episode in the geological and biological history of the two hemispheres. The main floral provinces of Eurameria, Angara, Cathaysia and Gondwana became sharply different from each other (Text-fig. 1). In the northern hemisphere the climate became warm and arid, the coal-swamp vegetation of the Carboniferous began to shrink and large areas were laid barren. On the contrary, the Carbo-Permian transition in Gondwanaland witnessed extensive glaciation which had already wiped away the last vestiges of the Arcto-Carboniferous flora. In the wake of glaciation a unique vegetation — the Glossopteris flora arose over the southern Gondwana lands and spread out far and wide with subsequent amelioration of climate in the Permian. The amazingly parallel development of the Glossopteris flora in space and time over Gondwanaland is a strong basis for the assumption that the southern continents including India were formerly close together permitting free intermigration of plants (Sahni, 1939; Schopf, 1970; Plumstead, 1970).

### India and Gondwanaland

In India, the Glossopteris flora is richly preserved in the Lower Gondwana formations which include the Talchir, Karharbari, Barakar, Barren Measure and Raniganj Formations in ascending order. The Lower Gondwana is typically developed in a series of basins in the Damodar Valley (Bengal) as well as in the Son-Mahanadi Valley and Narbada Valley. Extra-Peninsular occurrences are in Kashmir, Kumaun Hills, Nepal, Bhutan, Sikkim, Darjeeling and as far as Assam in the north east indicating the northern border of Gondwana during the late Palaeozoic (Jacob, 1952; Jacob & Banerjee, 1954; Gansser, 1964; Acharya, 1973). The base of the Peninsular Lower Gondwana is characterised by glacial or fluvio-glacial boulder beds (Carbo-Permian) which also carry miofloral counterparts of the Glossopteris flora (Lele & Karim, 1971; Lele & Chandra, 1973). In the Lower Permian (Talchir-Karharbari) the flora is dominated by *Gangamopteris* and *Noeggerathiopsis* while in the Upper Permian, (Barakar-Raniganj) *Glossopteris* is dominant. This is also paralleled by the dominance of monosaccate moispores in the Lower Permian and of disaccates in the Upper Permian (Lele, 1966).

In the Peninsular India, the Glossopteris flora is dominated by *Glossopteris* (45 spp.), and allied genera *Gangamopteris* (22 spp.), *Vertebraria*, *Rubidgea*, (2 spp.), *Palaeovittaria* (2 spp.), *Rhabdotaenia* (3 spp.) and probably *Pteronilssonia* (Maithy, 1974c; Chandra, 1974). Recent discoveries in India (Surange & Chandra, 1975 and references cited therein) of an amazing variety of fructifications found in association with or rarely attached to *Glossopteris* show beyond doubt that the Gondwanaland Glossopterids bore very unique types of male and female reproductive organs — the like of which is unknown in the northern hemisphere. The new group, Glossopteridales as now defined by Surange and Chandra (1975) includes naked, seed-bearing fructifications like *Dictyopteridium*, *Scutum*, *Ottokaria* and *Senotheca* which are known from several parts of Gondwa-


ANGARA
CATHAYSIA
GONDWANA
EURAMERICAN
GONDWANA
GONDWANA
EURAMERICAN
CATHAYSIA
MAJOR GEOBOTANICAL PROVINCES IN THE
LATE PALAEOZOIC (AFTER PLUMSTEAD, 1973)
Lower Gondwana outcrops
Subsurface Lower Gondwana proved by boreholes

TEXT-FIG. 1

naland. Apart from these there is a wide variety of cupulate pollen-bearing organs (*Eretmonia*, *Glossotheca* and *Kendostrobus* with monolete spores) as well as female cupulate structures (*Denkania*, *Partha* and *Lidgettonia*). The cupulate types resemble those of the northern families like Lyginopteridaceae, Coristospermaceae and Peltaspermaceae, but they can not be assigned to any one of these families. The cupulate types are provisionally accommodated within the Pteridosperms. More recently *Glossopteris* leaves have been found attached to divergent types of stems which accentuates the great diversity of these plants (Pant & Singh, 1974).

Some of these fructifications, e.g. *Cistella*, *Ottokaria*, *Lanceolatus*, *Dictyopteridium*, are widely known in other Gondwana countries (Table 2). *Eretmonia* and *Lidgettonia* are common to India and S. Africa, while *Hirsutum*, *Pluma* and *Vannus* are restricted to S. Africa. Several other fructifications whose affinities are still uncertain also occur in different parts of Gondwanaland (Table 2).

The Arthrophytes and ferns or fern-like plants stand next in significance and mostly occur in the later Permian. Among the Arthrophytes, *Phyllotheca* (5 spp. in India) is widely distributed in Gondwana countries (total 15 spp.). Of these, *P. australis* (including a closely allied species *P. indica*) is ubiquitous. *Schizoneura*, especially *S. gondwanensis* is also common in Gondwana and has a wide vertical range. *Stellotheca* possibly occurs also in Australia while several other plants (*Calamites*, *Annularia*, *Asterophyllites*, *Asterocalamites*) from S. America and S. Africa are suspected to belong to some southern Equisetales including *Stellotheca* (Surange, 1966). *Trizygia* is widely represented by *T. speciosa*. The probable Arthrophytes like *Raniganjia* and *Barakaria* are still not enough well-known. *Raniganjia* is also widely known outside India. *Barakaria* is particularly rare in India. *Gondwanophyton* — a probable Arthrophyte — has newly been discovered (Maithy, 1974b).

The Indian and other Gondwana ferns were so far referred to northern form genera like *Sphenopteris*, *Pecopteris*, *Alethopteris* and *Ptychocarpus*. Critical exomorphic and fructification studies of this complex has now been done in India by Maithy (1974, 1974a, 1975) and Pant and Khare (1974) which reveal that the Gondwana ferns are distinct which have now been placed under new taxa like *Neomariopteris* and *Damudopteris* (former *Sphenopteris*), *Dichotomorpteris* (former *Pecopteris*, and *Ptycocarpus*) or under southern taxa like *Dizeugotheca* (former *Alethopteris*). All these ferns seem to be widespread in Gondwana but critical studies in other countries of these and other genera like *Asterotheca* are warranted (Plumstead, 1973). Some of this fern foliage was apparently borne on the stems of *Palaeosmunda* Gould (1970), an australian plant. Such fern stems are not yet known in India. Among the Fern/Pteridosperms *Gondwanidium* (now *Botrychiopsis*) is an important common link between different parts of Gondwanaland. Other plants like *Angiopteridium*, *Caulopteris*, *Paranotheca*, *Merianopteris*, *Belemnopteris* etc. are somewhat peculiar in their distribution on Gondwana countries (Table 2).

In the Lower Permian of India, leaves of Cordaitalean appearance are represented by *Noeggerathiopsis* (10 spp.) and *Euryphyllum*. The former genus was originally discovered in the Upper Permian material and similar leaves seem to persist in the Triassic. *Noeggerathiopsis hislopi* is widespread on Gondwanaland.

Lycopsids are extremely poorly represented in Gondwanaland by the genera *Cyclodendron*, *Lycopodiopsis* and *Lycopodiophlois* Of these, *Cyclodendron lesleii* occurs in India, S. Africa and Australia. *Lycopodiopsis* is known from S. Africa, S. America while *Lycopodiophlois* is not known outside S. Africa. Recently *Eligodendron* is described from Bolivia (Archangelsky & de la Sota, 1966). A fossil *Selaginella* species has recently been found in Australia (Townrow, 1968). More intensive studies on the Gondwana lycopods is still desirable (Plumstead, 1973, 1973a; Archangelsky & Arondo, 1969).

All the Gondwana Permian conifers are also distinct from those of the north (Pant, 1975). The taxa are few but all of them are represented in India by *Paranocladus*, *Buriadia* and *Walkomiella* in the Talchir, Karharbari and Barakar formations respectively. The absence of former two conifers from Australia is somewhat striking. Ginkgophytes are represented by *Rhipidopsis* and *Platyphyllum*, (Maithy, 1974b) which occur in peninsular part sporadically and

**TABLE 2 — DISTRIBUTION OF GLOSSOPTERIS FLORA (CARBO-PERMIAN) IN GONDWANALAND. RECORDS INDICATED BY * NEED FURTHER CRITICAL STUDY. I (INDIA), A (AUSTRALIA & TASMANIA), S. Af. (SOUTH AFRICA), S. Am. (SOUTH AMERICA), An. (ANTARCTICA)**

| GENERA | I | A | S. Af. | S. Am. | An. |
|---|---|---|---|---|---|
| Glossopteris | + | + | + | + | + |
| Vertebraria | + | + | + | + | + |
| Noeggerathiopsis | + | + | + | + | + |
| Gangamopteris | + | + | + | + | + |
| Phyllotheca | + | + | + | + | + |
| Botrychiopsis | + | + | + | + | |
| Raniganjia | + | + | + | + | |
| Schizoneura | + | + | + | + | |
| Cyclodendron | + | + | + | + | |
| Walkomiella | + | + | + | + | |
| Lycopodiopsis | | + | + | + | |
| Trizygia | + | + | + | + | |
| *Pecopteris | | + | + | + | |
| Palaeovittaria | + | | + | + | + |
| Cistella (Plumsteadia) | + | + | + | + | |
| Scutum | + | + | + | + | + |
| Ottokaria | + | ? | + | + | |
| Arberia | + | | + | + | + |
| Rhabdotaenia (Taeniopteris) | + | ? | + | + | |
| Lanceolatus | + | | + | + | |
| Lidgettonia | + | + | + | | |
| Dictyopteridium | + | + | + | | |
| Buriadia | + | | + | + | |
| *Psygmophyllum | | + | + | + | |
| *Ginkgoites | ? | + | + | + | |
| Lycopodiophloios | | + | | + | |
| Stellotheca | + | + | | | |
| *Annularia | | | + | + | + |
| Samaropsis | + | + | + | + | |
| Arberiella | + | + | + | + | + |
| Cordaicarpus | + | + | + | | + |
| Carnucarpus | + | | + | + | + |
| Scale leaves | + | + | + | + | + |
| *Asterotheca (fertile) | | | + | + | |
| *Alethopteris/Cladophlebis | | + | + | | |
| *Lepidodendron | + | | | + | |
| Dizeugotheca | + | | | + | |
| Hirsutum | | + | + | | ? |
| Pseudoctenis | + | + | | | |
| Sphenophyllum | | | + | + | |
| Eretmonia | + | | + | | |
| Rubidgea | + | + | + | | |
| *Voltzia | ? | | + | ? | |
| Paranocladus | + | | | + | |
| Rhipidopsis | + | | | + | |
| Merianopteris | + | | | + | |
| *Baiera | | + | | ? | |
| Neomariopteris | + | | | | |
| Euryphyllum | + | | | | |
| Damudopteris | + | | | | |
| Belemnopteris | + | | | | |
| Dichotomopteris | + | | | | |
| Anthrophyopsis | + | | | | |
| Senotheca | + | | | | |
| Ginkgophyllum | + | | | | |
| Gondwanophyton | + | | | | |
| Stereocarpus | + | | | | |
| Senia | + | | | | |

