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Dominant gymnosperms of the Glossopteris flora

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ABSTRACT

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The paper presents new ideas about the Lower Gondwana forests which the author believes were dominated by deciduous gymnospermous trees of *Glossopteris* and its allied genera. It is suggested that the larger trees of glossopterids may have been 30 to 40 m or more in height and below them grew shorter trees and shrubs of *Glossopteris* and its allies. The large size of glossopterid trees is suggested by that of tree trunks assigned to *Dadoxylon* sp. from the Raniganj Stage where *Glossopteris* is the commonest fossil and the genus *Noeggerathiopsis*, to which they had been assigned earlier, is a rarity. Such trees could have been supported by horizontally spreading axes or roots at the base of the trunks as suggested by fossil axes or roots around missing trunks reported from the bed of Vaal River in South Africa which too had been assigned to *Noeggerathiopsis*.

The deciduous glossopterid trees are compared with those of modern *Ginkgo biloba*. It is suggested that the gradate series of glossopterid leaves with *Glossopteris* having a midrib and anastomosing laterals at one end of the series followed by leaves of *Gangamopteris* with anastomosing laterals and no midrib, *Rhabdotaenia* with a midrib and dichotomising non-anastomosing laterals *Palaeovittaria* with a midrib in the lower half and non-anastomosing spreading laterals, in the distal part, *Rubidgea* without a midrib and spreading arched laterals and *Noeggerathiopsis* with dichotomising spreading straight veins at the other end may form a series of leaves which may be related to each other. It is considered that *Noeggerathiopsis* may not be a cordaite.

The morphological nature of the fertiligers of glossopterids are discussed and compared with certain abnormal peduncles of *Ginkgo biloba* and it is pointed out that 10 per cent of the leaves of this genus show anastomoses and this genus may be allied to *Glossopteris*.

In addition, indubitable evidence in support of the *in situ* or autochthonous mode of formation of Lower Gondwana coal is also discussed.

Key-words — Deciduous trees, *Ginkgo biloba*, leaf-borne axillary fructifications, autochthonous coal.

सारांश

ग्लॉसोप्टेरिस वनस्पतिजात के प्रमुख अनावृतबीजी

दिव्यदर्शन पन्त

इस शोध पत्र में अधोगोण्डवाना वनों के विषय में कुछ नए विचार व्यक्त किए गए हैं, जिनके बारे में लेखक का विश्वास है कि ये *ग्लॉसोप्टेरिस* तथा इससे सम्बद्ध वंशों के पर्णपाती अनावृतबीजी वृक्षों द्वारा आच्छादित थे। यह प्रस्तावित किया जाता है कि *ग्लॉसोप्टेरिड* के दीर्घतर वृक्ष ऊँचाई में 30 से 40 मीटर के बीच रहे होंगे अथवा इससें अधिक ऊँचे रहे होंगे तथा उनके नीचे *ग्लॉसोप्टेरिस* एवं उससे सम्बन्धित लघुतर वृक्ष एवं गुल्म विकसित हुए होंगे। रानीगंज शैलसमूह से प्राप्त *डैडॉक्सीलॉन* प्रजाति के वृक्ष तने से ग्लॉसोप्टेरिड वृक्षों के दीर्घ आकार का अनुमान होता है। जहां *ग्लॉसोप्टेरिस*

अत्यंत सामान्य रूप से प्राप्त पादपाश्म है तथा जिस निओगैराथियॉप्सिस से वे पूर्व में सम्बन्धित किए गए थे, अत्यल्प है। ऐसे वृक्ष तनों के आधार विस्तृत क्षैतिज अक्ष अथवा जड़ों द्वारा अवलंबित हो सकते है, जिसका अनुमान दक्षिण अफ्रीका के वाल नदी संस्तर से प्राप्त लुप्तप्राय तनों के चारों ओर के पादपाश्म अक्षों अथवा जड़ों से किया जा सकता है, जो *निओगैराथियॉप्सिस* से भी सम्बद्ध हैं।

लेखक ने पर्णपाती ग्लॉसोप्टेरिड वृक्षों की तुलना आधुनिक *गिंको बिलोबा* वृक्षों से की है। उन्होंने ग्लॉसोप्टेरिड पत्तियों को एक श्रेणीकृत श्रेणी के रूप में प्रस्तावित किया है। इस श्रेणी के एक सिरे पर *ग्लॉसोप्टेरिस* है, जिसमें एक मध्यशिरा तथा शाखामिलनी पार्श्व है। तत्पश्चात क्रमशः *गैंगामॉप्टेरिस* है, जिसमें शाखामिलनी पार्श्व के साथ कोई मध्यशिरा नहीं है। इस श्रेणी की अगली कड़ी में *रैब्डोटीनिया* आता है, जिसमें मध्यशिरा तथा द्विभाजित अशाखामिलनी पार्श्व आते हैं, तत्पश्चात *पेलियोविट्टेरिया* आता है, जिसके निम्न अर्ध में मध्यशिरा तथा दूरस्थ अंश में अशाखामिलनी विस्तारित पार्श्व आते हैं। इसके पश्चात मध्यशिरा विहीन तथा चापाकार पार्श्वयुक्त *रूबिडजिया* आती है तथा श्रेणी के दूसरे सिरे की द्विभाजित एवं विस्तारित ऋजु शिराओं युक्त *निओगैराथियॉप्सिस* पत्तियों की एक श्रेणी बना सकती है, जो परस्पर अन्तर्सम्बन्धित हो सकते हैं। *निओगैराथियॉप्सिस* कार्डेट नही हो सकता।

लेखक ने ग्लॉसोप्टेरिड के फलनों के संख्यात्मक गुणों की भी चर्चा की है तथा इनकी तुलना *गिंको बिलोबा* के कुछ असामान्य पुष्पावलि वृन्तों से की है तथा इंगित किया है कि इस वंश की 10 प्रतिशत पत्तियाँ शाखामिलन प्रदर्शित करती हैं। अतः यह वंश *ग्लॉसोप्टेरिस* से सम्बद्ध हो सकता है।

