
The glossopterid group of plants in an evolutionary perspective

Hari K. Maheshwari & A. K. Srivastava

Maheshwari HK & Srivastava AK 1992. The glossopterid group of plants in an evolutionary perspective. *Palaeobotanist* 41 : 110-113.

The glossopterid group of plants was the most dominant constituent of the Permian vegetation of the Gondwana Supercontinent. During last one hundred and fifty odd years, an staggering amount of data has accrued on leaves, wood, root, fructifications, seeds and pollen that possibly belonged to this group. Evolutionary pathways within the group, however, are yet little understood.

Considering the venation and epidermal features of the leaves, two patterns are unfolded; one with leaves having dichotomising, almost parallel veins and stomata in linear rows, the other with dichotomising and anastomosing veins and stomata irregularly distributed in the mesh areas.

Oldest glossopterid fructifications, viz., *Arberia/Dolianitia* show a certain resemblance with the cordaitalean fructifications, thus suggesting that a group of plants with *Cordaites/Noeggerathopsis/Pantophyllum* type leaf and *Arberia/Dolianitia* type infructescence probably was the precursor of the glossopterids. Overall evidence suggests the development of this group of plants along two successive lineages.

Key-words—Glossopterids, Taxonomy, Evolution.

Hari K. Maheshwari & A. K. Srivastava, Birbal Sahni Institute of Palaeobotany, 53 University Road, GPO Box 106, Lucknow 226 001, India.

सारांश

ग्लॉसोप्टेरिड समूह के पौधों का विकास

हरिकृष्ण माहेश्वरी एवं अश्विनी कुमार श्रीवास्तव

गोंडवाना महासमूह के परमी कल्प की वनस्पति में ग्लॉसोप्टेरिड समूह के पौधों की बाहुल्यता थी। पिछले लगभग 150 वर्षों में पत्तियों, काष्ठों, मूलों, फलनों, बीजों एवं परागकणों के अश्विमत अभिलेखों के रहस्यपूर्ण आँकड़े प्राप्त हुए हैं जो सम्भवतः इसी समूह से सम्बद्ध हैं। पौधों के इस समूह में विकास किस प्रकार हुआ यह अभी भी स्पष्ट नहीं हो पाया है।

पत्तियों के शिरान्यास एवं उपचर्मी लक्षणों के आधार पर दो परिकल्पनायें प्रस्तावित की गई हैं, एक वह जिनमें पत्तियों में द्विभाजित शिरान्यास, प्रायः समानान्तर शिरायें तथा एक पंक्ति में विन्यस्त रन्ध्र विद्यमान हैं, तथा दूसरी वे जो शिराओं में द्विभाजन तथा शाखामिलन तथा अनियमित रूप से वितरित रन्ध्रों से युक्त हैं।

प्राचीनतम ग्लॉसोप्टेरिड फलन जैसे *आर्बेरिया/डोलियानिटिया*, कोर्डैटेली फलनों से कुछ समानता प्रदर्शित करते हैं। इससे यह व्यक्त होता है कि *कोर्डैटिस/नेग्रैथिऑप्सिस/पन्तोफिल्लम* प्रकार की पत्तियों द्वारा *आर्बेरिया/डोलियानिटिया* प्रकार के फलन से युक्त पौधों का समूह सम्भवतः ग्लॉसोप्टेरिडी पौधों के जन्मदाता हैं।

SINCE the first report of unique tongue-shaped leaves with a distinct midrib and dichotomously branched secondary veins anastomosing to form meshes, from the Permian sediments of India and Australia (Brongniart, 1828), their subsequent discoveries in the Permian floras of South America, South Africa, and Antarctica have attracted the attention of plant morphologists, taxonomists and evolutionary botanists. These leaves, referred to species of the genus *Glossopteris*, have variable

morphographical features, epidermal characters, and have now been shown to bear "attached" fructifications.

