The Palaeobotanist 65(2016): 159–167
0031–0174/2016

Glossopteridales: An intricate group of plants

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(Received 28 December, 2015; revised version accepted 23 February, 2016)

ABSTRACT

Srivastava AK & Srivastava R 2016. Glossopteridales: An intricate group of plants. The Palaeobotanist 65(1): 159–167.

The earliest representative of Glossopteridales is known by the leaves discovered from India and Australia (Brongniart 1822–28) under the genus *Glossopteris* as *Glossopteris browniana* var. *australasica* and *Glossopteris browniana* var. *indica*. Later discovery proved the presence of similar leaves in all the Gondwana continents, i.e. India, Australia, Antarctica, South America and Africa ranging from late Carboniferous to entire span of Permian to early Triassic. Such distribution pattern provides major evidence for the theory of continental drift. As a unified character, these tongue–shaped leaves show reticulate venation pattern and a midrib. Later, non reticulate and non midrib leaves were also considered as ally due to their close association with the leaves of *Glossopteris* and together they are assigned to Glossopteridales consisting of different genera, e.g. *Gangamopteris, Rubidgea, Euryphyllum, Palaeovittaria, Maheshwariphyllum, Rhabdotaenia, Sagittophyllum, Pteronilssonia, Surangephyllum, Gondwanophyllites, Laceyphyllum, Belemnopteris*, etc. Later, cuticular study, discovery of fertile structures in attachment with leaves increased the number of species. In addition, permineralized leaf fossils with anatomical features have also been described under new species of *Glossopteris*.

Fertile structures of glossopterids are mainly discovered in attachment with leaves or in attachment with scale leaves or bracts. Leaf borne fertile structures are known by multiovulate ovule/ seed bearing organ with or without stalk, e.g. *Ottokaria, Dictyopteridium, Scutum, Senotheca, Cistella, Plumsteadiostrobus, Jambadostrobu, Lanceolatus, Vanus, Pluma, Hirsutum,* etc. Scales or bracts showing branched and unbranched cupulate organs are other mode of fertile structures, e.g. *Lidgettonia, Partha, Denkania, Bifariala, Nogoa, Gladiopomum*, *Rusangea, Rigbya, Mooia*, etc. Distinct seed bearing *Arberia, Dolianitia*–type of fructifications, *Eretmonia*, *Glossotheca* type of sporangia bearing scale leaf or bract, *Arberiella*–sporangial mass and a variety of dispersed seeds are also accredited to glossopterids.

Ironically, leaves and fructifications have not yet been found in attachment with stem, however, fossil woods with araucariod pits, e.g. *Dadoxylon/ Araucarioxylon* found in alliance demonstrate their affiliation with glossopterids. *Vertebraria*–axes commonly observed in the sediments exemplify the rooting behaviour of the glossopterids.

Combination of different types of leaves consisting of more than 130 species under closely allied genera, thirty five to forty types of fructifications grouped under multiovulate and branched types together with seed–bearing structures, varied type of morphological, cuticular and structural features amply demonstrate that Glossopteridales had sundry approach for development, endurance and evolution and in all likeness represent different taxonomic characteristics.

Key–words—Glossopteridales, Glossopterid leaves, Fructifications, Evolution, Reconstruction, Gondwana, India.

ग्लॉसोप्टेरिडेल्स : पादपों का जटिल समूह

अश्विनी कुमार श्रीवास्तव एवं रश्मि श्रीवास्तव

सारांश

ग्लॉसोप्टेरिडेल्स का प्राचीनतम प्रतिनिधि *ग्लॉसोप्टेरिस ब्राउनियाना* उपजाति *ऑस्ट्रेलेसिका* एवं *ग्लॉसोप्टेरिस ब्राउनियाना* उपजाति *इंडिका* के रूप में *ग्लॉसोप्टेरिस* वंश के अंतर्गत पत्तियां भारत एवं आस्ट्रेलिया (ब्रॉग्नीआर्ट 1822–28) से खोजी गई। समस्त गोंडवाना महाद्वीपों अर्थात भारत, आस्ट्रेलिया, अंटर्कटिका एवं अफ्रीका में पश्च कार्बोनीफेरस से पर्मियन एवं पूर्व ट्राइएसिक की पूर्ण अवधि तक समान पत्तियों की

