

PALAEOCLIMATIC IMPLICATIONS OF GONDWANA FLORAS

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ABSTRACT

Among the Gondwana floras, the *Glossopteris* flora (Lr. Gondwana) appears remarkably unique in its origin, evolution and climatic responses. As the north hemispheric plant climatic indicators are found unhelpful, the *Glossopteris* flora is here judged on its own merits. A fresh approach is made to sort out certain plant-morphological characteristics and their appearance/dominance/disappearance patterns in time are examined for interpreting palaeoclimatic vicissitudes. The *Glossopteris* flora is composed of an earlier 'Gangamopteris floral phase' (Talchir Ser.) characterised by dominance of midrib-less and non-petiolate 'Gangamopteroid' foliage and the meagreness of pteridophytes (esp. ferns). This floral phase corresponds mainly with a cold (glacial) to cool temperate regime. The following *Glossopteris* floral phase is dominated by petiolate 'Glossopteroid' foliage, abundant pteridophytes (incl. ferns) and gymnosperm fossil woods with growth rings. This floral phase suggests a generally warm temperate, moist climatic regime with subsequent hotter trends. The main turn in the climatic balance corresponds with the Karharbari/Barakar transition. Adverse conditions in early Talchir times are indicated by poverty of floral record and a generally small-size and fleshy appearance of leaves. Subsequent amelioration is reflected by increase in leaf-size, improvement in floral record and coal formation in Karharbari times. Damuda times indicate availability of quite diverse habitats, frost-free conditions, substantial rainfall, marked seasons and forest-like plant communities. Hotter trends and open conditions towards late Damuda times are reflected in the increase of open-mesh *Glossopteris* species and robust fern types. At the Permian/Triassic transition the bulk of the *Glossopteris* flora rapidly declines, and organizationally distinct plants like *Lepidopteris* and *Dicroidium* subsequently characterize the *Dicroidium* flora (Mid. Gondwana). This major floral transformation indicates a shift in climatic regime. The general poverty and scanty distribution of Middle Gondwana plants and the xerophytic characters of some forms suggest adverse conditions involving widespread aridity, irregular rainfall and scanty water sources. The *Ptilophyllum* flora (Up. Gondwana) appears in the Jurassic. It comprises a rich vegetation of ferns, cycadophytes and conifers which, according to north hemispheric palaeoclimatic standards, would reflect a moist temperate to hot climatic regime with sufficient rainfall. Marked seasons are indicated by growth rings in woods. Climatic vicissitudes during Upper Gondwana, if any, are still difficult to interpret as there is no clear data on the distribution of plant-climatic indicators in space and time. The scope of further work in the various Gondwana floras is indicated for the reconstruction of past climates.

INTRODUCTION

The role of palaeobotany in the study of past climates was conceived as long back as the 18th century or even earlier (SEWARD, 1892; SCHWARZBACH, 1963; DORF, 1963) but Brongniart was perhaps the most notable among the early palaeobotanists to clearly realize the usefulness of fossil plants as climatic guides. According to the principle of uniformitarianism, the past plant distributions are believed to have been controlled by environmental conditions like those in present time. However the reliability of fossil plants as palaeoclimatic indicators suffers from several limitations—both botanical and geological. One of the important *botanical* handicap is that ecological relationship of plants is based on morphological similarities (DORF, 1969; KRÄUSEL, 1961) but it is also well-known that morphologically similar plants may differ widely in their ecological requirements. Then again the plant ecological requirements in the past could have differed from those

existing now. The *geological* limitations are imposed by floras which are relatively more remote in age. Thus in case of the Tertiary and the quaternary, plants can be closely matched morphologically with their extant representatives to enable ecological deductions. In relatively older floras, e.g. of the Mesozoic, although many plants are extinct, still some families and larger groups do persist even now; thus a broad comparison is possible to some reasonable extent. The greatest difficulty is encountered with very remote floras like those of the Palaeozoic which are almost entirely extinct. The palaeoclimatic requirements of these plants cannot therefore be assessed with any degree of confidence by comparison with modern plants. Here, the only method left is to depend on the morphological characteristics, specially of leaves and stems, which may independently reflect environmental conditions. In dealing with such fossil floras there are several other limitations as well; such as (1) megafossil assemblages may only give partial view of flora which probably thrived under a wide range of habitats. (2) In other cases, an assemblage may contain mixture of plants belonging to quite distinct habitats. (3) Normal environmental effects on plants can hardly be distinguished from abnormal or unnatural ones in a fossil flora (4) fossilization is a rather selective process and may mask the representation of the original floral assemblage. (5) In a fossil assemblage the determination of species is often arbitrary; qualitative and quantitative assessment of populations is rendered difficult. It is therefore evident that reconstruction of ancient climates is largely a subject of speculations and generalizations.

KNOWN PLANT CLIMATIC INDICATORS FOR FOSSIL FLORAS

In spite of these difficult situations, some useful criteria have been evolved for interpreting past climatic environments of floras. The criteria tend to vary and become less critical in successively older floras. It seems relevant to enumerate briefly these criteria in order to assess their bearing on Gondwana floral evidence.

(a) *Tertiary floras* have provided some fairly reliable criteria for interpreting palaeoclimates. (DORF, 1969; DILCHER, 1974). Leaf margin features, length of leaves and venation are considered more important than other features like texture, drip-points and organization of leaf. A *tropical* low land forest is indicated by an abundance of entire-margined, large (7-10 cm) leaves with pinnate venation. Veins are many with closed nets and small areols. (Text-fig. 1) On the contrary, a *cold temperate* forest is characterized by non-entire margined (toothed or lobed margin), small (<10 cm long) leaves with palmate venation. Veins are few, with open nets consisting of highly branched, free-ending tertiaryaries. Besides these characteristics, tropical lowland plants have a drip point to shed excess of water and the leaves have a thick texture. Cold temperate plants tend to be thin-textured.

(b) *Mesozoic floras* have been palaeoclimatically interpreted in few cases. Following indicators have been found useful.

Warm climate is indicated by (1) relatively larger size of coniferous trunks, fern fronds and equisetalean stems (2) sub-tropical to tropical conditions are inferred from abundance of cycads, cycadeoides, dipterid ferns, Marattiaceae, Matoniaceae and Osmundaceae (3) Temperate climate is deduced from the presence of conifers, ginkgoes and ferns of Schizaeaceae, Gleicheniaceae, Cyathiaceae and Polypodiaceae. Leaf-forms generally show greater dissection or lobing. (4) Seasonal variations (summer vs winter, dry vs wet) are indicated by presence of tree-rings. Absence of rings denotes more or less uniform, generally warm climate. (5) Dry climate is indicated by xerophytic features in the leaf

epidermis e.g. thickness, sunken stomata and their arrangement in grooves, protection by hairs, papillae etc.

(c) *Palaeozoic* climates were ingeniously worked out by H. Potonie in 1909 and later by White in 1913 on the basis of the Carboniferous Coal-Measures flora of Europe which indicated humid subtropical to tropical conditions. SCHOPF (1973) enumerates a total of 20 of these plant-climatic indicators : (1) General luxuriance, size and abundance of vegetation (2) Succulent nature of many plants, e.g., *Medullosa*, *Psaronius* (3) Tissues with large cells, thin walls, e.g., calamitalean cortex (4) Organs with large intercellular spaces and abundant lacunar tissue (5) General absence of growth rings in all plants showing secondary wood (6) Large size of fronds of bushy plants e.g., *Neuropteris* (7) Delicate foliage of climbers e.g., *Sphenophyllum* and some Sphenopterids, (8) Presence of aphanopores in ferns and pteridosperms. (9) Large size and texture of leaves e.g. *Megalopteris*, *Psymnophyllum* (10) Occurrence of stomata in grooves e.g., lycopods. 11) Presence of hydathodes to discharge excess water in certain Sphenopsids and Spheropterids (12) Profusion of large drooping fronds and pendant branches to shed rain. (13) Indications of delayed fertilization and adaptation for seed floatation. (14) Prevalence of the free-sporing habit and dependence on fluid moisture in reproduction (15) Inflorescences borne on central stems (cauliflory), e.g. calamites and sigillarians (16) presence of subaerial roots in Pteridosperms and ferns (17) Smoothness and thickness of bark, e.g., *Bothrodendron* and Lepidophytes (18) Occurrence of pneumatophores e.g., *Sigillaria* and some *Cordaites* (19) Dilation of tree bases e.g., large calamites, sigillarians, etc. and (20) presence of close relatives of modern types of tropical plants.

GONDWANA FLORAS

Palaeoclimatic speculations on the Gondwana fossil floras have been made rather sparingly during the last nearly fifty years. A significant step in this direction was taken as long back as 1937 in a symposium held during the International Geological Congress, Moscow in which KRÝSTHOFOVICH, ZALESKY, DU TOIT, FOX, WADIA and SAHNI and others expressed their views. KRÄUSEL (1961) has made some valuable observations on Gondwana floras and their palaeoclimatic bearing. In the last decade new ideas have grown through knowledge of other earth sciences which have been discussed during Gondwana Stratigraphy conferences held in Buenos Aires (1967) South Africa (1970) and Australia (1973). It must be however, confessed that the available floristic data on Gondwana palaeoclimates is still too meagre. What we know is of a generalized nature and largely based on the knowledge of plant-climatic indicators of the north hemispheric fossil floras. The Gondwana floras, especially the *Glossopteris* flora, are remarkably peculiar in many ways. The Gondwana plants, therefore, need to be studied very critically to evaluate the expression of their morphological peculiarities in relation to the palaeoclimatic history of the Gondwana regime. In short, we may have to evolve a plant-climatic key for Gondwana palaeoclimates based on Gondwana plants. In this symposium, which is probably the first significant step to synthesize knowledge on the subject of Gondwana palaeoclimates, I would like to make a preliminary approach to certain morphological aspects of the Gondwana plants and their appearance-dominance-disappearance patterns which seem to bear palaeoclimatic implications. Speculations are unavoidable at this stage of knowledge, but more intensive studies in future may yield substantial data.