In subsequent years, about half a dozen genera of morphographically related leaves were established from the Permian sediments of the Gondwana Supercontinent. On the basis of similarity

in their form, general pattern of venation, and epidermal features, leaf genera *Rubidgea* Tate, *Euryphyllum* Feistmantel, *Gangamopteris* McCoy, *Glossopteris* Brongniart, *Palaeovittaria* Feistmantel, and *Rhabdotaenia* Pant (non *Taeniopteris* Brongniart), have been referred to a single group of plants, informally called the glossopterids. Some palaeobotanists also include the leaf genera *Belemnopteris* Feistmantel and *Pteronilssonina* Pant & Mehra in this group. Certain new types of leaves discovered recently, viz., *Surangephyllum*, *Gondwanophyllites* and *Maheshwariphyllum* may also be related to the glossopterids (Chandra & Singh, 1986; Srivastava, 1987, 1992a).

Most species of the glossopterid leaves have been established on the basis of variation in gross morphology, i.e., shape of the leaf, extent of midrib, and the pattern of secondary venation (Maheshwari, 1965). In recent years, much work has been done on the epidermal features of these leaves and it has been suggested that variation in the cuticular features is also a very important component of characters used for species delimitation (see Chandra, 1974). A recent study (Maheshwari & Tewari, 1992), however, has shown that cuticular features may not always be species specific. This is one area where an exhaustive study is yet required to arrive at any definite conclusion.

Since most species are based on leaf specimens found in isolation, as single entities, it is difficult to taxonomically correlate one "species" with the other. Surange and Srivastava (1956) correlated and classified species of *Glossopteris*, *Gangamopteris* and *Palaeovittaria* into six groups on the basis of cuticular features. This classification is, however, not supported by gross morphology of the leaf. Srivastava (1991) classified the taxa into two categories, i.e., one category in which the veins dichotomise but do not anastomose, and the other category in which the veins dichotomise and anastomose to form a network (reticulate venation). The extent of the midrib in the two categories has been related to the evolutionary trend within each category. *Maheshwariphyllum* Srivastava, a leaf with parallel running dichotomising veins and a midrib running up to the apex, probably is the "missing link" between leaves without midrib and non-reticulate venation and leaves with a midrib and reticulate venation. It might also have given rise to leaves with non-reticulate venation and a midrib running only part of the length, viz., *Palaeovittaria*.

In spite of repeated search and exploration, it has not been possible so far to show an indubitable connection between these leaves and associated stems, roots, and fructifications. Due to this

drawback, the taxonomic position of this group and its classification are only vaguely understood. At times, we do get *Vertebraria*-type axes and certain fructifications associated in the sediments with species of the leaf genus *Glossopteris*. On the basis of accrued data, Pant (1977), and Gould and Delevoryas (1977) suggested that the plant that bore glossopterid type leaves was a large tree with *Araucarioxylon*-type wood. Schopf (1965) had earlier suggested that *Vertebraria*-axes represented the root of this plant.

The appearance of the glossopterid group of plants has generally been correlated with the end of glaciation phase in the Southern Hemisphere, sometimes during Late Carboniferous. Sahni (1939), however, believed that the group came on the scene before glaciation and that the Ice Age probably was a causative factor in emergence of the Gondwana Flora. Available records of glossopterid remains considered together with the contemporaneous floral elements in Late Carboniferous and Early Permian sediments of South America oblige our thinking to look forward for the ancestry of the glossopterids in the Carboniferous floras (Srivastava, 1992b). Apparent morphological and cuticular resemblances between glossopterid leaves, e.g., *Rubidgea*, *Euryphyllum*, *Maheshwariphyllum* and *Palaeovittaria* with the Angaran *Zamiopteris*, and Euramerican *Lesleya* suggest that non-reticulate glossopterid leaves possibly evolved from some element in the Carboniferous Flora that is supposed to have been cosmopolitan in distribution (Chaloner & Meyen, 1973).

Continued occurrence of non-reticulate, dichotomising parallel running veins in certain leaves of the Mesozoic floras, viz., *Pterophyllum*, *Ptilophyllum*, *Nilssonina*, etc. suggests their derivation from glossopterid leaves. Taxa such as, *Pseudoctenis*, *Ctenis*, *Zamites*, *Dictyozamites*, etc. having reticulate veins may indicate their affiliation with the glossopterid leaves having reticulate venation.