उपस्थिति प्रमाणित की है। इस प्रकार का वितरण प्ररूप महाद्वीप अपवाह के सिद्धांत हेतु विशाल प्रमाण प्रदान करता है। सम्मिलित लक्षण के रूप में जीभ आकारी पत्तियाँ जालिकारूप शिराविन्यास प्ररूप व मध्यशिरा दर्शाती हैं। बाद में उनके *ग्लॉसोप्टेरिस* पत्तियों की निकट संबंधता के कारण बिना जालिकारूप एवं मध्यशिरा की अनुपस्थिति वाली पत्तियाँ भी संबंधित मानी गईं और साथ–ही–साथ विविध वंश उदाहरणार्थ *गैंगमॉप्टेरिस, रूबिड्जिया, यूरीफिल्लम, पैलियोविटेरिया, माहेश्वरीफिल्लम, रैब्डोटीनिया, सजिटोफिल्लम, टेरोनिल्सोनिया, सुरंगेफिल्लम, गोंडवानोफायलाइटिस, लेसीफिल्लम, बेलेम्नॉप्टेरिस* इत्यादि सम्मिलित हैं। उनका संबंध ग्लॉसोप्टेरिडेल्स से निर्धारित किया गया है। बाद में हुए उपत्वचीय अध्ययन, पत्तियों से जुड़ी हुए जनन संरचनाओं की खोज ने जाति की संख्या में वृद्धि की। इसके अतिरिक्त, शारीरीय लक्षणों सहित अश्मीभूत पत्ती जीवाश्म भी *ग्लॉसोप्टेरिस* की अभिनव जाति के अंतर्गत वर्णित कर लिए गए हैं।

ग्लॉसोप्टेरिड में जनन संरचनाएं पत्तियों अथवा शल्क–पत्र या पत्राभ से जुड़ी हुए पायी गई हैं। पर्ण जनन संरचनाओं युक्त बहु–बीजांडी बीजांड/बीज धारी अवयव वृंत रहित अथवा समवृंत उदाहरणार्थ : *ऑटोकेरिया डिक्टीओप्टेरीडियम, स्कुटम, सेनोथिका, सिस्टेला प्लमस्टीडिओस्ट्रोबस, जमबडोस्ट्रोबस, लेन्सिओलेटस, वेनस, प्लुमा, हिर्सुटम* इत्यादि से ज्ञात हैं। शाखित एवं गैर–शाखित क्युपुलेट अंगयुक्त पर्ण या पत्राभ जनन संरचनाओं उदाहरणार्थः *लिटजेटोनिया, पार्था, डेंकानिया, बिफैरिआला, निगोआ, ग्लैडियोपोमम, रूसान्जिआ, रिम्बिआ, मूइया* इत्यादि जनन संरचनाओं के अन्य प्रकार हैं। सुस्पष्ट बीज धारण करने वाले फलनों का प्रकार – *आरबेरिया– डोलिएनीटिया, स्पोरैंजिया* युक्त शल्क पत्र या पत्राभ, *इरेटमोनिया, ग्लॉसोथिका, आरबेरियला* – स्पोरंजिअल मास तथा परिक्षिप्त बीजों की उपजाति भी ग्लॉसोप्टेरिड को अधिकृत की गई हैं।

यद्यपि तने से संलग्न पत्तियाँ एवं फलन अभी तक प्राप्त नहीं हुए हैं, फिर भी, आरोकैरियॉएड गर्त युक्त जीवाश्म काष्ठें उदाहरणार्थः *डेडॉक्सीलॉन/आरोकेरीऑक्सीलॉन* के साथ में प्राप्त ग्लॉसोप्टेरिड के साथ अपनी संबद्धता प्रदर्शित करती हैं। अवसादों में सामान्यतः देखे गए *वर्टेब्रेरिया* – अक्ष ग्लॉसोप्टेरिड की जड़ो के संबंध को परिलक्षित करते हैं।

विभिन्न प्रकार की 130 वंश से अधिक निकटतम संबंधित पत्तियाँ, पैंतीस से चालीस प्रकार के फलन, बीज युक्त संरचनाओं, आकारिकीय, उपत्वचीय व संरचनात्मक लक्षणों के साथ–साथ बहुबीजांडी व शाखित प्रकारों के अधीन समूहित फलनों के संयोजन प्रचुर मात्रा में प्रदर्शित करते हैं कि ग्लॉसोप्टेरिडेल्स ने विकास, स्थायित्व एवं क्रमिक विकास हेतु विविध सादृश्य किए तथा समस्त समरूपता विभिन्न वर्गिकीय अभिलक्षण निरूपित करते हैं।

