The origin, rise and decline of Glossopteris Flora: with notes on its palaeogeographical northern boundary and age

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In Africa impressions of two leaves of *Gangamopteris* were found lying below the glacial conglomerate and in Australia *Gangamopteris* and *Schizoneura* were found interbedded with the glacial beds at Bacchus Marsh. Microfossils, including pollen grains like those of the Glossopteris Flora, have been reported from the tillites, particularly from the Bacchus Marsh tillite. Similar microfossils have also been reported from the beds of the Talcher stage lying immediately above the glacial beds. All these fossils indicate that they were the pioneers of the Glossopteris Flora which may have come into existence in unglaciated and protected locations of Gondwanaland during the Ice Age itself. The early elements of the Glossopteris Flora thus seem to have lived in a cold temperate climate alongside glaciers. The flora of this stage was relatively poor but as the climate warmed up the forests became richer and their plants more diversified. However, this flora was living in a climate where a cold winter alternated with a warm summer and it abounded in deciduous plants. The climax of the Gondwana vegetation was reached during the Raniganj stage when a much warmer and more humid climate supported a rich forest vegetation again abounding in deciduous trees. Thereafter, there was a sudden change of vegetation during the Triassic when the plants of the Glossopteris Flora yielded place to new elements of the Dicroidium Flora.

The disappearance of the Rhacopteris-Lepidodendropsis Flora with the onset of the glaciation during the Carboniferous-Pennsylvanian times is easily understood but the sudden appearance of an entirely new Glossopteris Flora after, or even during the glaciation itself, and its almost simultaneous spread in all parts of Gondwanaland raise difficult questions about its origin and phylogeny. Besides dealing with the answers to these questions, the author discusses the factors and implications of the gradual decline of the Glossopteris Flora and the rise of the Dicroidium Flora during the Triassic. The estimates of the geological age and palaeogeographical limits of the Glossopteris Flora are also scrutinized in the light of recent work.

**Key-words**—Gondwanaland, Glossopteris Flora, Dicroidium Flora, Palaeogeography, Glaciation.

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DIGGING down into the sediments of geological time one finds that up to the Lower Carboniferous, the world’s land-mass formed a single continent which Wegener hypothetically called Pangaea (all lands) and this was surrounded by a universal sea Panthalasa (all seas). Evidence of this comes from our inability to recognise any clearly defined regional floras in this land-mass after the first invasion of land by plants in the Upper Silurian right up to the Lower Carboniferous. The last uniform flora which occupied Pangaea during the early Lower Carboniferous is called the Rhaeoepetis-Lepidodendropsis Flora. There is, however, some evidence to show that in the Middle Carboniferous the Angara area may have already separated from Euramerica and the flora of that area became different.

As we ascend into the Upper Carboniferous strata we find that our world has undergone a great divide into a northern continental mass called Laurasia, a name derived from Laurentia, the old name for North America and Asia, and this was separated by a median Tethys Sea from a southern land mass named Gondwanaland, by Sues, after the Gond tribe of central India. Remnants of this fission persist up to date. During this period Laurasia was having a warm, humid and swampy climate like that of present day tropics and it allowed the growth of the evergreen forests of the Pecopteris Flora. Abundant air spaces in the roots and stems of the flora indicate the existence of swamps and the absence of growth rings in the secondary xylem of the trees suggest the prevalence of a uniform climate all the year round. The remains of the forests of this rich flora are preserved in the form of coal seams of Europe and North America. In the flora of the northern landmass of this time we can also distinguish two other regional floras, the Angaridium Flora of Angarida and the Gigantopteris Flora of Cathaysia. Between the Angaridium Flora and the Pecopteris Flora of Europe was an ecotone which Meyen (1887) calls Sub-Angarida.