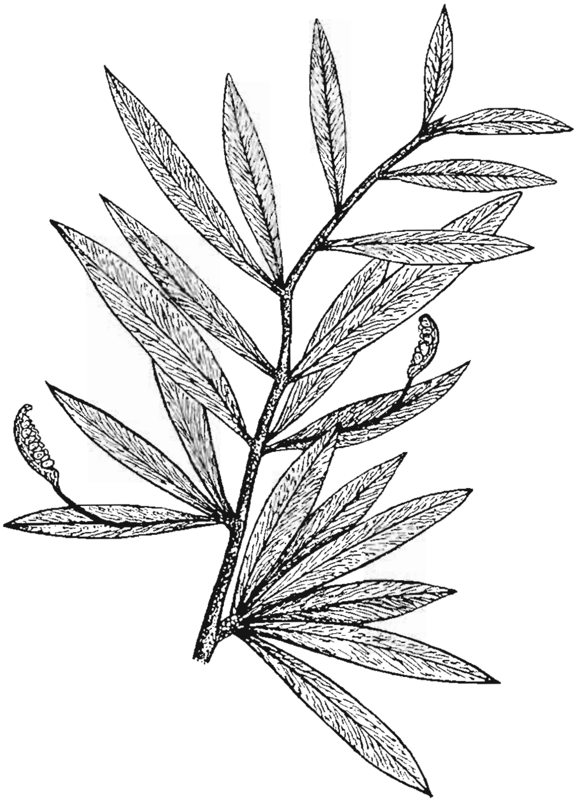
इसके अतिरिक्त लेखक ने अधो गोण्डवाना कोयले की निर्मिति के स्वस्थाने अथवा स्वस्थानिक मोड के समर्थन में कुछ असन्दिग्ध प्रमाणों की भी चर्चा की है।

INTRODUCTION

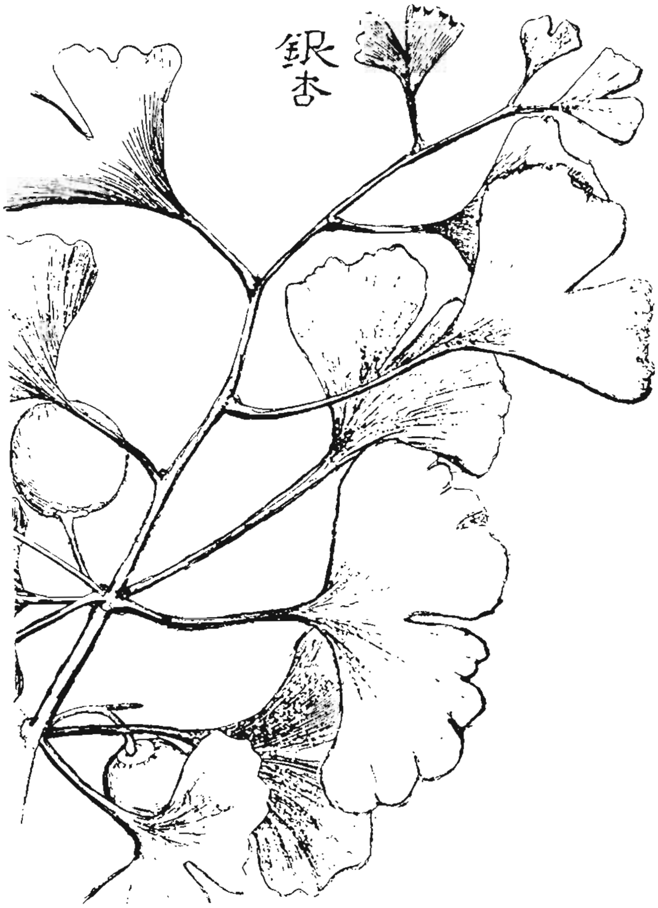
THE dominant constituents of the Lower Gondwana Glossopteris flora seem to have been the gymnosperms of the Glossopteridales which appear to have formed rich forests all over Gondwanaland. In India the coal deposits of Bihar, West Bengal, Madhya Pradesh and Maharashtra have thick coal-seams where a single seam may be as thick as 31 m, e.g., in Kargali and Korba of Bokaro and Hasdo valleys, respectively (Krishnan, 1949, p. 253) and about 46 m at Singrauli. In many coal basins there are multiple coal-seams placed one over the other interbedded with shale. The commonest fossils of the flora are leaves of *Glossopteris*. Some allies of *Glossopteris* e.g., *Gangamopteris*, *Rhabdotaenia*, *Rubidgea*, *Palaeovittaria*, *Pteronilssonia*, *Belemnopteris* and *Sagittophyllum* along with *Noeggerathiopsis* also occur. In the earlier stages of the flora, leaves of *Gangamopteris* and *Noeggerathiopsis* are predominant. Axes of *Vertebraria* and petrified woods showing well marked growth rings are quite common throughout the Lower Gondwanas. Among less frequent gymnospermous fossils of the Glossopteris flora there are a few narrow-leaved conifer-like remains as well but these are not discussed in the present article.

ATTACHED LEAVES OF GLOSSOPTERIDS

Although the leaves of *Glossopteris* and its allies generally occur in detached state, rarely some of them have been found attached to *Vertebraria* axes (Zeiller, 1896; Oldham, 1897; Arber, 1902; Dolianiti, 1954; Pant, 1977). In other cases glossopterid leaves have been found attached to axes which lack *Vertebraria* characters (Bunbury, 1861; Feistmantel, 1881; Etheridge, 1894; Seward, 1910; Walton & Wilson, 1932; Plumstead, 1956; Pant, 1967; Pant & Singh, 1974; Pant & Chauhan, 1995). Etheridge (1994) found leaves of *Glossopteris* attached in apical clusters to small axes which show rhomboidal leaf base scars below the clusters. Seward (1910) has illustrated a whorl of *Noeggerathiopsis hislopii* leaves from India which shows a stem in the centre. Bunbury (1861) and Feistmantel (1881) also found them attached around twigs which they mistook for raches of compound leaves and called them *Filicites* and *Sagenopteris*, respectively. Besides such clusters laterally attached single alternate leaves of *Glossopteris* have also been described by Pant, 1967. Accordingly, a reconstruction of the tree of *Glossopteris* made by Pant & Singh (1974) and Pant (1977) shows lateral spirally attached leaves around apical parts of the stem and apical clusters of leaves in short spur shoots as depicted in a reconstructed twig of *Glossopteris* in Text-figure 1. Attachment of leaves like that mentioned above for *Glossopteris* and allies actually occurs in modern *Ginkgo biloba* which has apical clusters of deciduous leaves in short spur shoots with rhomboidal leaf base scars below. Towards the tips of long shoots one can also see alternately attached deciduous leaves in whose axils arise the short shoots (see Text-figures 2 & 3) or the long shoot apices may themselves give rise to spurs (as seen in Text-figure 3). The manner in which this transformation takes place has been analysed by Gunkel & Wetmore, 1946 and Gunkel *et al.*, 1949.