In India three main floral successions can be marked out in the Gondwana time viz., (1) *Glossopteris* flora (Up. Carb. to Up. Perm : Lower Gondwana) (2) *Dicroidium* flora (Triassic : Middle Gondwana) and (3) *Ptilophyllum* flora (Jurassic to Lr. Cretaceous :

Upper Gondwana). The first two floras show a striking parallelism in their development all over Gondwanaland. The third floral succession is best known from India.

LOWER GONDWANA: GLOSSOPTERIS FLORA

ORIGIN, EVOLUTION AND CLIMATIC SETTING

Before the *Glossopteris* flora arose, there was a more or less cosmopolitan vegetation—the *Lepidodendropsis* flora—whose remains are imperfectly found in the Carboniferous beds of Spiti in India and in other parts of Gondwanaland (LELE, 1976). With the onset of glaciation this flora probably retreated from those areas which came under the influence of glaciers. The almost sudden and enigmatic arrival of the *Glossopteris* flora is deeply rooted in the glacial episode itself which presumably triggered genetic changes of rapid evolutionary significance (SAHNI, 1937, 1938). Early remains of the *Glossopterids* are well known from glacial strata from India (LELE, 1966) and other Gondwana lands which bear out the intimate relationship of the flora with the glacial climatic revolution. KING (1961) compares the habitat of the *Glossopteris* flora with “modern *Notofagus* (Southern beech) flora of Southern cold temperate latitudes which in Terra del Fuego maintains itself in forests close to the ice fronts.”

The rapid spread of the *Glossopteris* flora seems to have been brought about during the deglaciation phases when the ground became ice-free and the climate began to ameliorate. The maximum extent of the southern glaciation, therefore, approximately corresponds with the maximum spread of *Glossopteris*-bearing fossil localities on the Gondwana continent (CHALONER & LACEY, 1973). In view of this correspondence, CHALONER and LACEY (1973) envisage the possibility that the flora, especially *Glossopteris*, was adapted to relatively temperate conditions and could spread over high altitude areas previously covered by ice, which is approximately comparable to the modern distribution of *Picea* and *Abies* in North America and Europe vis-a-vis the maximum spread of Pleistocene glaciation. Sahni also assumed the possibility of some *Glossopterid* plants growing in hospitable places like nunataks. Although remains of *Glossopteris* are now found close to the south pole, no one would admit that it was a glacial flora or a polar flora (SAHNI, 1937; SCHOPF, 1973). The general consensus favours a temperate climatic setting for the *Glossopteris* flora, probably colder in the earlier phases but warming up later. (SAHNI, 1937; 1939; KRÄUSEL; 1961; SURANGE, 1966; RIGBY 1971; SCHOPF, 1973; PLUMSTEAD, 1973). SCHOPF (1973) even suggests that the Permian glacial climate was not necessarily polar; the glaciers were probably the result of abundant snowfall in cool temperate climatic regions.

The origin and evolution of the *Glossopteris* flora is, however, still enigmatic. Much of the early history seems to have been lost due to glacial erosion. Thus, the ancestors of this flora and their geographical situation are still controversial (SAHNI, 1938; CHALONER & LACEY, 1973; PLUMSTEAD, 1973; SCHOPF, 1973). PLUMSTEAD (1967) postulates that the *Protoglossopterideae*, whose remains are found in the Carboniferous of South Africa, are ancestral to *Glossopterids* of the post-glacial coal-bearing Gondwana strata. The *protoglossopterids* had *Glossopteris*-like simple leaves but they were strikingly small and devoid of midrib as well as vein-anastomoses. In these characters (e.g. in *Rubidgea*), the *protoglossopterids* show closer affinity to the *Gangamopteroid* leaves which characterise the earlier phase of the Lower Gondwana flora that follows the glaciation. This situation apparently reflects an aptitude of *Gangamopteroid* plants for colder climatic conditions. Later, in the mid-Permian, the climate must have become unfavourable as *Gangamopteroid* plants rapidly decline there. On the contrary the *Glossopteroid* plants—with leaves pos-

sessing strong midrib and petiole—show a marked rise. There is thus, some ground to surmise that Glossopteroid plants were on the whole more tolerant climatically and probably favoured a warming trend. *Glossopteris* in particular, shows a surprising adaptability; for not only did it survive the extreme colder phases of the early Permian glaciation but that the plant proliferated more rapidly with progressive amelioration and warming of climates and even lingered in the semi-arid conditions of the early Triassic in many parts of Gondwanaland. This wide range of tolerance and tendency to out-live climatic extremes exhibited by the Glossopterids, raises a pertinent question—can we hope to decipher in these plants any morphological characters which can serve as climatic guides? Let us test this by the known standards.

KNOWN PLANT-CLIMATIC STANDARDS AS APPLIED TO GLOSSOPTERIS FLORA

According to the Tertiary plant-climatic indicators the smooth-margined, simple, entire, large leaves of the Glossopterids and their more or less pinnate venation appear to be more compatible with tropical floral characteristics (Text-fig. 1). Indeed, Fox (1940) and Gothan were led to this believe which is no more tenable. It is now generally held that the *Glossopteris* flora emerged in the wake of glaciation and its further development took place under a more or less temperate regime (SAHNI, 1937; KRÄUSEL, 1961; SURANGE, 1966; RIGBY, 1971). But, curiously enough, Glossopterid leaf shapes are contrary to those of a temperate flora (i.e. lobed or dissected leaves, non-entire margin and palmate venation). It seems therefore as if the Tertiary plant climatic guides like leaf shape are either unhelpful in the case of the Glossopterid plants or that the Glossopterids were very versatile plants that could negotiate climatic vicissitudes without much alteration in their gross leaf architecture.

The Carboniferous tropical-subtropical Euramerian floras, also fail to provide any clear clues. The only points of resemblance seem to be (1) luxuriance, large size and abundance of plants and (2) suspected fleshy nature of the fructifications (PLUMSTEAD, 1963). In fact a large majority of features of the northern Carboniferous floras do not seem to apply; for example, the bulk of the Carboniferous flora is characterized by pinnate fronds, many of which belonged to free-sporing plants. Contrastingly in the *Glossopteris* flora, simple, entire-margined leaves predominate. The northern *Sphenophyllum* may externally resemble the southern *Trizygia* but there are no hydathodes in the latter which are so characteristically developed in the northern *Sphenophylls* and *Sphenopterids* for draining off excess water in a tropical humid rain-forest. Again, the absence of growth-rings in the northern woods stands sharply in contrast with the Gondwana woods which show marked seasonal changes. If one looks into the list of plant-climatic indicators of the Carboniferous coal-forest, perhaps more differences with the Gondwana than similarities would be found.

The conclusion seems almost inescapable that a palaeoclimatic reconstruction of the *Glossopteris* flora is not easy to achieve from standards known so far. Probably we have to give sufficient latitude to the Glossopterids whose morphological responses to climates were rather subtle and unorthodox. Evidently we will have to examine this unique flora at finer levels of morphology and anatomy, build up the organization and habit of the plants and relate them with some kind of habitat in order to understand the palaeoclimatic setting. In the present state of our knowledge, therefore, only an approach can be made to find out the morphological potential of the plants for possible palaeoclimatic interpretations.

PALAEOCLIMATIC REVALUATION OF LOWER GONDWANA FLORA

For a better understanding of the palaeoclimates, the *Glossopteris* flora can be grouped into two floral phases (1) an earlier *Gangamopteris* floral phase (= *Gangamopteris* Assemblage Zone of SHAH *et al.*, 1971) which spans the Talchir and Karharbari Stages of the Talchir Series and (2) a later *Glossopteris* floral phase (= *Glossopteris* Assemblages Zone of SHAH *et al.*, 1971) which spans the Barakar, Barren Measures and Raniganj Stages (Damuda Series). The beginning of the *Glossopteris* floral phase seems to overlap the later part of the *Gangamopteris* phase, and its end overlaps with the *Dicroidium* flora in the Triassic. The two phases, however, largely correspond with our present ideas that the Talchir Series was by and large cool while the Damuda Series was warm temperate (SAHNI, 1940). This can be outlined as below :

	Trias	Panchet	Semi-arid	Dicroidium flora	
Lower Gondwana	{ Damuda Ser.	{ Raniganj .. }	Warm	Glossopteris floral phase	} Glosso- pteris flora
		{ Barren .. }			
		{ Measures .. }	Tem- perate		
		{ Barakai .. }			
	{ Talchir Ser.	.. { Karharbari .. }	Cool	Gangamopteris floral phase	
		{ Talchir .. }	Glacial		
{ Boulder beds .. }					