सूचक शब्द—ग्लॉसोप्टेरिडेल्स, ग्लॉसोप्टेरिड पत्तियाँ, फलन, क्रम विकास, पुनर्सरचना, गोंडवाना, भारत।

INTRODUCTION

SINCE the first discovery (Brongniart 1822, 1828–30) *Glossopteris* has created a significant excitement in overall discoveries of different types of leaves, fructifications, stems, seeds, sporangia, roots and other related plant organs from different Gondwana continents, i.e. India, Australia, South America, South Africa and Antarctica (Srivastava, 1997; McLoughlin, 2011). The plant parts have not yet been discovered in attachment with each other and they are invariably discovered in dispersed condition and their occurrence in close association in the same bed indicates that they belong to similar faction. Together they are known as glossopterid group of plants. The group is a major component of the Glossopteris flora of Gondwana and survived during the late Carboniferous to entire Permian Period and some part of early Triassic (Seward, 1910; Rigby, 1966; Plumstead, 1973; Surange, 1975; Schopf, 1976; Appert, 1977; Pant, 1982; Srivastava & Rigby, 1983; Anderson & Anderson, 1985; Archangelsky, 1986; Pigg & Taylor, 1993; Pigg & Trivett, 1994; Prevec *et al.*, 2009; McLoughlin, 2011).

Brongniart (1828) for the first time while describing the leaves of *Glossopteris* observed dichotomizing and anastomozing secondary veins forming reticulation only near the mid vein but the examination of type and figured specimens by me indicate frequent presence of reticulation up to the lateral margin of the leaves as reproduced by Rigby *et al*. (1980). However, after Brongniart, researchers had a liberty to broaden and stretch the morphological characters of *Glossopteris* leaves and instituted a number of species on variable external morphological features. Hence, many leaf genera having analogous features were introduced in the flora especially by Feistmantel (1876–90), e.g. *Gangamopteris*, *Palaeovittaria*, *Euryphyllum*, *Rubidgea*, *Belemnopteris*. Since these leaf forms were found in association with *Glossopteris* they were considered as part of the same group of plants (Dana, 1849; Bunbury, 1861; Feistmantel, 1876–1890; Zeiller, 1902; Doilianiti, 1954). In recent years, many more genera, e.g. *Pteronilssonia* (Pant & Mehra, 1963), *Surangephyllum* (Chandra & Singh, 1986), *Maheshwariphyllum* (Srivastava, 1992), *Laceyphullum* (Chauhan, 2004), *Sagittophyllum* (Pant *et al.*, 1984), *Gondwanophyllites* (Srivastava, 1987) are instituted which are also assigned to glossopterids (Srivastava, 1991, 2004). Approximately 20 genera and 140 species based on impression, compression and permineralized fossils are associated with glossopterid–leaves. Leaves or bracts having attached fructifications constitute about 35–40 genera of glossopterids. Present study has been undertaken to analyze the character evaluation of morphologically allied genera and species of glossopterid leaves and fructifications. The cuticular and permineralized species are correlated with the morphologically identified species (Chandra & Surange, 1979).

GLOSSOPTERID LEAVES

Morphology, taxonomy, stratigraphy and geographical extension of the leaves of *Glossopteris* were discussed by Arber in 1905 for the first time in a monographic publication Catalogue of the Fossil Plants of the Glossopteris Flora in the Department of Geology, British Museum (Natural History) wherein, he discussed the detail history, collection, types of plant fossils described by different workers from different Gondwana localities. Comparison and relationship of Glossopteris flora were also examined with southern and contemporaneous floras of Northern Hemisphere.

Arber (1905) assigned *Glossopteris* to Filicales (?) and associated fossils of scale leaves as part of smaller frond of *Glossopteris*, re–examined the specimens preserved in the museum and redefined the leaves of *Glossoptreris* as "fronds often dimorphic, borne on rhizome–like structure (*Vertebraria*). The larger fronds simple, entire, sessile, petiolate, or contracted at the base to a short petiole. Size and shape greatly varied. Spathulate, lanceolate, ovate, linear, etc. Apex obtuse, acute or emarginated. Midrib well–marked, extending to the apex or impersistent. Secondary nerves numerous, more or less arched, dividing by dichotomy and anastomosing to form a net work, the meshes of which are polygonal and more or less elongate. The smaller fronds or scale–fronds varied in size and shape, strongly concave, as regards nervation similar to the larger fronds, but without a midrib. Fructification not known at present, quite beyond doubt", he further clarified that "the more important characters by which *Glossopteris* may be recognized are simple, entire fronds with a midrib (cf. *Gangamopteris*), and the anastomosing and dichotomising secondary nervation". Most of the description and identification of Glossopterid leaves in present context are based on the characters identified by Arber (1905).