THE GREAT GONDWANA GLACIATION

In contrast, all parts of Gondwanaland were in the grip of a widespread glaciation which is believed to have begun in the Upper Carboniferous times. In some parts the glaciation may have persisted up to the Lower Permian. According to some authorities this was the greatest Ice Age that the world has ever witnessed. Remains of this glaciation are preserved in the form of a characteristic basal scratched boulder bed overlain by glacial conglomerates in all parts of Gondwanaland. The glacial remains were first discovered at Talcher in India and hence all homotaxial beds of this kind can be called by the name Talchir Boulder Bed and tillites. They have been subsequently discovered in Africa, Australia and South America, etc. where names like Dwika tillite (Africa), Bacchus Marsh tillite (Australia), etc. are locally applied to them. Even in the Indian subcontinent glacial beds, homotaxial with the Talchir Boulder Bed and tillites are found in Kashmir and Kumaun Himalayas, Umaria (Madhya Pradesh) and Salt Range (Pakistan), etc.

The occurrence of varves in some Australian glacial deposits of this period (Sussmilch, 1923) indicates that even in the icy climate of Gondwanaland there was an alternation of colder winters and relatively mild summers. However, the vast stretches of ice bound Gondwanaland of this time seem to have been largely bereft of vegetation and the beds are generally lacking in fossils of any kind.

EARLIEST MEGAFOSSES OF GLOSSOPTERIS FLORA

The only exceptional reports of megafossils in beds of this ice age are from Africa and Australia. In South Africa Leslie (1921) and du Toit (1924) found leaves of Gangamopteris actually lying below the glacial conglomerate in the Dwika tillite at Vereening (see Pl. 3, figs 2, 3) and Strydenberg, respectively. In Australia, Sussmilch (1923) found Gangamopteris as well as Schizoneura interstratified with the glacial beds at Bacchus Marsh in Victoria. No megafossils have so far been reported from any tillite in India but Virkki (1938) found well preserved Gangamopteris, Schizoneura, Glossopteris and remains of other typical members of the Glossopteris Flora 25 feet above the Talchir Boulder Bed in Salt Range (Virkki, 1938 and Ph.D. Thesis,
Text-figure 1-145. Aleite, monolete, trilete and monocolpate spores. 1-7, show aleite spores; 1-3, show folds (see also Pl. 1, fig. 1) but 4-6, seemingly show thickened ridges (see also Pl. 1, fig. 2); 7, spore with ruptured wall (see also Pl. 1, fig. 3); 8, the exine of spore shows minute spines (see also Pl. 1, fig. 4); 9-11, monolete spores (see also Pl. 1, fig. 7); 12-19, smooth-walled spores are of Leiotriletes type (see also Pl. 1, figs. 8-11); 18, shows a spore with a peripheral flange around a triangular body (see also Pl. 1, fig. 16); 20-23, spores are trilobate; 20-22, Brachytrilistrium Naum.-type (see also Pl. 1, fig. 12); 23, Dicotriölistrium Naum.-type Trilete spores; 24, 25, Lophotriöites type (see also Pl. 1, fig. 14); 26-30, monocolpate spores are of Ginkgocycadophytes type (see also Pl. 1, fig. 15); 31-45, show monosaccates of Endosporites, Nuskoisporites, Potoniesporites and allied types; 31-38, spores are trilete; others are aleite; 42, spore shows a linear slit with thickening around the aperture (see also Pl. 1, figs. 18-23, 25-29). All figs. × 370.
Lucknow University see also Pl. 3, fig. 1). Earlier Jowett (1925) had reported plant remains lying directly over the glacial boulder bed in Karanpura Coalfield. Subsequently Surange and Lele (1956) also found a few megafossils only a few feet above the basal boulder bed. Lele (1966) assembled all the available data about the occurrence of megafossils in ten Indian localities of Talchir series and pointed out that *Gangamopteris* alone is found in all the ten localities while *Noeggerathriopsis* occurs in six and seeds of *Samaropsis* and *Cordaiacarpus* occur in four but *Glossopteris* is found only in the upper strata of the Talchir in two localities. The early occurrence of *Gangamopteris* in India agrees with its early occurrence in South Africa and Australia as mentioned above.

