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PALAEOWORLD full-text (Volume 15 –) available at:
http://www.sciencedirect.com/science/journal/1871174X

Permian Stratigraphy, Environments and Resources, v. 2
***Palaeoworld**, No. 9*, pp. 77-86
Jin *et al.* (Eds)
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CARBONIFEROUS-PERMIAN EVENT : RISE OF THE *GLOSSOPTERIS* FLORA ON GONDWANALAND

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Abstract: The present paper is an analysis of the impact of Late Palaeozoic glacial stress on the evolving patterns in the morphology of spore-pollen, which were produced by the floras at the beginning of Mid-Carboniferous on Gondwanaland. The episodic occurrences of glaciation in Carboniferous-Early Permian had triggered the evolutionary shift in the cosmopolitan *Lepidodendropsis* flora of Early Carboniferous. This is an important event. Astray records of *Glossopteris* leaf in early Late Carboniferous NBG (*Nothorachopteris, Botrychiopsis* and *Ginkophyllum*) flora, and the occurrence of a disaccate pollen with fair number of radial monosaccate pollen, in the cingulate-zonate spores dominant assemblage is significant in the Southern hemisphere. The recently determined Zircon dates of Upper Carboniferous strata in eastern Australia gives a younger aspect to the *Potonieisporites* assemblage zone. With this datum, the *Granulatisporites confluence* oppel zone of the Grant Formation in Australia, younger to *Potonieisporites* Assemblage zone, may now be considered to span from Early Asselian to Sakmarian. The record of Stephanian on Gondwanaland thus becomes doubtful.

Keywords: Gondwanaland, flora, event

INTRODUCTION

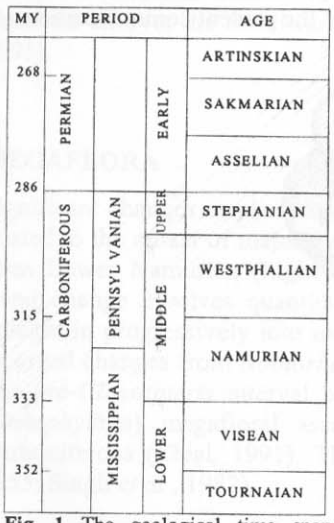

Fig. 1 The geological time span (adopted from Roberts *et al.*, 1993) during which the impact of Late Palaeozoic glaciation on the evolving patterns in flora has been discussed.

The Upper Carboniferous-Lower Permian passage (Fig. 1) has been recognised as a time of important event on the Gondwanaland. The widespread glacial regime caused the decline of *Rhacopteris* flora, followed by the rise of the *Glossopteris* flora (Lele, 1976; Vijaya, 1995). The intermediate *Nothorhacopteris* flora could not withstand the onslaught stress of the glacial environment, and hence did not survive for a long time. Although a continuity of the sequence is still debatable, these changes in the floral composition are reflected in the palynological assemblages recorded from Namurian to Sakmarian time in S. America, Africa, Australia, Antarctica and India (Cesari and Limarino, 1987; Vergel *et al.*, 1993; MacRae, 1991; Balme, 1960; Foster and Waterhouse, 1988; Vijaya, 1995). The appeareance of a non-striate disaccate with faint grooves on body (Fig. 2), and the bilateral and radial monosaccate pollen with a prepollen character having a prominent germinal aperture on the proximal face of the central body (Fig. 5), has been recorded in Namurian-Westphalian (see Vijaya and Tiwari, 1992). Evidences, although not direct, suggest that the striate disaccate pollen belonged to *Glossopteris* (Fig. 2), while the girdling monosaccate pollen has cordaitalean affinity. These two

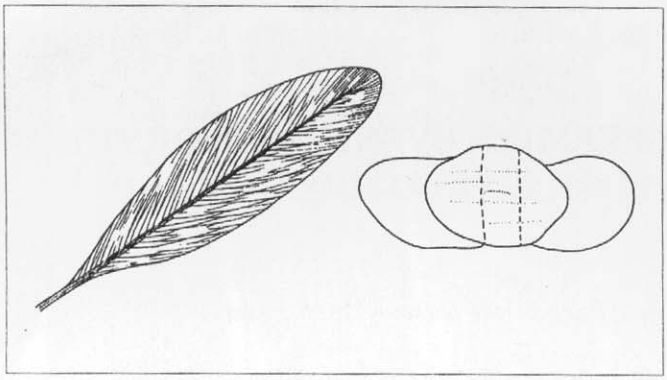

Fig. 2 Morphological characters of the first- *Glossopteris* leaf and a disaccate pollen, on record at the beginning of Mid-Carboniferous on Gondwanaland. The venation pattern in leaf is faint, and the central body of the pollen bears very faint grooves. In both, the characters are of primitive state.