Glossopterid species recorded from different Gondwana countries are mostly common, however, there are some species which are typical to their own region. The species are mainly based on external morphological characters, i.e. size, shape, apex, base, margin, venation pattern, angle of emergence of veins, dichotomy, anastomoses, shape, size of mesh and density of veins near the midvein and near the margin (Chandra & Surange, 1979). The cuticular species are identified on the basis of cellular structures and stomatal features (Pant & Gupta, 1968; Maheshwari & Tewari, 1992). Permineralized specimens collected from Australia and Antarctica have provided good information about the anatomical features of *Glossopteris* (Schopf, 1967, 1970; Pigg, 1990; Pigg & Taylor, 1993; Pigg & McLoughlin, 1997).

The morphologically allied leaf genus *Gangamopteris* originally described as *Cyclopteris angustifolia* by McCoy (1847) is very much similar with the leaves of *Glossopteris* in similar shape, size and reticulate venation pattern but differs remarkably in the absence of midrib. The genus was reported by Feistmantel (1879, 1881) from the early Gondwana sequences. Other related genus *Euryphyllum* introduced by Feistmantel (1879), contains ovate–spathulate leaf characterized by strong radiating veins, emerging from the base, frequently dichotomizing during upward course. There is no reticulation in the leaves. Arber (1905) included it under *Noeggerathiopsis*, but later workers (Maithy, 1965b; Chandra, 1974) included it under glossopterids.

In 1876, Feistmantel described a new genus *Palaeovittaria* consisting of simple leaf showing midrib only in the lower half, having erect spreading lateral veins, recurved near the margin, dichotomizing once or twice but never anastomosing. The genus is common in late Permian flora but now it is also recorded from early Permian sequence (Srivastava, 1992).

Maheshwariphyllum, a leaf very similar to *Palaeovittaria* but differing in having complete midvein is discovered from early Permian sequence of India (Srivastava, 1992).

The genus *Rubidgea* was instituted by Tate (1867) for the oblong, obovate, rounded leaves with obtuse apex; very slender secondary veins, dense, dichotomous, oblique venation pattern, with no indication of anastomosis. Kovacs–Endrody (1977) considers it as a leaf of *Glossopteris* but absence of reticulation makes it different (Maithy, 1965b; Iannuzzy & Tybusch, 2014).

Leaves of *Taeniopteris* described by Royle (1839) and Feistmantel (1876, 1880, 1881, 1882, 1886) from the Permian Gondwana are essentially from Mesozoic age. Pant (1958) and Pant and Verma (1963) observed that the cuticular structures of taeniopteroid leaves recorded from the Permian Gondwana sequences are distinct and compare closely with the cuticular structures of *Glossopteris*. Accordingly, Pant (1958) considered these as glossopterid leaves and instituted a new genus *Rhabdotaenia* to accommodate them. *Rhabdotaenia* has a strong midrib with secondary veins arising almost at right angles to the midrib, dichotomizing 2–3 times and showing absence of anastomosis (Srivastava & Agnihotri, 2010).

Feistmantel (1876) recorded a very interesting genus *Belemnopteris* having simple leaves with broadly sagittate, petiolate base bearing tricostate primary vein with strong median vein and side veins present in sagittate base, secondary veins frequently anastomosing to form reticulate venation pattern (Pant & Chaudhary, 1977; Kovacs–Endrody, 1990).

Dissected margin in *Pteronilssonia* (Pant & Mehra, 1963) having parallel running dichotomizing veins and *Gondwanophyllites* (Srivastava, 1987) showing reticulate venation pattern are also assigned to glossopterids on the basis of their morphology and cuticular features (Srivastava, 1991).

Tricostate nature of primary veins known in the net veined leaves of *Surangephyllum* (Chandra & Singh, 1986), *Sagittophyllum* (Pant *et al*., 1984) and *Laceyphyllum* (Chauhan, 2004) are also correlated as glossopterid on the basis of their morphology and cuticualr features, however, leaves are distinguishable on the basis of nature and extent of two basal veins in sagittate leaves (Srivastava, 2004).

Gangamopteris and *Glossopteris* leaf forms are the most dominant in the Gondwana flora. *Gangamopteris* is mostly found in the older horizons of Permian, whereas, *Glossopteris* is frequently distributed in younger horizons (Maithy, 1974; Kovacs–Endrody, 1976; Srivastava, 1992). Both the genera have extensively been studied and there are about 90 species based on external morphological features and cuticular characters.