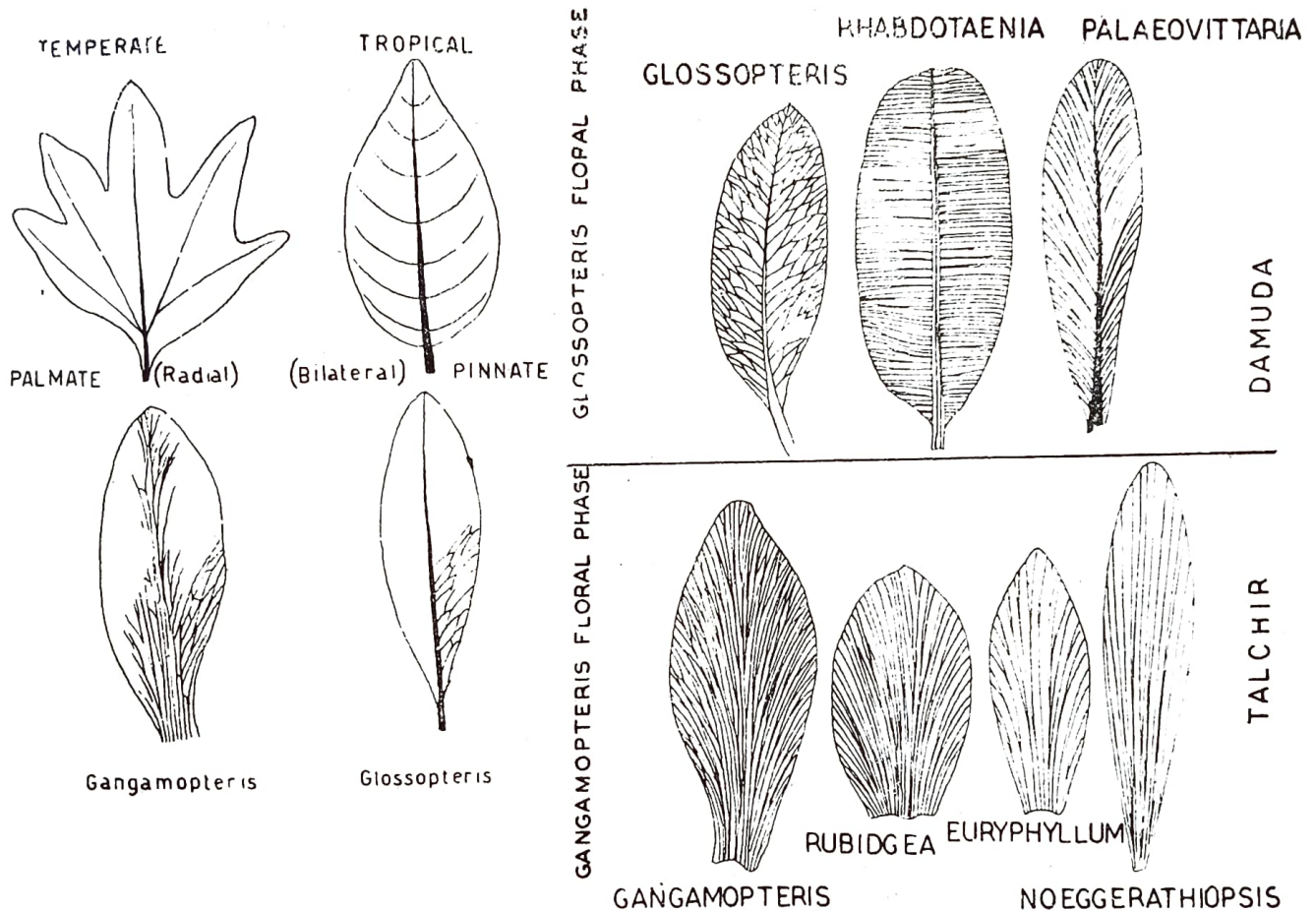
GANGAMOPTERIS FLORAL PHASE AND PALAEOCLIMATES

In the early phases of Talchir deposition, (more than 250 m. y. ago) the Indian Peninsula was presumably a land surface of high elevation, ice-covered and nearly barren of vegetation. Bizzare storms and winds must have swept across the irregular terrain from the mountainous country, still covered with unconsolidated till. A sea extended in parts of what is now Punjab and Kashmir. The early Talchir basins were embryonic, without any diastrophic control (GHOSH & MITRA, 1975). The glacial sedimentation in several Damodar Valley basins indicates a cyclic pattern governed by advancing and retreating ice fronts. There were thus interestadial climatic fluctuations within a single cycle. Perhaps more than one cycle may be present. The early Talchir flora, both mega—and microfossils, has been recovered from sediments close to the tillites (LELE & KARIM, 1971; SURANGE & LELE, 1956; LELE, 1975). This includes *Noeggerahiopsis*, *Gangamopteris* and some monosaccate pollen (*Plicatipollenites*, *Potonieiporites*). There is no doubt that some hardy plants could thrive even when the country was largely ice-covered. The records of the flora are, however, poor everywhere in the early Talchir. The vegetation was evidently very scanty thriving here and there on ice-free areas or in other relatively hospitable pockets (SURANGE & LELE, 1956). The leaves are strikingly small, sometimes fleshy, curled or folded up in sediments and the venation is often fine and crowded. These features are compatible with long dormant periods imposed on plants by the adversely frigid climate. *Glossopteris* has not been found in the early Talchir.

Towards the end of the Talchir, the flora shows a definite improvement suggesting an amelioration of climate brought about by the recession and melting of ice. (LELE, 1966; SURANGE, 1975) The flora must have quickly occupied the land as more ground became ice-free and opportunity for diversification became available with increased sunlight and temperature. As many as 8 species (including varieties) of *Gangampteris* are known in the topmost Rikba Beds. Some of these leaves are fairly large (mostly incomplete in length) and up to 8 cm. broad and well-built indicating improved climatic conditions

for growth. In addition there are some small conifers like *Paranocladus*. *Noeggerathiopsis* (mostly referable to *N. hislopi*) and winged seeds become more frequent. The sandy facies of the late Talchir often carry equisetalean stems.

It is remarkable that almost all the characteristic leaf forms of the Talchir flora (*Gangamopteris*, *Noeggerathiopsis*) are without a midrib (Text Fig. 2). Leaves with a distinct solid midrib appear only in the late Talchir; these are the narrow-mesh species of *Glossopteris* viz., *G. communis* and, *G. indica*. At any rate *Glossopteris* was very subordinate and significant in proportion into *Gangamopteris* in the Talchir and even in the overlying Karharbari. There is evidently a marked correlation between the abundance of midrib-less leaf-forms and cooler climate that prevailed throughout the Talchir-Karharbari times (*Gangamopteris* floral phase). (Histograms—1 & 2).



Text-fig. 1. Characteristic Angiosperm leaf-shapes of cool temperate and tropical climatic regimes as applied to Tertiary floras. In contrast, *Gangamopteris* and *Glossopteris*, though evolved and associated with temperate climatic regime, are rather 'tropical' in their shape.

Text-fig. 2. Leaf genera of the *Gangamopteris* floral phase (without midrib) as contrasted with those of the *Glossopteris* floral phase (with midrib).

The Karharbari climatic conditions were probably very optimum for a rapid rise in the *Gangamopteris* floral phase. As compared to the Talchir, the Karharbari leaves of *Gangamopteris* show a marked general increase in size; they may be as long as 35 cm. and as wide as 8.5 cm. This indicates a considerable improvement in the climatic setting. It is conceivable that by the Karharbari times glaciers had nearly disappeared from the ground and the climate became very hospitable for plant growth. Plants could therefore spread far and wide as is evidenced by the fossil occurrence of Karharbari plants in a large number of basins stretching from the Damodar Valley (in the east) to the Singrauli basin in the

central part of India. Substantial deposits of Karharbari coal also testify to the proliferation of vegetation that accumulated in the tectonically controlled coal-basins. The Talchir-Karharbari plants produced predominantly winged seeds as well as monosaccate pollen which suggests the important role of strong winds in the dispersal of the flora.

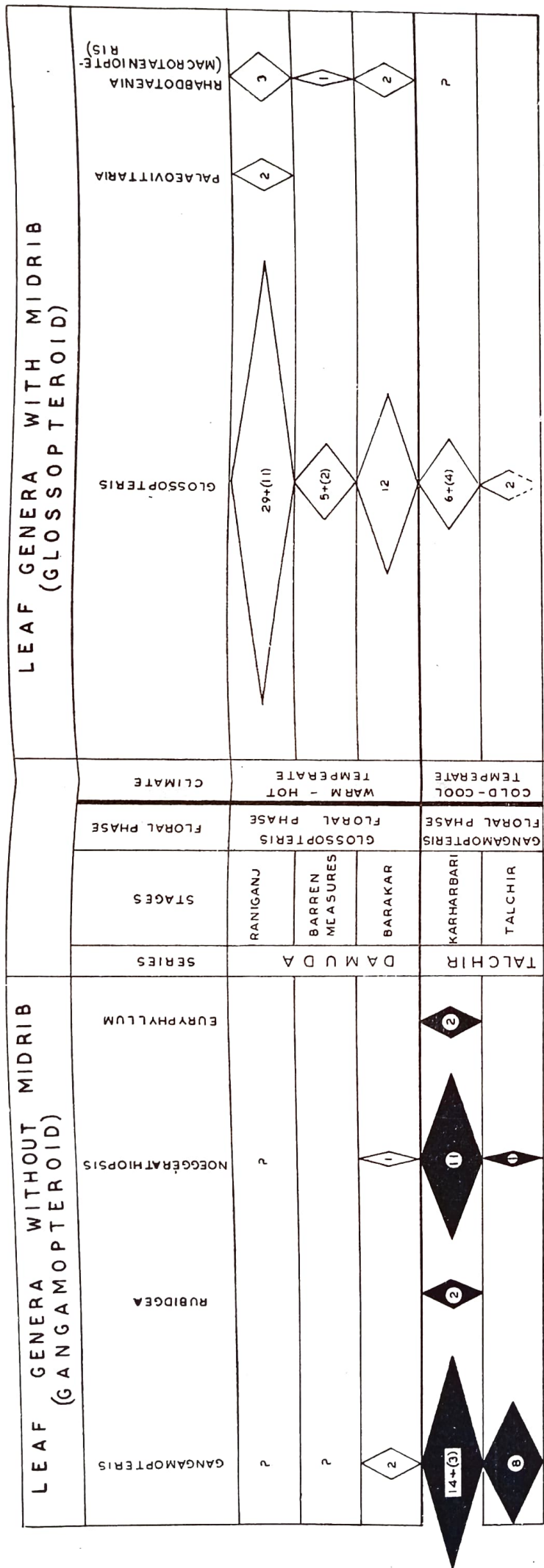
In the Karharbari flora both *Gangamopteris* and *Noeggerathiopsis* reach their epibole; the former rises to 14 species while the latter has about 11 species (SURANGE, 1966a, 1975). Two species of *Rubidgea* are also present. All these taxa are devoid of midrib. Gymnospermous plants (conifers ?) like *Buriadia* also become common at places. Ferns or fern-like plants (*Botrychiopsis*) were few and so were the Equisetales. Sometime the Equisetales are locally found concentrated in sandy to muddy shales which suggests their nearness to water sources. *Glossopteris* increases to 6 species (excluding cuticular ones) which is nearly treble of the Talchir incidence. No lycopod and fossil woods are known. The flora, on the whole, indicates a further amplification of the Talchir plant life. The communities were still dominated, as one could expect, by midrib-less leaves. The plants of the *Gangamopteris* floral phase were presumably weakly-built with pauceous wood (Text-fig. 3) which is also partly inferred from the lack of fossil tree trunks in the Karharbari times. On the other hand, plants like *Glossopteris*, which had a midrib, were much fewer in number, although they were comparatively better represented in the Karharbari than in the Talchir. This indicates availability of more favourable habitats, moist, frost-free conditions, sunlight, warmth and precipitation.