Text-figure 1—*Glossopteris*, reconstructed twig with spirally arranged leaves and axillary spurs. Two of the spurs bear fertiligers with *Ottokaria* fructifications.

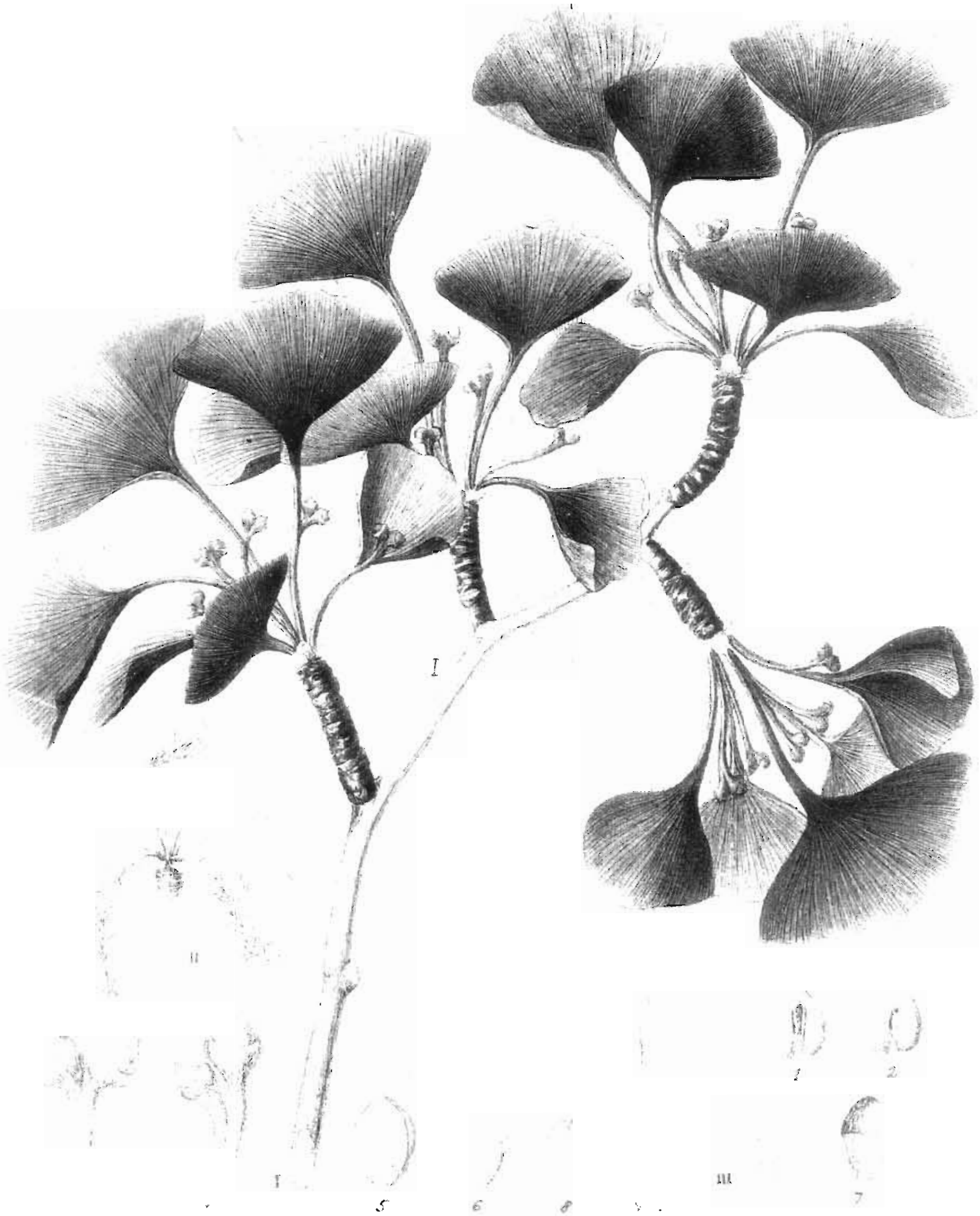


Text-figure 2—*Ginkgo biloba*, a twig from female tree with spirally arranged leaves; some of them have developed spurs in their axils (after Kaempfer, 1712).

MODIFIED RECONSTRUCTION OF TREES OF GLOSSOPTERIDS

The above mentioned similarities between the attachments of leaves of glossopterids and those of modern *Ginkgo* prompt me to review earlier reconstructions of trees of *Glossopteris* (see Pant, 1977) and I can hereby suggest a few additions and modifications. Firstly, the trees seem to have been deciduous as first envisaged by Plumstead (1958) and as the abundance of fallen leaves and paucity of attached ones in Lower Gondwana beds also indicates. Secondly, the presence of well marked growth rings in Lower Gondwana woods suggests that the glossopterid trees were producing and living in a cold or warm temperate climate with marked changes of seasons. They were bearing green foliage leaves during summers followed by their autumnal yellowing and fall during cold winters as they do in modern *Ginkgo biloba* (see Text-figures 4, 5 and 6). While growing in Lower Gondwana forests the larger trees of *Glossopteris* may have reached diameters of nearly a metre or more at their bases. Spreading branched roots or rhizomes and their usually upright, sometimes bifurcated trunks may have been about 30 to 40 m or more in height. The above ideas about the size of trees of *Glossopteris* are based on the dimensions of large tree trunks first discovered in 1923 by W.W. Whitney of the East Indian Railway at a place about 3 km from Asansol in an area which Bradshaw in Bradshaw & Sahni (1925) attributed to the Panchet Series of the Lower Gondwanas but which actually belongs to the coal beds of Raniganj Stage in the Damuda Series. The dimensions of one of these tree trunks (see Text-figure 7) which is bifurcated in its lower part (a major part of this tree is placed in G.S.I. Museum at Calcutta) are mentioned as being about 93 feet (= 28.6 m) and a maximum diameter of only the central preserved column of wood as 2 feet 7 inches (= 78.76 cm) by Bradshaw in Bradshaw & Sahni (1925). Making an allowance for the possible missing top and bottom parts of the tree, I estimate its length to have been at least 30 m or more. Its maximum diameter with surrounding soft wood and bark which are not preserved may have been about a metre or more.