Arber (1905) considered the institution of large number of species by Feistmantel superfluous and merged different species, and retained thirteen species for *Glossopteris* and four for *Gangamopteris*. Surange and Srivastava (1957) also tried to categorize the leaves of *Glossopteris*, *Gangamopteris* and *Palaeovittaria* under six groups based on the cuticular characters but this scheme did not get recognition because it has been observed that quite often morphologically identical leaves possess different cuticle and morphologically distinct leaves show similar type of cuticle (Pant & Singh, 1974; Maheshwari & Tiwari, 1992). Chandra and Surange (1979) after revising all the records of Indian species maintained only seventy species of *Glossopteris*. They also examined the cuticular species and tried to establish their identity on the basis of their external morphological characters.

Morphologically, all the leaf genera of glossopterids are grouped under two broad divisions–reticulate and non–reticulate. Reticulate leaves having frequent dichotomising and anastomosing veins include the genera *Glossopteris, Gangamopteris, Belemnopteris, Surangephyllum, Laceyphyllum, Sagittophyllum* and *Gondwanophyllites*, whereas, non–reticulate leaves are distinguished as *Euryphyllum, Rubidgea, Palaeovittaria, Maheshwariphyllum* and *Pteronilssonia*. Reticulate leaves are further divided into dissected margin and leaves having tricostate marginal vein. Correspondingly non reticulate leaves are also divided into simple and dissected leaves (Srivastava, 1991, 1999, 2004).

GLOSSOPTERID FRUCTIFICATIONS

In comparison to sterile leaf forms, fertile structures of glossopterids are limited but they possess variety of characters. Feistmantel (1881, 1882) for the first time described some round spots over the leaf surface and regarded them as the marks of sori. Arber (1905) classified these records under Filicales with a question mark. However, Seward (1910) doubted the spots as a mark of sori and proved it to be a mark of preservational arbritation. Later discovery of ovule/ seed bearing structures in attachment with leaves confirms the gymnospermic nature of glossopterids.

Feistmantel (1881) reported a small linear lanceolate specimen from India as *Dictyopteridium* bearing small tubercles, which was later described by Zeiller (1902) as a rhizome like structure of glossopterids, however, Maheshwari (1965), Surange and Chandra (1975, 1978), Schopf (1976), McLoughlin (1990a, 1995) confirmed the fertile nature of *Dictyopteridium*.

First glossopterid fructification in attachment with *Glossopteris* leaf was discovered by Zeiller (1902) as *Feistmantelia* (a post script changed the name to *Ottokaria*), and described the specimen as a leaf. Seward and Sahni (1920) reinvestigated the type specimen and proved its fertile nature where they found that long stalk of the fertile head is attached to the leaf of *Glossopteris indica*. Later, Plumstead (1956b), Pant and Nautiyal (1965) and Mukherjee *et al.* (1966) expressed various views regarding the nature and affinities of this genus. Surange and Chandra (1975) proposed a reconstruction model and McLoughlin (1990a) recorded new species from Australia. White (1908) instituted *Arberia* an ovule bearing fertile megasporophyll similar to the seed bearing fructification of *Dolianitia* Milan. Its association has been considered with the genus *Gangamopteris* (Chandra & Srivastava, 1981).

Discovery of large number of fertile structures, e.g. *Scutum, Cistella, Lanceolatus, Vanus, Pluma,* along with earlier forms in attachment and in association with glossopterid leaves from South Africa by Plumstead (1952, 1956a, b, 1958a, b) opened a new vision to scrutinize the taxonomic affiliation of glossopterids.

Thomas (1958) described a fertile structure *Lidgettonia* from South Africa. Later, Surange and Maheshwari (1970) and Surange and Chandra (1973a, b) instituted *Partha* and *Denkania*. Holmes (1973) instituted *Austroglossa* where seed bearing organ is attached near the confluence of lamina and petiole of *Glossopteris* leaf. White (1978) described cone type glossopterid fructification *Squamella* having male and female parts separately. Surange and Chandra (1974a, b) and Chandra and Surange (1977a–d) for the first time studied the structural details of the fructifications on the basis of cuticular study carried out by transfer preparation. They instituted genera like *Plumsteadiostrobus, Venustostrobus, Jambadostrobus* and *Kendostrobus.*

Lacey *et al*. (1975) described all together different organization of glossopterid fructifications under the genera *Rigbya*, *Rusangea* and *Mooia* where peltate cupulate structures were found in attachment with scales or bracts bearing number of seeds. Recently, number of glossopterid fructifications are recorded from South Africa and some of them are described under new genera, e.g. *Nogoa* (*Cometia*) (McLoughlin, 2011), *Bifariala* (Prevec *et al*., 2008) and *Gladiopomum* (Anderdorff *et al*., 2002). They are all comparable with multiovulate fructifications described by Plumstead from South Africa.