Available data on dispersed and "attached" fructifications attributed to the glossopterid group of plants has recently been thoroughly analysed by Maheshwari (1990). The *Arberia/Dolianitia* type, recorded from the oldest fossiliferous strata of the Gondwana Supergroup, or from equivalent formations, has an organisation perceptibly different from that of other fructifications. Schopf (1976) regarded the stalk and capitulum of such structures as a modification and proliferation of the cordaitan ovuliferous stalk, and the subtending leaf as a bract with which the stalk had become adnate, albeit partially. A comparative plan is seen in *Krylovia*, a cordaitan fructification from the Angara Flora. The

evidence indicates that plants having cordaitean leaf morphology (*Cordaites/Noeggerathiopsis/Pantophyllum*) with *Arberia/Dolianitia* type of fertile structures possibly were the ancestral stock of the glossopterid group of plants. The similarity observed between *Pantophyllum* (= *Noeggerathiopsis*) and *Palaeovittaria* also exemplifies the taxonomic relationship of the two groups of plants (Srivastava, 1992a).

Ottokaria, the first definite glossopterid fructification found in "attachment" with the leaf of *Glossopteris indica* (Zeiller, 1902) is known from the *Gangamopteris—Glossopteris—Pantophyllum* associated flora of Early Permian age. This bilateral foliose structure could have evolved through planation and modification of *Arberia*-type (Bajpai, 1992). Multiovulate fertile structures, viz., *Dictyopteridium* Feistmantel, *Scutum* Plumstead, *Senotheca* Banerji, etc. where a number of small ovules were borne on abaxial surface, the adaxial surface having a spreading venation, are the direct descendents of *Ottokaria*-type. In all such cases, the leaf that bore the fructification hardly showed any difference from the vegetative leaf. Branched fructifications appeared through condensation and reduction of ovules with a leaf quite different from the typical vegetative leaf. They bore six to eight ovules, either in a row on one side of the leaf, or in two rows, one on each side, e.g., *Lidgettonia* Thomas. A similar pattern is seen in the male fructifications also, e.g., *Eretmonia* du Toit and *Glossotheca* Surange & Maheshwari. Taking all the characters into account, two families of glossopterid plants are recognised, viz., Dictyopteridiaceae, and relatively younger Eretmoniaceae (Maheshwari, 1990).

Possible trends in the development of the branched fructifications (Eretmoniaceae) from the *Ottokaria*-type (Dictyopteridiaceae) have been outlined by Stewart (1983). These are the tendency to cover a large number of ovules on the inner adaxial surface of a megasporophyll (capitulum) by inrolling of the margins (*Glossopteris*, *Ottokaria*); reduction of ovules from a large number, more or less condensed on the lower surface of the megasporophyll, to a few ovules in one or two rows (*Lidgettonia*); reduction of ovule number to one and its enclosure by the revolute margins of the capitulum to form a "cupule" (*Denkania* Surange & Chandra). The revolute margins are clearly exhibited in *Satsangia* (Srivastava & Maheshwari, 1973), and the vertical sections of petrified glossopterid fructifications (Gould & Delevoryas, 1977).

The much lamented Gonophyll Theory advanced by Melville (1960) for the evolution of the

flowering plants suddenly focussed attention on the glossopterid group of plants as possible ancestors of the angiosperms. Melville (1969) further observed that the venation pattern of primitive angiosperms, e.g., *Pringlia*, *Foetidia*, *Lepinia*, *Lepiniopsis*, etc. is comparable to that in the glossopterid leaves, and was another evidence to support the view that the group was a forerunner of the angiosperms. Several other palaeobotanists have also commented on the significance of the glossopterid fructifications in assessing the place of this group in the evolutionary history of the angiosperms (Axelrod, 1952; Doyle, 1978; Retallack & Dilcher, 1981; Crane, 1985). Available data is too meagre to definitely trace the origin of angiosperms to the glossopterids; the probability, however, can not be ruled out, particularly because of direct observation of revolute margins of the seed-bearing foliose fructifications found "attached" to glossopterid leaves.

On the basis of available data it may thus be concluded that the glossopterids had their origin in a cordaitean ancestor, and during the Permian they developed along two different lineages, as exemplified by the two families recognised in the group.