Soon after the discovery of the trunks, Sahni (in Bradshaw & Sahni, 1925) assigned one of them to *Dadoxylon* sp. and thought that it may have belonged to *Noeggerathiopsis*, a *Cordaites*-like leaf genus which occurred in the Glossopteris flora and which had been assigned earlier to the genus *Cordaites* itself by Seward & Sahni (1920). Later, Sahni (1931)



Text-figure 3—*Ginkgo biloba* **I**, painting of a twig from a female tree showing a number of spur shoots with scars of fallen leaves and apical clusters of leaves with ovulate peduncles in their axils The lower spur shoot has broken off Note that the long shoot apex has also become a spur. **II**, a spur from a male tree showing peduncles with stalked paired sporangia. **III**, faintly drawn outline of a twig showing the long shoot apex; **1, 2**, pairs of pollen sacs below a hump, **3, 4**, details of apical portions of two ovulate peduncles with collars below two ovules; **5-8**, different views of seeds; **9**, a developing leaf (all from Siebold & Zuccarini, 1835-1842)

Text-figure 4—*Ginkgo biloba*, a part of a tree showing leafy branches during summer (from Michel, 1986).

reported several more trunks of the same kind and reaffirmed his earlier attribution of such *Dadoxylon* trunks to the Cordaitales. It is possible that he did not consider the eligibility of *Glossopteris* to be the leaf of such large gymnospermous trunks because Feistmantel (1886) had described structures which he believed to be sori in *Glossopteris* leaves and also due to a general belief at that time about the leaves of *Glossopteris* being those of a fern (as indicated by the inclusion of *Glossopteris* in the second volume of Seward's *Fossil Plants* 1910 and by the finding of sori of sporangia on the scales of *Glossopteris* (Arber, 1905b).

However, the situation has now completely changed and lately some leaves of *Glossopteris* and allies have emerged out as fertiligers producing seeds and pollen organs and their attached or detached stems, rhizomes or roots were first shown to have a good deal of secondary xylem with araucarioid or other types of gymnosperm-like pittings in the tracheids (Walton & Wilson, 1932). Grouped pitting like that of *Vertebraria* is also found in *Catervoxylon, Paracatervoxylon, Australoxylon, Tordoxylon, Myelontordoxylon* and *Paratordoxylon* as pointed out by Pant & Singh (1987) and these could be the woody trunk fragments of *Glossopteris*. Grouped pitting of this kind had been noticed earlier by Holden (1916) and Sahni (1931) who called it "somewhat *Callixylon*-like grouping of radial pits on the tracheids". However Sahni regarded it as a possible Cordaitalean character. The secondary xylem of the above mentioned wood genera show abundant narrow medullary rays and well marked growth rings

Text-figure 5—*Ginkgo biloba*, trees with golden leaves during autumn (from Michel, 1986).

which are typical of gymnospermous wood (Walton & Wilson, 1932; Pant, 1956; Pant & Singh, 1987; Pigg & Taylor, 1993; Pigg & Trivett, 1994). Moreover, the leaves themselves show thick cuticles with sunken stomata surrounded by papillate subsidiaries around sunken guard cells showing gymnosperm type of lignin lamellae (Pant, 1958). The midrib xylem of the leaves of *Glossopteris* often shows bordered pits (Pant, 1958; Surange & Maheshwari, 1962) and none of their well preserved leaves shows any sori. In contrast the cuticles of fern leaves are delicate and their stomata lack lignin lamellae. Further the fructification bearing leaves or fertiligers of *Glossopteris* bear seeds pollinated by disaccate *Striatites* type of pollen which are produced by *Arberiella* type of pollen sacs borne on male fertiligers called *Eretmonia*, *Glossotheca* or *Nesowalesia* (see Pant, 1977, 1987; Pant & Nautiyal, 1984; Pigg & Trivett, 1994; Chandra & Singh, 1995). Further the internal structure of axes of *Vertebraria* and leaves of *Glossopteris* and its allies as well as that of the attached or detached fructifications (fertiligers) attributed to them, as revealed by earlier studies of compressions, has been vividly confirmed by subsequent studies of their permineralized fossils (see Pant, 1997 and references cited therein). In addition to the above facts *Glossopteris* should be more eligible to be the leaf of the numerous large tree trunks called *Dadoxylon* sp. by Sahni (1925, 1931) instead of *Noeggerathiopsis*, since *Glossopteris* is the commonest leaf form occurring in the Raniganj Stage wherefrom the large tree trunks have been described, and *Noeggerathiopsis*, at this stage, had become quite a rarity.

Unlike the short, only 4 metres high, trees envisaged by Gould and Delevoryas (1977) dense forests of such high deciduous trees of glossopterids showing well marked growth rings in their secondary xylem would seemingly go well with the rich deopsits of coal in the Lower Gondwana beds and also with the frequent occurrences of petrified woods in association with remains of *Glossopteris* (Pant & Singh, 1987). I think that the thinner branches of a number of these diverse woods may have borne leaves of *Glossopteris* and its allies. However, leaves of some of the species of *Glossopteris* or its allies may have been borne on branches of small trees like the one reconstructed by Gould and Delevoryas (1977) and still others could have been borne by shrubs and lianas, e.g., *Belumoopteris* (Pant & Choudhury, 1977). All the same, the rather unnatural rosettes of leaves around the trees of *Glossopteris* depicted by Gould and Delevoryas (1977) may have been less regular with smaller and larger leaves in the apparent whorls.