The Karharbari coals are characteristically fusain-rich in contrast to the durain-rich coals of the later Damuda times. Fusain-rich coals are believed to have been formed under wet, aerobic conditions (NAVALE, 1975, in press). Prolonged exposure of plant debris to forces of oxidation may have been caused, among other factors, by inadequate tectonic control on coal basins, unstable drainage pattern and irregular rainfall. At any rate, the general floristic picture of the Karharbari bears the impression of a rather cool temperate regime.

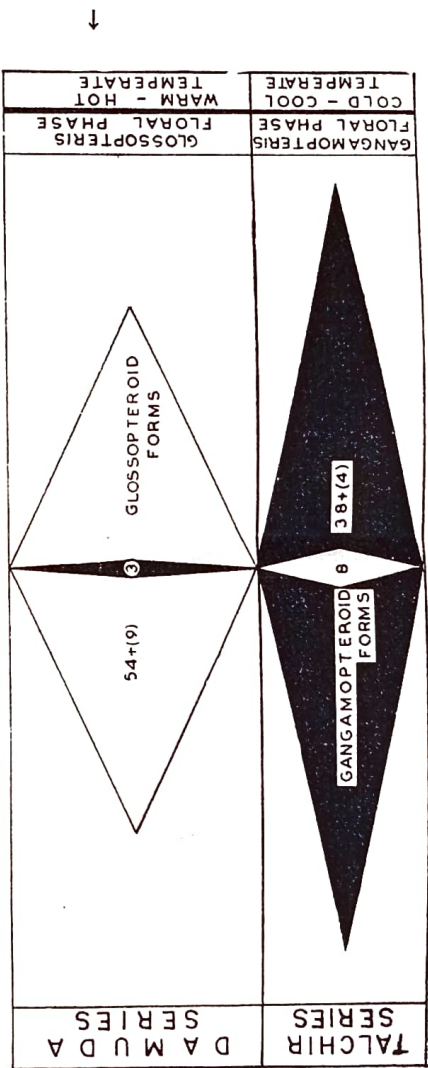
KARHARBARI-BARAKAR TRANSITION : FLORAL CHANGE AND CLIMATIC IMPLICATIONS

This transition demarcates the Talchir Series from the Damuda Series and is indicated by a conglomerate horizon at the base of the Barakar. It also seems to indicate a recognisable change in the flora from the *Gangamopteris* floral phase to the *Glossopteris* floral phase. A distinct turn in the climatic balance is, therefore, surmised at the beginning of the Barakar. The Talchir-Karharbari climate was by and large on the cooler side of a temperate regime. It is conceivable that by the beginning of the Barakar times the climate tended to become warm temperate. Probably a warm moist temperate regime prevailed in general throughout the Damuda, with intermittent hotter spells and wet seasons. It is evident that plants of the *Gangamopteris* floral phase (characterised by midrib-less leaves) which were adapted to cooler conditions could not adjust to the climatic change. The *Gangamopteris*—*Noeggerathiopsis* flora, therefore, shows an abrupt decline after the Karharbari (SURANGE, 1975). In the Barakar there is only one species of *Gangamopteris* (*G. cyclopteroides*)—probably a very hardy survivor that shows a remarkable persistence throughout the Lower Gondwana, irrespective of climatic vicissitudes. All other faithful associates of *Gangamopteris* like *Noeggerathiopsis*, *Buriadia* and *Botrychiopsis* also suffered a similar decline.

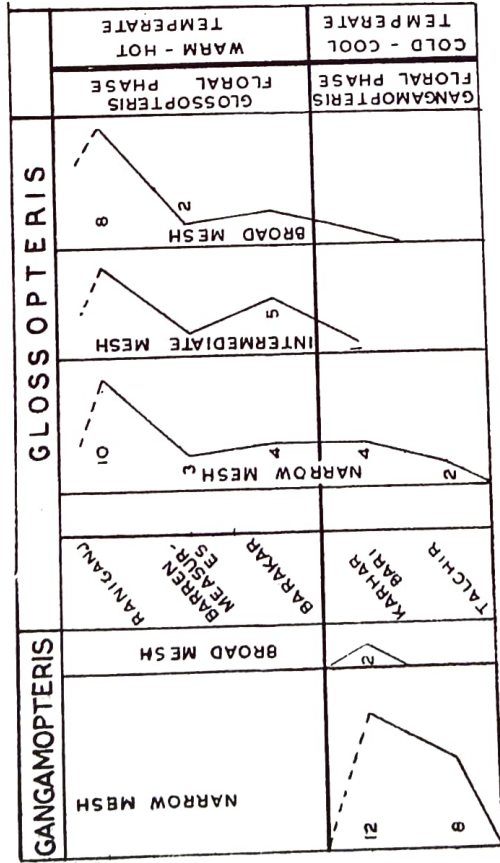
On the contrary, the climatic turn seems to have found favour with *Glossopteris*, which therefore rapidly proliferated in quantity as well as quality from Barakar onwards. From a low number of 6 species in the Karharbari, *Glossopteris* rose to 12 species in the Barakar (Histogram—1). Thus there is sufficient reason to believe that the fall of the



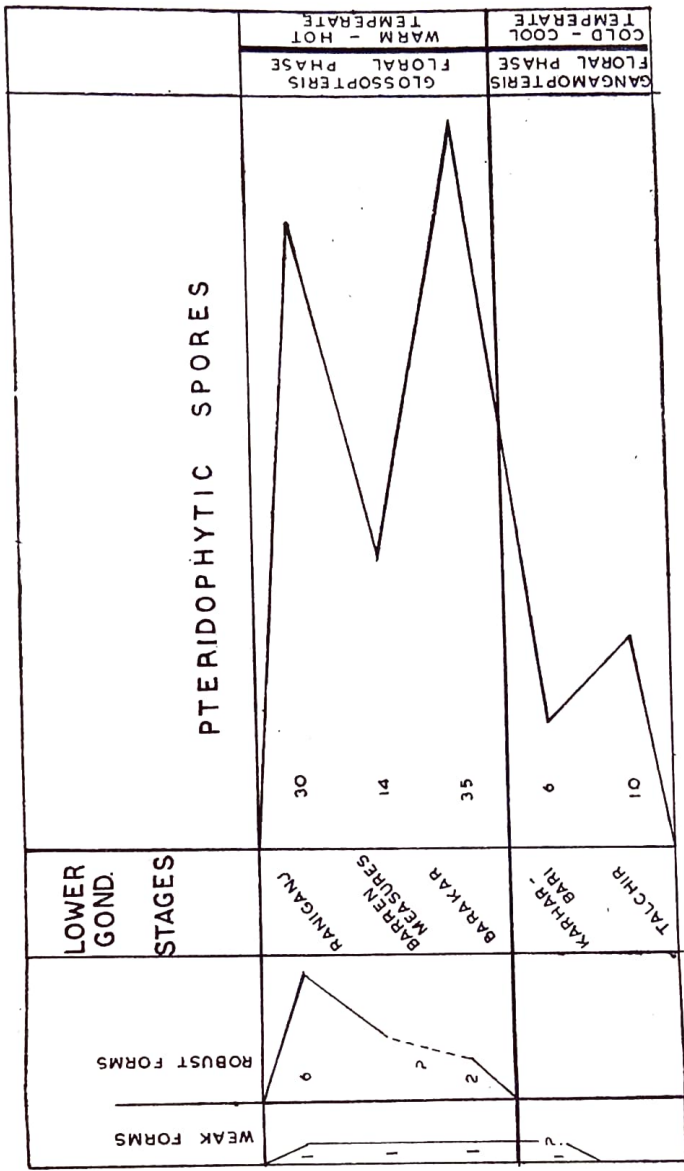
Histogram-1. Relative distribution of leaf species without midrib (Gangamopteroid) and species with midrib (Glossopteroid) in the Lower Gondwana Stages. Total number of impression-species is given inside the histogram. Cuticular-species are numbered within brackets. Source of data—Surange, 1966; Chandra, 1974.



Histogram-2. Relative distribution of total leaf species without midrib (Gangamopteroid) and species with midrib (Glossopteroid) in the Talchir and Damuda Series, Lower Gondwana. Number of impression-species is given inside the histogram. Cuticular-species are numbered within brackets. Source of data as for Histogram-1.



↑ Histogram-3. Relative distribution of different mesh-forms of *Glossopteris* and *Gangamopteris* in the Lower Gondwana Stages. Only impression-species are numbered inside the histogram. Source of data—Surange, 1966; Maithy, 1974.



↑ Histogram-4. Relative distribution of Ferns (probable weak and robust species) and Pteridophytic spores in the Lower Gondwana Stages.

Gangamopteris floral phase and the concomitant rise of the Glossopteris floral phase is a major event that may reflect a significant climatic change near the Karharbari-Barakar transition (Histograms—1, 2). An identical impression is also given by the miofloristic change at the Karharbari—Barakar transition where the monosaccate—rich microfloras are quickly replaced by disaccate-rich populations.

In the extra-Peninsular area of Kashmir, similar events are noticeable irrespective of the fact that this area was highly peculiar in its geotectonic setting and closeness to the Tethys shore line (WADIA, 1940). The older flora (lying below the Panjal trap) is richer in *Gangamopteris* but in the younger horizons it is replaced by *Glossopteris* and ferns (NAKAZAWA *et. al.*, 1975). This floral transformation occurred in Kashmir within the Permian much like that in the Peninsular India. Other peculiar elements in the Kashmir Lower Gondwana flora suggest extra-Gondwana affinities and a general coastal climatic influence on the Kashmir area (LELE, 1976).

