Morphological trends in Gondwana plants

Usha Bajpai

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The term Gondwana has recently been redefined to include the group of terrestrial rocks in the Indian Craton, that was initiated with a basal Permian glacigene epoch and terminated with the large hiatus at the top of the Triassic. The Gondwana Supergroup as redefined now comprises Talchir, Damuda, Panchet and Mahadeva groups and ranges in age from the earliest Permian to latest Triassic or earliest Jurassic (Venkatachala & Maheshwari, 1991).

The vegetational scenario of Gondwana shows mixture of plants belonging to quite distinct habitats. The morphological adaptations of plants that thrived at all levels on land, in continental water, upland and in environments of exeeding dryness are significant. Leaf size varies from small to large with variety of apex and base, midribless to prominent midrib, non-petiolate to petiolate, veins loosely arranged, narrow mesh type of venation to open mesh and narrow mesh type. Leaf cuticle of glossopterids also shows variations.

Most of the Gondwana woods show variation in pith and primary xylem and secondary xylem. Pith varies from homo- to hetero-cellular. Primary xylem shows variation from endarch to mesarch. The secondary xylem is pycnoxylic, homoxylous. Secondary xylem shows well-marked growth rings. There is a great variation in the pitting of secondary tracheids. Xylem rays vary from uni- to multi-seriate. The ray field-pits also show diversity.

Wide diversities are also seen in the morphology of pteridophytic megaspores and of reproductive organs of gymnosperms. The exosporium of megaspore is either smooth or variously ornamented. The mesosporium is with or without cushions. Reproductive organs are known only for the glossopterid group and are of two types.

The changing patterns in leaves, woods, megaspores and reproductive organs of Gondwana plants may provide significant data for charting of morphotrends in these organs. It can probably also be established if these morphotrends were ecologically controlled temporary and transient phase or were genetically controlled leading to evolution of new types.

Key-words—Gondwana, Lycopododophyta, Megaspores, Arthrophyta, Glossopteridopsida, Morphotrends.

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साराँश

गोंडवाना पौधों में आकारिकीय प्रवृत्तियाँ

ऊषा बाजपेयी

भारतीय क्रेटॉन में विद्यमान स्थलजात चट्टानों के समूह को सम्मिलित करने के लिए गोंडवाना शब्द को अभी हाल में पुनः परिभाषित किया गया है। इस क्रेटॉन का आधारी भाग परमी हिमानी कल्प का तथा उपरितम भाग त्रिसंघी कल्प की चट्टानों का निरूपण करता है। पुनः परिभाषित गोंडवाना महासमूह में अब तलचीर, दमुदा, पंचेत एवं महादेवा समूहों को सम्मिलित किया गया है तथा आयु में ये पूर्वतम् परमी से उपरितम् त्रिसंघी अथवा प्रारम्भिकतम् जूराई (वेंकटाचाला व माहेश्वरी, 1991) तक विस्तृत हैं।

गोंडवाना वनस्पति में विभिन्न जलवायु से सम्बद्ध पौधों का मिश्रण है। भूमि, पानी, ऊँचे स्थल तथा शुष्क वातावरण के अनुसार इन सभी पौधों का आकारिकीय अनुकूलन अत्यन्त महत्वपूर्ण है। पत्ती के आकार में अनेक विभिन्नतायें हैं कुछ पत्ती छोटी, कुछ बड़ी, कुछ मध्यशिराविहीन तो कुछ पूर्ण विकसित मध्यशिरा तथा चौड़े शिरान्यास एवं काफी सघन शिरान्यास से युक्त हैं। ग्लॉसॉप्टेरिडी पौधों की पत्तीयों की उपचर्म में भी विभिन्नताऐं हैं।

गोंडवाना से प्राप्त अधिकतर काष्ठों में मज्जा तथा प्राथमिक एवं द्वितीयक दारु में भी विभिन्नता प्रेक्षित की गई हैं। द्वितीयक वाहिनिकीयों के गर्तन्यास में भी विभिन्नता विद्यमान है। दारु किरणें एक अथवा बहुक्रमी हैं। किरण क्षेत्र-गर्त्त भी विविधता प्रदर्शित करते हैं।

यही नहीं अपितु टेरीडोफाइटी गुरुबीजाणु तथा अनावृतबीजीयों के जननांगों में भी विविधता प्रेक्षित की गई हैं। गुरुबीजाणुओं की बाह्यउपचर्म या तो चिकनी होती है अथवा विभिन्न प्रकार से अलंकृत। मध्यउपचर्म तल्पहीन अथवा किसी-किसी में तल्पयुक्त होती है। अभी तक जननाँग केवल ग्लॉसॉप्टेरिडी

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समूह में ही विदित हैं तथा दो प्रकार के होते हैं।

गोंडवाना पौधों की पत्तीयों, काष्ठों, गुरुबीजाणुओं एव जननांगों में उक्त विविधता से महत्वपूर्ण आँकड़े उपलब्ध हो सकते हैं। यह भी संभव है कि ये विविधता अस्थायी रूप से पारिस्थिति के कारण हो गई हैं अथवा स्थायी रूप से आनुवंशिक गुणों द्वारा निर्यंत्रित नये प्ररूपों के विकास के फलस्वरूप हुई हैं।

MORPHOLOGY implies the study of form. The adult form and structure of plants seems to be the outcome of a series of evolutionary changes extending over hundreds of million years. Most fossils represent the fragments of plants. The reconstructions of whole plants are made on the basis of morphology and anatomy. However, due to break in sequence of sediments and also due to uneven distribution of plant fossils in the sediments, usually it is very difficult to trace morphotrends which depict evolutionary tendencies and patterns. This is also true for the vegetation that thrived during the time when the Gondwana Supergroup of sediments was deposited in India and countries of the Southern Hemisphere. Available data being imperfect, there are several gaps in our knowledge which need to be investigated further.

LYCOPSIDA

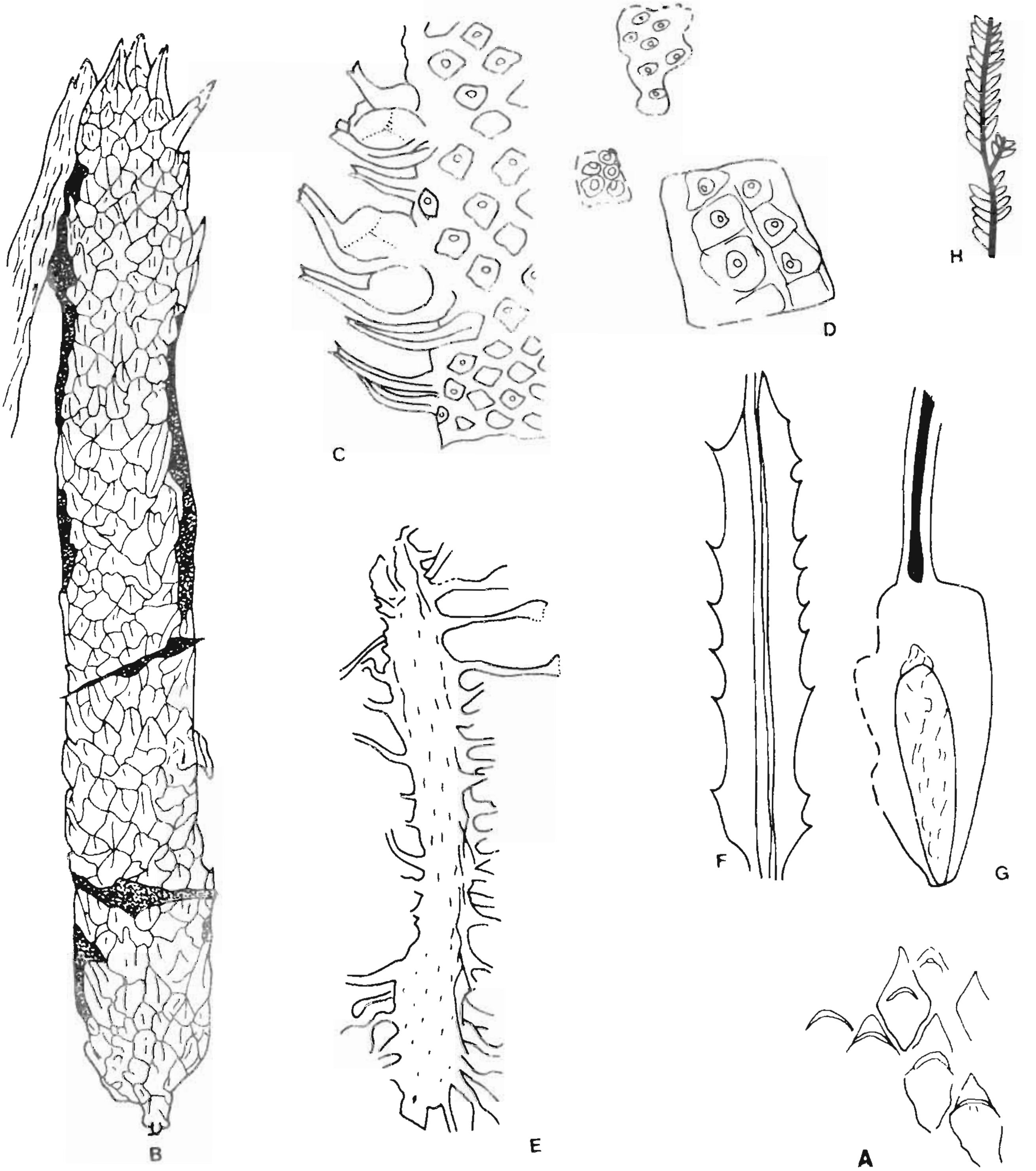
The Lycopodophyta, that appeared in the Upper Devonian, and constituted a major part of Carboniferous vegetation of the Northern Hemisphere, are meagrely represented in the contemporary and younger floras of the Gondwana Supercontinent, particularly so in India. In India, the oldest record of lycopsid megafossils is from the Early Permian *Gangamopteris* beds of Zewan Spur, Kashmir (Kapoor, 1968). The incomplete specimen shows crescentic ligular scars inside spirally disposed rhomboid leaf cushions (Text-figure 1A). Srivastava and Kapoor (1967) reported a lycopsid cone, *Lepidostrobus kashmirensis* from equivalent beds of the Liddar Valley, Kashmir (Text-figure 1B). Not many details are seen in this specimen, and hence its exact taxonomic position is yet to be decided.