**EARLIEST MIOSPORES OF GLOSSOPTERIDS**

Besides the above megafossils, Virkki (1939, 1946) and Pant (1942, 1943, 1949, 1955) and Pant and Mehta (1963) reported a large variety of miospores and other microfossils from Bacchus Marsh tillite. An extensive search for miospores in material of Lower Gondwana tillites was taken up by the present author in 1941 when the late Professor Birbal Sahni gave him rock samples from Talchir in India, Dwyka at Vereenigen and Strydenberg in South Africa and Bacchus Marsh in Australia and formulated the problem for his investigation in a rough sketch a fascimile of which is reproduced in Plate 3, figure 1. The author’s investigation of a rock sample from Goimadai Creek, Bacchus Marsh bearing the number "Off BM 1926, 965" which was obtained from Mr W. N. Edwards, Keeper of the Geology Department, British Museum (Nat. Hist.), London proved quite rich not only in the gross content of microfossils but also in their variety. Roughly about 1,200 miospores and a single megaspore were mounted on slides after macerating a rock piece which was hardly about 2 cm³ in volume. Statistical counts of miospores of different varieties show that 41 per cent of their total number are monosaccates with radially symmetrical circular, oval or triangular outlines and a uniformly wide saccus around a central corpus. In addition 1 per cent monosaccates are bilaterally symmetrical with a saccus which is wider on two sides. The central corpus of some monosaccates is aleate but in others it bears a trilete. The monosaccates are followed in descending order of frequencies by striate or non striate-disaccates 8 per cent, asaccate triletes 8 per cent; asaccate monoletes 6.5 per cent, trilobate triletes 6.5 per cent, monocolpates 5 per cent and the remaining about 24 per cent include a majority of aleates or other odd sporomorphs and about 3 to 4 per cent indeterminates. Some of these miospores have been reported already by Pant (1949, 1955) and Pant and Mehta (1963). The various kinds of miospores found in the tillites are illustrated in text-figures 1 and 2. A careful comparison of these with the figures and photographs of Lower Gondwana sporomorphs published by Virkki (1937, 1945), Balme and Hennelly (1955, 1956a, 1956b), Pierart (1959), Potonié and Lele (1960), Bharadwaj (1962), Bharadwaj and Tiwari (1964a, 1964b), Bharadwaj and Saluja (1964, 1965a, 1965b), Bharadwaj et al. (1965), Bharadwaj and Srivastava (1969), Bharadwaj et al. (1978) and others shows that practically all of them are referable to the same sporomorphs or closely similar ones. The high frequency of radial monosaccates in the mioflora and also the percentages of the different kinds of miospores in the tillite present an overall aspect which is closely comparable with that of the miofloras reported from the beds of Talchir and Karharbari stages which lie immediately above the glacial tillites in India (see Bharadwaj, 1974).

**CONTEMPORANEOUS EXISTENCE OF ICE AND EARLY GLOSSOPTERIDS**

As mentioned above the occurrence of *Gangamopteris* and a few other members of the Glossopteris Flora, interbedded with the glacial tillites and also occurring at the base of the tillites in Australia and South Africa, as well as the occurrence of the same kind of miospores in beds, which lie immediately above the tillites in India and other parts of Gondwanaland suggest that the Gondwana Ice Age and the earliest members of the Glossopteris Flora appeared almost simultaneously. Therefore, we can safely conclude that the pioneers of the Glossopteris Flora had come into existence during the Gondwana Ice Age. Seward (1933) compared the situation in ice bound Gondwanaland with that of present day Greenland and New Zealand. He pointed out that the present flora of Greenland has nearly 400 species of vascular plants growing in protected and unglaciated parts while in New Zealand one can see tropical looking "tree ferns cast shadows on the ice below them". A confirmation of these ideas comes from the miospores which have been reported from the Bacchus Marsh tillite. Such pollen grains from neighbouring vegetation seem to have been blown over the ice of Gondwana glaciers and later when the ice melted, they were deposited in the tillites. Pollen grains of surrounding vegetation become deposited in the same manner over the ice of modern glaciers, e.g., in Central Europe where Vareschi (1942) recovered them by melting the ice.
Text-figure 2—18. Monosaccate and disaccate spores: 1, 2, spores show monosaccates of Nuskoisporites-type with a wide and a narrow saccus, respectively (see also Pl. 2, figs 1, 2); 3, shows three adherent identical spores of Nuskoisporites-type possibly from the same tetrad; 4, 9, a new type of disaccate sporomorph, Rogasaccites marshalli gen. et sp. nov. where the two sacci are seemingly joined by narrow connections in front and/or rear and they have distinct radiating folds, the corpus is non-striate (see also Pl. 2, fig. 7); 5-8, spores are Alisporites-or of Striatites-type (see also Pl. 2, fig. 11-13); 10-18, show Ptysoisporites-type of spores of various sizes squashed in different aspects All figs × 370