THE GLOSSOPTERIS FLORAL PHASE AND PALAEOCLIMATES

The Damuda times exhibit the vibrant development of the Glossopteris floral phase. The dominant foliage of this floral phase was characteristically distinct from the earlier Gangamopteris floral phase in the possession of a strong solid midrib that was often continued into a petiole (Text-fig. 2). *Glossopteris* was the predominating plant which increased from 12 species in the Barakar to 29 species or more in the topmost Raniganj (SURANGE 1966a; MAITHY, 1974). The number would be further increased if we add several other species based on cuticular characters (CHANDRA, 1974; SURANGE, 1975). *Glossopteris* leaves were of very variable size and width and generally possessed an acute, but occasionally spatulate apex. Leaves with drip-points are rare. Some very large leaves in the collections of the Birbal Sahni Institute of Palaeobotany measure up to 2 ft in length and 6 inches in width and possess a strong, long-drawn petiole (up to 1.5 cm wide).

The Glossopterids include allied plants like *Rhabdotaenia* which also shared *Glossopteris* features such as large blade area, simple organization, entire margin, persistent strong midrib, petiole, thick texture of leaves and pinnate venation etc. but lacked anastomosis in veins. In *Palaeovittaria* the midrib is not persistent and net-venation is also absent. But such plants formed a minor proportion of the Glossopteris floral phase. *Glossopteris* bore several kinds of male and female fructifications which were often protected by a fertile bract. The female organs had a more or less fleshy receptacle which bore winged seeds in many cases. Such seeds are also found in dispersed state with bisaccate pollen in their micropyles. Dispersed pollen in the Damuda is predominantly bisaccate. This suggests the important role of wind in the life cycle of the plants. Large sized tree-trunks of different kinds, many of which presumably belonged to Glossopterid plants, are known from the Barakar and Raniganj Stages. Some of these show prominent growth rings that have long been known to indicate marked seasons. Many trees probably produced considerable resin as is indicated by the gum-canals (e.g. *Barakaroxylon*). The general consensus now favours the view that Glossopterids were well-built plants., many attaining tall tree sizes (Text-fig. 4) with an elaborate branch-system and varied foliage arrangements (PLUMSTEAD, 1958; PANT & SINGH, 1974). It is believed that the leaves were shed seasonally.

The profuse and widespread evidence of such well-organized plant life from the Damuda rocks leads one to believe that there could have been thick forests growing along river valleys with ample water, enough sunlight, rainfall and good soil cover. A moist warm temperate climate can be safely conceived for the Damuda times in general.

The durain-rich coals of the Damuda also support the presence of water-rich, anaerobic conditions and sufficient water cover over the plant debris that accumulated in the coal basins. Thus, the coalification history of the Damuda coals also supports a more stabilized drainage pattern, considerable rainfall and an adequate tectonic control on the coal basins. This picture is notably different from that of the Talchir-Karharbari times.

Away from the coal basins there could have been upland areas with drier and cooler habitats where a thick woodland flora could thrive. Leaves shed by the woodland plants were more likely to be destroyed before they could reach the low-lying coal basins. But in the pools of the woodland itself, there could have been seasonal accumulation of a wide variety of foliage and twigs carried by strong winds or storms from different trees (PLUMSTEAD, 1963).

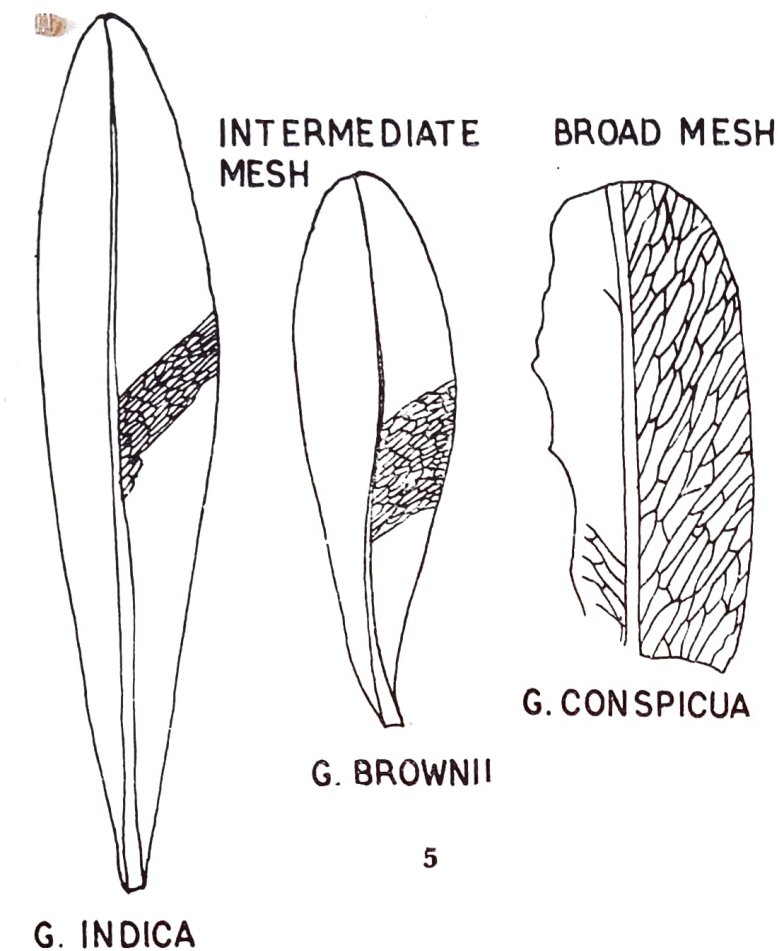
The mud flats and swampy areas of the flood plain with more pronounced semi-aquatic conditions, could also have been the growing place of some plants, especially the Equisetales and, may be, some Glossopterids as well. For, *Vertebraria* axes which were parts of the *Glossopeteris* tree (roots or stems?) show very conspicuous, large air-spaces, (SCHOPF, 1965; GOULD, 1975) that indicate proximity of the plant to water.

The Glossopterids, evidently lived under a wide range of habitats and were nearly versatile in their climatic-ecological tolerance. There is no doubt now that these were gymnosperms and a large proportion of them represented an entirely distinct class of plants called *Glossopteridales* (SURANGE & CHANDRA, 1975), the like of which is not known in the northern hemisphere. Probably some other Glossopterids developed pteridoppermous features but even these were different from the northern Palaeozoic and Mesozoic representatives.

Glossopeteris leaves of the Damuda flora show a number of venation patterns which have yet to be critically analysed for their palaeoclimatic value (Text-fig. 5). Generally three groups are recognized (CHANDRA, 1974) viz. (1) Narrow-mesh forms (2) Intermediate-mesh forms and (3) Open-mesh forms. Maithy (1974) attempted to study the distributional significance of the narrow-mesh forms v.s. open-mesh forms which revealed that the latter group is more prevalent in the upper part of the Damuda. The intermediate-mesh forms are somewhat gradational between the narrow-mesh and open-mesh groups.

If we study the distributional pattern of all the three groups in Lower Gondwana times we can discover some more significant features of probable climatic value. For instance it can be seen (Histogram—3) that the narrow-mesh species of *Glossopeteris* are amazingly persistent both in the Talchir-Karharbari as well as in the Damuda and even linger beyond it, but there is a marked rise in species in younger horizons (Raniganj). The intermediate-mesh forms behave differently. They are either absent or very rare in the Talchir-Karharbari but become rather suddenly recognisable in the Barakar and rise further in species in the Raniganj. The open-mesh forms nearly follow a pattern similar to the intermediate-mesh forms but they do not become truly conspicuous until the Raniganj times when they are almost as abundant as the other two groups. Broadly speaking, there is apparently a close correlation between the evolutionary diversification of *Glossopeteris* meshes and the progressively warming trend in the climates through the Lower Gondwana. Evolution of open (lax) mesh forms was probably influenced by the onset of a warm-humid trend in the climatic regime towards the beginning of the Barakar. Subsequently conditions might have become more humid with cool/hot and dry/wet intervals, towards the later Damuda times. The preference of open mesh *Glossopeteris* forms to warm climatic regime is also indirectly supported by their contrasting absence or extreme rarity in the colder climatic regime of the Talchir-Karharbari period (*Gangamopteris* floral phase). Even in

NARROW MESH



Text-fig. 3. Reconstruction of *Gangamopteris* plant (weakly built). After Plumstead, 1966.

Text-fig. 4. Reconstruction of *Glossopteris* plant (arborescent). After Pant & Singh, 1974.