As a matter of fact the coal and shales of the Lower Gondwanas appear to have been formed by thick layers of

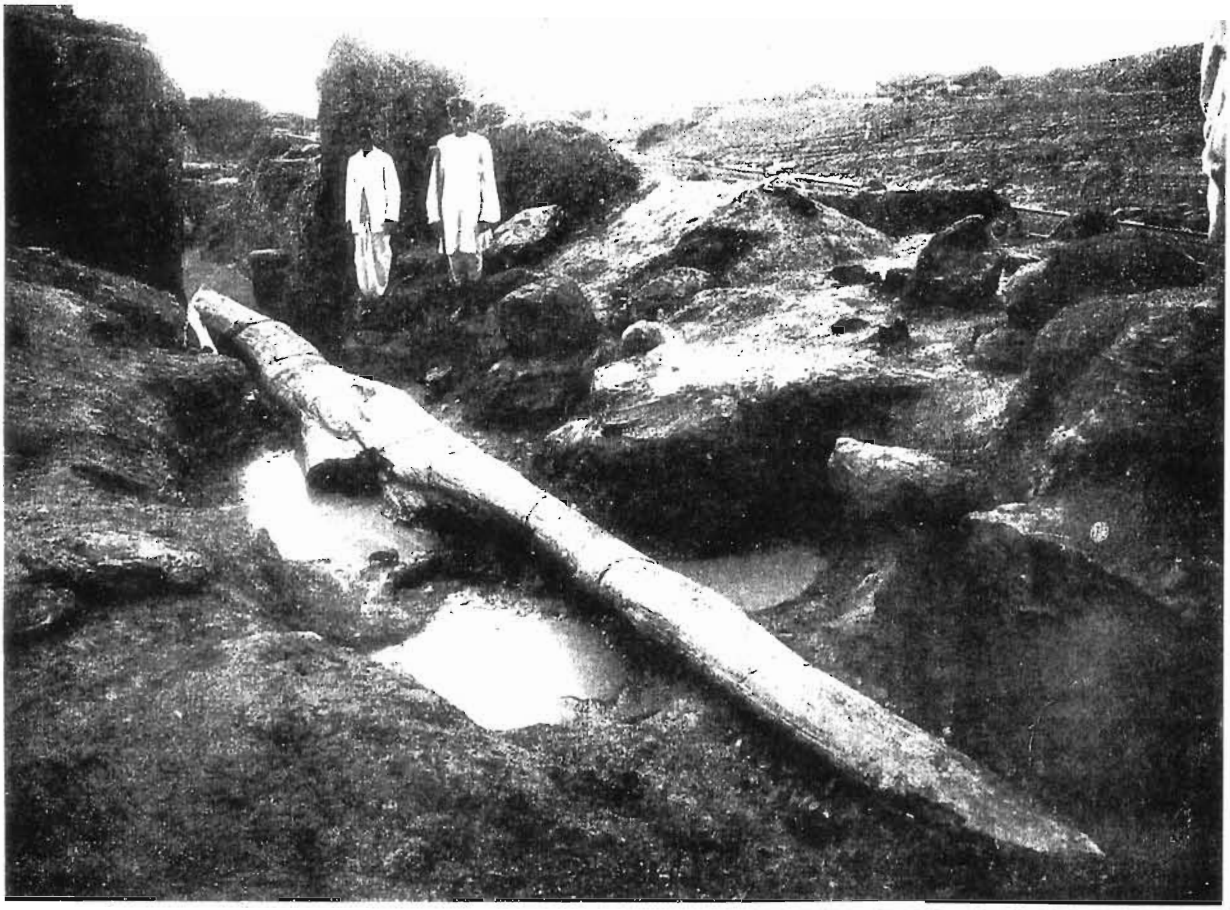
Text-figure 6—*Ginkgo biloba*, basal parts of tree trunks with fallen leaves around them forming a thick carpet in Toji Park, Tokyo during late autumn (photo by Random from Michel, 1986).

fallen leaves strewn heletr skelter and these may have accumulated repeatedly in thick annual carpets on the forest floor, as they do under the trees of modern *Ginkgo* (see Text-figure 6) whose size of 30 to 40 m, as mentioned by Pilger (1926) and Chamberlain (1935), seemingly corresponds with that of the fossil trees from Asansol. I therefore, imagine that during the Lower Gondwana times India was having rather dense deciduous forests of *Glossopteris* and its allies whose taller trees (see Text-figures 8, 9) were towering over shorter trees and shrubs so that in the words of Humboldt in these primeval woods "forest was piled upon forest" and dense humid shade of trees and shrubs provided ideal habitat for blattoid insects. The shrubs possibly had undergrowth of ferns, other pteridophytes and lower plants below them. The carpet of leaves on the undisturbed forest floor (Text-figure 10), with no records of any voracious consumers of fallen leaves, except some blatttoids (see Pant & Srivastava, 1995), in the course of time, must have piled up and become mixed up with broken twigs (rarely with attached leaves) and branches, as well as broken or fallen tree trunks as seen at the locality near Asansol.

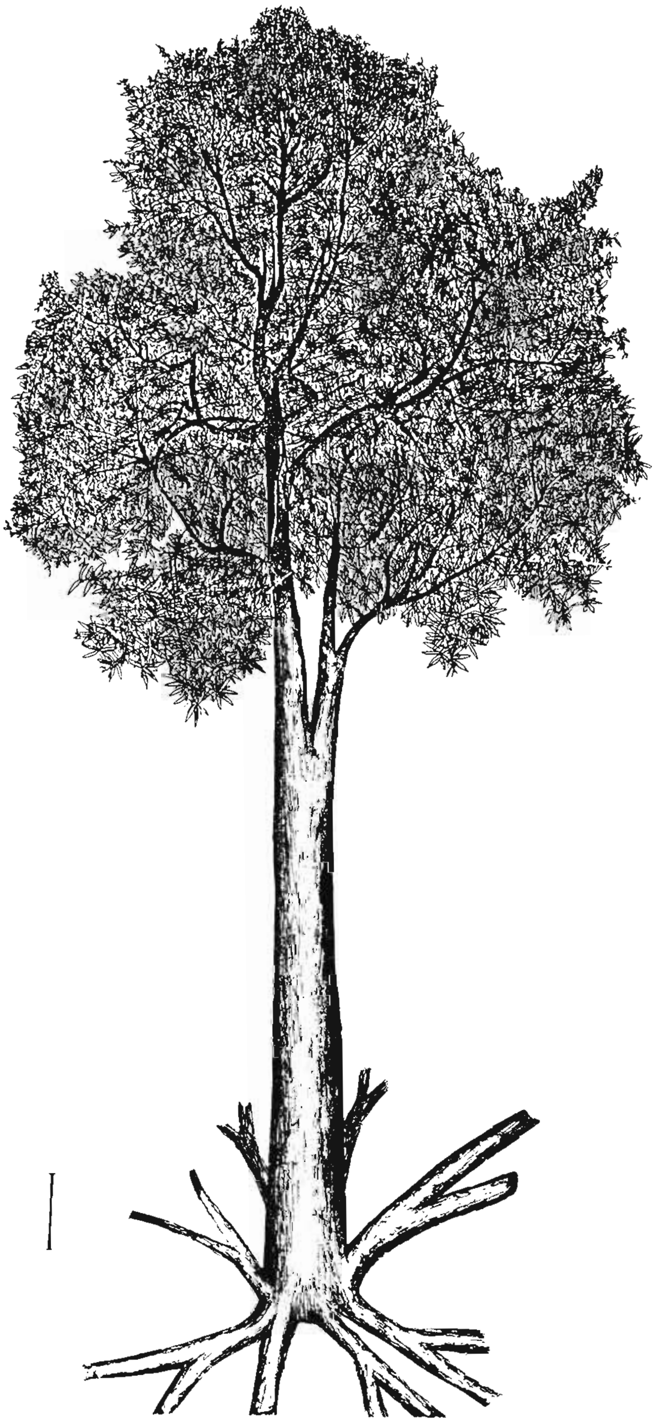
The underground or overground dead roots or root bearing axes of glossopterid trees and shrubs may also have ultimately become part of the dead organic material covering them in the forest floor. This is indicated by the greater frequency of *Vertebraria* axes at the bottom of coal seams. Wetting by rain water and fine silt displaced by rain or its drops between leaves and other plant material may have compacted the litter of leaves on the forest floor. New trees would have been coming up from germinating seeds on such a rising forest floor (Text-figure 10). In the course of millions of years the fallen leaves and other plant material became buried so that with arrested bacterial action due to lack of oxygen, it became further compacted and thereafter it was gradually converted by pressure and chemical processes of condensation and polymerisation under the influence of temperature, high pressure and time into the alternating dull and bright layered bands of the seams of coal. Occasional floods or advances of water bodies may have given rise to the intervening thin or thick layers of shale in between the coal seams.