*Contd.*

**TABLE 2 — DISTRIBUTION OF GLOSSOPTERIS FLORA (CARBO-PERMIAN) IN GONDWANALAND. RECORDS INDICATED BY * NEED FURTHER CRITICAL STUDY. I (INDIA) A (AUSTRALIA & TASMANIA), S. Af. (SOUTH AFRICA), S. Am. (SOUTH AMERICA), An. (ANTARCTICA)**

| GENERAL | I | A | S. Af. | S. Am. | An. |
|---|---|---|---|---|---|
| Alatocarpus | + | | | | |
| Pteronilssonia | + | | | | |
| Palmatophyllites | + | | | | |
| Palaeosmunda | | + | | | |
| Ginkgophyton | | + | | | |
| Caulopteris | | + | | | |
| Selaginella | | + | | | |
| Pluma | | | + | | |
| Lerouxia | | | + | | |
| Jongmansis | | | + | | |
| Plumsteadiella | | | + | | |
| Vannus | | | + | | |
| *Zeilleria | | | + | | |
| *Callipteridium | | | + | | |
| Belightfootia | | | + | | |
| Magistophyllum | | | | + | |
| *Psaronius | | | | + | |
| Eremopteris | | | | + | |
| Chiropteris | | | | + | |
| Derbyella | | | | + | |
| *Walchia | | | | + | |
| Cyclopitys | | | | + | |
| Abeitopitys | | | | + | |
| *Brachyphyllum | | | | + | |
| Eligodendron | | | | + | |
| Paranotheca | | | | + | |
| Nummulospermum | | | | + | |
| Eucerospermum | | | | + | |
| Genoites | | | | + | |

are also equally uncommon on Gondwanaland. *Ginkgophyllum* (former *Psygmophyllum*) occurs only in extra-peninsular Kashmir (Maithy, 1974b). Similar plants (*Psygmophyllum* and *Ginkgoites*) are also found in most Gondwana lands but they need more critical study.

A number of probably Glossopteridean leaves irregularly occur in different parts of Gondwanaland, e.g. *Chiropteris, Anthrophyopsis, Megistophyton* and *Belightfootia* etc. (Table 2). Seeds (*Samaropsis, Cordaicarpus, Carnucarpus*) are common in Gondwana countries. Sporangia like *Arberiella* are also widely known.

## NORTHERN HEMISPHERE

*Eurameria* — Unlike the Gondwana, in the Euramerian area the Carboniferous plants continued into the Permian although on a reduced scale. The same groups prevailed, viz., Lycopsids (*Sigillaria*), Arthrophytes (*Sphenophyllum, Calamites*), Ferns/Pteridosperms (*Odontopteris, Alethopteris, Neuropteris, Pecopteris, Taeniopteris* etc.), and Cordaitales (*Cordaites* etc.). Conifers (*Lebachia, Ernestiodendron*) were subordinate. *Callipteris* — a pteridosperm marked the beginning of the Permian. In the Upper Permian additional Arthrophytes (*Neocalamites*), Pteridosperms (*Lepidopteris*), Cycadophytes (*Pseudoctenis, ?Taeniopteris*), conifers (*Ullmannia, Pseudovoltzia*) and Ginkgopsids (*Sphenobaiera*) became characteristic. In the south western part of north America the Permian flora showed differentiation from the Euramerian flora by the appearance of *Glenopteris, Supaia, Protoblechnum* and *Gigantopteris* (Chaloner & Meyen, 1973).

Most of the Euramerian taxa are absent in the Gondwana. True Calamitales are not known in India and probably in Gondwanaland (Surange, 1966; Pant, 1975).

Contrarily, the Equisetales are endemic to Gondwana and so are the conifers and lycopsids (Edwards, 1952; Surange, 1966 & other references therein; Pant, 1975). All the Indian and some Gondwana ferns are now shown to be distinct from Euramerian forms. The remaining few will probably also prove to be different when they are more completely known. The Gondwana Cordaitales are also suspected to be different from the Euramerian, as is reflected by the epidermal structure and leaf morphology of the southern *Noeggerathiopsis* leaves (Lele & Maithy, 1964a; Pant & Verma, 1964; Surange, 1971). Besides it is important to note that (1) the Lower Permian climatic background and time-dominance of *Noeggerathiopsis* is distinct from that of *Cordaites* (2) no cordaitalean wood is found in *Noeggerathiopsis* — bearing Lower Permian beds. Most woods in India occur in the Upper Permian in association with *Glossopteris* (3) *Cordainthus* — like fructifications are not found in Gondwanaland. (4) True *Cordainthus*-type of pollen (*Florinites*) is virtually absent in *Noeggerathiopsis* — dominated Lower Permian strata. Contrarily, *Noeggerathiopsis* is associated intimately with organizationally distinct monosaccate pollen like *Plicatipollenites* and *Parasaccites* (Lele, 1966). These facts strengthen the assumption that the Gondwana plants were of a different kind, although their leaf-patterns are superficially comparable with northern *Cordaites*.

*Angara* — In the Angara region several endemic Carboniferous plants continued into the Permian (*Paragondwanidium, Angaridium, Angaropteridium*). New Permian elements were the lycopods *Viatscheslavia, Angarodendron, Demetria, Paichoia* and *Tundrodendron*, large Cordaites leaves and *Rufloria*, the Sphenospsids *Tschernovia, Annularia, Annulina, Phyllopitys* and the, Arthrophytes *Paraschizoneura* and *Umbellaphyllites*. Plants like *Zamiopteris* and the fructification *Vojnovskya* are also important. Towards the later Permian there were ferns like *Prynadaeopteris*, Pteridosperms like *Callipteris, Comia, Comsopteris, Tatarina* etc., several species of the Ginkgophytes *Rhipidopsis, Baiera, Ginkgophyllum* and *Dicranophyllum*, other gymnosperms like *Phylladoderma* and *Zamiopteris* and mosses-like *Intia* and *Polyssaievia*. The Angara flora shows regional differentiation within its own realm. Euramerian floral elements intermingle with those of the Angara along the western border while the Cathaysian influence is reflected in the Angara flora along its eastern contact with Cathaysia, (Kon'no, 1966; Chaloner & Meyen, 1973).

The Angara flora, as we can see from the above account, is mainly dominated by Arthrophytes, Pteridosperms, Ginkgophytes and Cordaitales. Among the Arthrophytes most are sphenopsid plants none of which occur in Gondwana. The cuticle of the Angara *Trizigia* is not known for comparison with Indian forms of *T. speciosa* and their placing under *Trizygia* is open (Meyen, 1969). The Gondwana Equisetalean taxa, are, on the other hand absent in the Angara (Surange, 1966, 1971; Meyen, 1969) *Barakaria* — a probable Sphenopsid — is possibly the only link between Angara and Gondwana floras. However, the Indian records are scanty and poorly known. The Angara *Barakaria* forms are better known from epidermal and morphological features but fructification evidence is lacking in all cases which does not solve the problem of real affinities. The Gondwana records of Angara plant *Umbellaphyllites* are now referable to *Raniganjia* (Meyen, 1969; Pant, 1975).

Most of the Angara Pteridosperms belong to Peltaspermaceae — a family not represented in the Permian of Gondwana. The possible Pteridosperms in the Glossopteris flora have distinct fructifications which can not be placed under Peltaspermaceae (Surange & Chandra, 1975). *Glossopteris* and *Gangamopteris* plants — referred to Glossopteridales — are the dominant class on Gondwana. The Angara records of *Glossopteris* and *Gangamopteris* have mostly been disproved (Meyen, 1969) and the few scarce records in the far Eastern Angara do not in themselves carry much weight. It is important to bear in mind that Glossopteroid net venation is shared by plants of different groups at different geological times (Alvin & Chaloner, 1971). What is more, we now difinitely know that a stereotype *Glossopteris* foliage is related to very divergent kinds of fructifications as well as stems (Surange & Chandra 1975; Pant & Singh, 1974). In view of this it is absolutely essential to obtain fructification and/or structural evidence of attached axes in the case of Angara and other northern Glossopteroid foliage to decide their

botanical and phytogeographical affinities (Pant, 1975).

As regards the Angara Cordaitales, quite a large proportion of these have been referred to the new genus *Rufloria* Meyen which is absent in India (Meyen, 1969). *Cordaites* also occurs in Angara which in the absence of cuticular evidence is indistinguishable from Euramerian forms. At epidermal level, a substantial part of Gondwana *Noeggerathiopsis* would seem to be distinct from Angara *Cordaites* (Meyen, 1969). The points that support the retention of *Noeggerathiopsis* have already been outlined earlier.

The Angara conifers are rare as in the case of Gondwana. However, there is no common point between the two.