Text-fig. 5. Three types of mesh-forms in *Glossopteris*.

the case of *Gangamopteris* the few broad-mesh forms seem to appear only in the later phases (Karharbari) when the climate had sufficiently ameliorated (Histogram-3). It seems therefore important to note that a detailed analysis of venatin morphology of *Glossopteris* and allied genera like *Gangamopteris* and *Macrotaeniopteris* (*Rhabdotaenia*) may yield important clues for palaeoclimatic interpretations. Certain characters relevant to such investigations are (1) emergence angle and course of veins from midrib towards margin of leaf (2) shape of meshes and mode of anastomosis (3) differential concentration of mesh-types in the same leaf and (4) linking and delinking trends in vein anastomosis. These and several other subtle features can only be found by closer analytical study of the leaf forms with refer-

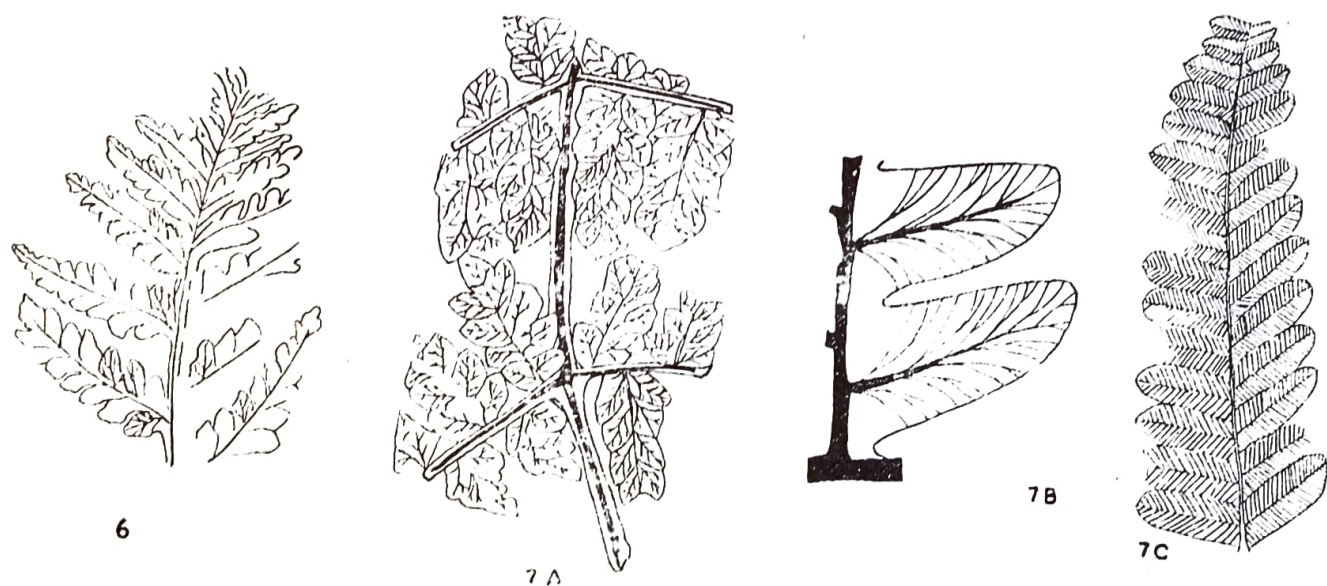
ence to space and time. An analysis of the epidermal structures of leaves can also be taken up to find out their value for ecological interpretation. Epidermal groups of Glossopteroid leaves envisaged by SURANGE AND SRIVASTAVA (1957) can help in going into further details of the problems. For the present no satisfactory clues seem to emerge. For instance, the group of broad-mesh leaves do not apparently show any correlation with their epidermal characters for palaeoclimatic interpretations. Indeed, a very critical morphological cum epidermal analysis is warranted to decipher aspects of correlative value.

The Glossopterids are often associated in the fossil flora with considerable proportion of arthrophytes like *Schizoneura*, *Phyllothea*, *Raniganjia*, and *Stellothea* which were probably distinct from the northern calamites. However in their habitat they might have been similar to some calamites in their preference to semi-aquatic conditions which could obtain along muddy or marshy places surrounding pools and lakes. Often these plants show a selective preponderance in silty to argillaceous shales and fine sandstones which probably indicates a mud flat like habitat for the plants.

Ferns are also an important component of the Damuda floras. The extreme poverty of ferns or pteridophytic spores in the Talchir-Karharbari indirectly supports the adversely cold conditions prevailing at that time. On the other hand, there is a substantial increase and also some diversification in the fern complex and pteridophytic spores during the Damuda times which indicates favourably warm and moist conditions (Histogram-4).

Some of the Damuda ferns appear to have been delicately built while others were probably robust forms. It is interesting to observe that the earlier ferns, like *Neomariopteris hughesi*, which prevailed in the Barakar, were rather delicate in construction with small pinnules having thin venation (Text-fig. 6). Their rachis is generally weak and unwinged. These plants could have favoured moist shady places, such as those available under the *Glossopteris* forest cover. Most of them have marattiaceous sporangia (MARTHY, 1974a, 1975). The presence of marattiaceous ferns favours a warm humid environment. *Damudopteris* (PANT & KHARE, 1974) was probably also a delicately-built fern of the Barakar times.

The later ferns, which prevailed in the Raniganj times, were apparently more robust in their construction, possessed an elaborate, open branching and their pinnules were firm with prominent veins. The main rachis was considerably wide, rigid, and often characteristically winged (Text-fig. 7 a-c). Some notable examples were *Neomariopteris polymorpha*,



Text-fig. 6. A probable weak fern—*Sphenopteris hughesi*.

Text-fig. 7. Some probable robust ferns (A) *Sphenopteris polymorpha* (B) *Dichotomopteris* and (C) *Dizeugotheca*.

species of *Dichotomopteris* and *Dizeugotheca* (MAITHY, 1974a, 1975). These ferns were evidently taller and probably were capable of standing open areas with bright sunlight and relatively higher temperature ranges. *Neomariopteris lobifolia* could have been one of these fern types. The records of this species are better known in the upper Permian of Australia than in India; and in the former area, RIGBY (1971) envisages the possibility that *Neomariopteris lobifolia* could have belonged to a large tree-fern like *Cyathea* or *Todea* indicating a tropical to sub-tropical or warm temperate, frost-free climate. Silicified osmundaceous tree fern trunks of *Palaeosmunda* are also known from Australia. However, in India we do not yet know anything definitely about tree-ferns. The earlier *Cyathea* records are now placed under *Neomariopteris* by MAITHY (1974a). It is obvious that the Indian Lower Gondwana ferns, when studied more intensively and extensively will yield meaningful data bearing on their morphology and palaeoclimatic value.

The Barren Measures Formation which intervenes the Barakar and Raniganj is somewhat peculiar in its geological background and lithological content and floral aspect. The intercalation of ferruginous bands, ironstone shales with highly carbonised shales and general poverty of workable coal is a characteristic feature. The fossil flora is strikingly impoverished. *Glossopteris* drops to 5 species. On the contrary *Cyclodendron* (a lycopod), is peculiarly restricted to this flora. *Cyclodendron*, in S. Africa, shows a kind of seasonal growth (PLUMSTEAD, 1961) as evidenced by the succession of large and small leaf-scar zones on the stem surface. There is reason to believe that plant life continued more or less uninterrupted through the Barakar—Barren Measures—Raniganj times as several species of the Barakar are seen in the Raniganj as well. The microfossil evidence also reflects considerable vegetation. Why then is the Barren Measures fossil record so poor? It may be due to several factors operating singly or in combination. A very plausible reason may be the temporary withdrawal of vegetation away from the swampy areas due to adverse conditions (SÜRANGE, 1966a). Could the vegetation recede to the uplands during Barren Measures and invade the swamps again in the Raniganj when conditions became better? Another possibility is that the environments of the Barren Measures swamps, lagoons and lakes could have been generally detrimental to preservation of plant-organic matter as well as to the formation of coal.

Since the Barren Measures times onwards there is, indeed, a notable reduction in the coal-bearing areas on the one hand (Raniganj and Jharia) and the rapid expansion of the non-carbonaceous, ferruginous—arenaceous, variegated, sediments (Kamthi facies) on the other. The Kamthi facies which is indicative of a deltaic sedimentation under a dominantly oxidizing environment (van HOUTEN, 1961), is extensively developed in the Son-Mahanadi valley basins and continues westward in the Satpura basin and southward in to the Wardha-Godavari valley basins. As opposed to this the carbonaceous facies of the Raniganj is nearly confined to the Raniganj and the Jharia basins of the Damodar valley. The carbonaceous Raniganj sediments carry abundant flora of Glossopterids, ferns, and Arthropytes in the Raniganj Coalfield. This indicates a lush, forest-like growth in particularly favourable areas of the lowlands. Even the Kamthi facies locally contain considerable floral evidence, as for example in Orissa (near Handappa), where large-sized *Glossopteris* leaves are found crowded together with some strongly-built large fern-types and a variety of *Glossopteris* fructifications. A strikingly similar facies in South Africa and Australia also seems to carry the bulk of Glossopterid fructifications and abundant fossil leaves. It is likely that these floral assemblages, associated with variegated sediments (Kamthi facies), represent an upland vegetation.

From the foregoing account, it may be safely contended that there is a close correspondence between the pattern of floral changes and climatic vicissitudes during course of the Lower Gondwana. It seems also possible to distinguish certain sets of morphological characteristics that are associated with plant communities of a particular climatic regime. I therefore venture to summarise below some plant morphological characteristics of the two main Lower Gondwana floral phases and their palaeoclimatic correlation. It is my hope that an approach like this, though open to further modification, may lead us to decipher more and more clearly the plant climatic indicators for the *Glossopteris* flora.

A : PLANT CHARACTERISTICS OF GANGAMOPTERIS FLORAL PHASE (COLD TO COOL TEMPERATE REGIME)

1. Gangamopterids, and ? Cordaiteans predominant. Equisetales, ferns, conifers and Glossopterids rare and associated more with amelioration in climate.
2. Gangamopterids probably weakly built, low shrubby plants, having small amount of wood, largely non-arborescent, vegetation scanty and dispersed, forest-like dense growth rare.
3. Cordaitean features not known except for leaves.
4. Leaves generally devoid of solid midrib and perhaps also non-petiolate. Main conducting system of leaves loosely arranged. Presumably composed of several vascular strands that enter the leaf from base upward and diverge in a straight to curved manner towards leaf margin. Strands dichotomise and/or anastomose in their course (examples 5 *Gangamopteris*, *Rubidgea*, *Euryphyllum*, *Noeggerathiopsis*).
5. Leaves associated with colder facies tend to be smaller and fleshy in texture, susceptible to curling or folding. Larger leaves associated more with amelioration in climate. Leaf-apex generally more or less obtuse.
6. Net-venation predominantly narrow-mesh type. Intermediate to open-mesh leaf-forms associated more with ameliorating climate. Veins generally not prominent.
7. Miospores predominantly monosaccate.
8. Seeds mostly winged.