Contrary to the *in situ* or autochthonous mode of formation of Lower Gondwana coal envisaged above and also suggested earlier by me (see Pant, 1989), some geologists like Fox, 1931 (see Krishnan, 1949) have earlier assumed that the Lower Gondwana coal is allochthonous or drift coal formed by plant material drifted into water bodies from unknown other localities. However, the presence of *Vertebraria* axes with thin roots spreading around them (Bunbury, 1861; Pant, 1956), broken tree stumps with horizontally spreading branched roots or rhizomatous axes around them as seen in a Permo-Carboniferous, sandstone bed of Vaal River at Vereeniging South Africa (Seward, 1917, p. 240, fig. 478), show that glossopterid trees were supported by such roots or axes. *In situ* vertically preserved *Vertebraria* axes called *Vertebraria radiata* by Royle (1840), vertically compressed seedlings of *Glossopteris* called *Diphyllopteris* (Pant & Nautiyal, 1987), occurrence of rootlet beds in the floor of coal seams reported by Chowdhury, 1985 and Manjrekar *et al.*, 1986 as mentioned by Banerjee *et al.* (1991), and horizontal roots and upright stems and *Vertebraria* axes later reported by Banerjee *et al.* (1991) and Singh and Chandra (1995) and Srivastava (1995) also vividly confirm that Lower Gondwana coal is autochthonous.

The paucity of genera of gymnospermous leaves and the multiplicity of species of *Glossopteris* has been noticed by Pant (1967) and Pant and Singh (1971) as a striking feature of the Glossopteris flora and this is particularly true about *Glossopteris* but the present day genus *Pinus* having over one hundred species spread over the entire north temperate zone from Japan in the East to western United States and western Canada in the West, with three species spreading northwards beyond the Arctic Circle in Eurasia and one species reaching or slightly overstepping the Equator in Sumatra (see Mirov, 1967; Little & Critchfield, 1969) presents a living parallel among the present day gymnosperms. Another parallel is provided by *Gnetum* which is distributed all over the tropical and humid regions of the world from Pacific Islands like New Guinea, Philippines and the East Indies, Siam, Malaysia, Indo-China, India, Tropical Africa, Guiana, Northern Brazil, Surinam and Amazon. Its diverse species are climbers, trees, shrubs and one of them, *Gnetum trinerve*, is a parasite (see Maheshwari & Vasil, 1961). Pant & Singh (1987) have already suggested that some Lower Gondwana woods showing excentric xylem cylinders could have belonged to lianas thereby implying that some glossopterids could have been woody climbers. Alternatively, the multiplicity of associated wood genera and leaf attached fructifications of *Glossopteris* and its allies may ultimately prove that they are divisible into a number of more natural genera, subgenera and sections on the basis of their stems and attached fructifications.



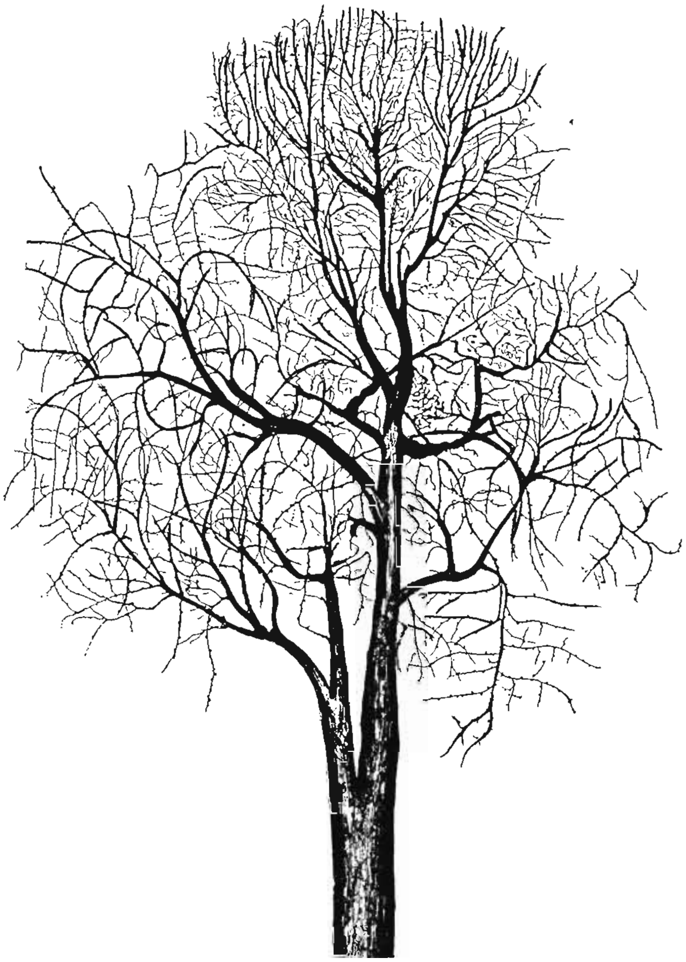
Text-figure 7—Fossil tree trunk discovered near Asansol by W.W. Whitney in 1923 (from Bradshaw & Sahni, 1925).



