FLORISTICS OF THE PERMIAN AND TRIASSIC GONDWANAS OF INDIA

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ABSTRACT

A synthesis of the floristics through the Upper Palaeozoic and Lower Mesozoic Gondwanas of India is presented. Definite lycopsids are known only from Middle Permian but could have been present in other ages as well. The solitary sphenophyll species ranges from Middle Permian to basal Triassic. Equisetales are known by vegetative shoots only, but a change in form through the time is noticed. Fertile filicinean remains known are mostly referable to the family Asterothecaceae of the Marattiales. The most important element of the period, i.e. *Glossopteris*-complex represents at least two orders, viz., Ottokariales and Lidgettoniales, as is evident from the fertile organs. This complex continues into the basal Triassic and is gradually replaced by Mesozoic 'Pteridosperm' families Corystospermaceae and Peltaspermaceae. Cordaitalean type of leaves are more common in the Lower Permian; their affinity, however, is uncertain. Cycadales, Ginkgoales and Coniferales though present are meagrely represented.

INTRODUCTION

THE Palaeophyte-Mesophyte in India is found preserved in a thick sequence of mostly continental deposits known as the Gondwana Sequence. This enormous sequence of rocks ranges in age from the Lower Permian (may be Upper Carboniferous) up to the Lower Cretaceous (inclusive). Parallel sequences of continental deposits are also known from the Southern Hemisphere continents, viz., Australia, Africa, South America and Antarctica. It is supposed that the rocks of the Gondwana Sequence in India were deposited in slowly sinking faulted troughs fed by rivers of the Gondwana country (Wadia, 1975, p. 165). In a few instances the deposits could have been laid down in lakes. The sequence starts with a boulder bed, containing the characteristically glaciated, striated and facetted blocks of rock embedded in a fine silt-like matrix, suggesting a fluvio-glacial agency of transport and deposition. The boulder bed forms a conspicuous and characteristic datum line in the geology of the Indian Peninsula. The boulder bed is overlain by green laminated shales and sandstones showing cold climate. The climate gradually warmed up as is seen from the diversification of the flora. The succeeding Permian strata contain thick coal seams which were laid down in a warm humid climate. The early Triassic, rocks contain undecomposed felspar which supposedly indicates arid conditions (Wadia, 1975). The younger Triassic has thick red sandstone deposits which are supposed to denote arid desertic conditions. Robinson (1967, p. 230) suggests a monsoon type of climate for the Indian Triassic. A classification of the Permian and Triassic Gondwanas of India is shown in the table (slightly modified from Shah, Singh & Sastry, 1971).

Plant fossils are quite abundant in the Permian and Triassic systems of the Indian Gondwana Sequence. These are of great biological interest as they comprise certain plant groups which are not represented in the contemporary floras of the Northern Hemisphere. In the period under review, two distinct floras have been found. The older, Glossopteris flora is characteristic of the Permian though it extends into the basal Triassic. The younger, the Dicroidium flora is confined to the Triassic System only. The plant groups represented in the two floras are: ?Bryophyta, Lycopodophyta, Arthrophyta, Pterophyta, Glossopteridopsida, 'Pteridospermophyta', Cycadophyta, Ginkgophyta and Coniferophyta. In addition there are certain plants whose taxonomic position is uncertain.

BRYOPHYTA

This group is probably represented by a solitary capsule-like structure, *Capsulites gondwanensis* Saksena, obtained from a Lower Permian shale. According to Saksena (1958), the distinct division of this structure into foot, seta and capsule, the possibility of the presence of an annulus and the indication of a spore-sac extending along the entire length of the capsule places it near the Muscineae. The exact affinities of the specimen, however, still remain uncertain. There is a distinct possibility that this structure represents a seed.

LYCOPODOPHYTA

Lycopsid megafossils in the Permian-Triassic of India are extremely rare. The oldest records of the lycopsids are from the Lower Permian *Gangamopteris* beds of Zewan Spur, Srinagar District, Kashmir. A fragmentary specimen showing crescentic ligular scars inside spirally disposed rhomboid leaf cushions has been tentatively identified with *Lepidodendron* (Kapoor, 1969, pl. 2, fig. 1). Another specimen shows a cone-like structure probably attached to a lycopsid stem (Kapoor, 1969, pl. 2, fig. 2). The presence of a ligule in these specimens has been doubted by Surange (1971, p. 65) who opines that " The scars described and figured as ligules seem to correspond to the elevations which are left on cushions when leaves dried without abscission like those in *Sublepidodendron*." A better preserved and almost complete lycopsid-like cone was found in the tuffaceous shales of Liddar Valley near Pahlgam, Anantnag District, Kashmir (Srivastava & Kapoor, 1969, pl. 5, figs. 1-3, text-fig. 1). The cone *Lepidostrobus kashmirensis* is cylindrical and pedunculate. The sporophylls are closely placed and spirally arranged. Detailed structure of this cone is not known and hence its affinities are as yet uncertain.

In the peninsula the oldest lycopsid megafossil record is from the Middle Permian Ironstone Shale Formation. The solitary species, *Cyclodendron leslii* (Seward) Kräusel is represented only by fragments of stems, which bear a number of spirally arranged, eye-shaped leaf-scars. Each leaf-scar has a more or less circular boss which perhaps indicates the position of the vascular supply. The ligular pit or the parichnos scars have not been found (Kar, 1968, pl. 1, figs. 1, 2). This species probably persisted into the Lower Triassic Mangali beds, from where a similar specimen was described as ?*Lepidodendron* by Hislop, and later as " *Stigmaria* ? (Portion of the Rhizome of a Fern ?) " by Bunbury (1861, pl. 12, fig. 2). The species is heterosporous, its sporophylls being distributed on normal leafy shoots, without any organized cone (Kräusel, 1961). In the latter character it resembles the Lower Carboniferous *Lepidodendropsis* Lutz, the Upper Carboniferous *Pinakodendron* Weiss and probably *Omphalophloios* White. This could probably represent an unique line of evolution from the Lower Carboniferous to the Permian or may be that the four genera evolved independently of each other (Chaloner & Boureau, 1967, p. 510).