PLATE 1

1-6. Smooth-walled aleate spores 1, 2 × 425, 3-6 × 380
7. Two monolete spores × 425
8-11. Leotretites-type of spores, all × 380.
13. Pterycotiletes-type of spore × 380.
15. Gnigocycadophytes-type of spore × 790
16. Hymenosporites-type of spore × 380
17-23. Trilete monosaccate spores of Endosporites-type all × 380.
ANCESTRAL STOCK AND ORIGIN OF GLOSSOPTERIS FLORA

The sudden appearance of an entirely new flora leaves us guessing about its ancestral stock and about the manner of its origin. No pre-Gondwanan plants of the area are closely comparable with the pioneers or even the later elements of the Glossopteris Flora. There is also no possibility of the glossopterids having invaded Gondwanaland from any other territory because nothing like its elements was existing in any previous or contemporaneous floras. The origin of the Glossopteris Flora with its predominantly simple leaved gymnosperms is therefore entirely unknown. In this connection, Seward (1922, 1924) suggested that the onset of catastrophic climatic changes in the geological history of the earth like the sudden chilling of Gondwanaland during the Carbo-Permian glaciation or the sudden rise of temperatures during widespread volcanic upheavals during some periods, etc. may have been responsible for large scale extinctions of old forms and the abrupt appearance of new forms. Sahni (1937, 1939) suggested that since it had become well known that radiations, chemicals, sudden heating and chilling, etc. can induce mutations, the Gondwan glacialization may have been itself responsible for the disappearance of the previous vegetation and the appearance of the Glossopteris Flora. Such mutations must have been induced on a large scale in pre-existing plants in a widespread area so that the flora spread rapidly all over Gondwanaland. At present this is the only plausible explanation known to us about the origin of the Glossopteris Flora.

RISE AND ULTIMATE CLIMAX OF GLOSSOPTERIS FLORA

With glaciers all around, the climate of Gondwanaland during the Talchir and Early Karharbari stages must have been of the cold temperate type with very cold winters. In this cold climate a few deciduous trees of Gangamopterus and Noeggerathiopsis were growing but Glossopteris was rare and appeared later. Some herbaceous forms like Schizonereia were also present.

Subsequently, during the deposition of the sediments of the Damuda Series with its three stages, viz., Barakar, Ironstone Shales and Raniganj, as the temperatures rose and glaciers receded, the forests of Gondwanaland became richer. Even at this time, the prevalent trees of the Glossopteris flora were deciduous but a few evergreen conifers also existed. Winters were still quite cold or dry and the secondary wood of tree trunks had marked seasonal rings. Ice had now melted away and Gondwanaland had developed a warm and humid temperature climate where ferns, sphenopsids and lycopsids formed the undergrowth in the shade of trees or along water courses in the forests.

The climax of this flora was reached during the last Raniganj Stage when the forests developed a greater variety of glossopterid genera like Gangamopterus, Glossopteris, Rhabdotaenia, Euryphyllum, Palaeovittaria, Belemnopteris, Sagittophyllum, Pteronissova, besides Noeggerathiopsis and some conifers, etc. There is now a far greater variety of species. Many of these gymnosperms were large leaved deciduous forest trees.

The litter of abscissed leaves and fallen plant parts and seeds on the forest floor must have provided shelter and food to many animals like those which live in present day warm temperate forests but so far only a few remains of cockroach wings have been observed in India (Patt & Das, 1987) and Africa (Rayner & Coventry, 1985). There is need for intensive search for animal remains among the fossils of the Glossopteris Flora.