Text-figure 8—*Glossopteris*, reconstructed tree with leaves during summer showing spreading axes or roots around the tree.

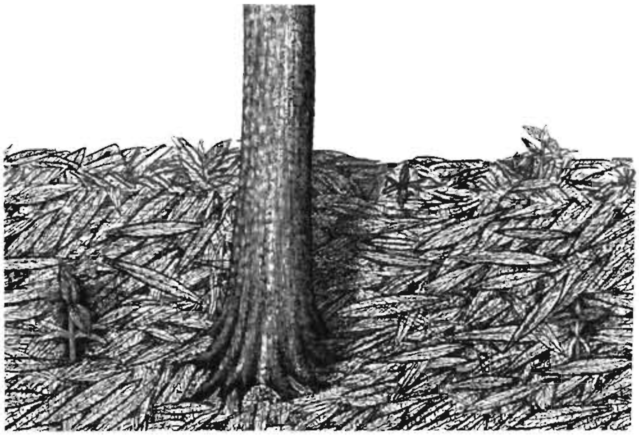
FERTILIGERS OF GLOSSOPTERIDS AND THEIR MORPHOLOGICAL NATURE

Plumstead (1952) described a number of leaf attached fructifications of *Glossopteris* and called them by separate adjectival generic names although as pointed out by Edwards, Krausel and Lakhanpal in the discussion of the paper by Plumstead (1952) and also as pointed out by me in 1977 the nomenclature is violative of two articles of the International Code of Botanical Nomenclature. The case of *Ottokaria* was different because Zeiller (1902) believed that the fructification was lying over a *Glossopteris indica* leaf. Subsequently after the discoveries of a number of leaf attached fructifications by Plumstead (1952), many other authors have also given separate generic names to such fructifications. So much so that the names of such fertile leaves or fertiligers have become legitimate by wide practice and accordingly I propose that such names may be treated as *nomina generica coservanda* and no longer violative of the code.



Text-figure 9—*Glossopteris*, reconstructed crown of leafless tree during winter.

However, the topic which I wish to discuss at this point is the morphological nature of the leaf attached fructifications. A search for comparable leaf attached fructifications among present day vascular plants leads me to (1) the fertile spikes of Ophioglossaceae, (2) the abnormal female "flowers" of *Ginkgo* described by Fujii (1896), which could be taken to be reversions, (3) the flowers of *Ruscus, Danae* and *Semele* at-



Text-figure 10—Reconstructed basal part of the trunk of a *Glossopteris* tree with fallen leaves forming a thick carpet around it. Note a few seedlings of *Diphyllopteris verticillata*.

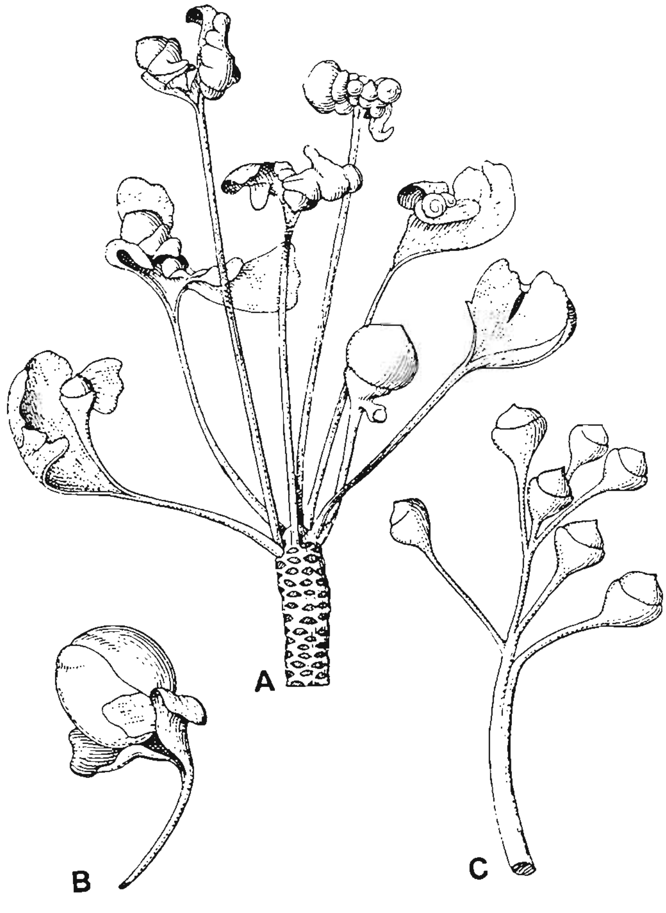
tached to their prophylls and (4) the bract attached inflorescences of *Tilia*. All these structures occurring in such diverse plants may be regarded as examples of the incorporation of the axillary fertile shoots in the subtending prophylls or bracts as suggested by Arber (1950). Indeed the widespread occurrence of such structures suggests that they are not peculiar to *Glossopteris* but they have arisen repeatedly in pteridophytes, gymnosperms, monocots and dicots. The latest interpretation of the fertile spikes of Ophioglossaceae regards the frond as a modified, reduced, dichotomous branch system (Zimmermann, 1942; Chrysler, 1945). In fact Nozu (1950, 1955) and Nishida (1957) regard the sterile and fertile segments as phylogenetically equivalent to fronds and therefore homologous. However, if we compare the two segments with the axillary fertile shoots of Rusceae and *Tilia* which become adnate to the subtending prophylls and bracts, they could be regarded as fertile axes adnate to phyllomes. The leaf attached fructifications of *Glossopteris* would thus appear to be quite comparable with those of the above living forms.

