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Some remarks on the glossopterids and stratigraphical distribution of their fructifications during the Permian on Gondwana Supercontinent

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ABSTRACT

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The paper summarises information available about different organs of the glossopterid group of plants. It has been found that various reconstructions proposed for the glossopterid plant and derivation of its phylogenetic relationships on the basis of cladistic analyses are yet to be validated. The relationship between the families Dictyopteridiumaceae and Eretmoniaceae is discussed. Distribution of various genera of glossopterid fructifications in the Permian of the Gondwana Supercontinent has been tabulated.

Key words—Gondwana Supercontinent, Glossopterids, Fructifications, Biostratigraphy.

गोण्डवाना अधिमहाद्वीप में परमियन कल्प के दौरान ग्लॉसोप्टेरिडों तथा उनके फलन के स्तरिकीय वितरण का विवेचन

ऊषा बाजपेई

सारांश

प्रस्तुत प्रपत्र में ग्लॉसोप्टेरिड समूह के पौधों के विभिन्न अंगों के विषय में प्राप्त सूचनाओं का समावेश किया गया है। यह पाया गया कि ग्लॉसोप्टेरिड पौधे के विषय में प्रस्तावित विभिन्न पुनर्रचनाएँ तथा क्लैडिस्टिक विश्लेषणों के आधार पर इनके जातिवृत्तीय सम्बन्धों के उद्गम को अभी व्याख्यायित किया जाना शेष है। डिक्ट्योप्टेरिड्यूमेसी तथा इरेटमोनिएसी कुलों के मध्य सम्बन्धन का भी विवेचन किया गया। परमियन कल्प के गोण्डवाना अधिमहाद्वीप के ग्लॉसोप्टेरिड फलनों के विभिन्न वंशों के वितरण सम्बन्धी तालिका भी निर्मित की गयी।

संकेत शब्द—गोण्डवाना अधिमहाद्वीप, ग्लॉसोप्टेरिड, फलन, जैवस्तरिकी.

INTRODUCTION

THE glossopterids are a group of fossil plants that has been known for almost one hundred and eighty years, and which constituted the major part of the Permian vegetation that grew on the Gondwana Supercontinent. However, as yet it has not been possible to reconstruct an indubitable glossopterid plant. The reconstructions proposed by Gould and Delevoryas (1977) and Retallack and Dilcher (1981, 1988), and others show the glossopterid plant as prolifically branched tree, with sparsely distributed leaves. These reconstructions are in fact based on certain presumptions and assumptions, for example, *Vertebraria australis* were the rootlets (roots are not named) and *Arberiella africana,* containing *Protohaploxypinus limpidus* pollen, was the pollen sac of *Dictyopteridium sporiferum* tree (Retallack & Dilcher, 1988, p. 1035). Nothing is said of other striate bisaccate pollen. It is further presumed that the plant was 'probably' wind-pollinated, the ovules were interconnected 'probably' by a good deal of mucilage, by the time of fertilization the fructification 'probably' shrivelled and decayed, seeds were 'probably' scattered by wind. The reason mainly is that, though root, stem, leaf, fertile organs, etc. have been assigned to this group, yet they mostly occur in disjointed condition, and their relationship is based mostly on association. Because of this reason, even the affinities of this group are not well understood. It has very casually been accepted that the glossopterids are pteridosperms, or pteridosperm relatives.

THE GLOSSOPTERIDS

Leaves—The glossopterids are mostly known through leaves that are simple, linear, lanceolate or obovate. Several genera of leaves are on record, some of which have a midrib, and some do not have a midrib, still others have only a partial midrib. Anatomical studies have shown that the midrib is just a concentration of veins identical to the laminar veins (Gould & Delevoryas, 1977; Pigg & Taylor, 1990). The secondary veins emanate either from the midrib or from a central strand of veins, dichotomise, and may or may not anastomose. These leaves also share a similar type of epidermal organisation. The other genera to which the glossopterid leaves are assigned are *Rubidgea* Tate, *Gangamopteris* McCoy, *Glossopteris* Brongniart and *Palaeovittaria* Feistmantel. The probability that leaf genera like *Pantophyllum* Rigby (=*Noeggerathiopsis* Feistmantel), *Euryphyllum* Feistmantel, *Rhabdotaenia* Pant & Verma, *Pteronilssonia* Pant & Nautiyal and *Belemnopteris* Feistmantel may also belong here is low. The leaves of *Pantophyllum* have a typical aspect in their morphology and cuticle (Pant & Verma, 1964; Maheshwari & Singh, 1999), the cuticle of the other genera is also differently organised than that of the glossopterid leaves (Pant & Mehra, 1963; Pant & Verma, 1963; Singh, 1998) and hence none of these genera are considered as belonging to the glossopterid group.