The Ginkgopsid flora is an important part of the Angara Permian, unlike the Gondwana. *Rhipidopsis* — the only common genus, is poorly known in India by *R. gondwanensis*. The other species (*R. densinervis*) is now transferred to *Platyphyllum* (Maithy, 1974b). The wide-spread Angara species *R. ginkgoides* is probably absent in Gondwana (Meyen, 1969). The Extra-Peninsular records of *Psygmophyllum* seem to bear no relation with Northern pinnate Psygmophyllums, and have been accommodated under *Ginkgophyllum* (Maithy, 1974b).

*Cathaysia* — In the Cathaysian province, although some Carboniferous plants lingered into the Permian, the scarcity of Lycopsids and the absence of *Sigillaria* is striking. The Cathaysian province became well-marked by Upper Permian. The flora is characterised by dominance of Arthrophytes (*Lobatannularia, Tingia, Sphenophyllum, Neocalamites, Manchuriostachys*), Pteridosperms (*Emplicopteris, Callipteris, Gigantopteris, Cathaysiopteris*), fern-like foliage, (*Cladophlebis, Pecopteris, Alethopteris, Odontopteris* etc), Ginkgophytes (*Sphenobaiera, Baiera, Ginkgoites, Psygmophyllum*) and Cycadophytes (*Taeniopteris*).

*Gigantopteris, Cathaysiopteris, Tingia* and *Lobatannularia* are peculiar to the Cathaysian flora as are *Glossopteris-Gangamopteris* for the Gondwana. These plants are mutually exclusive as far as the main realms of Cathaysia and Gondwana are concerned. Such dominance of Arthrophytes, Ferns/ Pteridosperms and Ginkgophytes as in Cathaysia is nowhere observed in Gondwana.

The only common plants between Cathaysia and Gondwana are *Schizoneura, Rhipidopsis, Palaeovittaria* and *Glossopteris*. However, now the Cathaysian *Schizoneura* leaves and its fructification (*Manchuriostachys*) are both found to differ in important respect from the Gondwana *Schizoneura* (Asama, 1969). Similarly the incidence of *Rhipidopsis* in Gondwana and of *Palaeovittaria* and *Glossopteris* in Cathaysia is too insignificant and their knowledge is very incomplete to be of any real phytogeographic importance (Kon'no, 1966).

*Sphenophyllum* in Cathaysia is very abundant and diverse (Trizygoid and non-Trizygoid). In India and Gondwana however, the only widespread species (*Sphenophyllum speciosum*) is trizygoid and its fructification is unknown. Contrarily the Euramerian *Sphenophyllum* is mostly non-trizygoid and has very elaborate reproductive structures. Until fructifications are also found in Gondwana it would be better to retain our Sphenophyllums under *Trizygia* (Maheshwari, 1963; Asama, 1969).

## TRIASSIC FLORAS

### India and Gondwanaland

The Indian Triassic deposits are mostly arenaceous, ferruginous and generally devoid of coal. This indicates extensive land conditions and general aridity. Similar conditions existed in the Permian of the northern hemisphere and continued into the early Trias. The sequence is composed of the Panchet, Pachmarhi and Maleri stages which together constitute the Middle Gondwana. Plant fossil localities are few and the flora is not as rich as in other parts of Gondwanaland. The type area (Satpura Basin) is nearly devoid of plants. The main information is based on floras collected from the Panchet of the Raniganj (Bengal) and Auranga coalfields (Bihar), from the Parsora Formation and Nidpur beds in South Rewa Basin (M.P.) and from the Maleri Beds of Andhra Pradesh (Lele, 1964; Bose, 1974; Anderson & Anderson, 1970). In most places fossils are preserved in ferruginous or non-coaly beds except in Nidpur where carbonised plants are now known.

The Triassic plant assemblages in India and all over Gondwanaland are character-

ised by the Pteridosperms *Dicroidium* and *Lepidopteris* and the flora is hence recognised as the Dicroidium Flora. In India about 7 species of *Dicroidium* (Corystospermaceae) and one species of *Lepidopteris* (Peltaspermaceae) are known.

In the lower part (Panchet) *Lepidopteris* and/or *Dicroidium* are scarce and often outnumbered by *Glossopteris* and other hardly survivers from the Permian (Lower Gondwana) including ferns like *Neomariopteris*, Equisetales like *Schizoneura* and Glossopterids like *Rhabdotaenia*. Higher up in the Nidpur beds (Lower-Mid. Trias), *Dicroidium* (usually unforked) and *Lepidopteris* become abundant together with *Pteruchus*, *Nidia*, *Satsangia* and other gymnospermous fructifications like *Nidistrobus* and scale leaves of *Glottolepis*. Some *Podozamites* and Permian survivers like *Rhabdotaenia*, *Glossopteris* and *Noeggerathiopis* are also known. The later Triassic Parsora Formation (near Parsora and Beli localities) contains three species of *Dicroidium*, including *D. hughesi*, which are not known in lower horizons of Trias (Lele, 1964). Associated with these are *Lycopodites*, *Neocalamites* (leaf-less) *Cladophlebis*, *Parsorophyllum*, *Marattiopsis*, *Danaeopsis*, *Pterophyllum*, *Pseudoctenis*, *Taeniopteris*, *Baiera Desmiophyllum* and *Araucarites*. Megaspores impressions and seeds (*Samaropsis*, *Cordaiocarpus*) are also abundant locally. *Glossopteris* and typical *Noeggerathiopsis* is very rare although strap-shaped leaves with parallel venation are locally common. The flora needs further exploration to know the plant entities more precisely (Bose, 1974).

In other Gondwana countries (esp. Australia, S. Africa, and S. America) the *Dicroidium* flora is better developed (Table 3). Some plants are now also known from Antarctica. A synthesis of the Triassic flora as given by Anderson and Anderson (1970) shows that at least 25 species of *Dicroidium* are represented in Gondwanaland Trias. This high content of *Dicroidium* has apparently resulted from the more comprehensive concept of the genus in the treatment of Anderson and Anderson. There can, however, be little doubt that *Dicroidium*, even if more closely circumsribed, would stand out prominently in the Triassic Gondwana flora. *Dicroidium odontopteroides* is ubiquitous and *D. feistmanteli*, *D. lancifolium*, *D. coriacium*, *D. narrabeenensis* etc. are also common. *D. hughesii* (including *Danaeopsis hughesii*) is widely known and is an important constituent of the Indian flora.

The other Pteridosperms *Lepidopteris*, *Pachypteris*, *Hoegia* and *Zuberia* are also significantly present in all parts of Gondwanaland. *Lepidopteris stormbergensis* is most widely known. Common Gondwana ferns are *Dictyophyllum*, *Asterotheca* and *Cladophlebis*. There are about 6 species of *Cladophlebis* in Australia, 4 in S. Africa and 16 in S. America. *Pecopteris* and *Todites* occur in Australia while Dipterids like *Thaumatopteris*, *Hausmannia* and *Clathropteris* and other ferns like *Chansitheca* and *Acrocarpus* are present only in S. America. In the fern/pteridosperm complex *Chiropteris* and *Kurtziana* are more wide-spread. *Sphenopteris*, *Neuropteridium*, *Alethopteris*, *Zeugophyllites* and *Hymmenophyllites* occur in Australia. *Harringtonia* is apparently confined to South America while *Odontopteris* is found in S. Africa only. Among the Cycadophytes, *Pseudoctenis* is widely represented in S. Africa (10 spp.), and S. America, while *Anomozamites* and *Ptilozamites* in S. America. *Taeniopteris* is represented by 10 species in Australia and 7 species each in S. Africa and S. America. Among the Ginkgophytes *Baiera* and *Ginkgoites* and widespread and abundant, the latter represented by 4 species in S. Africa, 2 in S. America and 10 in Australia. *Sphenobaiera* is also present. *Baierophyllites*, *Czeckanowskia*, *Saportaea*, *Ginkgoidium* and *Cardiopteridium* are present only in S. America. *Rhipidopsis* is not known outside S. Africa. Among the few conifers, *Rissikia* occurs in S. Africa while *Voltziopsis* is found in S. America. Australia has both plants Arthrophytes like *Neocalamites* are better known in S. Africa (4 spp.) and S. America (4 spp.). *Equisetites* is also commonly found. Lycopods are known only from Australia by *Lycostrobus* and *Caulopteris*. *Glossopteris* (esp. *G. verticellata*) persists in most parts, sometimes with *Phyllotheca*/*Schizoneura* and *Noeggerathiopsis*-like leaves. Among the plants of uncertain affinities, *Yabiella* is significantly represented by a striking number of species in S. America (7), Australia (4) and S. Africa (2). *Phoenicopsis* is also common. *Rhexoxylon* woods occur significantly in S. Africa as well as S. America. *Rienitsia* occurs in