From the Triassic of Beli, South Rewa Gondwana Basin, another lycopsid species, *Lycopodites sahnii* Lele (1962, pl. 1, figs. 1, 2, text-figs. 1, 2) is known. The fragmentary axis bears spirally disposed linear delicate leaves almost at right angles to the axis. The leaf-scars show a centrally situated minute depression probably representing the vascular trace. The genus *Lycopodites* continues into the Jurassic where it is represented by the species *L. gracilis* (Oldham & Morris) Seward & Sahni.

While the lycopsid megaplant remains are scarce in the Permian-Triassic Gondwana Sequence of India, a large number of microspores and megaspores, probably of selaginelloid affinity, have been recorded throughout the sequence (Bharadwaj & Tiwari, 1970; Maheshwari & Banerji, 1975). This does indicate the possibility that many more species of lycopsids flourished than is evident from the megafossil records. The paucity of lycopsid megaplant remains can probably be attributed to their delicate nature and their suppression by an overwhelming preponderance of gymnospermic megaplant remains (Maheshwari, 1974, p. 52).

ARTHROHYTA

EQUISETALES

The equisetalean remains, represented by vegetative shoots only, belong to the genera: *Schizoneura*, *Phyllotheca*, *Lelstotheca*, *Barakaria* and *Raniganjia*. In the absence of fructifications, the relationships of the above genera with one another or their affinities within the group Equisetales are as yet obscure. As far as their stems are concerned, they are all similar in being jointed and ribbed, the ribs continuing through successive nodes. In the latter character they resemble the stems of *Asterocalamites*. In that genus, however, the leaves are dichotomously forked many times. Such forking of leaves is known only in the genus *Barakaria*, and there is a report of a solitary forked leaf in *Phyllotheca australis* (Pant & Kidwai, 1968, pl. 30, fig. 6f). Fnrther in *Asterocalamites* the peltate sporangiophores are not subtended by bracts whereas in *P. australis* the strobili have alternating whorls of bracts and branched sporangiophores. The strobili of the Calamitaceae have sporangiophores subtended by bracts but branched sporangiophores are not known in the family except for *Protocalamostachys*. The fructification of the southern schizoneuras is not known but *Manchurostachys*, the strobilus of *Schizoneura manchuriensis*, is bracteate and has unbranched hexasporangiate sporangiophores. Thus, while the strobili of *Phyllotheca australis* and *Manchurostachys* are somewhat similar to those of the Calamitaceae, the latter family is differentiated by its foliage which lacks a cup-like sheath and by its stems in which the grooves alternate through successive nodes.

Examining the inter-relationship between these genera we find that *Phyllotheca* and *Schizoneura* are distinguished from the other three genera by their leaf-sheaths which are adpressed to the stem to a certain extent. Furthermore, the leaves of these two genera lack the characteristic transverse striations or wrinkling. This wrinkling, which may be due to a lamellate mesophyll or could represent a transfusion tissue, was formerly supposed to be of little or no taxonomic value (Seward & Sahni, 1920). But the association of this feature with the flat type of leaf-sheaths seems to give a certain taxonomic importance to this character within this assemblage. Meyen (1969) also believes that constant presence of this feature may be of taxonomic importance in some cases. *Barakaria*, however, stands out by its characteristically forked leaves which superficially resemble those of some sphenophyllums, e.g. *Sphenophyllum myriophyllum* Crépin. Whatever little that is known of the leaf anatomy of these genera, shows that most of them had a similar epidermal pattern. In *Raniganjia bengalensis* the guard cells are reported to possess obscure radiating striations like those seen in the modern *Equisetum* (Pant & Nautiyal, 1968). This character is not known either in *Schizoneura gondwanensis* (Srivastava, 1955) or in *Phyllotheca angusta* (Surange & Kulkarni, 1968).

Of the two species of the genus *Schizoneura*, *S. wardii* Zeiller is restricted to the Lower Permian formations only. The other species, *S. gondwanensis* Feistmantel ranges from the Lower Permian to the Upper Triassic but is more common in the Upper Permian and Lower Triassic. *Phyllotheca* makes it first definite appearance in the Lower Permian by two species, viz., *P. australis* Brongniart and *P. crassa* Maithy. The latter species is confined to the Lower Permian whereas the former continues into the Triassic. In the Middle Permian two new species, viz., *P. griesbachii* Zeiller and *P. ampla* Surange & Kulkarni (=*P. angusta*) appear. Only the former continues into the Upper Permian.

Lelstotheca robusta (Feistmantel) Maheshwari and *Barakaria dichotoma* (Feistmantel) Seward & Sahni are characteristic Middle Permian species. *Raniganjia bengalensis* (Feistmantel) Rigby is a typical Upper Permian plant. This species is sometimes found in the Lower Permian also (cf. *Phyllotheca sahnii* Saksena). *Neocalamites foxii* Lele from the Upper Triassic is just an equisetalean stem impression, its foliage is not known.

SPHENOPHYLLALES

The sphenophylls are probably represented in India by the vegetative shoots of *Trizygia speciosa* Royle (1839, pl. 2, fig. 8). *Trizygia speciosa* shoots have a slender articulate axis with swollen nodes. Each node bears 3 unequal pairs of leaves in a whorl, successive whorls being superposed. A single vein enters the leaf base, dichotomises a few times sending branches to the apical as well as lateral margins. The species made its first appearance in the Middle Permian and continued through Upper Permian into the basal Triassic where it died out.

Doubts have arisen as to whether this plant is a characteristic form of the Gondwanaland or is a migrant from the Northern Hemisphere and belongs to the genus *Sphenophyllum*. In fact, McClelland as early as 1850 renamed the species as '*Sphaenophyllum speciosa*'. Later workers mostly agreed with McClelland, till Maheshwari (1968b, 1974) reverted to the original name *Trizygia* after emphasizing the morphological differences between the genera *Sphenophyllum* and *Trizygia*, like the characters of the veins and the nature of the subsidiary cells. However, on the basis of shoot morphography, this Southern Hemisphere form can be referred to the Order Sphenophyllales, if not to the genus *Sphenophyllum*. Its exact affinities must await the discovery of the fructifications.