Leaves morphographically indistinguishable from glossopterid leaves are on record from locations outside the Gondwana Supercontinent (Meyen, 1982, 1984; Delevoryas, 1969). However, neither their cuticle is known nor any fertile organ related to the glossopterids is associated with them, hence they are not considered further.

Wood—Many taxa of wood are known from those sediments that contain glossopterid leaves (Kräusel *et al.,* 1961; Prasad, 1982). None of the wood has, however, been found with attached leaves. It is also not expected as the wood is found in decorticated condition, and most of it is known through secondary xylem only, which typically shows annual rings of growth, and has araucarioid pitting on the tracheid walls. The primary xylem is generally endarch, the pith is small, and may contain secretory cells, or canals. Xylem rays are generally uni- or bi-seriate.

Root—The root *Vertebraria*, which some people still argue bore leaves, has a characteristic segmented appearance, the like of which is not known in any of the other contemporary floras. Although *Vertebraria* has not been found in actual attachment with a stem, yet its consistent association with glossopterid leaves leads one to believe that it belongs to this group.

Fructifications—The female fructifications are the only organs that have been found attached to a glossopterid leaf. Male fructification is not known so far. The earliest described glossopterid fructification is *Dictyopteridium.* Feistmantel (1881) who reported this taxon from the Permian sediments of Damodar Graben, India thought it to be a fern pinnule. Chandra and Surange (1976) have convincingly illustrated the association of this fructification with a glossopterid leaf.

Zeiller (1902) described the female fructification *Ottokaria bengalensis* which is probably attached to a leaf of *Glossopteris communis* (Bose MN in Plumstead 1956b; Banerjee, 1978). White (1908) described *Arberia*, a putative glossopterid fructification (Rigby, 1972), from the earliest Permian of Brazil. Plumstead (1952, 1956a, b, 1958) described a host of other fructification genera found attached to leaves of *Gangamopteris*, *Glossopteris* and *Palaeovittaria* from the Permian sediments of South Africa. Since then many fructifications, both in organic connection with leaves and in detached condition, have been reported.

Maheshwari (1965) made a canada balsam transfer of one of the specimens of *Dictyopteridium sporiferum* and demonstrated that the fructification is foliose, bearing ovules on one surface, and showing venation patterns on the other. A somewhat similar pattern is evident in the fructification *Satsangia campanulata* found in the Nidhpuri beds (Srivastava & Maheshwari, 1973). A re-examination of the *Satsangia* fructification shows that it is neither bell-shaped, nor it bore sporangia. The fructification is only partially infolded at the margins, and the scars represent bases of dehisced seeds.

Gould (1975) reported glossopterid fructifications from a Permian petrified peat from Australia. The transverse section of a specimen has vindicated the interpretation of compression material that the fructification was foliose, and bore ovules only on one surface. There now seems to be hardly any scope of doubt in this regard. There is no indubitable evidence to suggest that the glossopterid fructification was a strobilus, or was bisexual, or was covered by a scale leaf (Surange & Chandra, 1975). The ovules/seeds mostly are platyspermic. No indubitable cupular structure has ever been reported. Bisaccate pollen with horizontal striations on the proximal face of the central body has been observed on the integument and in the micropyle of dispersed seeds/ovules (Pant, 1977).

As far as the location of the fructifications is concerned, many believe that it was borne in the axil of a vegetative leaf, while others say that the fructifications were epiphyllous megasporophylls. Very often the pedicil of the fructification was adnate with the midrib or the median strand of veins for some distance; by adherence it became incorporated into the vegetative leaf. Thus the glossopterids seem to belong to the caulosperms, rather than to phyllosperms.

Seedlings—Srivastava (1978) described *Diphyllopteris verticillata*, a taxon with heterophyllous leaves. The specimen has two oppositely placed *Glossopteris*-type leaves alternating with two dichotomously branched leaves. Pant and Nautiyal (1987) suggested that it was a seedling of the glossopterid plant. Banerjee (2000) is of the opinion that the specimen could as well be young *Rhipidopsis*. Banerjee (2000) described another putative glossopterid seedling *Deogarhia nautiyalii*, with two thick cotyledonary leaves and two *Glossopteris* leaves. Earlier Banerjee *et al.* (1991) have reported what they believed was an *in situ Glossopteris* plant with branched stems and spreading roots.