groups formed the major components of the "*Glossopteris*-flora" during the Early Permian time. The sporadic occurrence of the pollen group of "*Glossopteris*-flora" in Westphalian and their subtle but continued record upto Stephanian reveals that this was the period when the gene pool of *Rhacopteris* - *Nothorhacopteris* was shifting towards *Glossopteris* stock. This has happened under the pressure of glacial influence, which triggered a struggle for plants to survive under odd situation (Fig. 3). By the time of C/P boundary, the *Glossopteris* flora was established and in Early Asselian it captured the realm of the Gondwanaland. With the progressive withdrawal of the glacial ice, the *Glossopteris* flora diversified and first highest level of innovation was attained at the late Asselian time. Along the temporal span, climate continued to ameliorate and so also the floral diversity (Cleal, 1991a; Lopez-Gamundi *et al.*, 1992, 1993; Vijaya, 1995).

The palynofloras recognised through Asselian on to the Indian subcontinent are now determined to be more diversified than the Asselian part of *Granulatisporites confluence* oppel zone in Australia described by Foster and Waterhouse (1988). Because the recent taphonomic studies reveal that the earliest palynoflora recorded in the Talchir Formation of India is not so impoverished as was earlier thought to be (Tiwari *et al.*, 1994). This implies that the retreat of glaciers from India was predated than that from Australia, and also that the intensity of ice covers was lesser in India than in other continents of eastern Gondwanaland (Vijaya, 1995).

The changes which occurred across C/P boundary make the subject of the present communication.

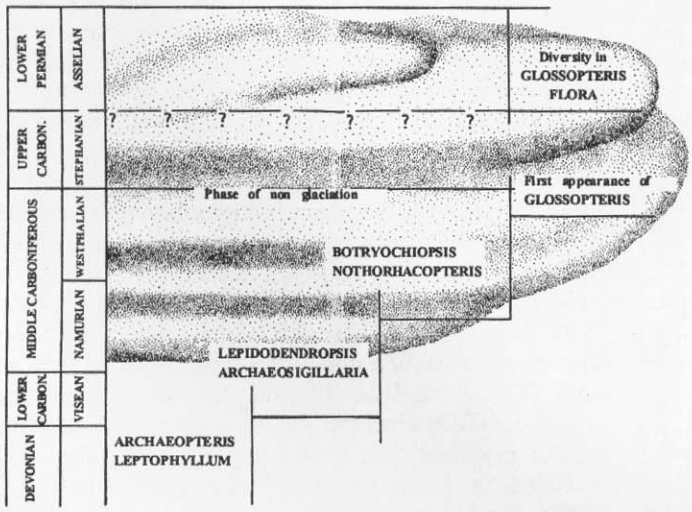

Fig. 3 Impact of episodic occurrences of glaciation in Carboniferous-Early Permian time which has triggered the evolutionary shift in the NBG flora. The advent of *Glossopteris* is recognised within the sudden non-glacial phase in Late Westphalian on southern hemisphere(no scale).

PALYNOFLORA

Within the Carboniferous, evolving patterns of potentially important radial monosaccate palynotaxa is regarded chronologically significant event, both in Northern and Southern hemispheres (Lopez-Gamundi *et al.,* 1993; Vergel *et al.,* 1993; Vijaya and Tiwari, 1992). The floral regionalism had begun during early Mid-Carboniferous (Cleal, 1991) but the data of the palynoassemblages at this level is meagre.

Recently, Playford (1990) has discussed the Lower Carboniferous palynoflora in the Southern Hemisphere with special comments about the status of known Upper Carboniferous palynoassemblages. The astray records of Middle to Upper Carboniferous palynoflora are known from South America and Australia (Vergel *et al.,* 1993; Roberts *et al.,* 1993). It is thus established that the appearance and consistent record of monosaccate pollen characterise the change-over in the composition of Carboniferous palynoflora in the Gondwana realm, and the exit of actual Carboniferous palynotaxa-*Retispora, Dibolisporites, Knoxisporites,* consistently mark the Carboniferous-Permian boundary (Playford, 1990).