In the Gondwana of the Peninsula, the oldest definite lycopsid megafossil has been reported from the Kulti Formation (Ironstone Shale/Barren Measures, ?late Early Permian) of Jharia Coalfield (Kar, 1968). 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 (Text-figure 1C). Each leaf-scar has a more or less circular boss which perhaps indicates the position of vascular supply to the leaf. The ligular pit or the parichnos scars have not been found. Better preserved specimens of this species are known from other Gondwana provinces, which are heterosporous, the sporophylls being distributed on normal leafy shoots, without any organized cone (Kräusel, 1961). A specimen described as *Bothrodendron* sp. by Seward and Sahni (1920, pl. 2, figs 28 a-c) from the Kulti Formation of the Raniganj Coalfield, probably also represents *C. leslii* (Text-figure 1D). The species possibly persisted into the Early Triassic Mangli beds, from where a somewhat similar specimen was described as *Lepidodendron* by Hislop (1856) and later as "*Stigmaria*" by Bunbury (1861) from the Kamthi Formation.

From the Late Triassic another lycopsid species, *Lycopodites sahnii* is known (Lele, 1962). 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 that probably represents the vascular trace to the leaf (Text-figure 1E). The genus *Lycopodites* continues into the Cretaceous where it is represented by the species *L. gracilis* (Oldham & Morris) Seward & Sahni. From the Early Cretaceous Bhuj Formation of Kutch Basin, Bose and Roy (1964) and Bose and Banerji (1984) have reported lycopsid taxa *Isoetites serratifolius* (Text-figure 1F), *I. indicus* (Text-figure 1G), and *Selaginellites* sp. (Text-figure 1H)

Evidently, lycopsid megafossils are meagrely known from the Indian Gondwana, yet the presence of lycopsid megaspores in almost all the sediments is indicative of their existence all through the Gondwana period. This indicates that many more species of lycopsids flourished than is evident from the megafossil record. The paucity of lycopsid megaplant remains may probably be due to the delicate nature of plants and their suppression by an overwhelming preponderance of gymnospermic megaplant remains (Maheshwari, 1974, p. 52).

The mesosporium in all the megaspore taxa, except in *Srivastavaesporites indicus* (Singh) Bharadwaj & Tiwari, recorded from the Early Permian Talchir Formation shows characteristic biseriately arranged, more or less rounded, projections or cushions in the inter-ray areas. In the succeeding Barakar Formation (Early Permian), the arrangement of cushions on the mesosporium changes and becomes irregularly organized, but the cushions remain confined within the inter-ray areas. However, in the ?late Early Permian Kulti Formation, the biseriate arrangement of cushions on the inner body reappears (e.g., *Duosporites congoensis*) and



Text-figure 1—**A.** Lycopsid stem; **B.** *Lepidostrobus kashmirensis*, **C.** *Cyclodendron leslii*, **D.** *Bothrodendron* sp., **E.** *Lycopodites sahnii*; **F.** *Isoetites serratifolius*; **G.** *Isoetites indicus*; **H.** *Selaginellites* sp. (Figure **B** redrawn from Srivastava & Kapoor, 1969, figure **C** redrawn from Kräusel, 1961; figure **D** redrawn from Seward & Sahni, 1920; figure **E** redrawn from Lele, 1962, figures **F-H** redrawn from Bose & Banerji, 1984).

exists alongwith irregular arrangement of the cushions (Text-figure 2A). This arrangement continues into the Late Permian and Early Triassic (Bharadwaj & Tiwari, 1970; Maheshwari & Banerji,

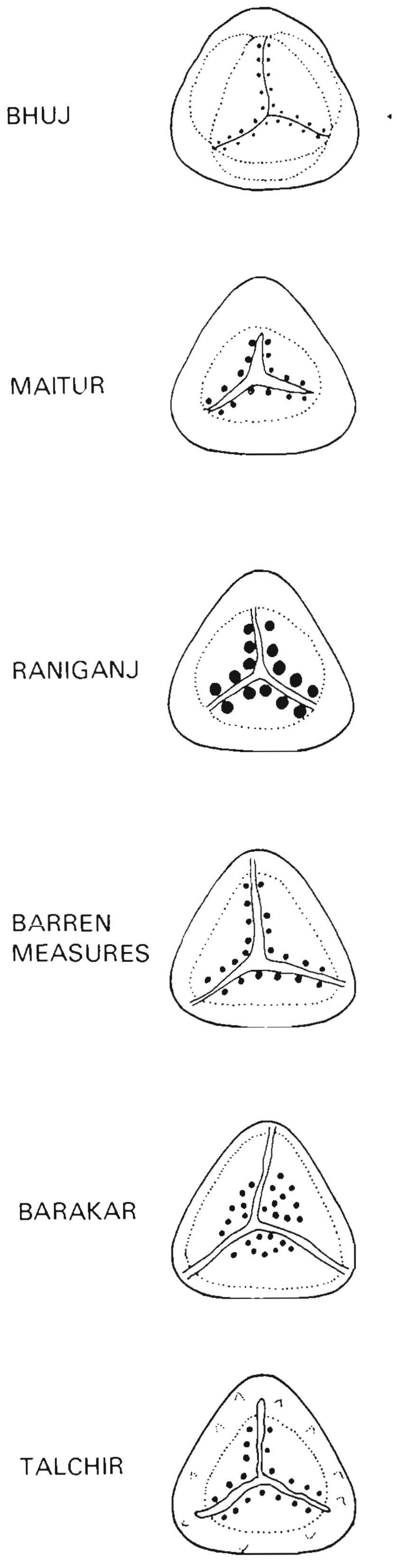
1975) but becomes associated with a megaspore type that is circular in polar view. One of the taxa, i.e., *Talchirella densicorpa* Bharadwaj & Tiwari, has massive cushions. Mesosporium with cushions is not known from younger horizons except for in three species of the genus *Minerisporites*, a zonate megaspore from the Bhuj Formation of Kutch Basin (Singh, Srivastava & Roy, 1964, Banerji, Jana & Maheshwari, 1984).

The sculptural elements on the megaspore sporoderm show a trend towards becoming more pronounced and robust in time (Text-figure 2B). The exine ornamentation in all the taxa of megaspores of Talchir Formation is from granulate to fine verrucate, except in *Trilaevipellites talchirensis* (Lele & Chandra, 1974), which is laevigate. The megaspore genus *Srivastavaesporites* continued into the Early Triassic without any significant change in the ornamentation pattern Megaspores assigned to the genus *Bokarosporites* are almost similar except that the sporoderm sculpture is psilate. Pronounced sculptural elements appear for the first time in the Barakar Formation. The megaspore genus *Jhariatriletes* with baculate exine also extended into the Early Triassic, different species having differentially baculate, closely baculate, and sparsely baculate elements. The baculae probably changed into ribbose pattern of *Singhisporites* in late Early Permian. Baculate elements reappear in *Bacutriletes* recorded from Late Triassic to Early Cretaceous (Text-figure 2C). The megaspore genera *Nathorstisporites* and *Paxillitriletes* seem to belong to this line. In Early Triassic megaspores appear with reticulate exosporium, e.g., *Maiturisporites*. Late Triassic megaspores of the genus *Hughesisporites* with finger-like interwoven projections could have been derived from *Maiturisporites* (Text-figure 2D).