**TABLE 3 — DISTRIBUTION OF IMPORTANT ELEMENTS OF THE DICROIDIUM FLORA (TRIASSIC) IN GONDWANALAND COUNTRIES AND NORTHERN HEMISPHERE. I (INDIA), A (AUSTRALIA), S. Af. (SOUTH AFRICA), S. Am. (SOUTH AMERICA), An. (ANTARCTICA), N.H. (NORTHERN HEMISPHERE). DATA MOSTLY DERIVED FROM BOCK (1969), ANDERSON & ANDERSON (1970) AND STIPANICIC & BONETTI (1970)**

| N.H. | Genera | I | A | S. Af. | S. Am. | An. |
|---|---|---|---|---|---|---|
| | Dicroidium | + | + | + | + | + |
| + | Lepidopteris | + | + | + | + | |
| + | Sphenopteris | + | + | + | + | |
| + | Neocalamites | + | + | + | + | |
| + | Cladophlebis | + | + | + | + | |
| + | Pseudoctenis | + | + | + | + | |
| + | Pterophyllum | + | + | + | + | |
| + | Baiera | + | + | + | + | |
| | Glossopteris | + | + | + | + | |
| + | Taeniopteris | + | + | + | + | |
| + | Ginkgoites | | + | + | + | |
| + | Phoenicopsis | | + | + | + | |
| + | Yabiella | | + | + | + | |
| + | Equisetites | | + | + | + | |
| | Noeggerathiopsis | + | | ? | | + |
| | Pteruchus | | + | + | | + |
| + | Schizoneura | + | + | + | | |
| | Phyllotheca | | + | + | + | |
| + | Podozamites | + | + | | + | |
| + | Sagenopteris (Phyllopteris) | | + | + | + | |
| + | Desmiophyllum | + | | + | + | |
| | Rissikia | | + | + | | + |
| + | Ctenis | | + | | + | |
| + | Czeckanowskia | | + | | + | |
| | Linguifolium | | + | | + | |
| + | Nilssonia | | | + | + | |
| + | Dictyophyllum | | | + | + | |
| + | Pachypteris | | | + | + | |
| | Umkomassia | | | + | + | |
| + | Chiropteris | | | + | + | |
| + | Elatocladus | | | + | + | |
| | Voltziopsis | | | + | + | |
| + | Brachyphyllum | | + | | | + |
| + | Williamsonia | | + | | | + |
| + | Sphenobaiera | | | + | + | |
| + | Asterotheca | | | + | + | |
| | Kurtziana | | | + | + | |
| | Rhexoxylon | | | + | + | |
| + | Danaeopsis | + | | + | | |
| + | Marattiopsis | + | | + | | |
| | Stenopteris | | + | + | | |
| | Conites | + | | + | | |
| + | Conipteris | | + | | + | |
| + | Araucarites | + | + | | + | |
| | Rhabdotaenia | + | | | | |
| | Glottolepis | + | | | | |
| | Nidistrobus | + | | | | |
| | Satsangia | + | | | | |
| | Vertebraria | + | | | | |
| | Cyclopteris | + | | | | |
| | Samaropsis | + | | | | |
| + | Lycopodites | + | | | | |
| | Cordaicarpus | + | | | | |
| | Parsorophyllum | + | | | | |
| + | Lycostrobus | | + | | | |
| + | Caulopteris | | + | | | |

*Contd.*

**TABLE 3 — DISTRIBUTION OF IMPORTANT ELEMENTS OF THE DICROIDIUM FLORA (TRIASSIC) IN GONDWANALAND COUNTRIES AND NORTHERN HEMISPHERE. I (INDIA), A (AUSTRALIA), S. Af. (SOUTH AFRICA), S. Am. (SOUTH AMERICA), An. (ANTARCTICA), N.H (NORTHERN HEMISPHERE). DATA MOSTLY DERIVED FROM BOCK (1970), ANDERSON & ANDERSON (1970) AND STIPANICIC & BONETTI (1970)**

| N.H. | GENERA | I | A | S. Af. | S. Am. | An. |
|---|---|---|---|---|---|---|
| + | Todites | | + | | | |
| | Hymmenophyllites | | + | | | |
| | Zeugophyllites | | + | | | |
| | Rhipidopsis | | + | | | |
| | Cyclostrobus | | + | | | |
| + | Doratophyllum | | + | | | |
| + | Fraxinopsis | | + | | + | |
| | Psygmophyllum | | + | | | |
| | Hoegia | | + | | + | |
| | Frenolepis | | + | | | |
| + | Hepaticites | | + | | | |
| | Muscites | | + | | | |
| + | Pachypteris | | + | | | |
| + | Cycadopteris | | + | | | |
| + | Otozamites | | + | | | |
| | Sphenozamites | | + | | | |
| | Leptostrobus | | + | | | |
| + | Anthrophyopsis | | + | | | |
| + | Voltzia | | | + | | |
| + | Odontopteris | | | + | | |
| | Strobilites | | | + | | |
| | Stormbergia | | | + | | |
| | Antevsia | | | + | | |
| | Peltaspermum | | | + | | |
| | Pilophorosperma | | | + | | |
| | Spermatocodon | | | + | | |
| + | Zamites | | | + | | |
| | Moltenia | | | + | | |
| | Dadoxylon | | | + | | |
| + | Stachyopitys | | | + | | |
| + | Neuropteridium | | | + | | |
| | Cyparissidium | | | + | | |
| | Cupressinocladus | | | + | | |
| | Rienitsia | | | + | | |
| + | Eoginkgoites | | | | + | |
| | Feruglioa | | | | + | |
| + | Thallites | | | | + | |
| + | Pelourdea | | | | + | |
| | Sphenolepis | | | | + | |
| + | Cycadocarpidium | | | | + | |
| + | Anomozamites | | | | + | |
| | Ginkgoidium | | | | + | |
| | Cardiopteridium | | | | + | |
| | Baierophyllites | | | | + | |
| | Saportaea | | | | + | |
| | Chansitheca | | | | + | |
| + | Hausmannia | | | | + | |
| + | Acrocarpus | | | | + | |
| + | Thaumatopteris | | | | + | |
| | Sphenopteridium | | | | + | |
| | Kopiapaea | | | | + | |
| + | Ptilozamites | | | | + | |
| | Annulariopsis | | | | + | |
| + | Barrealia | | | | + | |
| | Lepidanthium | | | | + | |

Australia and S. Africa while *Linguifolium* is found in S. Africa and S. America. Taxa apparently confined to S. America are *Lesleya, Copiapeae* and *Desmiophyllum.*

A comparative look at these southern floras (Table 3) will easily reveal that the chief floral links between India and other Gondwana components rest largely on the Pteridosperm families — Corystospermaceae (*Dicroidium, Pteruchus* etc.) and Peltaspermaceae (*Lepidopteris*). However, in respect of other plant groups, which are no less significant in the Dicroi ium flora, the Indian share is extremely small as compared to Australia, S. Africa and S. America. For instance, all the Dipteridaccous ferns and *Chiropteris* are absent in India but shared well by other components especially S. America. Cycadophytes are comparatively richer in S. Africa and S. America than in Australia but the Indian records are still very scanty. *Ginkgophytes* are more diverse and abundant in S. America than in S. Africa and Australia, but in India Ginkgoalean records are almost negligible. Conifers are rare on Gondwanaland in general, but the few genera (*Voltziopsis* and *Rissikia*) are significantly present in most parts except in India where conifers are indeed, very imperfectly known. As to the Lycopsids there is some evidence from India and Australia but this group is on the whole poorly developed on Gondwanaland.

## Northern Hemisphere

In the northern hemisphere the Permian desiccation apparently touched its peak in the Lower Triassic as evidenced by the continental facies.

*Eurameria* — Unlike the Gondwana the change in the flora is more well-marked at the base of the Upper Permian in Eurameria when the earlier Lycopsids, Sphenophylls and almost all ferns and Pteridosperms disappered due to sudden increase in aridity (Vakhrameev, 1973). The Gymnosperms which took over the position of dominance were represented by Cycadophytes like *Taeniopteris, Pseudoctenis,* Ginkgophytes like *Sphenobaiera* and conifers like *Pseudovoltzia* and *Ullmannia. Neocalamites* also appeared.

In the early Triassic there were Lycopsids (*Pluromeia*). Pteridopserms (*Neuropteridium, Lepidopteris*), conifers (*Pseudovoltzia, Ullmannia, Albertia*) broad *Cordaites* and *Yuccites* leaves along with some Ginkgophytes (*Sphenobaiera*). In later Triassic and Rhaetic, with the return of more favourable climate, the flora became more diversified in Arthrophytes (*Neocalamites*), ferns (*Dictyophyllum, Thaumatopteris, Hausmannia, Clathropteris, Todites* etc.), ferns/Pteridosperms (*Psaronius, Cladophlebis, Asterotheca*), Peteridosperms (*Callipteridium Lepidopteris, Stenopteris, Thinnfeldia*), Cycadophytes (*Pterophyllum, Nilssonia, Pseudoctenis, Anomozamites, Ptilozamites, Wielandiella Taeniopteris,* etc.), Ginkgophytes (*Ginkgoites, Baiera, Czeckanowskia*), conifers (*Sagenopteris*). The aspects of the later Triassic and Rhaetic floras are decidely closer to the Jurassic floras than to the early Triassic flora. General distribution of Triassic flora is given by Bock (1969).

*Angara* — Unlike Eurameria, climate in Angara was more favourable (humid) even in the Permian and continued to be so in the Triassic (Vakhrameev, 1973). In the Triassic several Mesozoic forms of ferns (*Acrostichides, Todites, Phlebopteris, Cladophlebis, Tudovakia*) Peltasperms (*Tatarina*), Ginkgophytes (*Rhipidopsis, Glossophyllum, Sphenobaiera*) and conifers (*Araucarites, Pseudoaraucarites*) and *Imamia* (standing between *Sagenopteris* and *Scorsbya*, see Krassilov & Schorochova, 1970) flourished. The floral aspect was not very different from the Euramerian.

*Cathaysia* — In the Cathaysian area also a similar uniformity in the floral texture was developed during the Triassic. In the region of China, Tonkin and Japan, for instance, there were similar Arthrophytes, ferns/Pteridosperms, Cycadophytes, conifers and Ginkgophytes (Bock, 1969). The uniformity can be noted even at the level of families and genera. There were only few plants of peculiar significance in the Cathaysian flora. For example *Yabiella* — a characteristic southern plant was present in Japan but was not known elsewhere in Euramerica. *Protoblechnum*-a probable Pteridosperms — was a Cathaysian plant although closely comparable forms are found in other parts, e.g. *Comsopteris* in Angara, *Supaia* in N. America, and *Dicroidium hughesii* in India. *Glossopteris* and *Palaeovittaria* are also recorded from the Triassic of Tonkin, but we need more adequate proof to confirm them.

At any rate, the composition of the floras all over the northern hemisphere became fairly uniform. This was evidently related to the progressive return of more equitable, humid climate by the Middle Triassic and the disappearance of earlier arid belts of the Lower Triassic (Vakhrameev, 1973).