The axillary fructifications of *Glossopteris taenioides* described by Pant and Singh (1974) seemingly support the axillary nature of the fructifications of *Glossopteris* even when they seem to be coming out of their midribs. The abnormal female fructifications or "flowers" of *Ginkgo* described by Fujii, 1896 (see Text-figure 11A, B) could likewise be interpreted as fused to the leaves in whose axils they were produced. Some of the abnormal fructifications of *Ginkgo* described by Sprecher (1908) are branched (see Text-figure 11C) and in this connection it is important to point out that such branched fructifications of *Ginkgo* and the multiple fertile spikes of *Ophioglossum palmatum* too have their parallels in *Eretmonia, Glossotheca, Partha, Denkania, Lidgettonia* and these would perhaps require to be explained as being branched and the branches being adnate to the lamina.

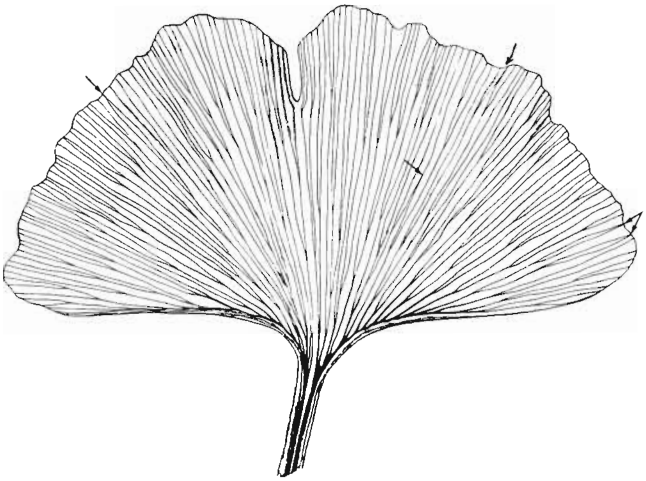
The position of the fertile leaves on the plants of *Glossopteris* is, however, unknown and we do not even know whether they are similar to or different from ordinary leaves of their plants (cf "bracts" of *Tilia*). Accordingly the term fertiliger used by Schopf (1974) seems to be quite appropriate. Further, we are completely ignorant about the plants of glossopterids being monoecious or dioecious. A method of determining this could be the occurrence of male and female fertiligers in close proximity or far away but this too is presently unknown.

RELATIONSHIPS OF GLOSSOPTERIDS

The similarity of the size of trees, deciduous habit and abnormal female fructifications of *Ginkgo* (Text-figure 11A, B) with the envisaged size of the deciduous trees and the leaf attached fructifications (fertiligers) of *Glossopteris* could even prompt us to look for relationships between the Ginkgoales and the Glossopteridales. Both the groups appear to be having deciduous leaves borne on short as well as long shoots,



Text-figure 11—*Ginkgo biloba*. **A**, spur shoot with a number of abnormal ovulate peduncles fused to leaf stalks, some of them showing seeds borne on laminae and single almost normal peduncle. **B**, a single abnormal peduncle with a seed showing longitudinal striation along fleshy part of seed and the lamina below the seed. **C**, an abnormal peduncle with seven stalked single ovules and their collars (A, B, from Fujii, 1896; C, from Sprecher, 1907).



Text-figure 12—*Ginkgo biloba*, cleared leaf showing dichotomous venation with a few anastomoses of veins marked by arrows (redrawn after Arnott, 1959).

and both kinds of shoots showing secondary xylem with well marked growth rings. The haplocheilic stomata of *Ginkgo* (Pant & Mehra, 1964) and glossopterids have similar rings of papillate subsidiaries overarching sunken guard cells. However, the net veined leaves of *Glossopteris* having well defined midribs would, appear to be quite different from the dichotomously veined leaves of *Ginkgo* and the Ginkgoales. All the same Arnott (1959) has reported various kinds of cross connections in 10% leaves of *Ginkgo biloba* (Text-figure 12) and there are other glossopterids which seemingly bridge the gap between acostate leaves with fan like spreading furcate veined leaves of Ginkgoales and net veined costate leaves of *Glossopteris*. These are *Gangamopteris* which is netveined but it has no midrib, *Rhabdotaenia* which is costate but its lateral veins are usually non-anastomosing, and there are species like *Glossopteris angustifolia* var. *taeniopteroides* with almost complete absence of anastomoses between lateral veins (see Seward, 1910) which are quite like *Rhabdotaenia*. Next comes *Palaeovittaria* which has an ill-defined midrib in the basal half of the leaf and only furcate non anastomosing parallel or sub parallel veins in the lamina and there is *Rubidgea* which has no midrib and only furcate veins in the distal part of the lamina which are, however, arched and not straight like those of *Ginkgo*. At the end of the series is *Noeggerathiopsis* which is acostate with furcate and spreading parallel veins. This genus is believed to be a cordaite, so much so that Seward & Sahni (1920) had actually merged it with the genus *Cordaites*. However, it appears to me that *Noeggerathiopsis* may not only be different from *Cordaites*, as already suggested by Pant & Verma (1964a) on the basis of (1) prevalent differences in structural features of its leaves from those of *Cordaites*, (2) the usual absence of stems with discoid pith or *Artisia* pith casts and (3) the absence of *Cordaitanthus*-like fructifications in the Lower Gondwana beds. Indeed, it occurs to me now that it may belong to an alliance approaching the Glossopteridales which I have earlier called Noeggerathiopsidales (Pant, 1882).

Another resemblance between *Ginkgo*, Cordaitales and Glossopteridales (Arberiales of Meyen, 1987) lies in their platyspermic seeds which, according to Meyen (1987), is a character of fundamental importance and he actually includes his Arberiales in his Ginkgopsida. Although he regards *Ginkgo* as having evolved from some pteridospermous ancestors which were rather different from cordaites and conifers. On the contrary Crane (1985), Doyle and Donoghue (1986) and Hart (1987) regard *Ginkgo*, conifers and *Cordaites* as having evolved from a common ancestor. Another point which may favour the relationships of glossopteridales and ginkogoales is the early appearance of ginkgophytic leaves in the Jurassic (Archanelsky, 1965) and Lower Permian (Cuneo, 1987) of Argentina and also those of *Ginkgophyllum diazii* in the carboniferous of Rioja Province of the same country as mentioned by Taylor & Taylor (1993) after S. Archangelsky. These finds may suggest the dispersal of the group from the southern latitudes as also envisaged by Stewart & Rothwell (1993). My conclusions about the habit of the deciduous plants of *Glossopteris* and its allies and the series of leaves of the glossopterids with *Palaeovittaria* and *Rubidgea* placed between them and *Noeggerathiopsis* also seemingly support the relationships of Glossopteridales Ginkgoales and Cordaitales.

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