PTEROPHYTA

Earliest records of fern-like plants in India are from the Lower Carboniferous Po Series of Spiti. In the Gondwana Sequence unquestioned fern megaplant remains are not known in the basal Permian, the first fern-like fronds occur at the top of the Lower Permian. Later on they increase in genera and species through the Middle and Upper Permian and continue into the Triassic. Most forms have been attributed to Marattiales. There is no indication of the presence of Osmundaceae or any other tree fern in the Permian-Triassic. However, fertile fern-fronds are rarely found in the Gondwana Sequence and hence the affinities of most of the species remain open.

The oldest fern-like form from the Gondwana of India is *Botrychiopsis* (*Gondwanidium*) *valida* (Feistmantel) Archangelsky & Gamerro, which is a marker species of the Lower Permian Karharbari Formation. The fronds are long and bear two rows of large and more or less deeply lobed leaflets. The fertile structure of this species is not known and hence its pteridophytic affinities have been questioned. Seward (1903) presumed that *Gondwanidium* had gymnospermous, rather than filicinean, fructifications. Similar forms from the Kuznetsk Basin were supposed to have bore gymnospermous fructifications of the type *Gondwanotheca sibirica* Neuburg. The Kuznetsk forms are now supposed to be different from *Botrychiopsis*-*Gondwanidium* and hence the affinity of the Southern Hemisphere form still remains undecided.

The other fern-like forms were usually described under various Northern Hemisphere genera, such as: *Alethopteris*, *Cladophlebis*, *Cyclopteris*, *Merianopteris*, *Pecopteris*, *Sphenopteris* etc. Recently Maithy (1974a, 1974c, 1975), on the basis of a reinvestigation of sterile as well as fertile specimens, has separated almost all of the Indian Permian ferns from the Northern Hemisphere fern genera. The Indian forms are now placed under the genera *Dichotomopteris* Maithy, *Dizeugotheca* Archangelsky & Sota and *Neomariopteris* Maithy. Pant and Khare (June, 1974) established a new genus *Damudopteris* for some sterile and fertile *Sphenopteris*-like fronds from India. The genus is, however, nomenclaturally superfluous as it has the same type (*Sphenopteris polymorpha* Feistmantel, 1876) as the earlier published genus *Neomariopteris* Maithy (May, 1974).

In the genus *Dichotomopteris*, 4-6 free sporangia form superficial sori, which are arranged in two distinct rows, one on either side of the midvein, upon lateral vein endings on the underside of the pinnules. Annulus is absent. Spores are trilete and sculptured. Forms earlier described as *Pecopteris* (*Alethopteris*) *phegopteroides* (Feistmantel) Arber have now been transferred to the genus *Dizeugotheca* as they show groups of 4 free sporangia, arranged in linear fashion on the pinnule margins. Of the 4 known species of the genus *Neomariopteris*, only *N. hughesii* (Feistmantel) Maithy and *N. polymorpha* (Feistmantel) Maithy are known in fertile state. The sporangia are arranged in groups above lateral veinlets, a little removed from the margin. Each group probably comprises 4-6 sporangia in *N. hughesii* and 2-9 sporangia in *N. polymorpha*. In *N. polymorpha* the sporangia are exindusiate, shortly stalked and annulate. The annulus is transverse and multiseriate (Pant & Khare, 1974). Sporangial details are not known in *N. hughesii*. Spores are not known in the former whereas in the latter these are triangular trilete, echinate, similar to those of *Dichotomopteris major* (Feistmantel) Maithy. *Asterotheca santhalensis* Vimal & Singh (1971) is incompletely known. The genera *Dichotomopteris* and *Dizeugotheca* can provisionally be referred to the family

Asterothecaceae of the Marattiales. The sphenopterid *Neomariopteris* shows some resemblance to the gleicheniaceous *Oligocarpia*.

In the Lower Triassic the group is probably represented by *Sphenopteris* (? = *Neomariopteris*) *polymorpha* Feistmantel and *Sphenopteris* spp. Two forms, viz., *Pecopteris concinna* Presl and *Cyclopteris pachyrhachis* Göppert are restricted to the basal Triassic (Feistmantel, 1881a) but their identifications need confirmation (Bose, 1974, p. 285). In the Upper-Middle Triassic we find *Marattiopsis* sp. and *Danaeopsis gracilis*. In the former species at each vein ending is situated a sorus-like swelling. The position of the sorus appears to be Marattiaceous (Lele, 1962b). *Parsorophyllum indicum* Lele could be another fern, characteristic of the Upper Triassic. On the whole the records of Triassic ferns in India are extremely poor and their relationships with the Permian types are as yet uncertain.

GLOSSOPTERIDOPSIDA

This is the most dominant group of plants in the Indian Permian floras appearing almost at the base of the Gondwana Sequence, reaching its zenith in the Upper Permian and then continuing through the Lower Triassic and becoming extinct before the Liassic. *Glossopteris* is the most important member of the group and gives the name Glossopteris flora.

At present five leaf genera, viz., *Gangamopteris*, *Glossopteris*, *Palaeovittaria*, *Rhabdotaenia* and *Rubidgea* are tentatively assigned to this group. The most important genus *Glossopteris* has tongue-shaped leaves with a definite midrib giving off secondaries which dichotomize and anastomose. The anastomoses either only connect the lateral veins in which case the secondaries can easily be traced throughout the lamina, or change the venation to a regular reticuloid pattern (Maheshwari, 1965a, 1966). *Palaeovittaria* and *Rhabdotaenia* also possess a midrib but lack vein anastomoses. In the former the secondary veins meet the leaf margin at acute angles whereas in the latter they reach the margin almost at right angles. *Gangamopteris* and *Rubidgea* both lack a midrib, but in the former the secondaries anastomose whereas in the latter the secondaries dichotomize but do not anastomose. The genus *Euryphyllum* is also sometimes included in this group.