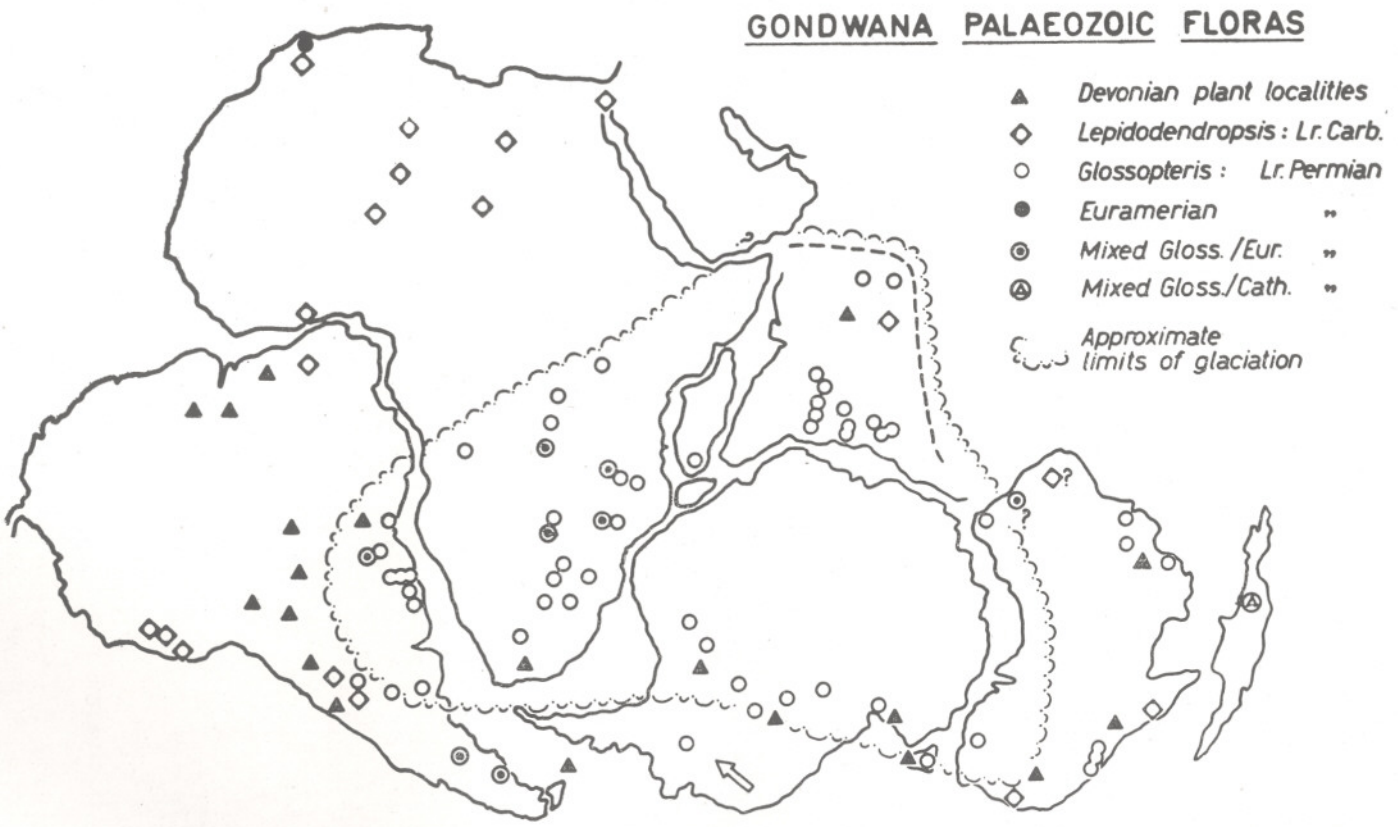
In the southern hemisphere, however, arid conditions persisted somewhat longer in the Triassic, particularly in India as is reflected by the ferruginous, arenaceous, and almost non-coaly facies of the Upper Triassic strata everywhere in India. Coal is however found in S. Africa, Australia, Tasmania and Antarctica which indicates fluctuations in Triassic climates over Gondwanaland (Ahmad, 1969). The differences in the floras of the two hemispheres were no longer as sharp as in the Permian (Table 3), yet the individuality of the southern Gondwana remained well-marked by the exclusive dominance of *Dicroidium*. In the northern hemisphere, *Dicroidium* is only doubtfully present; most forms belong to *Pachypteris* (*Thinnfeldia*) which is distinct (Doludenko, 1971). Apart from *Dicroidium*, there were some more Pteridosperms like *Lepidopteris* and *Hoegia*. Although *Lepidopteris* is found in both hemispheres, it is striking that the earliest northern records are from the Permian but on Gondwanaland *Lepidopteris* is so far not known below the Triassic. Also, the northern and southern species are mutually exclusive (Townrow, 1960). *Hoegia* appears to be southern. Besides, there are other fructifications like *Satsangia, Nidia, Nidistrobus* and *Bosea* in India (Srivastava, 1974), which suggest the presence of more pteridospermous plants. The few conifers (*Rissikia, Voltziopsis*) are also indigenous to the southern continents. Then, there is a large number of *insertae sedis* plants which are typical of the Gondwana, e.g. *Linguifolium, Kurtziana,, Feruglioa, Chansitheca, Bariophyllites, Ginkgoidium, Stormbergia, Moltenia, Reinitsia, Yabiella,* and *Rhexoxylon* etc.

## GENERAL DISCUSSION

The Devonian floras, it is generally accepted, were cosmopolitan though comparatively much more well developed in the northern than in the southern hemisphere. A similar impression largely prevails even in the early carboniferous world except perhaps in the Angara where the flora began to diverge from the contemporary Arcto-Carboniferous (Lepidodendropsis) vegetation. The progressive isolation of the Angara province from Europe (Euramerian) in the west and from Cathaysia in the east within almost similar latitudinal range is attributed to epicontinental sea barriers (Vakhrameev, 1973).

On the Gondwana supercontinent, events took an entirely different turn. About fifty years ago, Sahni (1926) had visualised that "during the Devonian and Early Carboniferous the original cosmopolitan flora probably evolved along similar lines in the two hemispheres. Then the balance was disturbed by the great southern cold period which ushered in the Glossopteris flora". At that time and on several occasions later, Sahni (1935a) exposed his views on the Permo-Carboniferous life-provinces with special reference to India and clearly pointed out that "in several parts of Gondwanaland, particularly in S. America and S. Africa, species related to or identical with members of the European floras have been found associated with the indigenous southern flora. The so-called 'northern/elements may be interpreted as remanants of the pre-existing southern flora which could have persisted through the glacial period in regions relatively free from the regours of ice". These prophetic remarks now seem to receive new support from recent studies on the palaeobiogeographical distribution of Devonian, Carboniferous and Permian fossil localities on Gondwanaland in relation to the phenomenon of glaciation (Chaloner & Lacey, 1972).

It is now known that ice sheets occupied different lands at different times during the Lower Carboniferous to the Early Permian interval. This had a profound and multi-directional influence on the development and evolution of the Lower Carboniferous plant life on the southern Supercontinent. According to Chaloner and Lacey (Text-fig. 2) floras of Euramerian (*Lepidodendropsis*) aspect could evolve in those areas which were not glaciated. In parts of western south America, for instance, such a flora could continue its development, though in a restricted manner, in the later Carboniferous when some of its members apparently got mixed up with those of the