RECORD OF DISACCATE POLLEN

The palynoassemblages which contain fair number of radial monosaccate pollen (*Potonieisporites, Plicatipollenites*) in association with *Cristatisporites* dominance, are on record from Argentina (Cesari and Limarino, 1987; Archangelsky and Cesari, 1986) dated to be of Namurian-Westphalian age. However, these assemblages do not have disaccate pollen at this level (Fig. 4).

The other palynoassemblages recovered in succession in widely separated areas of -- Australia and Argentina are of Late Westphalian-Stephanian age (Balme, 1960; Lopez-Gamudi *et al.,* 1993; Vergel *et al.,* 1993), which also contain relatively high incidence of cingulate-zonate spores -- *Cristatisporites-Densosporites.* But in these, the occurrence of increased speciation in radial and bilateral monosaccate pollen is significant. The record of a disaccate pollen (Fig. 4) at this level in Anderson Formation, Fitzroy Basin, northwestern Australia (Balme, 1960) is a bench-mark event. Subsequently as seen in the palynocomposition of the zone *Potonieisporites* (Cesari and Limarino, 1987) the kind and number in the striate disaccate pollen had started to diversify as it has been observed all over the Gondwanaland during Early Sakmarian (Foster and Waterhose, 1988; Vijaya, 1995).

MEGAFLORA

Significant changes in plant fossil assemblages, known as floral break (Kidson, 1894) are probably related to the on-set of major glaciation in Mid-Carboniferous (Wagner, 1982; Meyen, 1987) that is, from Lower Namurian (highest Mississipian) to Middle Namurian (Lower Pennsylvanian). This floral change involves quantitative variation, and also the appearance of newer taxa which had brought-in progressively into more than one floral change. By the end of Carboniferous there were recorded changes from *Nothorhacopteris* flora to NBG flora, and then to *Glossopteris* flora (Fig. 3). The pre-*Glossopteris* interval had been succeeded by NBG (*Nothorhacopteris, Botrychiopsis* and *Ginkophyllum*) megafloral assemblage, which is now recognised to range in time of Late Carboniferous (Cleal, 1991). This flora is widely distributed on the Gondwanaland (Hoeg *et al.,* 1955; Singh *et al.*, 1982).

ENIGMA OF RISE OF GLOSSOPTERIS

The *Glossopteris* is a leaf genus -- based on its unique morphology, tounge-shaped outline with a midrib and parallel venation (Fig. 2). This leaf morphology had maintained its identity as a diagnostic constituent of *Glossopteris* flora. Rise of *Glossopteris still* remains the subject of debate.