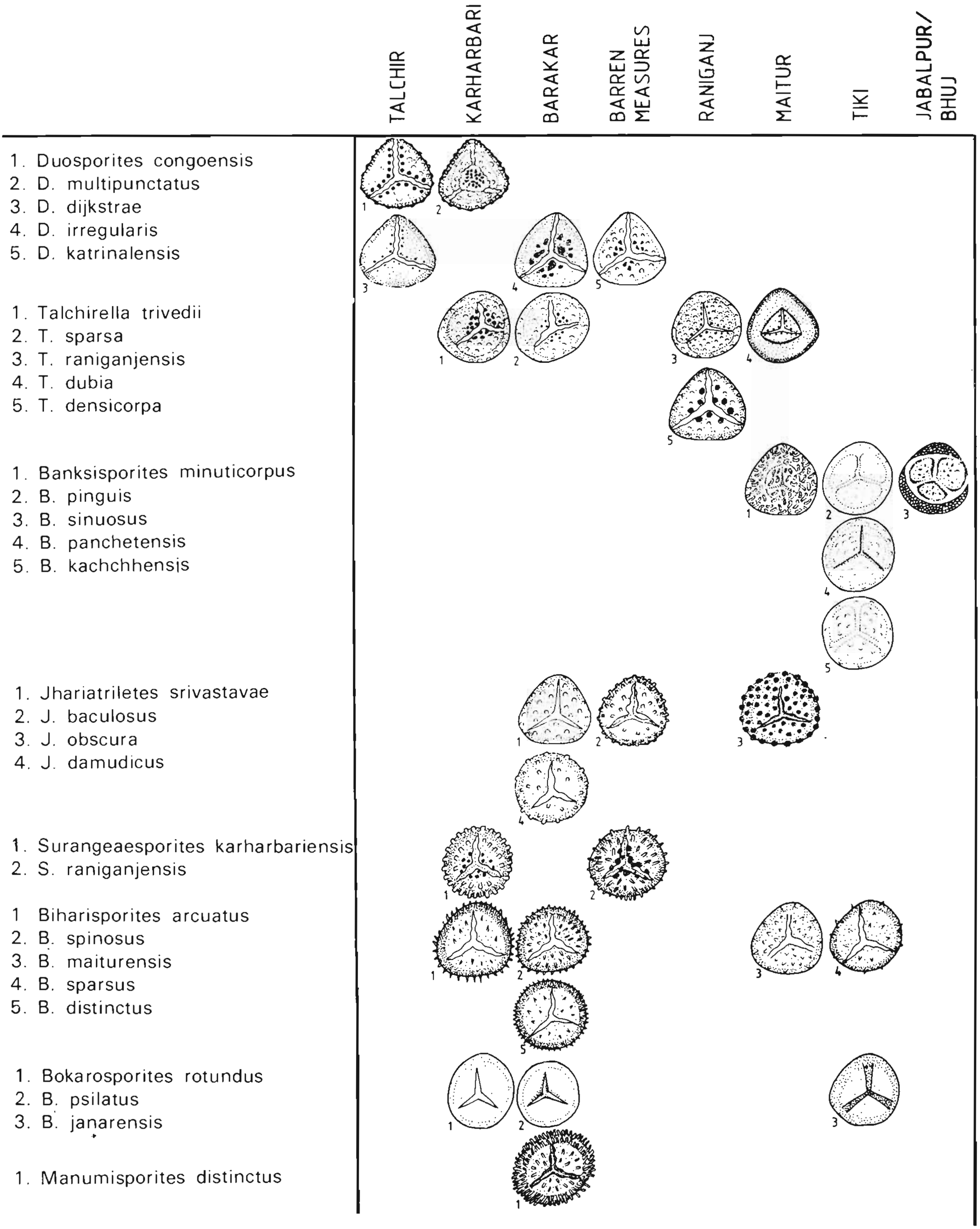
ARTHROPHYTA

The group is largely known through vegetative shoots. In the absence of well-preserved fertile parts, except for *Giridia indica* (Text-figure 3A; Pant *et al.*, 1981), the plant remains can only provisionally be assigned to two orders, viz., Equisetales and Sphenophyllales.

The equisetalean stems are all similar in being jointed and ribbed, the ribs continuing through successive nodes (Surange, 1971). Adpressed leaf sheaths are known in the genera *Phyllotheca* Brongniart (Text-figure 3B) and *Schizoneura* Schimper & Mougeot (Text-figure 3C). Both appear simultaneously in the Early Permian (Lower Barakar Formation) and continue almost into the Early



Text-figure 2A—Schematic drawing showing arrangements of cushions on the mesosporium.



Text-figure 2B—Schematic drawing showing sculptural pattern on megaspore sporoderm.

Contd.

1. Singhisporites surangei
2. S. radiales

1. Maiturisporites indicus
2. M. distinctus
3. M. spinotriletus

1. Erlansonisporites triassicus
2. E. indicus

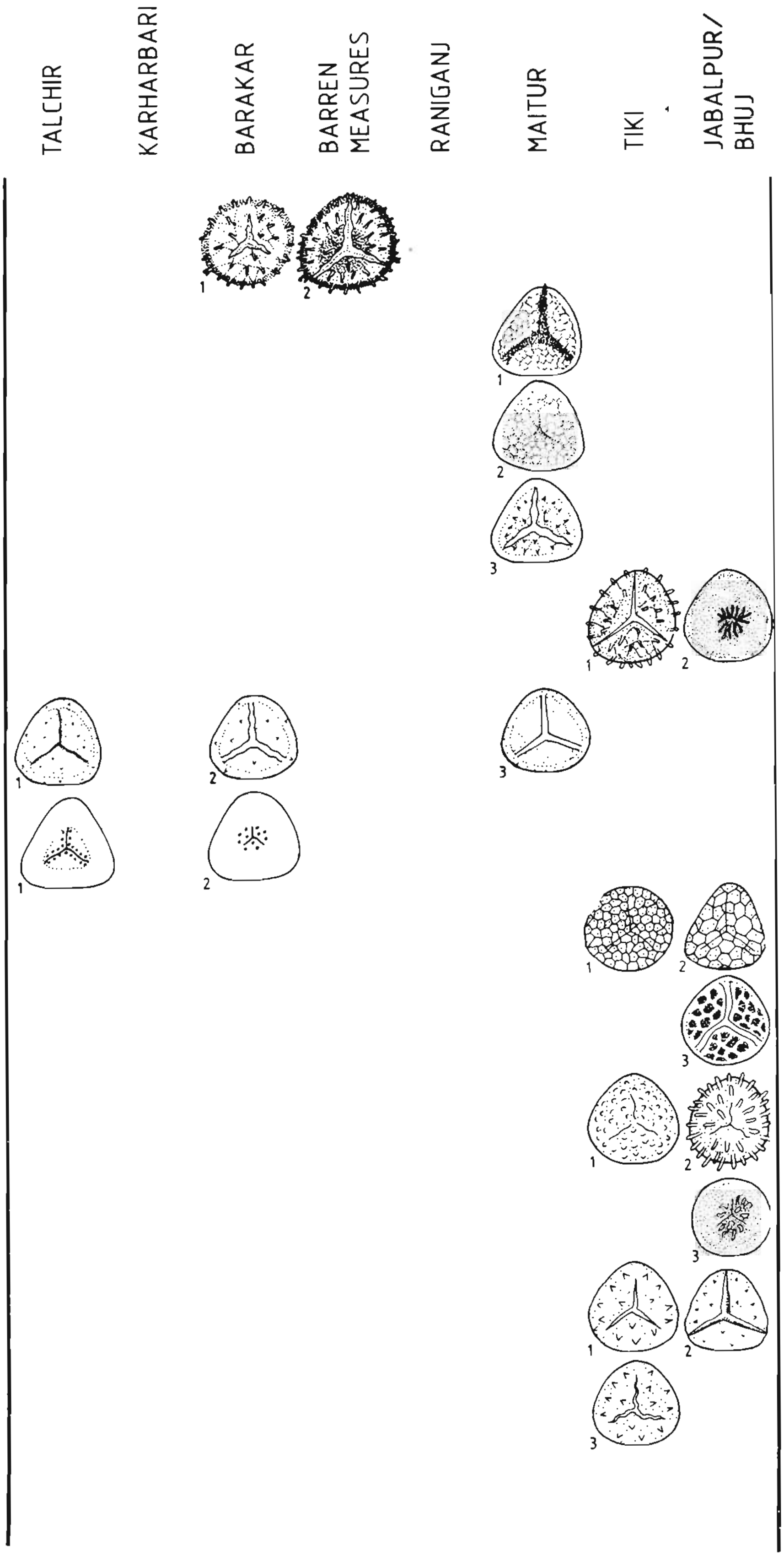
1. Srivastavaesporites indicus
2. S. utkalensis
3. S. panchetensis