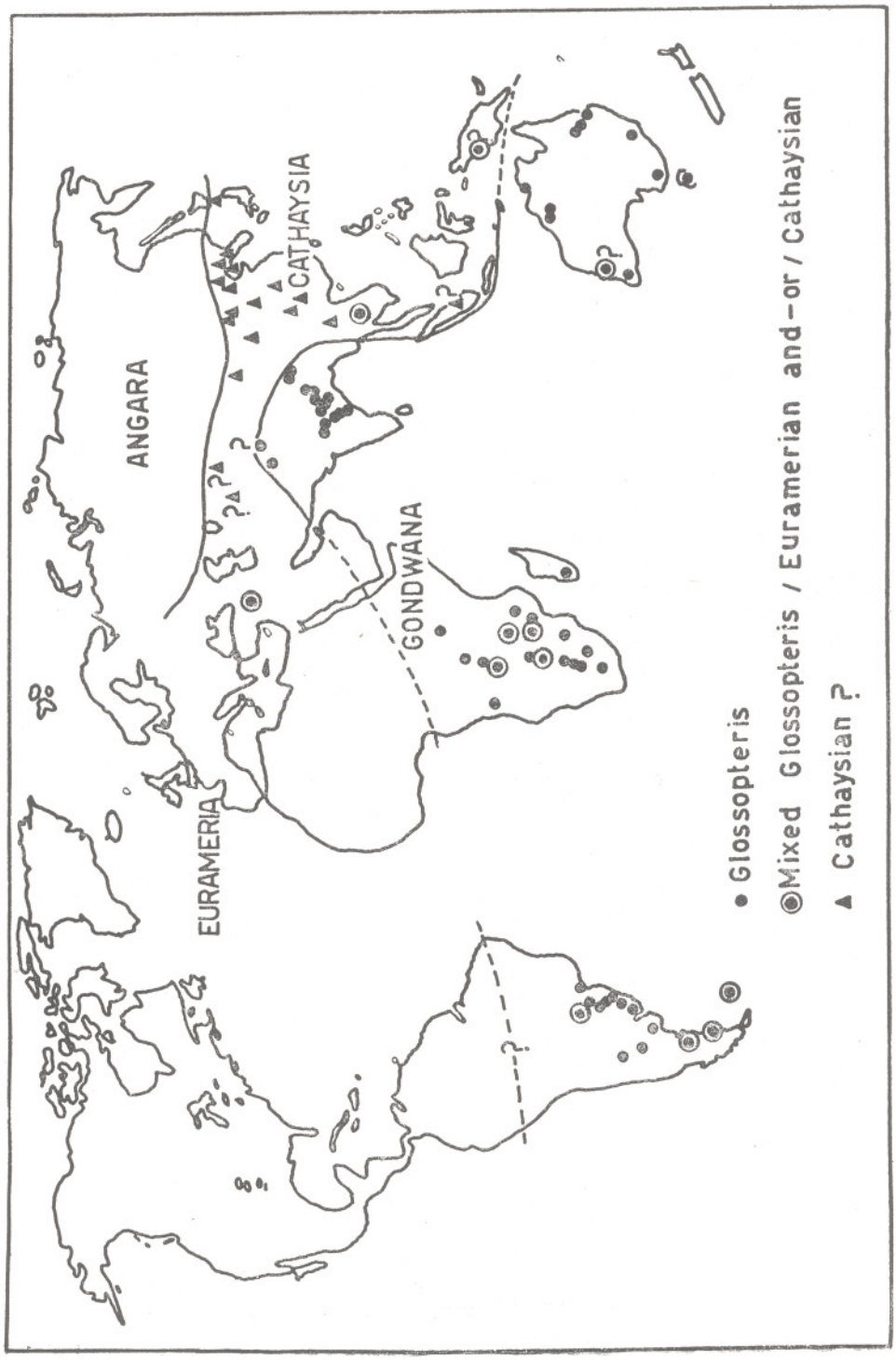

TEXT-FIG. 2 — Permian assembly of Gondwanaland, showing main fossiliferous localities for Devonian, Early Carboniferous and Carbo-Permian floras. The maximum extent of Carbo-Permian glaciation apparently coincides with subsequent spread of the Glossopteris flora. While several Devonian localities lie 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 *Glossopteris* occurrences. (After Chaloner & Lacey, 1973).

incoming Glossopteris flora (Carbo-Permian). Contrastingly, on glaciated regions, such Euramerian floras could not evolve (or thrive) but in their turn we find, as in S. Africa during the Lower to Middle Carboniferous interval, the appearance of a unique vegetation — the Protoglossopterideae (Plumstead, 1967) which is believed to have later evolved into the true Glossopteris flora which rapidly established itself far and wide with progressive amelioration of climate (Plumstead, 1973). We now need more wide spread knowledge of Proto-glossopterids from other southern countries to understand the origin and evolution of the unique Glossopteris flora.

The northern Arcto-Carboniferous flora essentially thrived under warm humid environments. Migration of this flora to the frigid Gondwanalands is hardly conceivable. The apparent similarities between the two floras may be, as several palaeobotanists think now, the result of homoplasmy or parallel evolution (Asama, 1969; Plumstead, 1970; Meyen, 1969). Moreover, the Lower Carboniferous Gondwana plants are still too imperfectly known to reveal differences, if any. The same holds equally good for the Carbo-Permian plants (esp. *Pecopteris*, *Annularia* and *Sphenophyllum*) which are still considered by a few workers as northern migrants in the Glossopteris flora of S. America and S. Africa (Archangelsky & Arrondo, 1969) (Text-fig. 3). Critical investigation of these so-called mixed elements is also warranted (Surange, 1966; Plumstead, 1973, 1973a). It may be pointed out that in the Indian Permian flora, similar plants are now distinguishable into different taxa like, *Trizygia*, *Dizeugotheca*, *Dichotomopteris* and *Stellotheca* etc. Indeed, recent studies have gone to show that all the Permian ferns in India and all the lycopods of Gondwanaland are distinct from their northern hemisphere counterparts and that the presence of Calamitales in the southern hemisphere is extremely doubtful (Sahni, 1926; Surange, 1966 and other references cited there in; Maithy, 1974, 1974a, 1975; Pant & Khare, 1974). The presence of northern Cordaitalean elements in Gondwanaland is also open to doubt. It is certain that, in the Carbo-Permian times the Gondwana flora, in its main ingredients like the Glossopteridales, was distinctly marked out from all the contemporary northern floras of Euramerica (typified, e.g. by *Pecopteris*), Angara (typified, e.g. by *Rufloria*) and Cathaysia (typified, e.g. by *Gigantopteris*) (Text fig. 4). What is now needed is that all the so-called 'northern' elements especially their fructifications should be intensively investigated in all Gondwana countries, preferably by a joint working group, so as to arrive at a common understanding about their systematics, affinities and distribution.

During the early Permian, climatic zones became more sharply defined over the globe and the floral development took different courses under the environmental influences of each geobotanical realm. Euramerica became arid, Angara remained temperate, Cathaysia was damp (Kon'no *et al.*, 1970) while Gondwana was still passing through the last phases of glaciation. About the Mid-Permian times, there was intense volcanism and crustal movements ('Tungwu Revolution') in the southern parts of Cathaysia (South China and Malayasia), as well as in the extra-Peninsular India (Kashmir) which presumably brought about repeated emergence and subsidence of land in the Tethys. Some chance contacts between the Gondwana and Cathaysia floras, e.g. in New Guinea and Thailand, (Text-fig. 3), probably resulted under these physicogeographic influences (Kon'no, 1966). However, most of these so-called Gondwana plants in Cathaysia are either proved to be distinct or they are very rare and fragmentary which limits their phytogeographic significance (Kon'no, 1966; Kon'no *et al.*, 1970; Asama, 1969). The floras in the heart of Gondwana (Glossopteris flora) as well as in Cathaysia (Gigantopteris flora) remained pure and isolated throughout the Permian by the vast Himalayan geosynclinal barrier. The present juxtaposition of the two provinces, according to Sahni (1936, 1937) was the result of 'drifting together' of the Cathaysian and Gondwana blocks which squeezed and folded the Himalayan geosyncline around the Assam promontory and produced the mountain range of Burma.

Indeed, from phytogeographical standpoint the entire northern border of India is full of interest. From Assam to Kashmir in the west and as far as the Salt Range of Pakistan (Text-fig. 5) there are a number of Lower Gondwana patches (with *Gloss-*


ANGARA
CATHAYSIA
EURAMERIA
GONDWANA
• Glossopteris
◉ Mixed Glossopteris / Euramerian and-or / Cathaysian
▲ Cathaysian ?

TEXT-FIG. 3

*opteris* and *Vertebraria*, and rarely with other typical elements of the Glossopteris flora) which indicate the former northward extent of the Gondwana (Jacob, 1952; Jacob & Banerjee, 1945). But perhaps the most interesting area is the northernmost outpost of Kashmir whose tectonic features and plant fossil records have, at one time, led Sahni (1926, 1936a) to envisage intermigration between Gondwana and Angara plants. We know that his contention, although based on incomplete palaeobotanical evidence, was fully supported by the geological work of Wadia (1931, 1937) in the Kashmir region and of Mushktov in Eastern Ferghana that demonstrated the existence of a chain of volcanic islands in the Carbo-Permian across the Tethys. This archipelago which stretched from Punjab to as far as the Pamir plateau, could permit plant intermigration. As around Kashmir in the west, Sahni (1936) further postulated that in the east "the Assam promontory of Gondwanaland may similarly mark the position of a former land connection with the Gigantopteris Flora".

In recent years some more additions have been made to the flora of the *Gangamopteris* beds of Kashmir which seem to add further interest to the phytogeographic aspects of the area. There are, no doubt some typical Gondwana plants like *Glossopteris* and *Vertebraria*. But at the same time there are a number of other plants which do not occur in the main Peninsular Lower Gondwana. These include *Psygmophyllum* (now *Ginkgophyllum*) and the somewhat peculiar species *Gangamopteris kashmirensis*. More recently Kapoor (MS) has been able to discover plant assemblages from at least five distinct stratigraphic levels in the Gangamopteris beds which are believed to be Lower Permian (Artinskian) in age, (Chakravarti, 1960-64). The lowest plant bed lies below the main Panjal Trap. *Gangamopteris* is apparently more common in the lower horizons but the flora becomes more diversified and richer in *Glossopteris* in the upper levels. A number of quite strange plants of apparently extra-Gondwana orientation have been found. The peculiar *Lepidostrobus* cones and *Lepidodendron* stems have already been described (Srivastava & Kapoor, 1969; see also Surange, 1971). Plants under study (H.M. Kapoor, personal communication) include several bipinnate leaves of *Comsopteris* (Angara) or *Protoblechnum* (Cathaysian) aspect, some extra-Gondwana (?Cathaysian) species of *Pecopteris* and several strap-shaped *Cordaites*-like leaves but with peculiar venation and other morphological differences.

The whole plant assemblage admittedly needs critical investigation before any categorical statement could be made. But it is all the same evident that the Kashmir Permian flora contains a significant proportion of plants of extra-Gondwana character. It is also apparent that the flora of the Gangamopteris beds is different from what we know so far from other extra-Peninsular Gondwana fossil sites including the Salt Range (Virkki, 1938) (Text-fig. 5). This probably suggests that the Kashmir region was, on the one hand somewhat isolated from the main Peninsular Gondwana, while on the other, it was also in a position to receive influences of other contemporary botanical provinces. It seems uncertain at present whether Kashmir was a northern outpost of Gondwana or a southern outpost of any other province, for example Angara as Sahni once thought. That Kashmir was a dry land, an island or a chain of islands of volcanic origin has been postualated from time to time in the past and this region has featured in the concept of intermigration (Sahni, 1926, 1936a; Wadia 1937, 1966; Lacey, 1975). Kapoor (MS) also believes that the northern types of elements were probably developed due to their migration from north or east in the 'supposed Kashmir island' which was close to the mainland of the Gondwana continent; the possibility

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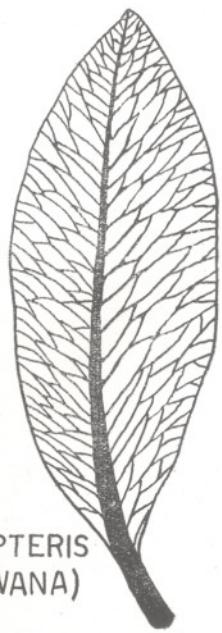
TEXT-FIG. 3 — Permian geobotanical provinces of Euramerica, Angara, Cathaysia and Gondwana on present world map. Occurrence of mixed-floras (involving Gondwana + Euramerian and/or Cathaysian elements) are shown. Note the doubtful Gondwana site of Kashmir which is here referred to the 'Middle Asiatic floras of uncertain affinity' which also includes the Hazro locality (Turkey) and the two doubtful Cathaysian localities east of the Caspian sea.