Detailed epidermal studies on the leaves of the above genera have shown that certain generalized epidermal types are common to more than one genus. According to Surange and Srivastava (1957) the various glossopterid species studied by them " fall into six groups which may provisionally be considered as of generic rank ". This is if we take it for granted that each glossopterid genus will have only one generalized epidermal type. However, during my investigations on the glossopterid cuticles, several times I noted a marked inconsistency in epidermal structure of different portions of the same specimen, as well as in different but morphographically similar specimens of the same species. Features, like the degree of cutinization of the guard cells, the surface papillae, and the thickness of the lateral cell walls etc. seem to be affected by preservation as well as laboratory processes. On the other hand, the epidermal structure of *Pteronilssonia gopalii* Pant & Mehra, having large pinnate leaves, is like that of certain glossopterid leaves. While the importance of cuticular characters in delimitation of species within a genus can not be denied, it is doubtful if this character can be utilized for delimitation of generic or higher categories of taxa. Discussing the importance of epidermal features, Seward and Sahni (1920, p. 7) have said that " the direct utility of this line of work in phylogeny is open to doubt."

Records of foliage shoots with glossopterid leaves in organic connection are rather few, probably due to " an extraordinary efficiency in abscission " (Schopf, 1967, p. 114). That the glossopterids were deciduous is suggested not only by the occurrence of a very large number of isolated leaves but also by the presence of sharp growth rings in almost all the Gondwana fossil wood (Maheshwari, 1972). Leaves or shoots have not been found attached to a main stem and, therefore, the various reconstructions of the habit of the glossopteridean plants are largely based upon subjective extrapolation of the available circumstantial evidence.

There seems little doubt, however, that the glossopterid leaves were borne in terminal clusters in a tight spiral (Feistmantel, 1881a, pl. 40, fig. 1, pl. 41, figs. 3, 4; Rigby, 1967, pls. 25, 26). The records showing lateral attachment of leaves are not convincing enough and may probably be due to chance overlapping (cf. fig. 2, in Schopf, 1967). Therefore, views postulating a dimorphic arrangement of leaves on short and long shoots need more evidence. The axes which bore glossopterid leaves have sometimes been identified with *Vertebraria* (Surange & Maheshwari, 1962) but mostly these axes are without any characteristic exomorphic features. In anatomical details these axes are reported to be not significantly different from those of *Vertebraria* (Pant & Singh, 1974). The surface striations found in some of these axes probably represent the growth rings in radial view. In the smooth axes it is further possible that preservation of a thick cortex masked the characteristic transverse septae of *Vertebraria*. The ribbed axes could represent young vertebrarias which were probably penta- to septagonal in cross-section. As *Vertebraria* represents only the stelar aspect of an axis, leaves, even if borne on such an axis, will be difficult to find in organic connection. But Schopf (1965) insists that *Vertebraria* is a root. He of course agrees that it is allied to the glossopterids. Gould (1975) thinks that " *Vertebraria indica* was part of the underground system of *Araucarioxylon arberi* (Seward) Maheshwari type of wood and possibly represents an adaptation to a semiaquatic environment ". Whether *Vertebraria* was a root or shoot, its very characteristic stelar construction seems to preclude its alliance with the known petrified tree trunks of the Glossopteris flora. Therefore, it could have been allied only to some of the glossopterids which were large shrubs or small trees. Other glossopterids were large trees as is evident from the length and diameter of some of the petrified tree trunks found in the Gondwana sediments.

Fructifications of the glossopterids are infrequent, organically attached ones being more so. Leaves with attached fructifications and having a cuticular crust are extremely rare. In recent years, however, well-preserved glossopterid fructifications have been described (Sen, 1955; Maheshwari, 1965b; Mukherjee, Banerjee & Sen, 1966; Banerjee, 1969; Surange & Maheshwari, 1970 and Surange & Chandra, 1975). Some of these were pollen producing members while others bore ovules. The affinities of the pollen producing types are uncertain but the ovule-bearing fructifications seem to indicate the presence of two orders, which presently are informally named as Ottokariales and Lidgettoniales. In Ottokariales, a multiovulate capitulum was born in the axil of an ordinary foliage leaf and closely adpressed to its petiole or midrib. In Lidgettoniales, the fertile leaf was scale-like and had 2 or more ovule-bearing capitula, arising from its midrib region.

The male fructifications, *Eretmonia* du Toit emend Surange & Maheshwari, *Glossotheca* Surange & Maheshwari and *Kendostrobus* Surange & Chandra, stand apart, in their organization, from the known southern or northern hemisphere male fructifications. In *Kendostrobus*, groups of 4-5 sporangia were disposed in close spirals on an axis. The sporangia were exannulate and produced monolete, sculptured spores. Superficially, *Kendostrobus* resembles the spike of *Helminthostachys* but according to Surange and Chandra (1975, p 174) these two are quite distinct in their detailed structure. *Eretmonia* and *Glossotheca* possessed one and three pairs of sporangial clusters respectively, borne on a pedicel which was fused with the petiole of a scale-like glossopterid leaf. The fructification was probably axial. These fructifications show some superficial resemblance with the Peltaspermaceae whose male organ *Antevsia* was a bipinnate sporophyll, ultimate branches of which bore 4-12 sporangia. *Eretmonia* and *Glossotheca* also carried their sporangia on a branch system but it can not be regarded as a sporophyll, and moreover each ultimate branch carried a single sporangium only. In external characters an individual sporangium resembles those of the genus *Arberiella* Pant & Nautiyal instituted for dispersed sporangia. These two genera probably come under the order Lidgettoniales.

The ovulate glossopterid fructifications belonging to the order Ottokariales are referred to the genera *Dictyopteridium* Feistmantel, *Ottokaria* Zeiller, *Gonophylloides* Maheshwari, *Scutum* Plumstead and *Senotheca* Banerjee. These organs have been interpreted as receptacles of various sizes and shapes around which ovules are attached in close spirals, without bracts or ovuliferous scales; the whole receptacle, however, is believed to have been subtended by a scale.