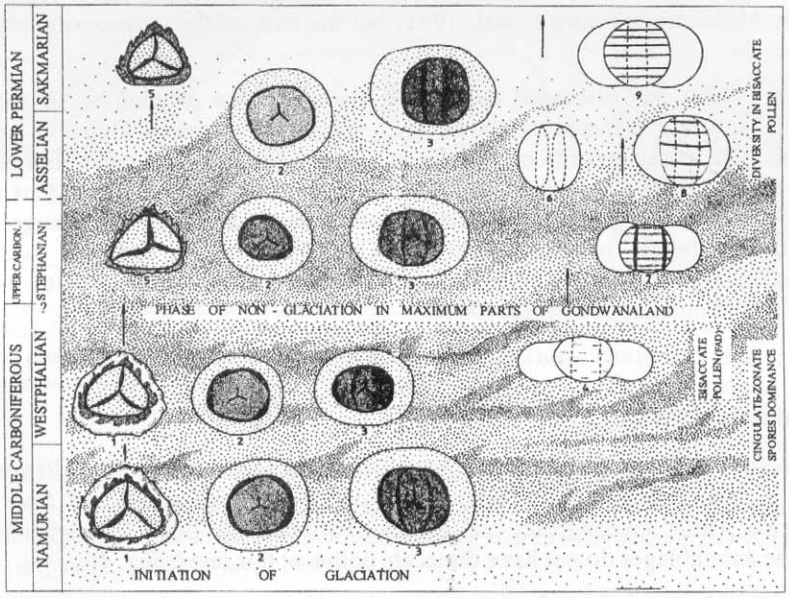

Fig. 4 Evolving patterns in spore-pollen morphology during the glacial stress of Carboniferous and Early Permian time span. Cingulate-zonate spores (1. *Cristatisporites*) are major elements of Namurian-Westphalian palynoassemblages with fair number of radial monosaccate pollen (2. *Plicatipollenites,* 3. *Potonieisporites*). The radial pollen taxa bear prominent germinal aperture on the proximal face of body -- a prepollen character. In subsequent horizon represented by Westphalian-Stephanian time, first record of a disaccate pollen (4. *Pityosporites westphalensis*) still in a cingulate-zonate spore dominated palynoassemblage, is a benchmark event. This disaccate pollen is thought to be an ancestral morphology for striate as well non-striate disaccate pollen (8. *Faunipollenites,* 9. *Stratopodocarpites,* 7. cf. *Crescentipollenites.*, and 6. *Scheuringipollenites,* in the younger Early Permian Talchir Formation. The cingulate-zonate spore (5. cf. *Dentatispora*) recognised at this horizon, again retains its affinity with the older morphology. The density of dotted pattern in the background indicates varying intensity of glaciation during the time of floral shifts.

First record of *Glossopteris* leaf within the NBG flora is from Argentina although its venation pattern has been described as faintly anastomosing (Lopez-Gamundi, *et al.,* 1992).

A probable ancestral relationship of *Glossopteris* leaf had been postulated with the leaf genus *Lesleya* (Leary, 1993) which occurred in North America in the Early Pennsylvanian flora. Both the leaf taxa -- *Lesleya* and *Glossopteris,* are apparently the same in their shape and pattern of venation. Such basic resemblance had arisen the probability of their being linked through a common gene-stock.

ADVENT OF *GLOSSOPTERIS*

The diversification of plants has speeded up the differentiation in *Glossopteris* flora, along with the increase of endemic plant elements by the Late Carboniferous (Cleal, 1991a). It is widely recognized that tropical vegetation underwent a significant change and a probable decline during Late Carboniferous. Virtually all of the lycophyte/fern dominated forests had disappeared by the Early Permian. The reasons for this kind of destruction of vegetation seems to be a consequence of changing climatic pressure of the tropical areas, due to the formation of the Pangaea "super-continent".

The establishment of the glossopterid-dominated assemblages in top-most Carboniferous or basal Permian in Gondwana certainly reflects a significant retreat of palaeo-antarctic ice-sheets (Cleal and Thomas, 1991; Rowley *et al.,* 1985).

CARBONIFEROUS-PERMIAN : GLOBAL EPISODES

On the existing biostratigraphic evidences it is difficult to correlate precisely the glacial episodes, and the evolution of flora during the Carboniferous and Early Permian times on the Gondwanaland. The sedimentary deposits through this span are a package of terrestrial as well as marine sediments (Visser, 1993; Wopfner, 1980, 1991). It includes an array of changing palaeoclimate, and also the flora and fauna.

During this span of time, two major events had been recognized at the global level: (i) Carboniferous glaciation, (ii) and the formation of Pangaea. Carboniferous glaciation had not been an uninterupted episode through the time of 55 ma. Thus, the cyclicity of increased or decreased volumes of glaciation (Veevers and Powell, 1987) seems to be the major causal factor for the shifting in floral community of Carboniferous. Similarly, Pangaea — a supercontinent extending from pole to pole, widened the continentality on the palaeoequator of the globa surface area. Thus, the more openland resulted in the rise of temperature and aridity effecting the vegetation of the palaeo-equatorial region. This phenomenon triggered the migration of plant groups, which were well-suited to wet climate, to higher latitudes (Wagner, 1993).

With reference to these global episodes in the Carboniferous, certain phases of events have been identified:

The early Lower Carboniferous period represents relatively a uniform cosmopolitanism in the megaflora as well as the palynoflora which seems to retain a continuation with several Devonian elements (Cleal, 1991a; Playford, 1990). The Middle Carboniferous witnessed extensive glaciation, provincialism in flora, and record of monosaccate pollen. The transition from Middle to Late Carboniferous has been recognised presently the Phase of major events by the occurrence of disaccate pollen and the *Glossopteris* leaf (Figs. 3, 4).