PECOPTERIS
(EURAMERIA)

GIGANTOPTERIS
(CATHAYSIA)

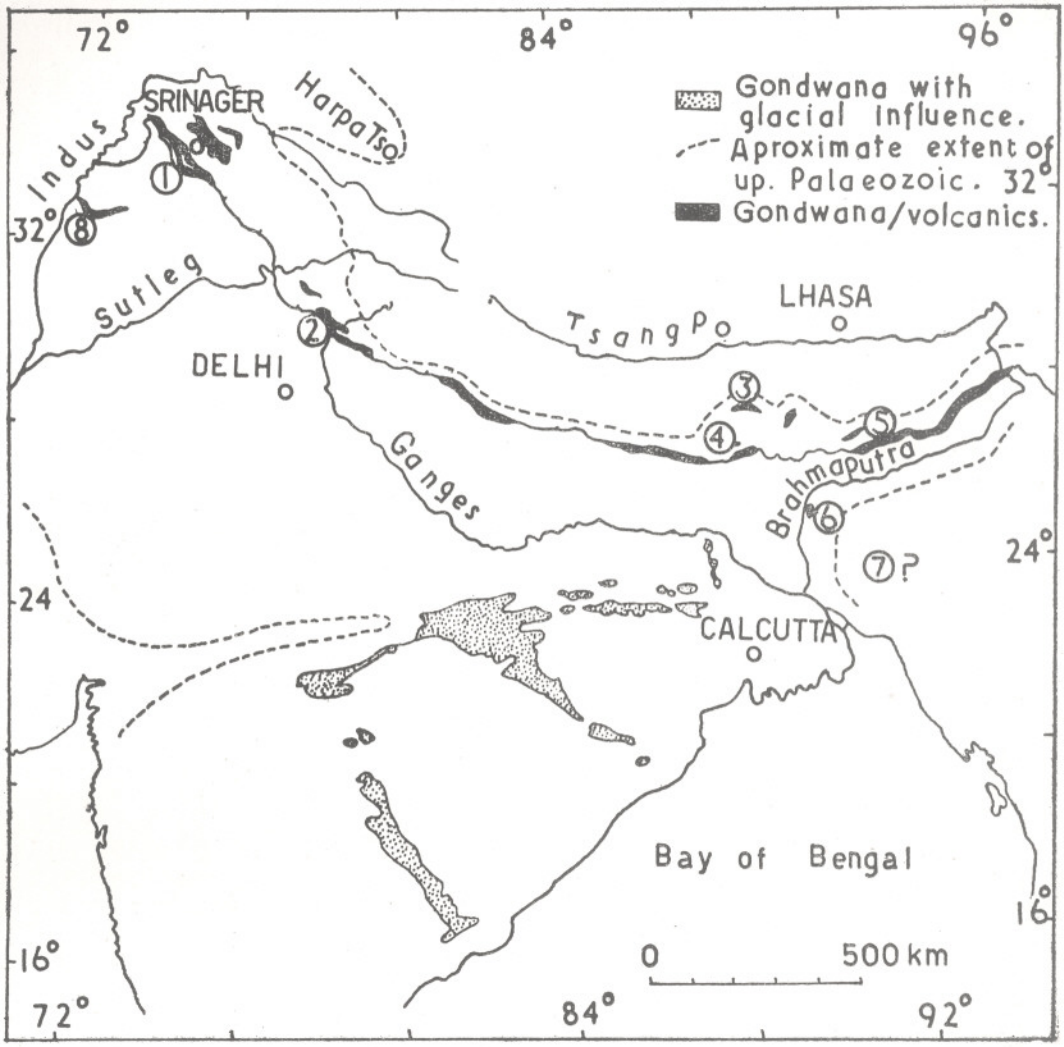
| | EU | AN | CA | GL |
|---|---|---|---|---|
| ALETHOPTERIS | + | | | |
| CALAMITES | + | | | |
| SIGILLARIA | + | | | |
| CORDAITES | + | + | + | |
| PECOPTERIS | + | + | + | |
| CALLIPTERIS | + | + | | |
| SPHENOPHYLLUM | + | + | + | |
| ANNULARIA | + | + | | |
| INTIA | | + | | |
| TSCHERNOVIA | | + | | |
| ANNULINA | | + | | |
| ANGARIDIUM | | + | | |
| PARAGONDWANIDIUM | | + | | |
| RUFLORIA | | + | | |
| GIGANTOPTERIS | | | + | |
| PROTOBLECHNUM | | | + | |
| TINGIA | | | + | |
| LOBATANNULARIA | | | + | |
| GONDWANIDIUM | | | | + |
| GLOSSOPTERIS | | | | + |
| NOEGGERATHIOPSIS | | | | + |
| LYCOPODIOPSIS / CYCLODENDRON | | | | + |
| DIZEUGOTHECA | | | | + |
| WALKOMIELLA | | | | + |

RUFLORIA
(ANGARA)



GLOSSOPTERIS
(GONDWANA)

TEXT-FIG. 4




TEXT-FIG. 5 — Distribution of typical Peninsular Gondwana rocks (Stippled) with glacial influence. Equivalent Late-Palaeozoic rocks in the extra-Peninsular region, along the Himalayan foot-hills, include Lower Gondwana beds with glacial or volcanic influence. In the extra-Peninsular part, palaeobotanical evidence of typical Glossopteris flora comes from localities no. (2) Kumaun area, (3) Sikkim (4) Darjeeling (5) Sela area, Arunachal, (6) Garo Hills, (7) Tripura (doubtful) and (8) Salt Range (Pakistan). The Kashmir locality (No. 1) contains definite mixed-flora of extra-Gondwana affinities. Data mainly derived from Jacob and Banerjee (1954), Gansser (1964) and Acharya (1973).

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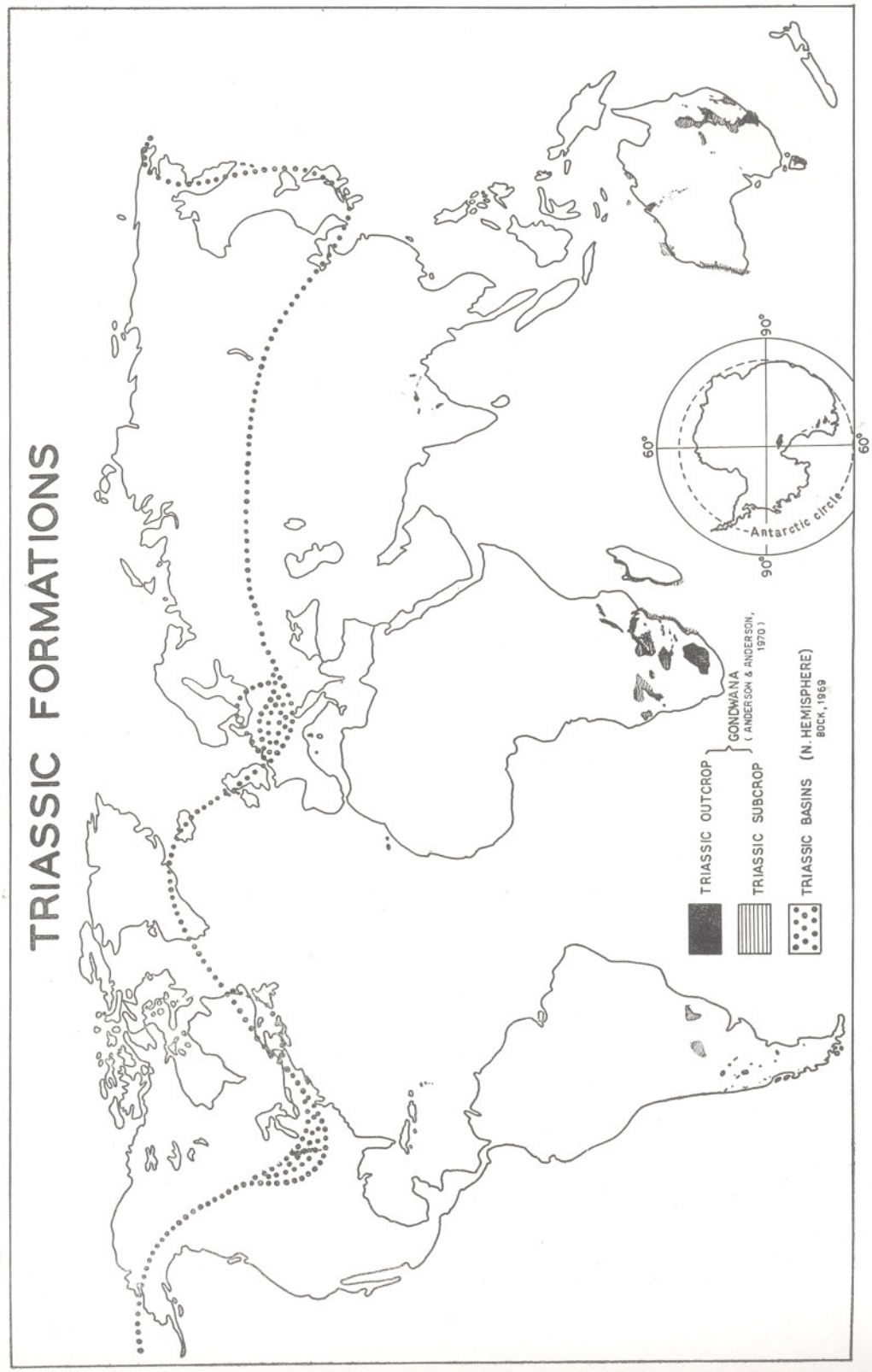
TEXT-FIG. 4 — Distinctive distribution of some important Permian plants in the Euramerian (EU), Angara (AN), Cathaysia (CA) and Gondwana (GL) geobotanical provinces. A typical plant representative for each province is drawn to emphasize its individuality.