REFERENCES

- Axelrod DI 1952. The theory of angiosperm evolution. *Evolution* **6** : 29-60.
- Bajpai U 1992. Morphological trends in the Gondwana plants. In Venkatachala BS & Singh HP (editors)—*Symposium on Four Decades of Indian Palaeobotany, Palaeobotanist* **40** :
- Brongnart A 1828-1837. *Histoire des végétaux fossiles ou recherches botaniques et géologiques sur les végétaux renfermés dans les diverse couches du globe*. Masson et Cie, Paris.
- Chaloner WG & Meyen SV 1973. Carboniferous and Permian floras of the northern continents. In Hallam A (Editor)—*Atlas of paleobiogeography* : 169-186.
- Chandra S 1974. *Glossopteris* and allied genera—cuticular studies. In Surange KR, Lakhanpal RN & Bharadwaj DC (editors)—*Aspects and appraisal of Indian palaeobotany* : 144-153. Birbal Sahni Institute of Palaeobotany, Lucknow.
- Chandra S & Singh KJ 1986. *Surangephyllum* gen. nov. from the Kamthi Formation of Handapa, Orissa. *Indian Soc. Geoscient. Bull.* **1** : 15-18.
- Crane PR 1985. Phylogenetic analysis of seed plants and the origin of angiosperms. *Annls Mo bot. Gdn* **72** : 716-793.
- Doyle JA 1978. Origin of angiosperms. *Annl Rev. Ecol. Syst.* **9** : 365-392.
- Gould RE & Delevoryas T 1977. The biology of *Glossopteris* : evidence from petrified seed-bearing and pollen-bearing organs. *Alcheringa* **1** : 387-399.
- Maheshwari HK 1965. Studies in the *Glossopteris* Flora of India—31. Some remarks on the genus *Glossopteris* Sternb. *Palaeobotanist* **14** : 36-45.
- Maheshwari HK 1990. The glossopterid fructifications: an overview. In Douglas JG & Christophel DC (editors)—*Proc. 3rd IOP Conf., Melbourne 1988* : 11-15.

- Maheshwari HK & Tewari R 1992. Epidermal morphology of some Indian species of the genus *Glossopteris* Brongniart. *Palaeobotanist* **39** : 338-380.
- Melville R 1960. A new theory of the angiosperm flower. *Nature Lond.* **188** : 14-18.
- Pant DD 1977. The plant of *Glossopteris*. *J. Indian bot. Soc.* **56** : 1-23.
- Retallack G & Dilcher DL 1981. Arguments for a glossopterid ancestry of angiosperms. *Paleobiology* **7** : 54-67.
- Sahni B 1939. The relation of the *Glossopteris* Flora with the Gondwana glaciation. *Proc. Indian Acad. Sci.* **9** : 1-6.
- Schopf JM 1965. Anatomy of the axis in *Vertebraria*. In Hadley JB (Editor)—*Geology and paleontology of the Antarctic. Am. geophys. Union Antarctic Res. ser.* **6** : 217-228.
- Schopf JM 1976. Morphologic interpretation of fertile structures in glossopterid gymnosperms. *Rev. Palaeobot. Palynol.* **21** : 25-64.
- Srivastava AK 1987. *Gondwanophyllites*, a new genus from the Raniganj Coalfield, West Bengal. *Proc. natn. Acad. Sci. India* **B57** : 153-156.
- Srivastava AK 1991. Evolutionary tendency in the venation pattern of Glossopteridales. *Geobios* **24** : 383-386.
- Srivastava AK 1992a. Plant fossil assemblages from the Barakar Formation of Raniganj Coalfield, India. *Palaeobotanist* **39** : 281-302.
- Srivastava AK 1992b. Alien elements in the Gondwana flora of India. In Venkatachala BS & Singh HP (editors)—*Symposium on Four Decades of Indian Palaeobotany*, *Palaeobotanist* **40** .
- Srivastava SC & Maheshwari HK 1973. *Satsangia*, a new plant organ from the Triassic of Nidpur, M.P. *Geophytology* **3** : 222-227.
- Stewart WN 1983. *Paleobotany and evolution of plants*. Cambridge Univ. Press, Cambridge.
- Surange KR & Srivastava PN 1956. Studies in the *Glossopteris* Flora of India-3. Generic status of *Glossopteris*, *Gangamopteris* and *Palaeovittaria*. *Palaeobotanist* **5** : 46-49.
- Zeiller R 1902. Observations sur quelques fossiles des Lower Gondwanas. *Mem. geol. Surv. India Palaeont. indica*. n. ser. **2** : 1-40.