Taxonomic position—Initially regarded as a fern, there is now no doubt that the glossopterids are gymnosperms. But opinions differ as to whether the group merits the rank of a division, a class, an order, or just a family. Some people place the glossopterids in almost as many families as there are genera of female fructifications. Taking into the general organisation of the fructification, all the known fructifications seem to have the same organisation, and hence it is likely that all the glossopterids belong to one family only, that is, the Dictyopteridiumaceae.

The main question that yet remains to be solved is where to place this family? Andrews (1961) classified it as gymnosperms of uncertain affinities, not closely related to any other group. Sporne (1965) placed it under the Pteridospermales. Pant (1982) placed the group at the rank of an order, the Glossopteridales, "the unique leaf attached fructifications of Glossopteridales" suggesting some relation to the Pteridosperms. Some others have suggested that the group represents an independent class - the Glossopteridopsida (Banerjee, 1984). One thing, however, seems certain that the glossopterid group of plants is not closely related to the northern pteridosperms (see Maheshwari, 1990). Some cladistic analyses place glossopterids very close to various seed-fern groups (Crane, 1985). These, however, need further testing as they take into consideration certain premises that are debatable, for example, the occurrence of a cupular structure in the group or the leaf-like nature of the fructification (Schopf, 1976). Doyle and Donoghue (1986, p. 332) observed that Crane "omitted many potentially useful characters", "his interpretation of characters predisposes the analysis toward particular theories" and that "his methods of scoring groups are sometimes questionable". It is not clear as to why Doyle and Donoghue (1986, p. 340, 412) consider pinnately compound leaves/once-pinnate leaves as the derived state in the Glossopteridales, or that "the pinnate arrangement, as in the pollen organs and the ovulate organ *Lidgettonia*, is the basic condition."

Many of us very casually use the term Pteridosperm, like the so-called Mesozoic pteridosperms where nothing is known about the relationship of the leaf and the supposedly related fructification, except that based on similarity of the cuticular organisation. Harris (in Plumstead, 1952, p. 322) had suggested that "such strange plants should not be placed in the Pteridosperms...". Pant (1977, p. 20) remarked that "the Glossopteridales are very different". The glossopterids are thus best placed in the order Dictyopteridiumales in the Class Glossopteridopsida.

IS ERETMONIACEAE, TOO, A GLOSSOPTERID?

Another group of plants, the Eretmoniaceae, has sometimes been placed with the glossopterids. Except for its occurrence in some of those sediments that contain the glossopterids, not much is common between the two. In the Eretmoniaceae, the fructifications are branched 1-4 times; each branch terminates into a head. Both pollen-bearing (*Eretmonia* du Toit, *Glossotheca* Surange & Maheshwari) and ovule-bearing (*Lidgettonia* Thomas =?*Partha* Surange & Chandra) fructifications are known. The leaf to which the fructification is attached is scale-leaf like, which shows reticulate venation but no midrib (Surange & Maheshwari, 1970). Anatomical details are also lacking for this group. At present there is no evidence to suggest that the Eretmoniaceae had a close affinity with the Dictyopteridiumaceae. In fact, some other detached, profusely branched fructifications have been reported from the Indian Gondwana, which are quite unlike the glossopterid fructifications. For example, *Utkalia dichotoma* (Chandra, 1984), *Veekaysinghia durgavatiae* Maheshwari & Bajpai and *Birbalsahnia divyadarshanii* (Bajpai & Maheshwari, 1991)

Thus in Dictyopteridiumales and Eretmoniales we have two different orders of plants, that may be related, within the Class Glossopteridopsida.