TRIASSIC FORMATIONS
TRIASSIC OUTCROP
TRIASSIC SUBCROP
GONDWANA
( ANDERSON & ANDERSON, 1970 )
TRIASSIC BASINS (N. HEMISPHERE)
BOCK, 1969
90°
60°
Antarctic circle

TEXT-FIG. 6

of an island is supported by the underlying formation of the 'Agglomeratic' formation as well as by the Trap activity.

Until more is known about the flora and palaeogeography of the Gangamopteris beds, it would perhaps be best to accommodate the Kashmir fossil site under the Middle Asiatic Floras of uncertain affinities (Vakhrameev, *et al.*, 1970) which also includes the Hazro locality of Turkey (Wagner, 1962) and one or two localities of the Madgyn flora, east of the Caspian Sea (Dobrunskina, 1970; Chaloner & Lacey, 1973) (Text-fig. 3). In Hazro, an originally Euramerian flora is believed to have received typical Cathaysian as well as some controversial Gondwana elements (e.g. *Glossopteris*). According to Kon'no *et al.* (1970) plant migration from Cathaysia towards south (and probably up to Hazro) became possible by the repeated emergence and subsidence of land in and around the Tethys in the Middle of the Permian crustal activity and volcanism in South China. A similar phenomenon was evidenced almost contemporaneously around Kashmir, and closely comparable geotectonic situations seem to have existed at other points along the northern border of Gondwana during the Upper Palaeozoic, (Text-fig. 5) e.g. in Abor country and Darjeeling area in north eastern India, (Gansser, 1964; Acharya, 1973 & other references therein). Does it indicate that the northern border of India was involved in plant migration across the Tethys in a manner similar to Cathaysia (China)? How did typical plants from Cathaysia reach as far west as Turkey (Hazro) crossing the enormous barrier of the Tethys?. Is it likely that Kashmir, Assam or other places had any relevance to this puzzle, for these sites do appear ideally positioned between China and Turkey. The extra-Gondwana character of the Kashmir plants adds a promising touch to such speculations. However, we need to know the Kashmir plant taxa with more exactness while in the case of the flora of north eastern India and that of the Salt Range, the available data (with exclusively Lower Gondwana plants) is without much relevance.

As an alternative hypothesis, Meyen (1969) includes Hazro site within the belt of Hydrophylic Permian floras which covers near East, Middle East, part of North Africa and Central North America. These regions are characterised by marine Permian strata or younger sediments of considerable thickness. The plant associations of this belt are regarded as derivatives of Cathaysian floral aspect along with some Gondwana derivatives (e.g. *Glossopteris*). The relations of Kashmir with this provisional belt, if any, can be judged only when the floral picture of the Gangamopteris beds becomes clear. There is no doubt, as Sahni (1935) pointed out, that "the great belt of mountains which form out landward border is therefore a region of very special interest both from the tectonic and from the plant-geographical points of views: it represents an important line of junction between at least three originally distinct land areas: in the south Gondwanaland, in the north-east and east Gigantopteris-land and in north west and west the Arcto-Carboniferous continent". The maritime floras of these palaeofloristic provinces surrounding the Tethys could have, conceivably, been environmentally modified, as compared to the floras growing in the heart of the provinces. The hydrophylic floral belt of Meyen probably provides for such a coastal vegetation but its structure and distribution are still not clearly understood (Kon'no *et al.*, 1970). It is fortunate that interest of workers in the northern (extra-Peninsular) and Gondwana (Peninsular) regions of India has lately been revived from palaeomagnetic and geotectonic standpoints (Acharya, 1973; Athavale, 1973 & other references therein). These studies would eventually clarify many points with regard to the Late Palaeozoic palaeobiogeography and geology of the maritime areas, which now largely cover the Middle Asiatic region. From palaeobotanical point of view this region needs extensive exploration for un-

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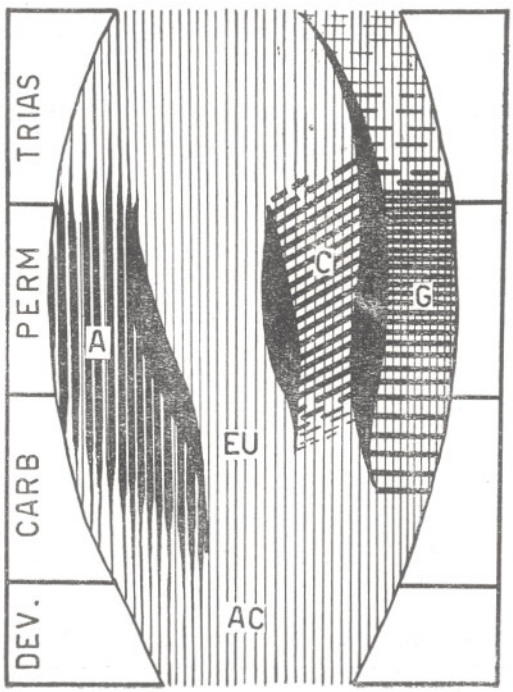
TEXT-FIG. 6 — Distribution of Triassic rocks in the southern hemisphere (Gondwanaland) and contemporary basins in the northern hemisphere. Data mainly derived from Anderson and Anderson (1970) and Bock (1969).

ravelling the history of Late Palaeozoic and Triassic plant-life (for example localities mentioned by Diener, 1912, p. 95).

The climatic shift from the Permian to the Triassic and the accompanying floral change probably occurred at different times and does not necessarily coincide with the palaeontological Permian/Triassic boundary (Vakhrameev, 1973). In Europe, the major plant break appears to lie in the Middle Permian, in Angara it conforms with the Permian-Triassic boundary or may be in the late Permian whereas in Gondwana (e.g. India) it is somewhat transitional at the Permian/Triassic or may be a little later. In Eurameria the Permian was a period of increasing aridity and desiccation (non-coaly), the Angara was still humid (with coal), the Gondwana was warm humid (rich coal-bearing) whereas in Cathaysia arid conditions appeared towards the later part of the Permian. Arid belts became a characteristic feature of the early Triassic globe. The climatic adversities caused the extinction of the bulk of the Permian lycopods and other Pteridophytes, the Cordaitales and Pteridosperms. The floras that emerged on the Triassic scene were mostly dominated by Gymnosperms notably Cycadophytes, Ginkgophytes along with some Conifers, Pteridosperms and ferns (esp. Dipteridaceae). The southern Gondwana floras also responded in a similar manner. With the return of favourable (humid) climate during the later Triassic, the general texture of the floras all over the world became relatively more uniform, especially in the northern hemisphere geobotanical areas of North America, Greenland, Europe, China and Japan (Bock, 1969). However, the Gondwana climate remained more or less arid throughout the Triassic and correspondingly some salient differences existed between the floras of the northern hemisphere and those of the southern Gondwana realm: in fact these were the two main natural floral domains in the Triassic (Harris, 1937) (Text-fig. 6).

The Gondwanaland vegetation was characterised by the dominance of Pteridosperms, especially *Dicroidium* (Corystospermaceae) and *Lepidopteris* (Peltaspermaceae). *Dicroidium* is a typically southern plant whose structure is now well known. It is distinct from *Pachypteris* (*Thinnfeldia*) that typically prevailed in the northern hemisphere. The southern records of *Thinnfeldia* need reexamination (Townrow, 1957; Lele, 1962; Rao & Lele, 1962). *Dicroidium* is also rather polymorphous and some workers




TEXT-FIG. 7 — Diagrammatic representation of the evolution and geobotanical diversification of floras on the globe from the Devonian to the Triassic period. Note the global uniformity in the floras of the Devonian Arcto-Carboniferous province (AC), the subsequent diversification of the Euramerian (EU), Angara (A), Gondwana (G) and Cathaysian (C) floral provinces during the Carbo-Permian and the eventual return to global uniformity in the floras of the Triassic.

treat it in a more comprehensive sense including several other plants like *Xylopteris, Jhonstonia, Stenopteris, Displasiophyllum, Zuberia, Protoblechnum* etc.). A somewhat similar synthesis was recently proposed by Anderson and Anderson (1970) as a preliminary basis for further detailed work. It seems very essential to resolve *Dicroidium* more precisely from the abundant foliage and fructification material available all over Gondwanaland so that its phytostratigraphic value could be realised for more detailed correlations. This genus undoubtedly plays a central role in distinguishing the Dicroidium flora that represents the Middle Gondwana unit all over Gondwanaland (Lele, 1964; Plumstead, 1970).

Apart from *Dicroidium*, there were probably several other pteridospermous plants including *Hoegia, Zuberia* and *Pachypteris* and a number of fructifications in the Dicroidium flora of India and other Gondwanalands which did not occur in the northern hemisphere. Many plants of unknown affinities also appear to be entirely southern. The few better known conifers were also endemic. Plants like *Yabiella* and *Rhexoxylon* were more typical of the Gondwana province. These floristic features, no doubt, contributed to the peculiarities of the Gondwana province but the general texture of the southern hemisphere vegetation was strongly tending to be in harmony with that of the northern hemisphere towards the later part of the Triassic. This is borne out especially well by the similarities or even identity among the Cycadophyte and Ginkgophyte plants and some Dipterid ferns of the two hemispheres. This reflects withdrawl of physical barriers and greater scope for the interchange of floras between the two hemispheres during the Triassic (Bock, 1969; Meyen, 1969).

Thus when we perceive the march of plant life from the Late Palaeozoic to the Triassic in one look, we can not miss the essential rhythm underlying the floral events: beginning with a note of global uniformity in the Devonian/Carboniferous, then rising to a high pitch of diversity in the Permian and again returning back to global harmony in the Triassic. (Text-fig. 7).

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