B : PLANT CHARACTERISTICS OF GLOSSOPTERIS FLORAL PHASE (WARM TO HOT, MOIST TEMPERATE REGIME)

1. Glossopterids, Arthropytes, ferns and ? Pteridosperms predominant. Lycopods, conifers, ? cordaiteans and Gangamopterids rare or absent.
2. Glossopterids strongly built, with abundant wood, generally arborescent. Vegetation dense, forest-like; covering diverse habitats of low lying river-valleys, flood-plains, lakes, swamps (semi-aquatic) and uplands.
3. Glossopterid leaves characterized by a solid, more or less persistent midrib and often petiolate. Main conducting system of leaves compactly arranged, presumably composed of a solid vascular strand (midrib) from which the secondaries pass into the lamina in various manners. Veins dichotomise and/or anastomose in their course.
4. Leaf-blade area generally large, texture rigid (not leathery). Drip-points rarely present; leaf apex generally more or less acute.
5. Net-venation types diversified into narrow-mesh forms, intermediate-mesh forms and open-mesh forms. The latter two types of mesh-forms associated more with increased warm to hot humid conditions. Veins generally prominent, thick.

6. Fossil wood generally gymnospermous, picnoxylic, often with resin-ducts. Growth-rings prominently developed.
7. Some plants probably growing in semi-aquatic swampy areas developing large air spaces in their axes. (e.g. *Vertebraria*).
8. Leaf epidermis generally thick, often relatively thicker on one side, stomatal distribution more often hypostomatic, haplocheilic; stomatal complex well-developed, stomatal index high, stomatal pore \perp exposed, subsidiary cells and/or other epidermal cells may be sometimes papillate. Epidermal features generally indicating mesophytic conditions.
9. Pteridophytes well represented. Arthropytes probably growing in proximity to water. Sphenophyllums without hydathodes. Ferns, both weak as well as robust types, present; the former adapted to shady places; the latter probably adapted to increased warmth (? hot conditions) and open areas with bright sunlight. *Aphlebica*, etc. not found in ferns.
10. Miospores predominantly bisaccate.
11. Seeds winged or unwinged.

MIDDLE GONDWANA: DICROIDIUM FLORA

The Permian-Triassic transition in India as well as in several other Gondwana countries is characterized by the disappearance of the *Glossopteris* flora and the appearance of a new kind of vegetation called the *Dicroidium* flora (= *Thinnfeldia* flora of du Toit and earlier workers) which characterizes the Middle Gondwana (LELE, 1964).

In India, the Triassic is believed to have been a period of extensive land conditions, epi-erogeny and widespread erosion. The red bed sequences (with haemetite) indicate oxidizing condition of deposition. Fox (1940) envisaged an arid tropical region for much of the Triassic period in India. However more recent sedimentological and faunal evidences support a semiarid regime (SHAH; DUTTA—in this symposium). The semiaquatic to aquatic reptilian fauna tends to indicate water-sources and hence rainfall. Later Triassic sequences suggest humid conditions (DUTTA—in this symposium). ROBINSON (1967) completely rules out semi-arid or arid conditions and in its stead, envisages a monsoon type of climate but with heavier and longer seasonal rainfall and high mean annual temperature. The climatic picture is, obviously, not very clear still and more work seems necessary. Unfortunately the Triassic floral record is neither rich nor widespread; hence only some observations can be made at present.

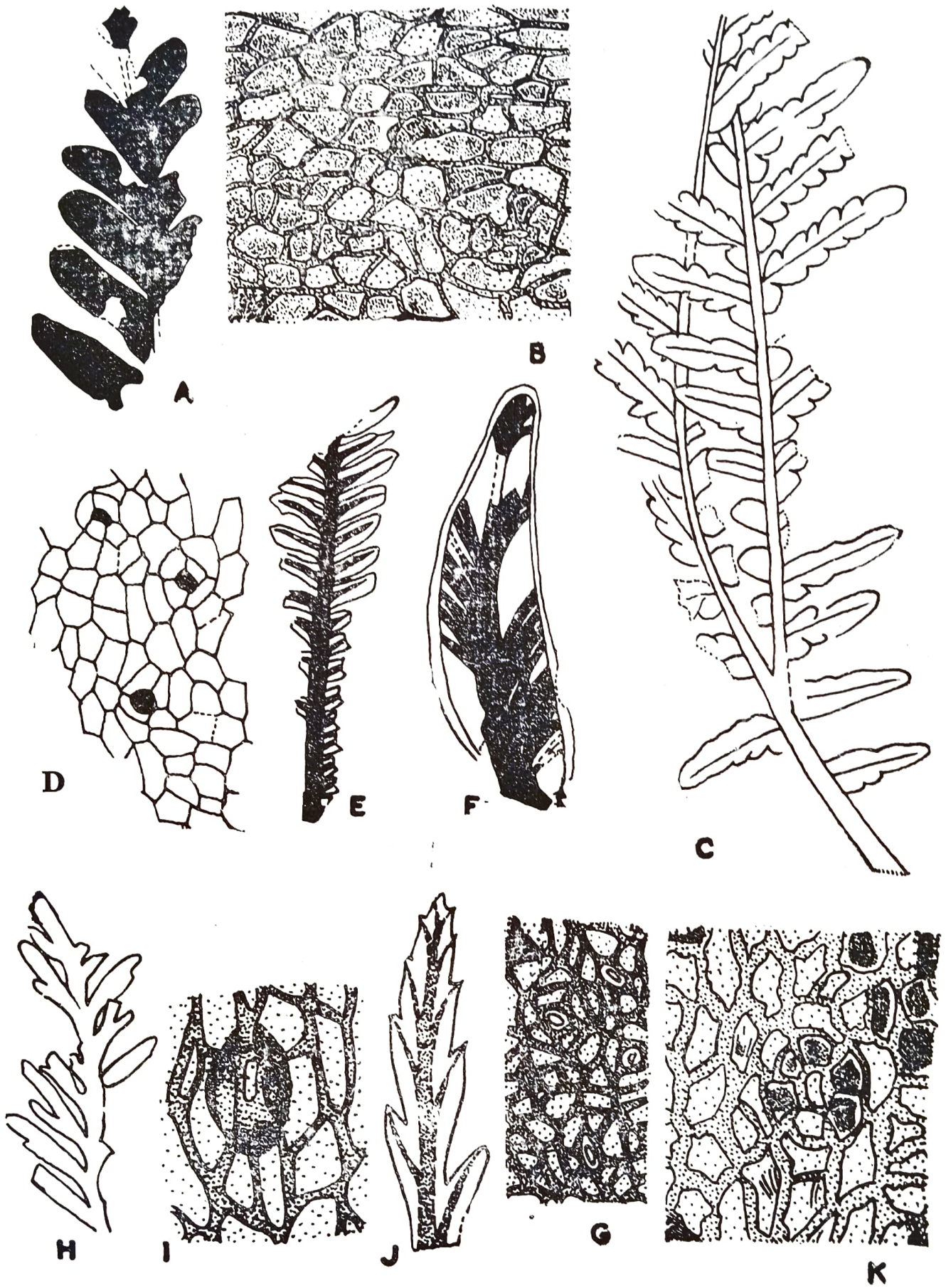
Relatively better Triassic floral assemblages occur in the lower part of the sequence (Panchet, Nidpur etc; ROY CHOWDHURY *et al.*, 1975) where plants may be associated with carbonaceous sediments. In the upper part (Parsora beds) the fossil flora is found in the red-bed facies. It is probable that the Permian climatic conditions lingered on into the Lower Triassic in a somewhat restricted sense; for, some older *Glossopterids* (*Glossopteris*, *Rhabdotaenia*), Equisetales (*Schizoneura*) and ferns (*Neomariopteris*) persist in these beds. At any rate, a floral change is noticeable at the beginning of the Triassic which reflects a distinct turn in the climatic setting, perhaps involving aridity. The Permian species considerably reduced in number by the Triassic times both in the mega—and mio-floras. From about 40 species of *Glossopteris* in the Raniganj, the number abruptly dropped to about 8 in the Triassic as a whole. Many of the *Glossopteris* 'hold-overs' like *G. indica*, *G. angustifolia*, *G. communis* and *G. browniana* are indeed exceptional forms which show outstanding long vertical ranges and an obvious tolerance to climatic vicissitudes. The more typical *Glossopteris* species of the Raniganj flora, which were adapted to moist,

warm temperate (or hot) conditions, however, nearly disappeared from the Triassic scene. This reflects an adverse climatic turn, probably caused by ensuing aridity. In later Triassic times *Glossopteris* was a straggler, seldom represented by one or two species with relatively much reduced blade area. Fox (1940) had suggested, and perhaps correctly, that the disappearance of the *Glossopteris* flora was caused more due to the aridity, rather than the heat during the Triassic.

It was during this transition that some quite distinct plants began to appear on the Gondwana Triassic scene. These were *Lepidopteris* and *Dicroidium* which had a characteristically pinnate organization and often a forked rachis. No such plants were present in the Permian floral regime of the *Glossopteris* which had on the contrary, simple, entire, smooth-margined leaves. The question is naturally raised as to how the *Dicroidium* plants appeared suddenly on a rather adversely changing climatic scene. Is it probable that the Gondwana *Dicroidium* had a northern ancestry? SCHOPF (1973) postulates such a probability and temporary floral contacts with Gondwanaland during the late Permian. The question is admittedly open, but there is little doubt that earlier (Permian) distributional barriers were progressively withdrawn after the Triassic permitting fresh means and opportunities for an intermingling between the northern and southern elements across the Tethys (LELE, 1976 and other references cited therein).

Probably part of the northern floral migration was also influenced by a factor that relatively suitable climatic conditions were still available on Gondwanaland around the Perm/Triassic transition when the northern Permian landscape was under the full grip of desiccation detrimental to plant life. *Lepidopteris* could be one such northern migrant on Gondwana, for it appears earlier in the northern hemisphere (Late Perm.) as compared to the south (Triassic) and the species of the two hemispheres are also different.