GLACIATION

The Carboniferous period had experienced dramatic climatic changes on the Gondwana continents. However, there exists a controversy about the duration and extent of glaciation (Gonzalez, 1990; Dickins, 1984).

Evidences allow to estimate the initiation of glaciation in Argentina and probably in other Gondwana continents in latest Visean/Early Namurian. And it is assumed that the ice had totally vanished from all over the Gondwanaland around Early Sakmarian (Gonzalez, 1990), encompassing the time span of c 55 m.y. There seems to be no major synchroneity between glacial episodes (Eyles *et al.*, 1993); the reasons for such diachroniety is assigned to the migration of South pole through southern hemisphere (Lopez-Gamundi and Espeyo, 1993).

During the Mid-Carboniferous Namurian time with the initiation of warming in climate along the palaeoequatorial belt, the monosaccate-pollen-producing plant-group cordaitales migrated to higher latitude in southern Hemisphere (Wagner, 1993), as these plants were suited to cool-climate. The sudden emergence of *Glossopteris* in NBG flora may be traced back in time with the similar-looking Early Pennsylvanian (Late Carboniferous) genus *Lesleya* of North America.

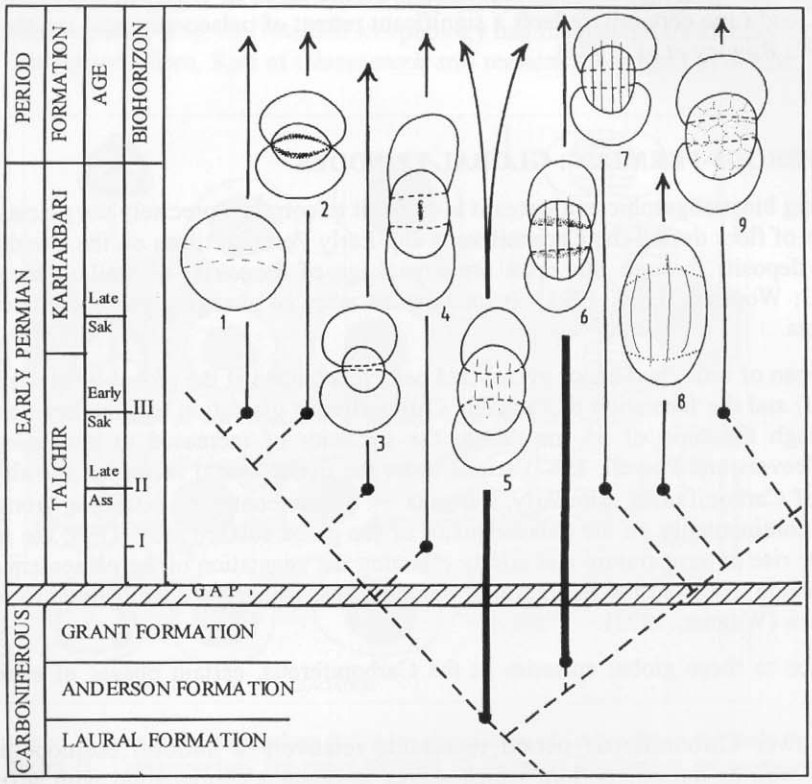

Fig. 5 Progressive withdrawl of glaciation had brought-in further diversification among the striate disaccate pollen, and the first highest level of innovation is attained by late Asselian. The various pollen taxa observed are - 1. *Scheuringipollenites,* 2. *Cuneatisporites,* 3. *Platysaccus,* 4. *Vestigisporites* comprising the group of non-striate disaccate pollen. The striate disaccate pollen are represented by, 6. *Crescentipollenites,* 7. *Striatopodocarpites,* 8. *Faunipollenites,* 9. *Rhizomaspora.* The genus 5. "*Pityosporites*" remained the ancestral stock. This cladistic figure is drawn from Vijaya and Tiwari (1992). Solid dots - level of First occurrence; vertical arrows-continuity in time; broken line - cladistic relationship of morphos; vertical thick lines - beginning of major striate stocks.

DISCUSSION AND CONCLUSION

The available sedimentological evidences from Australia and western Argentina indicate that at least late Westphalian was a phase of non-glaciation in the maximum parts of the Gondwanaland (Gonzalez, 1990). Such transitional palaeoclimatic conditions with the increase in humidity and relative warming correspond with the advent of *Glossopteris,* and faintly grooved (striate) disaccate pollen in this time span (Figs. 3, 4). From the preceeding account it is concluded that the occurrence of a disaccate pollen -- *Pityosporites westphaliensis* in the beginning of Late Carboniferous (Balme, 1960) may indicate its distant relationship to the glossopterid group of plants represented by *Glossopteris* leaves (Fig. 2).