But the stroblus-like organization for all of these fructifications is as yet far from proved. It is possible that in certain types the ovules/seeds were borne embedded on the adaxial surface of a scale-like leaf (see Maheshwari, 1965, pl. 1, figs. 4, 5; Banerjee, 1969, pl. 2, figs. 6-8; Schopf, 1970, fig. 6; Rigby, 1971, p. 3; Holmes, 1974, p.l 6, fig. 1; Pant & Singh, 1974, pl. 31, figs. 64, 65). Some of these fructifications are borne on a stalk which seemingly arises from the petiole of a typical glossopterid leaf. If that is the case then the petiole can be considered as forked, and the fructifications as foliar modifications. It is also possible that the fructifications were borne in the axil of a leaf and the stalk of the fructification is fused with the petiole of the leaf to various extents giving the appearance of the fructification as coming out of the midrib. In that case the fructifications will be axial (Pant & Singh, 1974, pl. 31, figs. 64, 65).

As the glossopterid fructifications are extremely rare, their evolutionary aspect is unknown. The oldest fructification is *Ottokaria bengalensis* Zeiller (1902) which is so far known only from the Lower Permian. This fructification arising from the midrib of a leaf, probably *Glossopteris indica* Schimper, is supposed to have been protected by a bell-shaped veined bract which was borne on a common stalk with the fructification (Surange & Chandra, 1975, p. 171, text-fig. 14A-B). *O. kathwaiensis* Virkki (1943, photo 1, text-fig. 1) is an elliptic-obovate frond attached to a slender stalk. If it is an *Ottokaria* at all, then it probably represents the protective scale of the fructification. In the Middle Permian comes up another fructification, viz., *Dictyopteridium sporiferum* Feistmantel (1881) which is so far known only in detached state. Maheshwari (1965b) observed that one surface of the fructification bore oval scars aligned in oblique rows, while on the other surface a regular reticuloid venation was present. Surange and Chandra (1973), however, opined that the net venation belonged to a closely adpressed subtending scale and that the fructification proper has ovules or seeds of *Platycardia* type attached all around the central receptacle. However, the specimens studied by Maheshwari had evidently shed their seeds, and as such it is unlikely that a subtending bract will remain closely adpressed to a dehisced fructification. Even a fructification with mature ovules will require exposure to pollen rather than protection. The genus continued through the Upper Permian into the basal Triassic. It is in the Upper Permian, where the glossopterid leaves reached their acme, that the largest number of ovulate fructifications is known, other types being *Scutum*, *Senotheca* and *Gonophylloides* (= *Cistella*, probably also *Plumsteadia*). The seeds of *Scutum* and *Senotheca* are *Indocarpus* and *Cornuspermum* respectively. *Protohaploxypinus* type of pollen has been found inside the micropyle of *Cornuspermum* ovules (Banerjee, 1969). It has been suggested that some of the *Gonophylloides* type of fructifications might be the seedless receptacles of *Scutum* (Surange & Chandra, 1974, p. 12).

In their organization the 'strobilate' ovulate fructifications compare with the Jurassic *Rajmahalia paradoxa* Sahni & Rao emend Bose (1966), where, too, the seeds/ovules are arranged in close spirals on a receptacle. Another Jurassic fructification *Carnoconites* also had a similar mode of attachment of seeds (Banerjee, 1969, p. 365). Therefore, Surange and Chandra (1975, p. 176) suggested that the plant group to which *Rajmahalia paradoxa* belonged could have had its roots in the Glossopteropsida and if *Rajmahalia* and *Carnoconites* of the Pentoxyleae are related to each other, it is possible that the Pentoxyleae had its roots in the Permian strobilate ovulate types.

The order Lidgettoniales comprises the genera *Denkania* Surange & Chandra, *Lidgettonia* Thomas and *Partha* Surange & Chandra, all known from the top of Upper Permian only. These fructifications, show superficial resemblance to the pteridospermous fructifications, but are not identical with any of the known forms. In *Denkania* about 6 seed-bearing appendages (cupules) are attached by long pedicels on the petiolar part of a scale-like glossopterid leaf. Each 'cupule' probably contained a single seed. It seems possible that each 'cupule' was borne on the tips of ultimate branches of a pinnate structure which in turn arose from the leaf-scale petiole. Thus the whole structure becomes compound with a forked rachis. If this was the case then this plant could have led to the

Corystospermaceae. In *Partha* and *Lidgettonia* the seeds are arranged on the underside of disc-like heads probably borne on tips of the ultimate branches of a branched structure as in the Peltaspermaceae. However, the cupules of Peltaspermaceae are borne spirally whereas in *Partha* and *Denkania* the capitula are borne in one plane.

A relationship between male and female fructifications is not known. But it is possible that *Kendostrobus* is related to the Ottokariales whereas *Eretmonia* and *Glossotheca* might be related to Lidgettoniales. The latter types could have led to the Triassic 'pteridospermous' plants.

'PTERIDOSPERMOPHYTA'

As discussed earlier there is no definite evidence of the presence of Pteridospermales in the Permian Gondwanas of India though certain plants with 'cupulate' female fructictifications have provisionally been referred to this group. Two families of 'Pteridosperms', viz., Peltaspermaceae and Corystospermaceae, are, however, known in the Triassic Gondwanas of India. Peltaspermaceae is known only in sterile state by the fronds of *Lepidopteris indica* Bose & Srivastava (1972). The fronds are bipinnate, have an unforked rachis, and a few pinnules are attached directly on to the rachis in between the pinnae. The pinnules have a well-marked midrib and forked lateral veins. Recently Srivastava (1975) has described a microsporangiate fructification, *Bosea indica* which he suspects to be the pollen-producing organ of *Lepidopteris indica*. Organizationally *Bosea* is quite different from *Antevsia* which is supposed to be the pollen-producing member of the genus *Lepidopteris* (Harris, 1937, p. 35). *Lepidopteris,* therefore may not be an organ genus.