The knowledge of the Indian Triassic plant life is still very meagre as compared to the better records from other Gondwanaland countries (LELE, 1976). Later Triassic floras (Mahadeva, Tiki, Parsora Stages) are particularly poor in content, although *Dicroidium* is well represented. The striking deterioration in floral record, though in itself not a very reliable guide, may suggest wider extension of adverse conditions in which no substantial plant life could thrive or be preserved. MAHABALE (1966) opines that the vegetation was discontinuously developed at distant places "wearing a xerophytic garb". Certain xerophytic features in the epidermal cell walls and stomatal complex of *Dicroidium*, *Lepidopteris*, *Pachypteris* and *Cycadopteris* as well as the thick and scaly nature of the rachis of *Lepidopteris* and the thick cuticle of *Dicroidium hughesi* (preserved as ferruginous cast in some localities, see LELE, 1962) may provide some support to a dry environment (Text-fig. 8). Presumably these plants might have grown like a scrubby vegetation in some hospitable areas which were fed by irregular rain fall. Besides *Dicroidium*s, there were plants with wide stems of *Neocalamites* appearance which probably favoured nearness to water. Cycadophytes like *Pterophyllum*, *Taeniopteris*, *Pseudoptenis* are significant to the upper Triassic of India and are much more abundant in other Gondwana lands. These plants indicate a warm humid environment. Rare conifers (*Podozamites*, *Araucarites*) could have lived in cooler habitats (? higher ground) along with *Ginkgo* and *Baiera*. Ferns (viz. *Parsorophyllum*, *Cladophlebis*, *Danaeopsis*) are rare in India but a large number of them, especially the dipterids are characteristic of other Gondwana Triassic and in the northern hemisphere. These ferns indicate sub-tropical to tropical conditions. There are undoubtedly some differences in composition details of the Indian flora and other Gondwanaland floras during the Triassic (LELE, 1976) which may be due to regional differences in physical/climatic conditions coupled with the relative latitudinal positions of different



Text-fig. 8. Some characteristic plants of the Dicroidium flora (Triassic) (A) *Dicroidium odontopteroides* (B) *Dicroidium papillosum*—thick, papillate cells (C-D) *Dicroidium feistmanteli*—forked frond and leaf epidermis (E-G) *Cycadopteris*—leaf, its rolled margin, (F), thick cuticle and sunken stomata (G). (H-J) *Pachypteris*—leaves and stoma (K) *Glottolepis rugosa*—thick cells and sunken stoma of a thick scale leaf recalling xerophytic features.

Gondwana areas during the drift of the southern landmass. On the whole there is a noticeable change towards more favourable climate in many parts of the late Triassic world (LELE, 1975) and the rejuvenated plant life appears to foreshadow the vegetation that subsequently characterized the Jurassic floras.

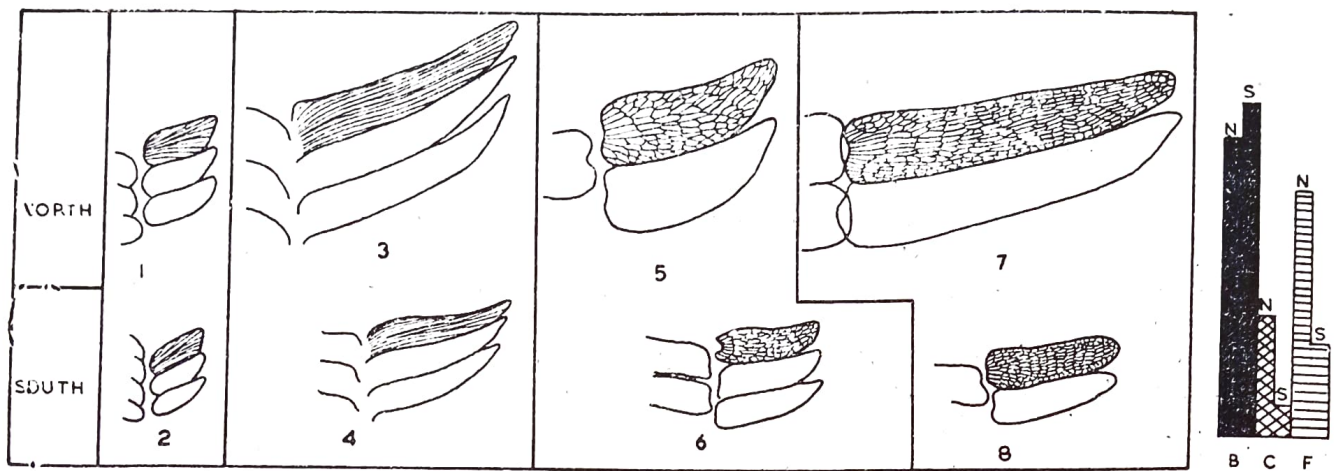
UPPER GONDWANA—PTILOPHYLLUM FLORA

The Triassic period seems to have passed into the Jurassic without much disturbance. India was then perhaps across the equator. Jurassic climates are believed to have taken a favourable turn due to increased humidity, possibly caused largely by the gradual spread of sea along the Indian Gondwana coast-line in the Upper Gondwana times (Fox, 1940). Volcanic activity was evidenced in several successive phases in the Jurassic of the Rajmahal area, but it was nothing compared to the enormous volcanism witnessed by the close of the Triassic and throughout the Jurassic in some other Gondwana continents like South Africa. Evidently, the best floral records of the Jurassic-Lower Cretaceous floras are only available from India. This is called the Ptilophyllum flora, remains of which are richly preserved in various lithologies ranging from freshwater shales, clays, sandstones marine intercalations and intertrappean cherts.

The Upper Gondwana flora is undoubtedly characterised by *Ptilophyllum* which also sets the lower limit of the Jurassic (LELE, 1964) and forms the principal biozone of the Ptilophyllum flora (SHAH *et al.*, 1971), comprising a rich proportion of Equisetales, Filicales, Pteridosperms, Cycadophytes (Cycadales & Bennettitales), Coniferales and Ginkgoales.

According to Shah *et al.* in the older assemblages, (Lr.—Mid. Jurassic) Cycadales are common and conifers are subordinate. Conifers seemingly increase in proportion and replace the Cycadales in the middle part of the succession (Up. Jurassic) and some Pteridophytes like *Onychiopsis* also appear. In the uppermost assemblages (Wealden) conifers and ginkgoes like *Brachyphyllum*, *Araucarites* and *Ginkgoites* become constitutinally important together with several characteristic ferns like *Gleichenites*, *Onychiopsis* and *Weichselia*. Cycadophytes dwindle out. Abundance of cycadophytes and presence of deperid ferns, Marattiaceae, Matoniaceae and Osmundaceae in the flora would seem to suggest a hot, moist subtropical to tropical climate. On the other hand the prevalence of conifers and Ginkophytes as well as ferns of Schizaeaceae, Gleicheniaceae and Polypodiaceae reflect a temperate realm (VAKHRAMEEV, 1965). It is generally believed that the earlier part of the Upper Gondwana is relatively richer in cycadophytes and ferns whereas later floras are richer in conifers and ginkophytes. Was there a gradual change in the climatic trend through the Upper Gondwana times? The answer is very unclear especially because there is yet no clear cut distinction between the floral assemblages of the various Upper Gondwana horizons. Even in the same formation e.g. Rajmahal Formation, there are often noticeable differences in the floral composition (Cycadophyte/Conifer/Ferns) of different localities within the single area of the Rajmahal Hills. This kind of floral differentiation is probably linked with some climatic difference but at the same time some geological factors are also involved.

An interesting study, although of a preliminary nature, was carried out by GUPTA (1966) in the Rajmahal Hills which is relevant to the above points. Gupta observed demonstrable qualitative and quantitative differences in the morphological characters of the plants and their distribution in the southern and northern parts of the Rajmahal Hills. (Text-figs. 9 & 10). The northern zone was characterized by (1) bigger size of leaves and fructifications with marked size-variation (2) numerical abundance of species. (3)



Text-fig. 9

Text-fig. 10

Text-fig. 9. Smaller and bigger fronds of the same species of two different genera in the northern and southern zones of the Rajmahal Hills (Jurassic). 1 & 2-*Ptilophyllum cutchense*, 3 & 4-*P. acutifolium*, 5 & 6-*Dictyozanites indica*, 7 & 8-*D. falcata*. After Gupta, 1966.

Text-fig. 10. Distribution of Bennettitales (B), Cycadales (C) and Ferns (F) in the northern (N) and Southern (S) Zones of the Rajmahal Hills (Jurassic). After Gupta, 1966.

prevalence of sinuous epidermal cell-walls (4) frequent association of Cycadophytes and ferns, esp. *Gleichenites* and (5) Sinuous and thin cell-walls in *Ptilophyllum* species. The southern zone, on the contrary, was characterized by (1) generally smaller size of fronds and fructifications (2) prevalence of smooth cell walls and (3) *Ptilophyllum* species with xerophytic features, smooth and thick cell-walls. As the north and south zones were not separated by any considerable distance, the only plausible conclusion was that the fossiliferous outcrops of the two areas belonged originally to different periods of volcanic activity the records of which are obliterated by subsequent erosion. The floral characters of the two areas also suggest that the plants grew in different seasons (or climate) : one hot-dry type, the other humid, That there were distinct seasons (hot/cold or wet/dry) is also borne out by the prominent growth rings in some Jurassic woods (*Sahnioxylon*). Also there could have been arid habitats where some xerophytic ferns like *Matonidium* and *Weichselia* could grow.

There can be little doubt that the Upper Gondwana scene provided a number of habitats for varied and luxuriant plant growth. Palaeo-physiographic details of the landscape may prove useful in strengthening the nature of habitats which may have ranged from coastal areas, river valleys and flood-plains, open low lands, and even some uplands permitting ecological and floristic differentiation. Another important need is to collect extensive statistics on the floristic compositional patterns together with morphometric assessment of the plant characters in different fossil sites of the same or different areas. Work on such lines was apparently begun by GUPTA (1966) but has not been followed up critically. In the northern fossil floras exhaustive work on Jurassic plants have amply demonstrated their palaeoclimatic value (VAKHRAMEEV, 1965). As the northern floras were, by an large, of the same kind as those in the southern hemisphere it should seem possible to use with advantage some of the well known Mesozoic plant-climatic indicators for interpreting the Upper Gondwana palaeoclimates.

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