The assemblage containing monosaccate pollen and its megafloral component - *Lepidodendropsis* flora, is now considered to be of Middle Carboniferous (late Early Carboniferous-Namurian) age, as discussed by Playford (1990). The change-over passage of NBG flora to *Gangamopteris* flora occurred during Late Carboniferous Stephanian to Asselian which is characterised by first appearance of *Glossopteris* leaves (*G. wilsonii*) in Late Carboniferous. And the corresponding *Potonieisporites-Lundbladispora* (*Densoisporites*) palynozone (Cesari, 1986) to the remains of NBG megafloral zone,

is presently dated as Late Westphalian-Stephanian (Lopez-Gamundi *et al.*, 1993). However, the recently published information of the zircon analysis from Early Permian sediments of Australia (Roberts *et al.*, 1993) had raised the doubts about the stratigraphic status of *Potonieisporites* assemblage-zone, which had so far been dated to be of Westphalian age. This provides a doubtful situation for the Late Carboniferous palynoassemblages on Gondwanaland.

Major climatic impact on flora and fauna seems to have commenced in Mid-Carboniferous, after the definitive on-set of Late Palaeozoic Ice age on Gondwanaland (Wagner, 1993). There are records of wide-spread ice sheets, mainly on south western Gondwana during Mid-Carboniferous to late Early Permian (Visser, 1993). Waning of Late Carboniferous glaciation had been a more gradual event than that of its onset in Namurian, as it is evidenced from the kind and number of spore-pollen taxa of the Carboniferous - Early Permian palynoassemblages during the present analysis.

Summarizing the floristic evidences, a general trend of gradational mode of diversity could be derived in the time span of Namurian to Early Asselian. The increased diversification had been introduced in later part of Asselian-Sakmarian transition (Archangelsky, 1990; Venkatachala *et al.*, 1994).

Stephanian-Asselian glaciation had created high stress levels through Carboniferous-Permian boundary on Gondwana continent, which resulted into waning of *Nothorhacopteris* flora and sudden prominence of Glossopteris flora (Vijaya, 1995). This fact is further supported here by the increased evolving morphos in the lineage of a disaccate pollen - *Pityosporites westphalensis* through the passage of time from latest Stephanian to Asselian as illustrated here in Fig. 5. By the latest Carboniferous, the luxurient growth of *Glossopteris* vegetation from western Argentina (Lopez-Gamundi, 1993) flourished gradually in other parts of Gondwanaland - Australia, India and Antarctica along with the decreasing glacial stress.

ACKNOWLEDGEMENTS

The author extends her grateful thanks to Dr. R.S. Tiwari, Director, Birbal Sahni Institute of Palaeobotany, Lucknow, India, for his useful suggestions during thye preparation of this manuscript. The kind consideration of the authorities of the BSIP to sanction a major grant towards my participation in the International Symposium on Permian Stratigraphy, Guiyang, China (Aug. 28-31, 1994), is thankfully acknowledged. To Prof. Yin Hongfu, China University of Geosciences, Beijing, the author is thankful for his kind support that made my participation possible. The partial financial assistance (PFA) by Council of Scientific Industrial Research, New Delhi is also acknowledged.

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Plate 1

Characteristic spore-pollen taxa in the Talchir Formation Lower Permian palynoassemblage on peninsular India.