	Taxon	Australia	India	Africa	South America	Antarctica	Arabian Plate
LATE PERMIAN	*Satsangia*	-	+	-	-	-	-
	Utkalia	-	+	-	-	-	-
	Escourtia	-	-	+	-	-	-
	Squamella	+	-	-	-	-	-
	Cometia	+	-	-	-	-	-
	Rigbya	+	-	+	-	-	-
	Nesowalesia	+	-	-	-	-	-
	Eretmonia	+	+	+	+	+	-
	Glossotheca	-	+	-	+	-	-
	Lidgettonia	+	+	+	-	-	-
	Senotheca	-	+	-	-	-	-
	Austroglossa	+	+	-	-	-	-
	Scutum	+	+	-	-	+	-
	Plumsteadia	+	+	+	-	+	-
	Dictyopteridium	+	+	-	+	+	-
	?Arberia	-	-	-	-	-	?
MIDDLE PERMIAN	*Rigbya*	-	-	-	-	-	+
	Eretmonia	-	?	-	-	-	-
	Senotheca	-	-	-	-	-	-
	Hirsutum	-	-	+	+	-	-
	Scutum	-	+	+	+	-	+
	Plumsteadia	+	-	-	+	-	+
	Dictyopteridium	+	+	-	-	-	-
	Ottokaria	-	?	-	+	?	-
	Arberiopsis	-	-	-	+	-	-
	Arberia	-	-	-	+	-	-
	Birbalsahnia	-	+	-	-	-	-
	Veekaysinghia	-	+	-	-	-	-
EARLY PERMIAN	*Hirsutum*	-	-	-	+	-	-
	Plumsteadia	+	-	+	+	-	-
	Ottokaria	+	+	+	-	-	-
	Arberiopsis	-	-	-	+	-	-
	Arberia	+	+	-	+	-	-

Fig. 1—Distribution of glossopterid and other fructifications, in time and space, on the Gondwana Supercontinent.

STRATIGRAPHICAL DISTRIBUTION OF FRUCTIFICATIONS

Fructifications assigned to the glossopterids have been reported from most regions of the Gondwana Supercontinent. The possible use of these fructifications in phytostratigraphy was discussed at a workshop during the 10th Meeting of the Palaeobotanists and Palynologists held at Guarulhos, Brazil during December 2000. No consensus could be arrived at. The main stumbling block seems to be the extreme paucity of the glossopterid fructifications in the sediments throughout, and more particularly so in the South American and Antarctic continents. Rigby (2000) opined that "*Glossopteris* and its fructifications may prove to be better indicators of environmental and climatic conditions than as stratigraphic correlators". Even so, it is possible to arrive at broader zonations based on the available database.

In Australia, McLoughlin (2000) recognises three levels of fertile glossopterids, that is, Lower Permian (containing *Arberia*), Middle-Upper Permian (containing *Dictyopteridium* and *Lidgettonia*) and Upper Permian (containing *Rigbya, Cometia* and *Senotheca*). It would thus seem that in Australia *Lidgettonia* appears earlier than *Senotheca.*

In India, too, a similar broad zonation could be recognised (Bajpai, 2000). *Arberia*, supposed to be a fructification of the genus *Gangamopteris* (Rigby, 1972), is restricted to the Talchir and Karharbari formations (Early Permian). *Ottokaria* is known from the lower part of the Barakar Formation (= Karharbari Formation, Early Permian). The reported occurrence of *Ottokaria* in the Raniganj Formation (Banerjee, 1978) and Illawarra Coal Measures (White, 1978) is to be confirmed by further finds. *Dictyopteridium* ranges from late Early Permian to the latest Permian, whereas other foliose fructifications are confined to the Late Permian. Contrary to the situation in the Australian Gondwana, in the Indian Gondwana the genus *Lidgettonia* appears later than *Senotheca.*

In Africa, Anderson and Anderson (1985) have recognised four families of glossopterid fructifications. They have postulated a stratigraphic zonation based on glossopterid fructifications; these zones correspond to the Dwyka, Middle Ecca, Upper Ecca and Estcourt formations, respectively.

A general summary of distribution in time and space of major glossopterid fructification genera is shown in Fig. 1 (data collated from different sources, e.g., Anderson & Anderson, 1985; Archangelsky, 1992; Archangelsky *et al.*, 1981; Banerjee, 1984; Benecke, 1976; Bernardes de Oliveira, 1978; Bose *et al.*, 1990; Broutin, 2000; Chandra & Srivastava, 1981; Cuneo *et al.*, 1993; Holmes, 1974; Lacey & Huard-Moine, 1966; Lacey *et al.*, 1975; le Roux & Anderson, 1977; McLoughlin, 1990a, b; Maheshwari, 1992; Maithy, 1974; Millan, 1967; Rigby, 1972; Schopf, 1976; White, 1964, 1978).

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