The family Corystospermaceae is represented in the Triassic of India by the foliage of the genus *Dicroidium* Gothan and pollen-bearing organs *Pteruchus* Thomas and possibly *Indotheca* Sitholey. The fronds of typical *Dicroidium* have a forked rachis. The epidermis of *Dicroidium* is amphistomatic, subsidiary cells are 4 in number (rarely more) but do not form a ring and normally the cell surface is papillate. But in most of the Indian forms forking of the rachis has not been observed. It is believed that these were large forms and only their small parts have been preserved. Such leaves with unforked rachis are included in the genus *Dicroidium* on the basis of their epidermal structure. Recent opinion is that some of the so-called dicroidia may in fact be *Lepidopteris* or may even belong to a separate genus (Bose, 1974, p. 287). In fact, the epidermal structure of *Dicroidium* fronds described from Nidhpuri beds by Bose and Srivastava (1971) does not strictly conform with that prescribed for typical dicroidia (see Lele, 1962a). The separate identity of the Nidhpuri dicroidia is further confirmed by the discovery, in the same beds, of two fructifications *Nidistrobus harrisianus* and *Nidia ovalis* whose epidermal structure resembles most that of *Dicroidium nidpurensis* (Bose & Srivastava, 1973, p. 78). In case these two fructifications were borne on dicroidia fronds, the plant would be quite unlike any of the known pteridosperm families. *N. harrisianus* has spirally disposed 'pad-shaped' pollen-bearing organs. Each 'pad' has a row of 7-8 pollen sacs on its adaxial surface. Pollen grains were probably bisaccate, non-striate. Lacey (1974, p. 40, pl. 1, figs. 1-3) has recently described apparently similar, though comparatively larger, 'ribbed object' associated with *Dicroidium lancifolium* in the Molteno flora (Middle-Upper Triassic) of Rhodesia. *Nidia ovalis* has spirally disposed megasporophylls, each bearing two peltate seeds-ovules. Thus it is more cycad-like.

Satsangia campanulata Srivastava & Maheshwari (1973) is another fructification-like structure. It shows oval scars arranged in oblique rows as in the genus *Dictyopteridium*. However, in *Satsangia* the scars seem to be present on the inner surface of a bell-like organ. The organ probably bore ovules at the scars. Details are, however, not known.

Typical corystospermaceous pollen-bearing organs are also known from the Nidhpuri bed. *Pteruchus indicus* Pant & Basu (1973) is known from sporangiferous stalks, borne spirally at wide angles around a central axis. Each sporangiferous stalk gradually widens out terminating in an 'umbrella-like' head, on the under surface of which are arranged sporangia. Pollen is bisaccate, non-striate. A somewhat similar organ is

Indotheca sakesarensis Sitholey (1943b, pl. 2, figs. 14-16) from the Triassic of Salt Range. *Indotheca*, however, differs from *Pteruchus* in having a definite lamina which bears the sporangial cluster.

CYCADOPHYTA

The group Cycadophyta is poorly represented by foliage only. One of the species known is *Pseudoctenis balli* (Feistmantel) Seward. Feistmantel (1881b) described the species under *Anomozamites* but later (1886) changed to *Platypterigium*, Schimper. Seward (1917) transferred the species to his genus *Pseudoctenis* without reasoning out the necessity for such a change. From the Generic Index (Andrews, 1970, p. 165) the species *balli* of Feistmantel (1886) seems to be the type species of the genus *Platypterigium* Schimper ex Feistmantel (1886). Under the International Code of Botanical Nomenclature, it is doubtful if the type species of an older genus can be transferred to a younger genus. This species which was originally described from the Middle Permian was later discovered in the basal Triassic (Lele, 1962b). The frond is pinnately divided, the segments are of unequal width and attached at right angles or obliquely to a slender rachis. The veins are generally forked near the point of emergence and show a few cross connections.

Another leaf, *Pterophyllum burdwanense* (McClelland) Feistmantel was originally described as *Zamia burdwanense* by McClelland (1850). Here the veins do not bifurcate, run parallel and are spaced fairly apart. The species is known from Middle to Upper Permian strata. Because of this, the identification of the genus has been doubted. Arber (1905) suspected that the species may represent a torn fragment of *Taeniopteris*-like leaves. Pant and Mehra (1963) studied the epidermal structure of similar leaves and described them as *Pteronilssonia gopalii*. As there is hardly any morphographical difference from the species *burdwanense* it would have been better to describe it as *Pteronilssonia burdwanense*. Pant and Mehra (1963) suspect that this species may not have cycadean but pteridospermous affinities. It is, however, doubtful if one can postulate affinities to higher taxa of Gymnosperms simply on the basis of epidermal characters; the Bennettitales being an exception. The genus *Pterophyllum* has also been reported from the Upper Triassic beds (Lele, 1956, 1962b). The species *Pterophyllum sahnii* is pinnately segmented, segments being closely set, attached to the rachis by the whole base. Veins usually fork close to the emergence, rarely forking again.

Senia reticulata Khan (1969), from the top of Upper Permian, is a very imperfectly known cycad-like leaf. *Taeniopteris spatulata* from the Parsora Formation and *T. glandulata* from the Nidhpuri beds are also suspected to have had cycadean affinities.

'GINKGOPHYTA'

Some of the leaf types present in the Indian Gondwana Sequence show a general resemblance to the leaves of *Ginkgo*. But, in the absence of fructifications their relationships with one another or with the Ginkgoales are not definitely established. These are, therefore, sometimes placed in the noncommital order Palaeophyllales. The Upper Palaeozoic ginkgoalean type of leaf belongs to two genera, viz., *Psygmophyllum* and *Rhipidopsis*.