1. Trilaevipellites talchirensis
2. T. multipulvinatus

1. Horstisporites areolatus
2. H. semireticulatus
3. H. biswasii

1. Hughesisporites variabilis
2. H. rajnathaii
3. H. singhii

1. Verrutriletes minuticorpus
2 V. obscura
3. V. royii



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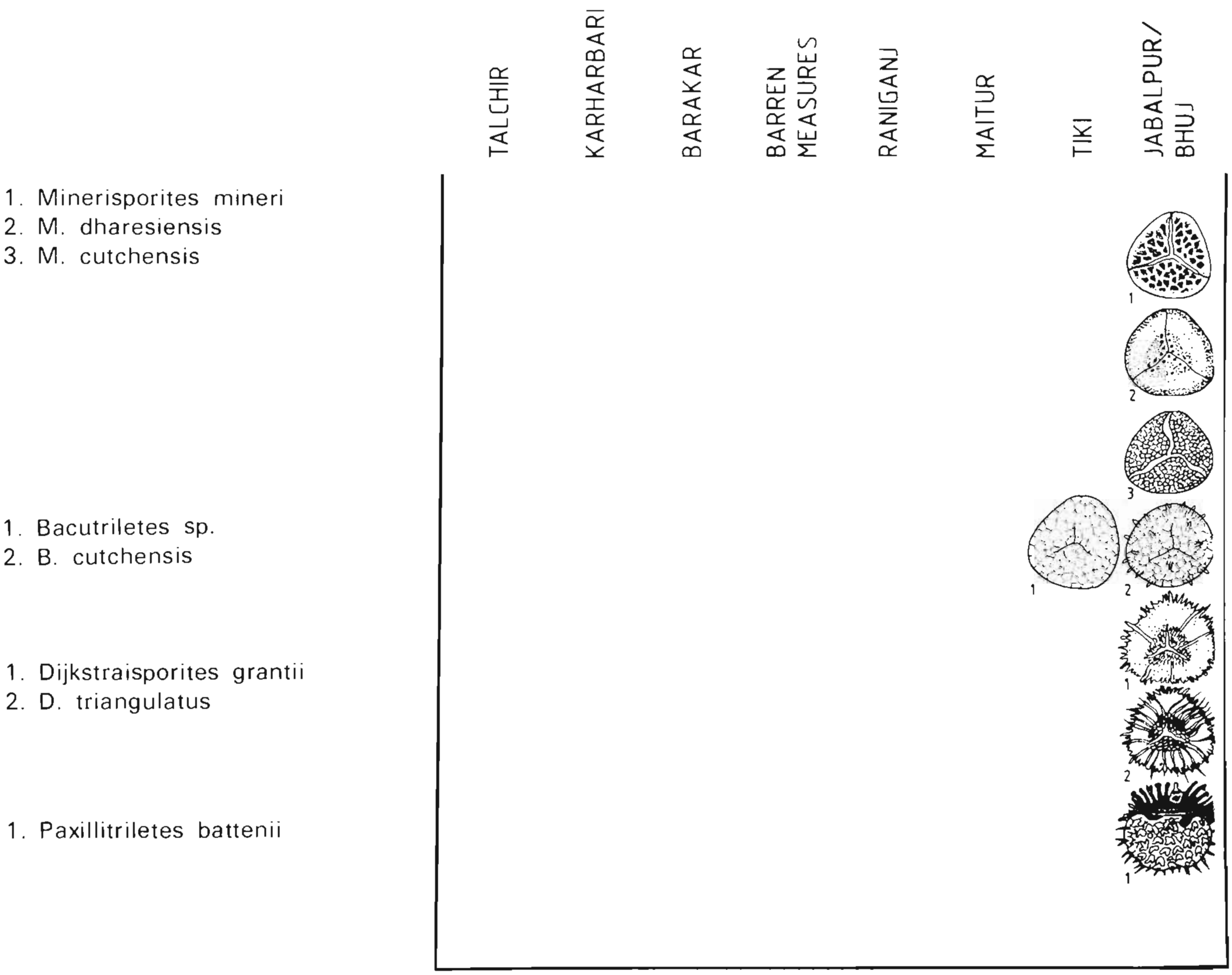
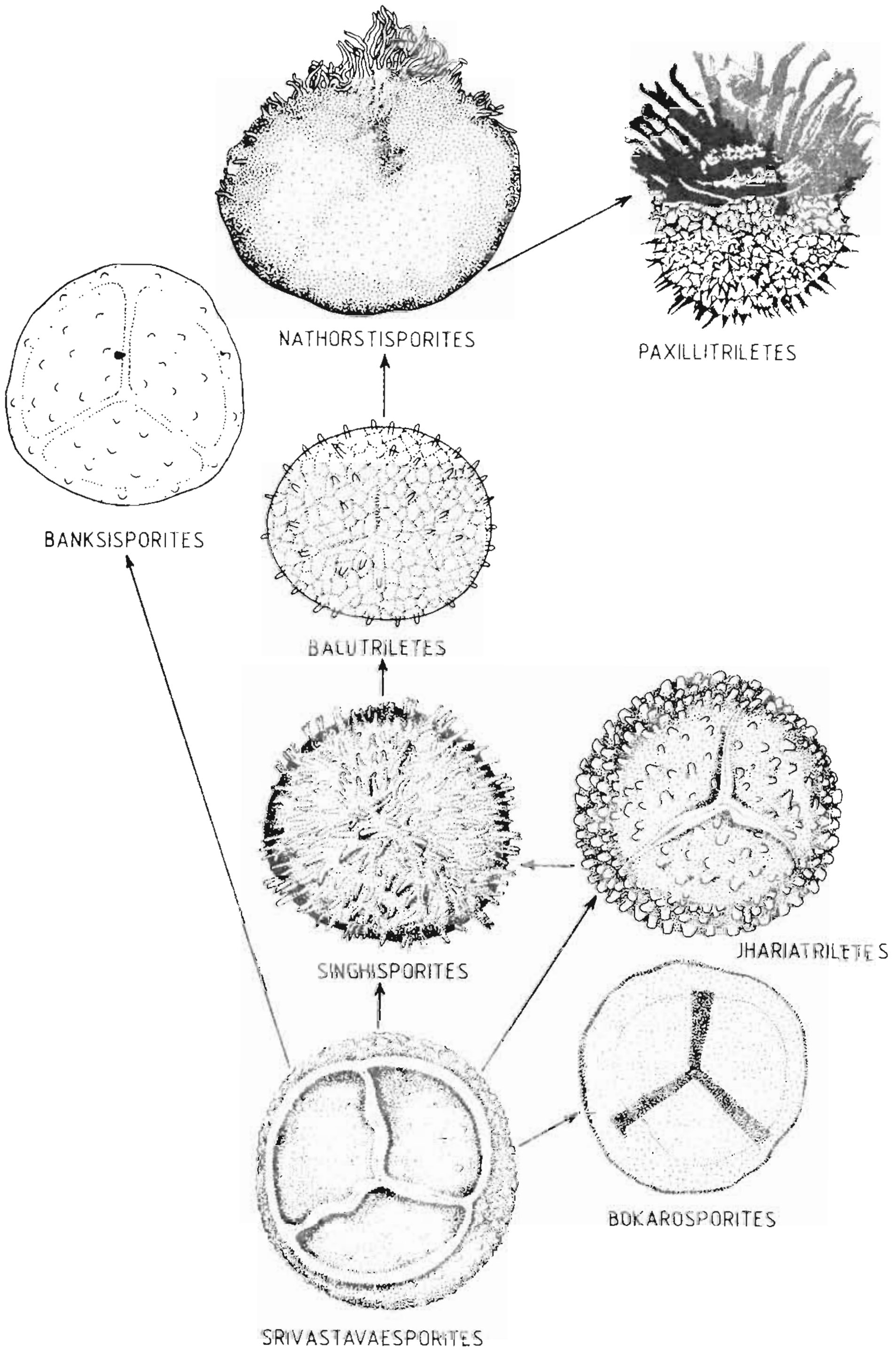


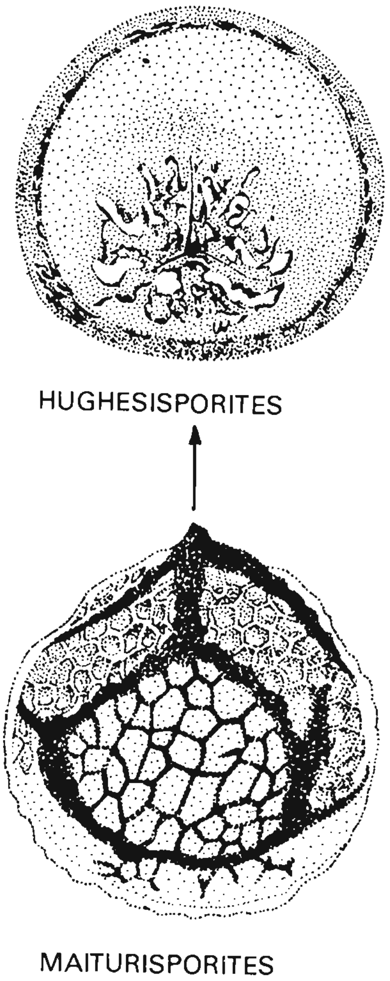
Triassic. The genus *Lelstotheca* Maheshwari (Text-figure 3D) apparently resembles shoots of the genus *Phyllotheca*, but is distinguished by the absence of an adpressed leaf sheath. The genus appears later than *Phyllotheca* and is so far known only from the Barakar Formation (Maheshwari, 1971; Srivastava & Maheshwari, 1986). The genus *Barakaria* Seward & Sahni (Text-figure 3E) has a restricted distribution and is a very rare form, having been reported only once (Feistmantel, 1881, 1886; Seward & Sahni, 1920). *Raniganjia* Rigby (Text-figure 4A), a characteristic form of the Late Permian (Raniganj Formation), has a typical disc-like leaf whorl which may have arisen from the leaf-whorl of *Lelstotheca* through an increase in number of segments, and in length of continuity of margins. *Bengalia raniganjensis* Maheshwari, Singh & Bajpai from the Late Permian Raniganj Formation (Text-figure 4B), probably is also related to *Lelstotheca robusta* (Feistmantel) Maheshwari. In the epidermal features of most of the genera of the Equisetales there is hardly any difference (Meyen, 1969; Pant & Nautiyal, 1968). In *Raniganjia bengalensis* (Feistmantel) Rigby, the guard cells show radiating striations (Pant & Nautiyal, 1968) like those on the leaf-segment and stems of some of the modern Equisetums (Pant & Kidwai, 1968). This feature, however, is not known in the cuticle of *Schizoneura* (Srivastava, 1954) and *Barakaria* (Meyen, 1967). Leaf segments of the genera *Barakaria, Lelstotheca, Raniganjia* and *Bengalia*, all have transverse running striations that simulate lateral veins, and mucronate apices. These characters are lacking in leaf segments of *Phyllotheca* and *Schizoneura*.

The Sphenophyllales are represented by two genera, viz., *Trizygia* Royle (Text-figure 4C) and *Sphenophyllum* Koenig (Text-figure 4D). The former, represented by a single species, *T. speciosa* Royle, is the most common form and continues unchanged from the Early Permian Barakar Formation into the



Text-figure 2C—Schematic drawing showing changes in ornamentation pattern in time.

Early Triassic Maitur Formation (Bose & Banerji, 1984). The genus *Sphenophyllum* is comparatively rare in the Indian Gondwana. Fragments have been reported from Barakar and Hinjir formations of the Raniganj and Talcher coalfields, respectively A characteristic heterophyllous *Sphenophyllum* has been reported from the Early Permian Barakar Formation of the Rajmahal Hills (Singh, Srivastava & Maheshwari, 1986) The two genera are distinguished on the basis of the difference in the nature of leaf whorls at the nodes; there is no difference in the epidermal features of the leaves



Text-figure 2D—Schematic drawing showing changes in ornamentation pattern in time.

(Pant & Mehra, 1963; Boureau, 1964). Recently, Prasad and Maithy (1990) have reported a new genus of fossil leaves from the Barakar Formation of the Bansloi Valley Coalfield in the Rajmahal Basin. The epidermal features of this leaf, *Pachwarophyllum santhalensis* (Text-figure 4E) which is morphologically indistinguishable from leaves of the genus *Benlightfootia* Lacey & Huard-Moine (Text-figure 4F), qualify for the placement of this taxon also under the Sphenophyllales. So far, no fructification has been assigned to the Gondwana taxa of Sphenophyllales; the genus *Kendostrobus* Surange & Chandra, with its monolete spores, probably belongs here.

PTEROPHYTA

The oldest fern-like foliage from the Indian Gondwana is *Botrychiopsis* (*Gondwanidium*) *valida* (Feistmantel) Archangelsky & Gamerro. The fronds, known only from the early Early Permian (Lower Barakar Formation), are long and bear two rows of large and more or less deeply lobed leaflets. Reproductive biology of this 'fern' is not known.