DECLINE OF GLOSSOPTERIS FLORA

Unlike the abrupt rise of the Glossopteris Flora, its decline was gradual. Many of its elements lingered on in the Triassic Dicroidium Flora (see Pant & Patt, 1987). The climate of the area seems to have become drier and warmer as the spread of the flora and reptiles also indicate. Once again mutational changes may have been responsible for

PLATE 2

1-3. Aleate spores of Nuscoisporites-type 1, 2 × 380, 32 × 560.
6,11-13 Striatis spores. Spore in 13 is a more magnified view of spore in 12, 6, 12 × 380, 11 × 487, 13 × 585.
7. Rugasaccites marsbensi gen et sp. nov.
8-10. Large disaccate spores of Aisporites and Pityosporites, all × 380.
14,15. Spores of Sabnites, both × 380.
16,17. Spores of Pityosporites-type seen in a side and a top view, both × 380.

Type specimen. × 380.
the coming in of new elements but other new forms may have migrated from other parts. Some old forms adapted themselves for the changed conditions and continued their existence with dwindled strength of numbers.

**PALAEOGEOGRAPHICAL NORTHERN BOUNDARY OF GONDWANALAND**

The northern limit of Gondwanaland towards the north of India has lately become quite uncertain. Earlier *Glossopteris* and *Gangamopteris* containing beds were reported only up to the Himalayan region in Kashmir, Kumaon and Darjeeling areas which were believed to mark the southern shore of the Tethys sea and the palaeogeographical northern boundary of Gondwanaland. However, lately the boundary has been suggested to have been lying far towards the north of the Himalaya, after Yin and Guo (1976) and Hsü (1976) reported a rich *Glossopteris Flora* of an early stage of the Late Permian in the northern slope of Qomolangma Feng (Mount Everest Area) in southern Xizang (Tibet) and Crawford (1974) emphasized the occurrence of the cladoceran *Daphniopsis* and the reptile *Lystrosaurus* in Lower Triassic of Tibet. According to Termier and Termier (1981) *Lystrosaurus* occurs simultaneously in Tarim Basin, India, South Africa and Antarctica and Crawford has used this for postulating his hypothesis of Greater Gondwanaland which extended up to the Tarim basin.

The finds of mixed Cathaysian and Gondwana elements in the Mamal Bed in Kashmir and the occurrence of *Glossopteris* in Hazro in Anatolia up to Soviet far east complicate the boundary problem of Gondwanaland and it could indicate the existence of an ecotone in the north of Gondwanaland.

**AGE OF THE GONDWANA GLACIATION AND GLOSsopteris FLORA**

Although it is generally agreed that the Gondwan glacia tion started sometime in the latter part of the Palaeozoic, it is not settled whether it started in the Carboniferous or the Permian times so that it is often called the Carbo-Permian glaciation. Along with the age of the glaciation, the age of the Glossopteris Flora has also been discussed by geologists and palaeobotanists and there is hardly any unanimity in the matter.

In 1875, Blanford (in : Oldham, 1893) had suggested that the Talchir Boulder Bed of India was contemporaneous with the Permian glacial beds of England. Feistmantel and Vredenberg (see Schuchert, 1929) believed that it was of Permian or *Early Triassic* age. It was at one time even correlated with beds which are regarded to be Jurassic. Warth (1887, 1888 as quoted by Virkki, 1945) and Waagen (as quoted by Schuchert, 1929) held that the glaciation took place in the Carboniferous. In later years Seward (1924, 1929), Sahni (1926, 1938), du Toit (1926, 1927), David (1932), Thomas (1929), Walton (1929) and others have suggested that although the glaciation did not begin simultaneously in all parts of Gondwanaland, it began as early as the Upper Carboniferous, while Schuchert (1929, 1936), Teichert (1941, 1943, 1943a, 1943b) and others hold that the glaciation began in the Permian and according to Schuchert in "early Middle Permian". Geological evidence supporting the views of the various authors is partly palaeobotanical and partly palaeozoological as mentioned below:

*Palaeobotanical evidence—*It comes from the occurrence of mixed florais containing typical European and Cathaysian Carboniferous plants in Lower Gondwana beds. The occurrence of these mixed floras according to Thomas (1929) indicates a Carboniferous age not only for the underlying glacial beds but also for the origin of the closely associated Glossopteris Flora. In the Irwin River District of Australia Teichert (1941) mentions the occurrence of *Bothrodendron*, *Sphenophyllum* and *Lepidodendron* intermingled with Glossopteris, Gangamopteris and other typical members of the Glossopteris Flora in the Coal Measure Series which overlie the tillite. Seward and Sahni (1920) thought that *Bothrodendron* was also present in India. Seward (1908) believed that it also occurred in South Africa and Seward and Leslie (1908) reported it from Vereeniging in association with *Lepidodendron* and *Sigillaria*. In the Wankie flora of South Africa, Walton (1929) found Glossopteris and

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**PLATE 3**

1. Sahni’s rough sketch showing the Talchir Boulder Bed and tillite at the base and Triassic (Fanchet) beds at the top both with question (?) marks to indicate the problematic downward and upward extensions of the Glossopteris Flora.
2. T. N. Leslie’s sketch of Dwyke tillite beds at Vereeniging, South Africa showing position of layer containing Gangamopteris impressions.
3. One of Leslie’s hand-specimens of Gangamopteris obtained from the layer indicated in fig. 3. × 1.
other Lower Gondwana plant remains mixed with *Pecopteris* and other typical European Carboniferous plants. In South America, too, du Toit and others discovered *Rhacopteris szajnochait* and *Cardiocarpus polymorphus* between glacial beds and *Asterocalamites, Sigillaria, Lepidodendron larchius, Psaronius* with *Glossopteris, Gangamopteris* and *Noeggerathiopsis* and according to du Toit (1937) this indicated an Upper Carboniferous age for the glaciation. However, the reports of the above mixed elements require to be re-examined in the light of recent knowledge since most of the reports of European Carboniferous elements are based on surface impressions of sterile parts and some of them have, and others may prove to belong to homoplastic Gondwana forms which were different from European Carboniferous elements, although they were externally similar (see Edwards, 1952; Chaloner & Lacey, 1973; Lacey, 1975; Xingxue, 1986).

The miolfloras reported from the Lower Gondwana tillites and beds immediately overlying them are dominated by radial monosaccates which first appeared in the Lower Carboniferous but the presence of disaccates, which are first reported in the Upper Carboniferous and continue upwards, may only rule out a Lower Carboniferous age. However, the agewise vertical distribution of characteristic miospores has to be confirmed on a world-wide scale before the miospores reported from the tillites and overlying Lower Gondwana beds can be used for age determination.

*Palaeozoological evidence*—In the Indian subcontinent, according to Reed (1932), the occurrence of *Eurydesma* and other marine fossils in a horizon lying above the boulder bed in *Salt Range* (Pakistan) indicates an "Upper Carboniferous rather than Lower Permian" for the horizon. Accordingly, this author points out that the boulder bed lying immediately below that bed could not be younger. In Kashmir, the *Gangamopteris beds* (Noetling, 1902 as mentioned by Hayden, 1908) which lie above the trap are overlain by the *Zewan Stage* which is equivalent to *Fenestella* shales of Spiti. Therefore, according to Reed the *Gangamopteris* bed could not be younger than Upper Carboniferous. Reed also believes that the marine fossils (discovered by Sinor, 1923) overlying the Talchir tillite in Umaria in central India also favour a similar conclusion.

In South Africa du Toit and Thomas regard the occurrence of *Eurydesma, Pygocephalus* and the fish *Palaeoniscus* in the Dwyka shales above the Dwyka tillite to suggest a Carboniferous age for these beds.

In South America marine fossils collected from two horizons over the glacial matrix in Brazil and Argentina (du Toit, 1927—appendix by Reed) indicate, according to Reed, a Carboniferous and possibly Lower Middle Carboniferous age for the Gondwana glaciation and the Glossopteris Flora.

In Australia, the fauna of the *Eurydesma* and *Conularia* horizons of New South Wales and the occurrence of *Paralegodoceras jacksonii* in the Lower Marine beds below the Irwin Coal Measures in Western Australia, according to Thomas (1929), indicate an Upper Carboniferous age for the beds and the glacial beds below could not be younger. Other workers in Australia, e.g., Teichert (1941) suggests that the glaciation in that area started sometime in the beginning of Permian (Sakmarian) or at a time only slightly preceding the Permian.

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