Leaves of *Psygmophyllum* are known only from the Permo-Carboniferous strata of the extra-peninsular Gondwanas of Kashmir. Three species of the genus are known, all of which have simple, lobed leaves. These, therefore, should be taken out of the genus *Psygmophyllum* Saporta emend Schimper which is characterized by pinnate leaves. Maithy (1974b) suggests the use of the generic name *Ginkgophyllum* Saporta for the Indian leaves. These forms are more or less intermediate between *Ginkgophyllum* and *Ginkgophytopsis* Høeg.

Ginkgophyllum (*Psygmophyllum*) *hollandi* (Seward) is known from the Lower Permian of Kashmir. The lamina is divided by a deep median sinus into two bilobed segments. *G.* (*Psygmophyllum*) *haydenii* (Seward), also from the Permo-Carboniferous of Kashmir, is a petiolate, flabellate leaf deeply incised into a number of radiating, cuneate segments. *G.* (*Psygmophyllum*) *sahnii* (Ganju) is represented by a branch, bearing spirally disposed leaves with a short petiole and flat, wedge-shaped lamina divided by a median sinus into two equal bilobed segments. Each segment is again cut into equal lobes. Ganju (1943, p. 203) remarks that *P. sahnii* bears a striking resemblance to the leaves of *Ginkgo*, and therefore there may be some relation between the two.

The genus *Rhipidopsis* was reported by Feistmantel (1881, 1886) from the Permian of the peninsula. His specimens of *R. ginkgoides* Schmalhausen from the Middle Permian were later put under a new species, *R. gondwanensis* by Seward (1919). Here the lamina is divided, almost to the base, into 6-10 segments; the larger are cuneate and the smaller obovate and obtuse. In *R. densinervis* from the Upper Permian the lamina is deeply divided into obcuneate segments that appear to be irregularly lobed at the truncate margin. Sitholey (1943a, p. 188) remarked that *R. densinervis* may belong to the same genus as *Psygmophyllum haydenii*. But, Maithy (1974b) has transferred *R. densinervis* to the genus *Platyphyllum* Dawson. He also describes a somewhat similar form as *Gondwanophyton indicum*. *R. densinervis* is probably also present in the Lower Triassic (Bhattacharyya, 1963).

The only other Triassic ginkgoalean type of leaf known is *Baiera indica* Lele (1962b, pl. 3, figs. 27, 28). The leaf is deeply dissected into a number of narrow, linear, segments, each having 4-5 thin, parallel veins. Sitholey and Bose (1974) have doubts about the affinity of the specimen with the genus *Baiera* due to former's peculiar mode of dissection.

CONIFEROPHYTA

CORDAITALES

In the Lower Permian certain strap-shaped, parallel-veined leaves, known as *Noeggerathiopsis*, are very common (Feistmantel, 1879). The genus has stray representation not only through the Permian but in the Triassic as well (Feistmantel, 1882). The leaves are very much similar to the leaves of the Northern Hemisphere *Cordaites* and are therefore taken as representing the group Cordaitales. However, assignment of *Noeggerathiopsis* to the group Cordaitales is not free from doubt. Epidermal structure of *Noeggerathiopsis* leaves has been found to be distinct from that of *Cordaites* (Lele & Maithy, 1964). The leaves were borne in close spirals (Seward & Sahni, 1920, pl. 1, fig. 10). Further *Cordaitanthus* like fructifications are totally absent in the Gondwana Sequence. Maithy (1970, p. 169) is of the opinion that *Noeggerathiopsis* could as well be a glossopterid. However, presently there is no evidence to support such an opinion. The problems met with in systematics of cordaitalean type of leaves have recently been discussed by Maheshwari and Meyen (1975, p. 199).

A large number of fossil wood with annual rings and araucarioid tracheidal pits are known from the Barakar and Raniganj formations (Maheshwari, 1964, 1965c, 1967; and others). Sahni and Singh (1926) thought that such wood probably bore *Noeggerathiopsis* type of foliage. Kräusel, Maithy and Maheshwari (1962) on the other hand, suggested that some of the Lower Gondwana wood with endarch protoxylem may represent conifers. Maheshwari (1972, p. 37) finds it most likely that most of the fossil wood belonged to the Glossopteridopsida as almost all records of fossil wood are from horizons where the glossopterids predominated and the conifers or *Noeggerathiopsis* were extremely rare.

The only fructification which has been correlated with *Noeggerathiopsis* is a megasporophyll-like organ originally described by Feistmantel (1881a, p. 59, pl. 28, fig. 5) as an "inflorescence" probably belonging to *Noeggerathiopsis hislopi*. This was later named *Arberia indica* by White (1908) and correlated with *Gangamopteris*. Another species known from India is *A. umbellata* Surange & Lele. Similar specimens have also been figured by Ganguly (1959, fig. 14), Pant and Nautiyal (1966, *Ottokaria*-like head) and Maithy (1970, *Dolianitia karharbarensis*). The megasporophyll has a slender stalk which expands distally and bears a number of abruptly truncate lobes or recurved processes. It is presumed that the lobes or processes bore ovules as is seen in a specimen figured by Pant and Nautiyal (1966, pl. 1, fig. 1) as *Ottokaria*-like head. Similar specimens were described by Millan (1967) under the genus *Dolianitia* and were supposed to have affinity with *Noeggerathiopsis*. But according to Rigby (1972), *Arberia* (= *Dolianitia*) while not belonging to the same plant which bore *Noeggera-*