However, there are other genera of fern-like foliage that are known both as fertile and sterile forms. The Permian forms are species of the genera *Asansolia, Tritbecopteris, Damudosorus* and *Damudopteris*. The sterile foliage ranges throughout the Permian but the fertile foliage is known only from the Late Permian Raniganj Formation. All the known ferns are exindusiate, some forms are characterized by free eusporangia with a transverse annulus, while the others have synangia. The forms with synangia (i.e., *Asansolia, Tritbecopteris*) are referred to the family Asterothecaceae while forms with free eusporangia constitute the family Damudopteridaceae. The latter family could have been the progenitor of gleichenaceous forms. The spores of these ferns do not show any major trend. They are a mixed lot, except that all have a surface sculpture (Lele, Maithy & Mandal, 1981) that ranges from grana to bacula (Text-figure 5A-D).

The records of Triassic ferns in India are poor, and therefore their relationship with the Permian forms is uncertain. In the Early Triassic, two types of sphenopterid foliage, viz., *Sphenopteris polymorpha* and *Sphenopteris* spp. are found. Two new ferns, viz., *Marattiopsis* and *Danaeopsis* appear in the Late Triassic (Parsora Formation) of South Rewa Basin. These forms are again found in the Early Cretaceous (Rajmahal Formation) of Rajmahal Hills. There being a sedimentary hiatus, as well as geographical discontinuity, intervening story is not known, except that the pinnules of *D. rajmahalensis* Feistmantel are larger and more linear than those of *D. gracillis* Lele.

GLOSSOPTERIDOPSIDA

The most dominant and important group of plants that thrived during the Permian times in India is the Glossopteridopsida. This group appeared almost simultaneously with the Gondwana sedimentation. Due to non-deposition of older, Ordovician to Carboniferous sediments in the peninsular basins, forms ancestral to the glossopterids are not known. Five genera based on leaves, viz., *Rubidgea* Tate (Text-figure 6F), *Gangamopteris* McCoy (Text-figure 6D), *Maheshwariphyllum* Srivastava (Text-figure 6B), *Glossopteris* Brongniart (Text-figure 6A) and *Palaeovittaria* Feistmantel (Text-figure 6E) are definitely assigned to this group. The leaf genus *Belemnopteris* Feistmantel (Text-figure 6C) probably also belongs here.

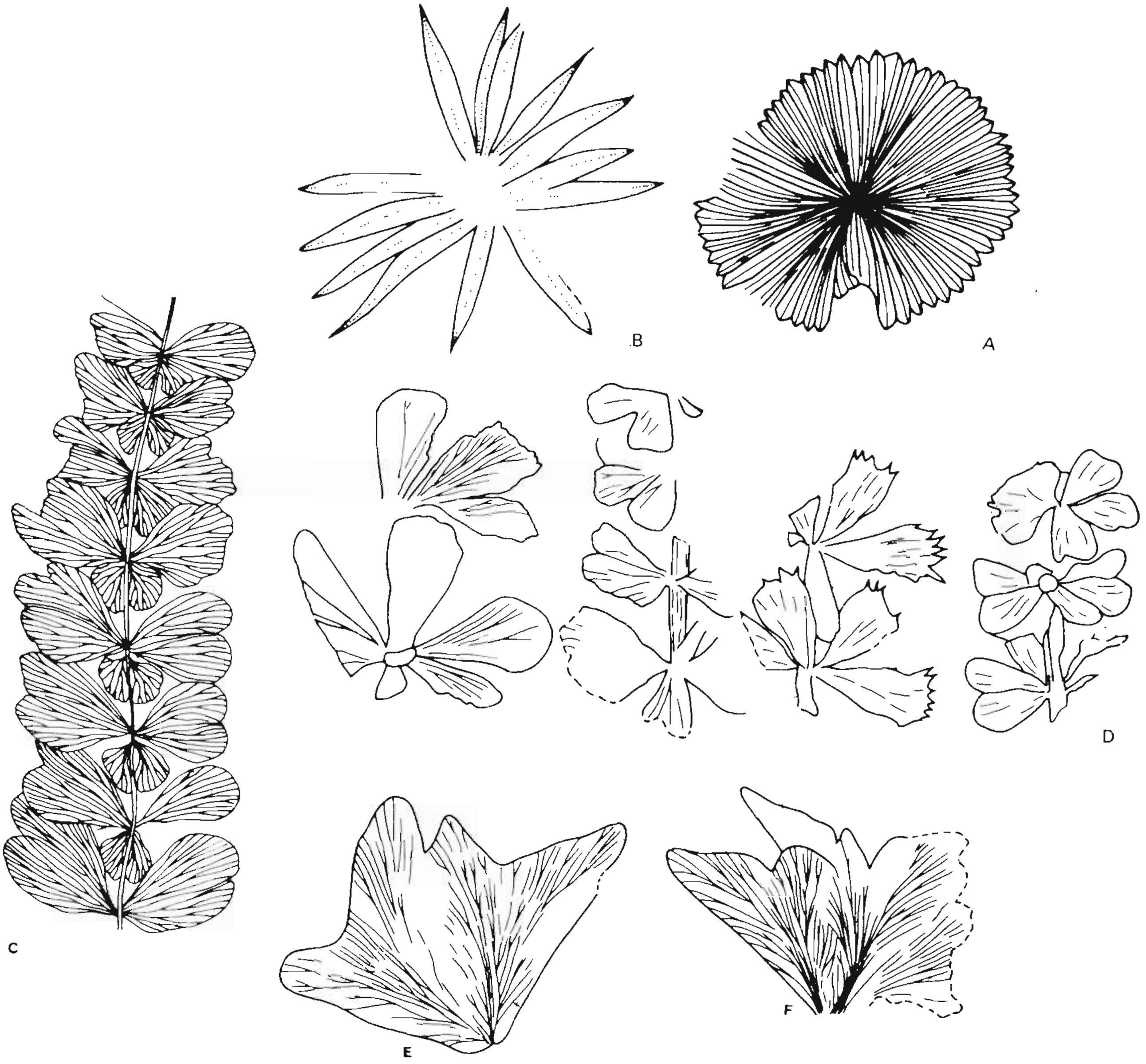
Text-figure 3—A. *Giridia indica*; **B.** *Phyllotheca australis*; **C.** *Schizoneura gondwanensis*; **D.** *Lelstotheca robusta*; **E.** *Barakaria dichotoma* (Figure **A** redrawn from Pant *et al.*, 1981; figure **B** redrawn from Pant & Kidwai, 1968).

The most important genus is *Glossopteris* which has tongue-shaped leaves with a midrib that gives off dichotomizing and anastomosing secondary veins. *Palaeovittaria* leaves have a midrib only in basal part. Leaves of the genera *Gangamopteris* and *Rubidgea* are devoid of a midrib. Anastomoses are present only in *Gangamopteris* and *Glossopteris*, and also in *Belemnopteris*.

The glossopterid group when put in a stratigraphic perspective reveals that leaves without a midrib were probably the first to appear. Alongwith the earliest forms, occurs a Cordaite-type of leaf, *Pantophyllum spatulata* (Dana) comb. nov. (Basionym: *Noeggerathia spatulata* Dana 1841; earlier known as *Noeggerathiopsis hislopii* (Bunbury) Feistmantel/*Noeggerathiopsis spatulata* (Dana) Rigby, Maheshwari & Schopf). The name *N. hislopii* should be restricted only to latest Permian forms from the Kamthi Formation (Bunbury, 1861), and which may have ginkgopsid, rather than cordaitalean affinities. The leaves of *Pantophyllum* were strap-shaped, lacked the midrib and the veins ran straight from the base to the apical region dichotomizing once or twice and never anastomosing.

An almost similar leaf is *Euryphyllum* Feistmantel (Text-figure 6G) which appeared slightly late, i.e., in basal Barakar Formation (Feistmantel, 1879) and is so far known only from the Giridih Coalfield (Lakhanpal, Maheshwari & Awasthi, 1976). Alongwith *Euryphyllum* also appears *Rubidgea* where too the leaves lack a midrib and anastomoses. The genus *Rubidgea* is also known only from the basal Barakar Formation of the Giridih Coalfield.

It is presumed that sometimes in the earliest Permian, the Cordaite-type of leaf gave rise both to *Euryphyllum* and *Rubidgea* (Text-figure 7). Morris (1975), however, believes that certain aphlebiae found alongwith leaves of *Dactylophyllum digitata* in the Late Carboniferous of New South Wales, Australia could have been precursors of the glossopterid lineage. From *Rubidgea* could then have arisen leaves of *Gangamopteris* which though lack a midrib, yet have a well-defined central strand of