1. *Plicatipollenites* Lele 1964
2. *Potonieisporites* Bharadwaj emend. Bharadwaj 1964
3. *Scheuringipollenites* Tiwari 1973
4. *Parasaccites* Bharadwaj and Tiwari 1964
5. *Rugasscites* Lele and Maithy 1969
6. *Sahnites* Mehta emend. Tiwari and Singh 1984
7. *Vestigisporites* Balme and Hennelly emend. Tiwari and Singh 1984
8. *Microfoveolatispora* Bharadwaj 1962
9. "*Pityosporites*" Mehta 1944
10. *Crescentipollenites* Bharadwaj, Tiwari and Kar 1974
11. *Dentatispora* Tiwari 1964
12. *Jayantisporites* Lele and Makada 1972
13. *Brevitriletes* Bharadwaj and Srivastava emend. Tiwari and Singh 1981
14. *Striatopodocarpites* Soritch. and Sedova emend. Bharadwaj 1962.
15. *Verrucosisporites* (Ibrahim) Potonie and Kremp 1954
16. *Platysaccus* (Naumova) Potonie and Klaus 1954
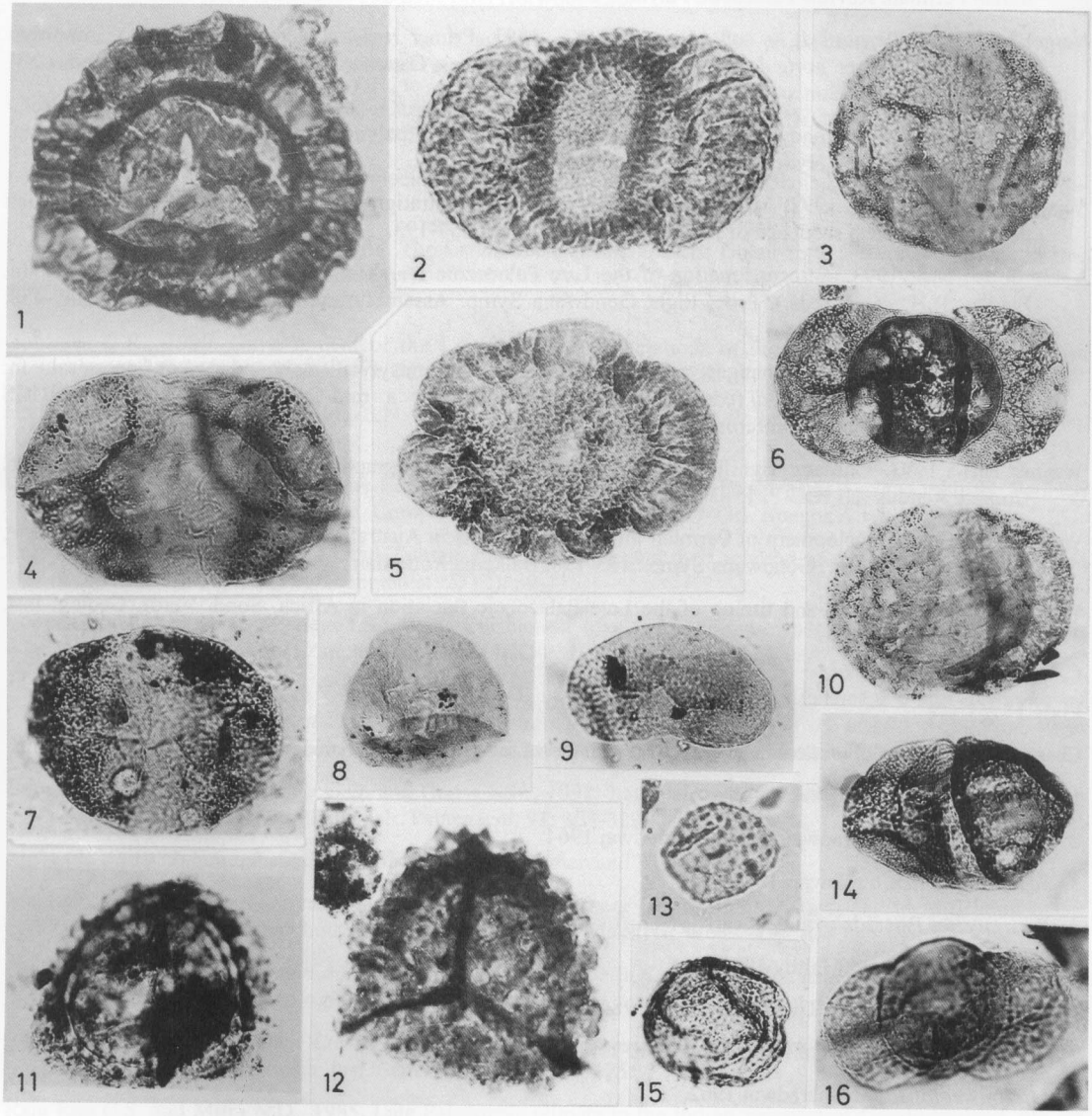
Plate 1