			DAMODAR VALLEY	SATPURA BASIN	SOUTH REWA BASIN	SON VALLEY	RAJMAHAL HILLS	WARDHA-GODAVARI	MAHANADI VALLEY	RAJASTHAN	KASHMIR
TRIASSIC	UPPER TO MIDDLE	MAHADEVA Gr	SUPRA-PANCHETS		PARSORA Fm		DUBRAJPUR Fm	DHARMARAM Fm			
				DENWA Fm	TIKI Fm			MALERI Fm			
				PACHMARHI Fm	NIDHPURI beds			BHIMARAM Fm			
		PANCHET Gr						YERRAPALLI Fm			
	LOWER		HIRAPUR Fm			PANCHET Gr		MANGALI beds			
			MAITUR Fm	ALMOD beds	DAIGAON beds			KAMTHI Gr	HIMGIR Fm		
PERMIAN	UPPER	DAMUDA Gr	RANIGANJ F	BIJORI Fm	PALI Fm		? RANIGANJ Fm				
	MIDDLE		IRONSTONE Sh.Fm	MOTUR Fm	BARREN MEAS.Fm		BARREN MEAS.Fm	IRONSTONE Sh.Fm	BARREN MEAS.Fm		
			BARAKAR Fm	BARAKAR Fm	BARAKAR Fm	BARAKAR Fm	BARAKAR Fm	BARAKAR Fm	BARAKAR Fm		
	LOWER	TALCHIR Gr	KARHARBARI Fm	KARHARBARI Fm	KARHARBARI Fm	KARHARBARI Fm		KARHARBARI Fm	KARHARBARI Fm	BADHAURA Fm	*Gangamopteris* beds
			TALCHIR Fm	TALCHIR Fm	TALCHIR Fm	TALCHIR Fm	TALCHIR Fm	TALCHIR Fm	TALCHIR Fm	BAP beds	
?UP. CARB			Boulder bed	Boulder bed	Boulder bed	Boulder bed	Boulder bed	Boulder bed	Boulder bed	Boulder bed	

LITHOSTRATIGRAPHICAL CLASSIFICATION OF PERMIAN - TRIASSIC GONDWANAS OF INDIA

TEXT-FIG. 1

thiopsis leaves, also does not seem to be related to known pteridosperm families.

CONIFERALES

The oldest conifer-like foliage known from the Indian Gondwana Sequence is the Lower Permian ?*Paranocladus indica* Surange & Lele (1957, pl. 1, fig. 13, 15). The shoots are irregularly branched, branches being covered by somewhat spreading, spirally disposed homomorphic leaves.

A somewhat younger species is *Buriadia sewardii* Sahni. The vegetative shoot shows trimorphic leaves which may be bifacial or trifacial, and bear cutinized unicellular hairs at the margins. The epidermal structure of the leaves is characteristically conifer-like. Anatropous, platyspermic seeds, borne on slender stalks, replace a leaf here and there in the phyllotactic spiral. Because of the absence of an organized female cone, the genus does not exactly fit in the coniferales. According to Pant and Nautiyal (1967) the plant is "either a conifer of an unusual type or a curious plant which is not assignable to any known group of gymnosperms".

Replacement by an ovule, of a leaf on an ordinary foliage shoot is also found in the Middle Permian *Walkomiella indica* Surange & Singh. The species is known by a small dwarf shoot carrying several spirally arranged scales and a single orthrotropous platyspermic seed/ovule, probably lateral to the axis (Surange & Singh, 1955, pl. 1, fig. 1). The leaf epidermis has sinuous and often smooth anticlinal walls of the cells. The marginal hairs are 1-3 celled.

Pant and Bhatnagar (1975) have recently described an interesting conifer-like shoot, viz., *Searsolia oppositifolia* from the Upper Permian. Here the leaves are two-ranked and inserted in opposite pairs. A few stalked globose heads are seen attached to the axis, but their structural details are not seen. The affinity of this taxon is not known.

Triassic records of conifers in India are poor. The oldest known Mesozoic conifer-like plant is *Podozamites* which is comparable to *P. lanceolatus* Schimper. Leaves earlier referred to *Desmiophyllum* by Lele (1962b) are now believed to be fragmentary or incomplete leaves of *Noeggerathiopsis* type (Bose & Maheshwari, 1974, p. 212). Little is known about conifer fructifications though some forms have been described as *Araucarites* cone scales or *Conites*.

CONCLUDING REMARKS

Till late there was no evidence of plant life in the basal boulder bed horizon of the Gondwana Sequence although Sahni (1939) opined that the rise of the Glossopteris flora overlapped with the later phases of the Palaeozoic glaciation in India. Recently a microflora, predominated by gymnospermic pollen, has been recovered from two intercalated boulder beds (Lele & Karim, 1971). Some of these pollen, particularly the bisaccates, could have belonged to the Glossopteridopsida. It is thus seen that in the Indian Gondwana Sequence there is now evidence of the existence of gymnospermous plants overlapping with the Upper Palaeozoic glaciation. The glossopterids, which are the characteristic elements of the Southern Hemisphere Permian floras, had already come up along with cordaitalean type of foliage in the basal Permian. Conifers were probably present but ferns and lycopsids, if present at all were extremely rare. Ginkgoalean type of leaves are known by *Ginkgophyllum*. The sphenopsids and ferns make their first appearance in the upper part of the Lower Permian. A characteristic probable fern-like form is *Botrychiopsis*; while another characteristic form *Buriadia* might represent the conifers. The lycopsids are missing here, as well as in the lower part of the Middle Permian, where the sphenopsids become more diversified, *Trizygia* making its first appearance. *Lelstotheca* and *Barakaria* are plants characteristic of the age. In the Glossopteridopsida, *Glossopteris* supersedes *Gangamopteris* in dominance, and a new element, *Rhabdotaenia*, probably of the same group makes its first appearance. Some cycadalean and ginkgoalean type of foliage is also known. Not much information is available about the upper part of the Middle Permian. But the only definite lycopsid megafossils are known from here. The Upper Permian has the richest flora of all. Most of the Middle Permian forms continued though in greater quantity; the characteristic forms are *Raniganjia* and

Palaeovittaria. The *Glossopteris*-complex is best known from the Upper Permian strata. Besides leaf morphography and wood anatomy we have data about epidermal features and the fructifications. The information available so far does not favour the inclusion of this complex in the Pteridospermophyta. The *Glossopteris*-complex is therefore referred to an independent class — the Glossopteridopsida. This class comprises at least two orders, viz., the Ottokariales and the Lidgettoniales.

The basal Triassic flora is extremely poor but not much different from the Upper Permian floras. In the Upper part of the Lower Triassic the 'pteridospermous' families Corystospermaceae and Peltaspermaceae appear and continue at least up to Upper Triassic.

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