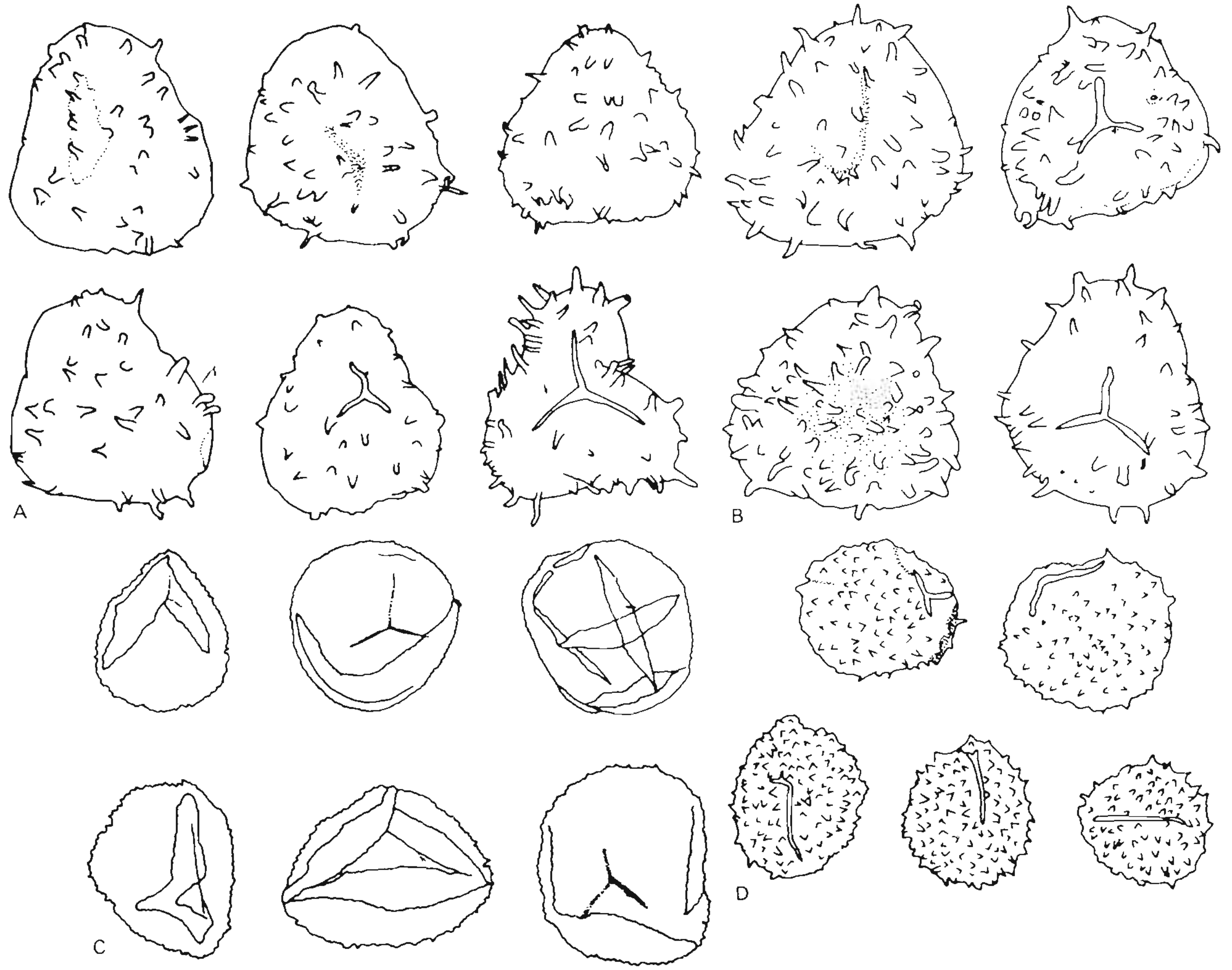


Text-figure 4—A. *Raniganjia bengalensis*; **B.** *Bengalia raniganjensis*; **C.** *Trizygia speciosa*; **D.** *Sphenophyllum gondwanensis*; **E.** *Pachwarophyllum santhalensis*; **F.** *Benlightfootia*. (Figure **A** redrawn from Pant & Nautiyal, 1968; figure **C** redrawn from Pant & Mehra 1963; figure **D** redrawn from Maheshwari *et al.*, 1986, figure **E** redrawn from Prasad & Maithy, 1990; figure **F** redrawn from Singh & Chandra, 1990).

straight veins. For the first time, anastomoses of veins appear. *Maheshwariphyllum*, a leaf with definite midrib recently discovered from the Barakar Formation (Srivastava, 1992), probably also had its origin in the earliest Permian. Slightly later appeared *Glossopteris* leaves having both a midrib and anastomosing veins, combining characters of *Maheshwariphyllum* and *Gangamopteris*. All this must have happened within a very short span of time in the earliest to Early Permian. The Maheshwariphyllum-line continued into the Late Permian (Raniganj Formation) as *Palaeovittaria*, a leaf with midrib reduced in length, running only up to 1/2-3/4 of lamina.

The leaves of many plants are characterized by distinctive leaf forms. The blade or lamina is most important and conspicuous part of the leaf. But as an adaptation to extreme climate, it may be reduced, modified or even absent; the leaves directly interact with the atmosphere and adapt themselves accordingly.

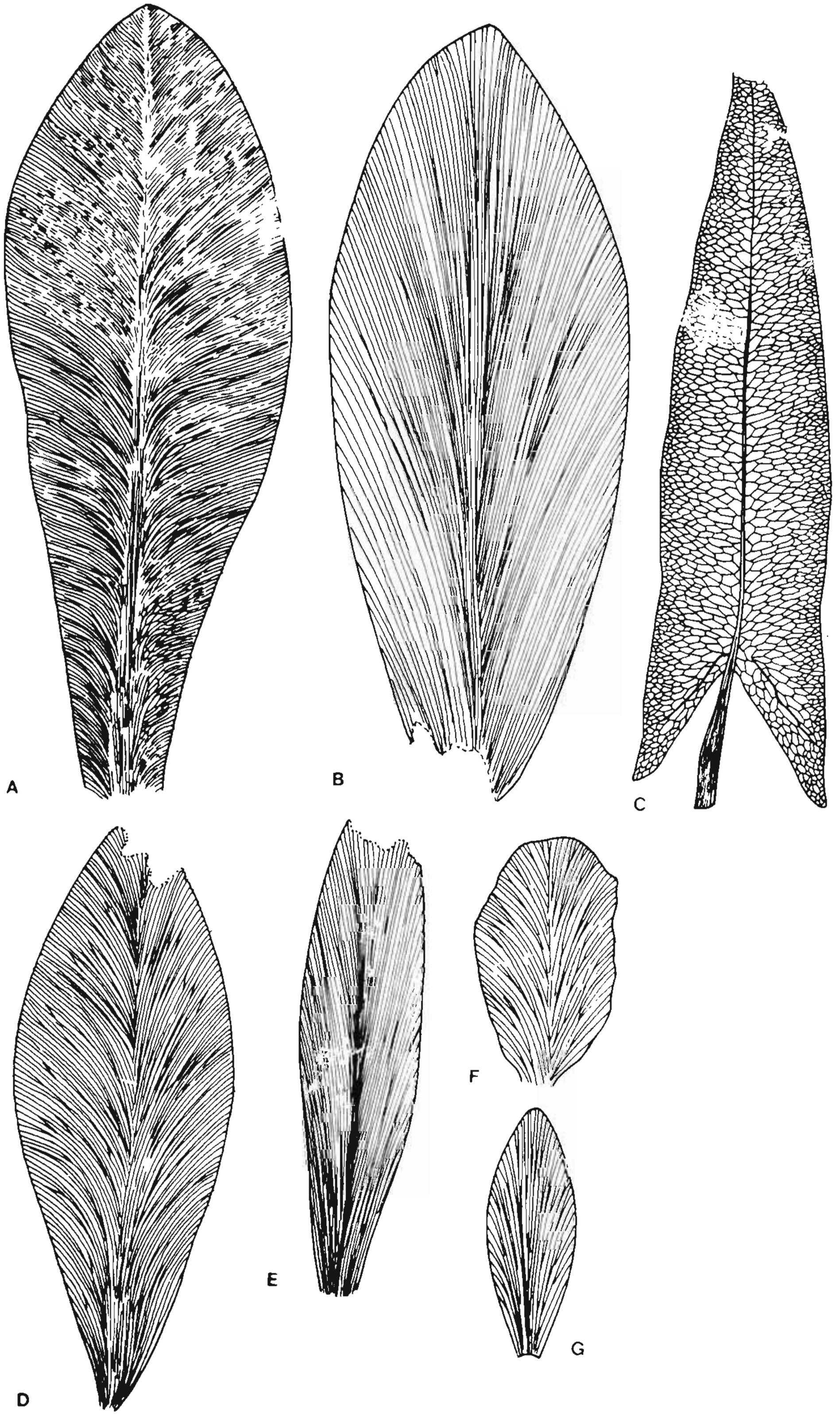
After the pioneering efforts of Sahni (1923) in



Text-figure 5—Showing variation in surface ornamentation of microspores in Late Permian ferns: **A.** *Dichotomopteris major* **B.** *Neomariopteris hughesii*; **C.** *Dichotomopteris lindleyii*; **D.** *Dizeugotheca phegopteroides* (All redrawn from Lele *et al.*, 1981).

chemically isolating cuticles from a *Glossopteris* leaf, much work has been done in recent years. A number of new species has been established under the belief and observation that cuticular morphology is taxon specific. Latest study on certain leaves of *Glossopteris* from the Barakar Formation of the Raniganj Coalfield (Maheshwari & Tewari, 1992) shows that this may not always be true. These authors have found that some morphographically different leaves show similar cuticular features.

The cuticle covers the aerial parts of the plants and plays an important role. The deposition of cuticle can be affected by light intensity and availability of water. In plants under continuous water stress twice as much cuticle is laid down as compared to plants growing under optimal water conditions (Martin & Juniper, 1970). The development of wax is also affected by light, being greater at higher light intensities. In leaves stomata may occur on both the surfaces or on one surface only. In temperate climate with an adequate water supply, stomata are more frequent on the abaxial surface. In aquatic plants stomata may be absent, or in floating leaves restricted to the upper or lower surface. In many xerophytes, plants which usually have a restricted water supply, the stomata may be deeply sunken. Therefore, these are the adaptive characters which develop in a plant depending on the ecological niches not necessarily genetic characters. However, one thing is certain that the syndetocheilic stomata did not appear in the Indian flora prior to the Early Cretaceous and there too are confined to a single order, the Bennettitales. Similarly development of trichomes and frequency of stomata are also governed by the environment. A trichome is formed by the outgrowth of an epidermal cell; it is protective in function and may prevent undue water loss. Therefore, these are the



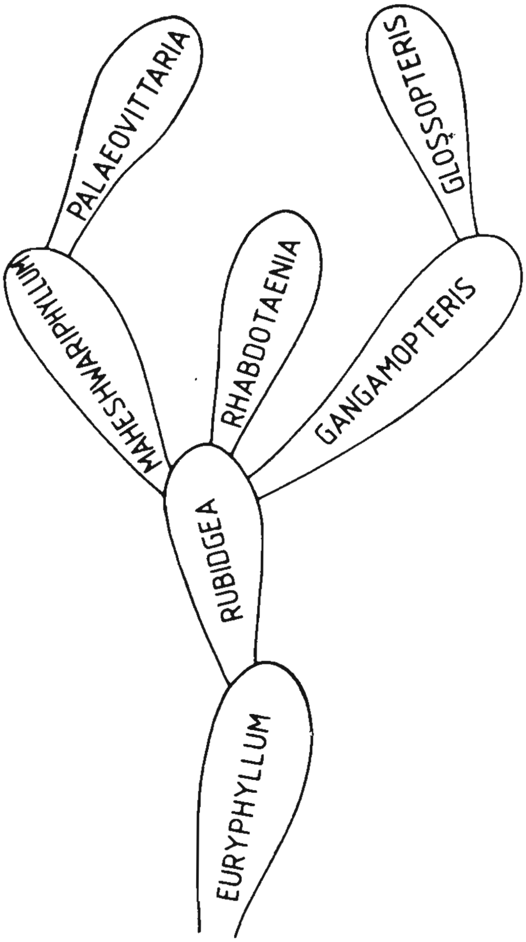
Text-figure 6—A. *Glossopteris*; **B.** *Maheshwariphyllum*, **C.** *Belemnopteris*; **D.** *Gangamopteris*; **E.** *Palaeovittaria*; **F.** *Rubidgea*; **G.** *Euryphyllum* (Redrawn from Pant, 1982).

characters which develop in the plant as a reflection of its surrounding environment and, hence are not necessarily indicators of phylogenetic relationships or morphological trends within a group of plants.

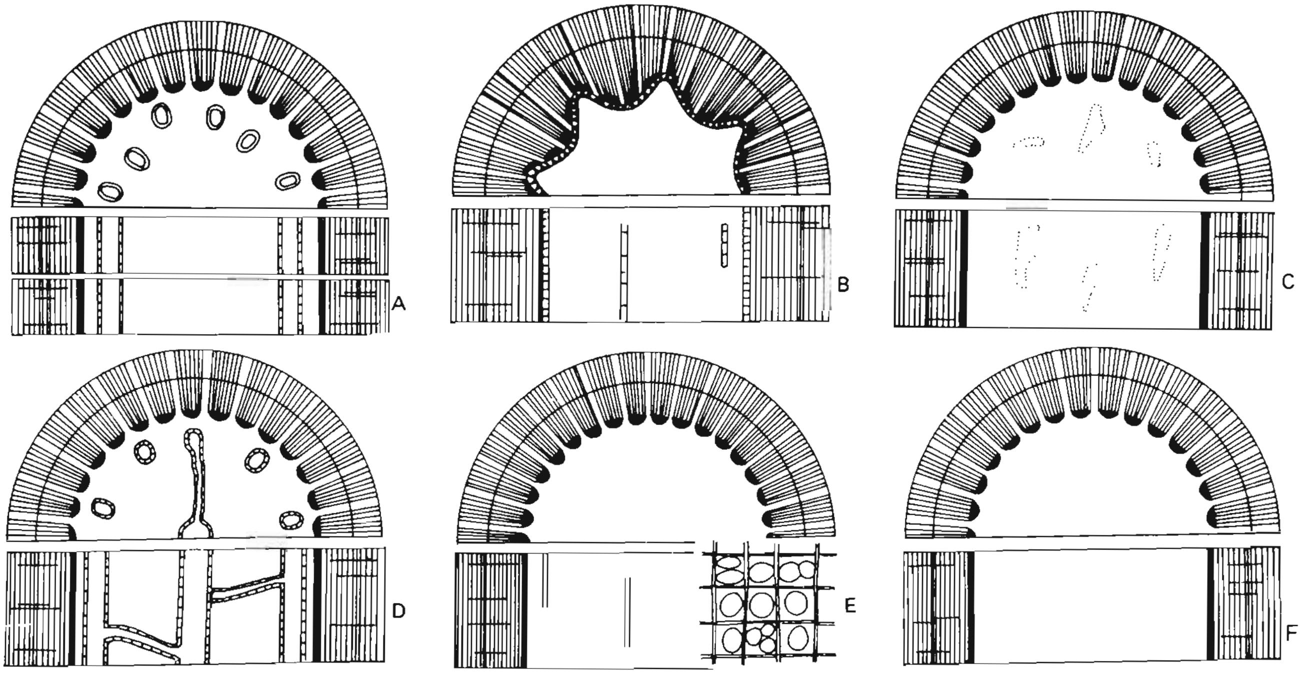
In most of the Gondwana woods, comparatively more delicate tissues like pith, primary xylem, phloem and cortex are not preserved. The taxa are usually known through pieces of secondary wood only. The secondary xylem in Gondwana woods is relatively uniform, but it may be combined in different arrangements with the pith and primary xylem. The wood taxa with pith and primary xylem known from the Permian Gondwana of India are *Trigonomyelon* Walton, *Damudoxylon* Maheshwari, *Megaporoxylon* Kräusel, *Kaokoxylon* Kräusel, and *Polysolenoxylon* Kräusel & Dolianiti.

In India, the oldest record of wood with heterogeneous pith and primary xylem is from the Early Permian Barakar Formation. The pith in this wood, viz., *Solenoxylon* (Text-figure 8A) and *Polysolenoxylon* (Text-figure 8D) is solid but with well-distributed 'secretory' cells and vertical running canals, supposed to have had some undefined secretory function. The primary xylem is endarch and the secondary xylem is with araucaroid and mixed pitting. This type of pith is restricted only to the Barakar Formation. Elsewhere, it is known from Brazil (Kräusel & Dolianiti, 1958) and Antarctica (Maheshwari, 1972). In the same horizon is also found wood with homogeneous pith, usually referred to the genus *Dadoxylon*. No woods have so far been reported from the Kulti Formation or equivalent beds.

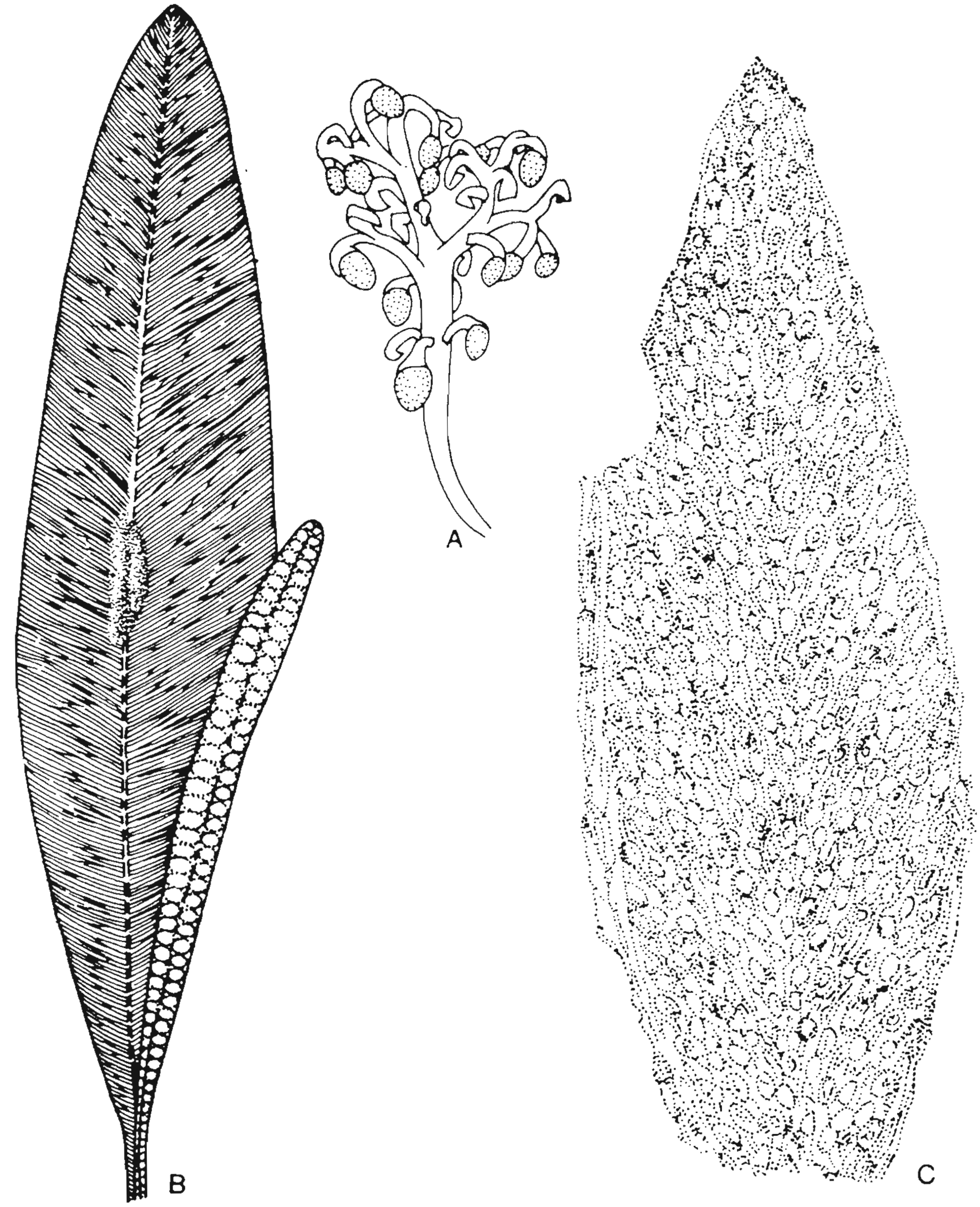
Fossil woods found in the Late Permian Raniganj Formation also have a solid pith which is heterogeneous. It may contain 'secretory' cells as in *Damudoxylon* Maheshwari (Text-figure 8C), *Trigonomyelon* Walton (Text-figure 8B), and



Text-figure 7—Sketch delineating assumed origin of glossopterid foliage.



Text-figure 8—Schematic transverse sections through various taxa of fossil wood. **A.** *Solenoxylon* sp.; **B.** *Trigonomyelon raniganjense*; **C.** *Damudoxylon* sp.; **D.** *Polysolenoxylon canalosum*; **E.** *Megaporoxylon kraeuselii*; **F.** *Kaokoxylon zalesskyii* (Redrawn from Kräusel *et al.*, 1961).



Text-figure 9—A. *Senotheca murulidihensis*; **B.** *Arberia umbellata*; **C.** *Dictyopteridium sporiferum* (Figure **A** redrawn from Banerjee, 1980, figure **B.** from Rigby, 1972; figure **C.** from Surange & Chandra, 1973).

Megaporoxylon Kräusel (Text-figure 8E), or sclerenchyma as in *Kaokoxylon* Kräusel (Text-figure 8F). The pith is lobed in the genus *Trigonomyelon*, originally reported from South Africa (Walton, 1925). Most of the Gondwana woods show endarch protoxylem. The secondary xylem is pycnoxylic, homoxylous and shows well-marked growth rings. The presence of growth rings in the wood is generally regarded as indicative of a response to climatic fluctuations and periodicity as against lack of growth rings which is believed to be indicative of equitable climate. Pitting in the secondary wood tracheids of Gondwana woods is generally araucaroid but many of them show dual combination of araucaroid and abietoid pits or araucaroid pits with taxinean tertiary spirals or triple combination of araucaroid and abietoid pits with taxinean tertiary spirals.

The xylem rays of these woods are always homogeneous and one to many cells high. They are usually uniseriate or partly biseriate; rarely a xylem ray is multiseriate. The cross-field pits may be one to

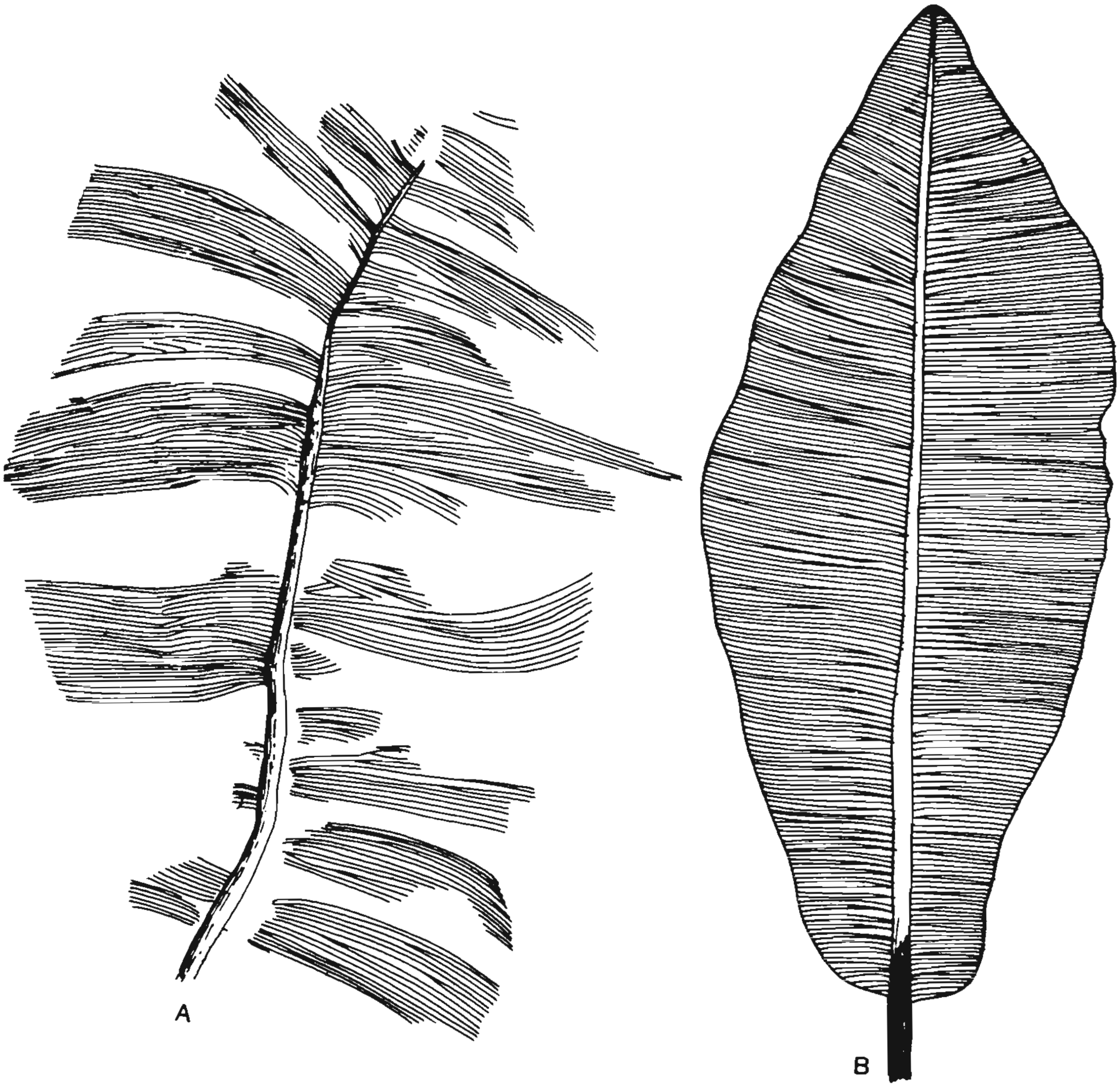
Text-figure 10—**A.** *Eretmonia*; **B.** *Glossotheca utkalensis*; **C.** *Lidgettonia indica* (Figure **A** redrawn from Surange & Maheshwari, 1971; figure **B** from Surange & Chandra, 1974).

many in number, simple or single dacrydiod or pinoid, simple or multiple bordered araucaroid, piceoid, cupressiod and taxadiod, podocarpoid or of intermediate types. The shape of cross-field pits may be circular, oval or elongated oval, may be isolated or contiguous.

On the basis of organisation of the fructification and the nature of subtending leaf, the glossopterids are grouped under two families, viz., Dictyopteridiumaceae and Eretmoniaceae (Maheshwari, 1990). The family Dictyopteridiumaceae includes the fructification genera *Dictyopteridium, Ottokaria, Scutum, Senotheca, Satsangia*, and probably *Vannus*. The family Eretmoniaceae includes the fructification genera *Eretmonia, Lidgettonia, Glossotheca* and probably *Denkania*.

The fructifications of the family Dictyopteridiumaceae are simple, dorsiventral and foliose (Text-figures 9B-C). A large number of ovules are borne on the abaxial surface. On the basis of an indepth analysis of all the characters, it is visualised that the basic structure of the dictyopterid ovule-bearing fructification is represented by the genus *Arberia* Rigby (Text-figure 9A) where the ovules are present on terminal branches of an axis subtended by a sporophyll. Through overtopping and syngenesis the Dolianitia-type of fructification could have given rise to the basic identity of the dictyopterid fructification. The dichotomies became unequal and eventually gave rise to a pinnate arrangement through syngenesis, where the photosynthetic area increases and ovules become transferred to the adaxial surface.

In the family Eretmoniaceae the fructifications are pinnately branched, axillary to a leaf; the subtending leaf is modified and looks like a scale leaf (Text-figures 10A-C). The fructification has 1-4 pairs of branches, each branch terminating in a fertile head. In the female fructification each fertile head is dorsiventral and bears 1-7 ovules on abaxial surface. In the male fructification each fertile head bears a large number of pollen-sacs, in a manner not yet clearly known. These fructifications show a superficial resemblance to the peltaspermaceous fructification—*Antevsia*. The *Eretmonia-Glossotheca*



Text-figure 11—A. *Pteronilssonia gopalii*, and **B.** *Rhabdotaenia danaeoides* (Redrawn from Pant, 1982).

complex probably resulted in the androclad *Pteruchus* (Pant & Basu, 1973) found in the Tiki Formation of terminal Permian age.

Birbalsahnia divyadarshanii Bajpai & Maheshwari is an incompletely known pollen-sac bearing organ. The main axis of the androclad is dichotomously branched, and subsequent branches are lateral and alternate to one another. No pollen grain was recovered from the pollen-sacs. This form alongwith pinnately branched gynoclads *Utkalia dichotoma* Chandra and *Veekaysinghia durgavatiae* (Bajpai & Maheshwari, 1991) are without any subtending scale leaf. These possibly do not belong to the glossopterid lineage.

CYCADOPHYTA

The group is poorly represented in the Gondwana. In the Early Permian it is represented by a frond which is pinnately divided, and 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. The leaf type, i.e., *Pseudoctenis balli* (Feistmantel) Seward reappears in the Early Cretaceous, e.g., *Pseudoctenis footeana* (Feistmantel) Seward & Sahni. *Pterophyllum sahnii* reported from the Late Triassic Parsora Formation (Lele, 1956) may also be a *Pseudoctenis* as the veins in the specimens show a few cross connections. *Pterophyllum burdwanense* (McClelland) Feistmantel and *Pteronilssonia gopalii* Pant & Mehra (Text-figure 11A) probably also belong here alongwith leaves of the genus *Rhabdotaenia* Pant (Text-figure 11B) as evidenced by the cuticular morphology. *Pteronilssonia* probably belonged to the same plant that bore *Rhabdotaenia* leaves.

GINKGOPHYTA

Definite records of the ginkgopsid group are mostly from the Early Cretaceous sediments of India (Lakhanpal, Maheshwari & Awasthi, 1976). In recent years Ginkgo-like leaves have also been recorded from older formations (Maheshwari & Banerji, 1978; Bajpai, 1991; Maheshwari & Bajpai, 1991). Most of these leaves have been assigned to the genus *Ginkgoites* and have the same morphology as the younger forms. However, definite ginkgoalean ovules are known only from the Early Cretaceous Rajmahal Formation (Bano, Maheshwari & Bose, 1979). A number of Early Permian leaves, e.g., *Saportaea, Psygmophyllum* and *Rhipidopsis* have also been assigned to the ginkgopsids (Maheshwari & Bajpai, 1991).

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