Apparently, thirty–four ovuliferious genera are found to be associated with glossopterids (Banerjee, 1979, 1984; McLoughlin, 2011). Sporangia bearing glossopterid male fructifications mainly belong to *Eretmonia* and *Glossotheca* having *Arberiella*–like sporangial mass attached with scale leaf or bract (Surange & Maheshwari, 1970; Chandra & Surange, 1977d, e).

Arberia and *Dolianitia* type fertile structures mostly occur in the older horizons of early Permian and apparently demonstrate an archaic plan where pinnate rachis is repeatedly branched and branchlets bear ovules terminally or just below the apex. The fertile structure is not associated with any type of laminar structure (Maithy, 1965a; Rigby, 1972). Schopf (1976) considered the structure as modification and proliferation of cordaitalean fertile structure and hypothesised the cordaitalean origin of glossopterids (Maheshwari & Srivastava, 1992).

Significantly, there are two types of ovulate fructifications, one is associated with vegetative leaves and the other one is found in association with bract or scale. The leaf borne fructifications are mainly comprise different ovule bearing structures attached with the midvein of leaves with or without stalk, their number and positions vary and they may be attached near the base or in middle part of leaf, e.g. *Dictyopteridium, Ottokaria, Scutum, Plumsteadia, Hirsutum, Pluma, Lanceolatus, Vanus, Jambadostrobus, Venustostrobus, Plumsteadiostrobus, Senotheca, Gladiopomum*, *Austroglossa*, *Isodictyopteridium*, *Rigbya* and *Bifariala*. Variously shaped ovulate structures are characterized by dorsiventral compressed receptacle, ovules single or some times more in number, pedicillate or sessile, winged or without wing, normally attached with the midrib of glossopterid–like leaves, in middle or basal portion, often with petiole of the leaf, small in size, large in number, situated over the surface of receptacle. In rolling ovule bearing structure of *Austroglossa* Holmes (1973) is very characteristic where it is attached with the petiole of *Glossopteris* leaf.

Other types of fertile structures, e.g. *Denkania, Lidgettonia*, *Partha*, *Mooia* are found in attachment with scale leaf or bract and their alliance with glossopterids is considered mainly because of the fact that they are discovered in association with its leaves. The ovule bearing stalks (single or many) are arranged in a row on one or both the sides of leaf and are mostly attached with the middle part, and rarely to the lower part of scale or bract. Each stalk bears ovulate structure having single or four ovules.

Rigbya Lacey *et al*., *Rusangea* Lacey *et al*. and *Nogoa* (*Cometia*) McLoughlin show a different pattern where ovules are found on dissected apical margin of cupulate structure having very long contracted base and may represent a modified structure of scale or bract leaves. McLoughlin (1990a, b) doubted the ovulate (?) structure of *Nogoa* since the ovule position in supposedly two fused scales was not specified in the generic diagnosis. While comparing the structural pattern of *Nogoa* he discussed its relative similarity with *Rigbya* and *Rusangea* indicating another line of contraction of glossopterid fructification.

Arber (1905) and Walkom (1928) noticed sporangium–like structure in association with scale leaves. White (1978) instituted the genus *Squamella* for cone–like fructification which occurs in association with scale leaves. In this genus, sporangia and seeds are found separately in attachment with scale leaves in a cone–like structure. According to White (1978) "Cones formed by aggregation of squamous scale–fronds, each composed of a scale and a laminal segment, and each bearing a reproductive structure at the line of junction of scale and lamina. The scale–fronds of *Lidgettonia australis* White are incorporated in *Squamella.* There are small, gangamopteroid, sterile leaves associated with the cone and some of these show serial modification towards scale–fronds with induration of tips. Squamae are deciduous and are mostly fossilised separately from the laminal segments, sporangial clusters, and residual cores. The cones were borne at the ends of branchlets which had leaves in whorls or close spirals. Modified leaves formed a whorl between the cone and the foliage leaves. There is evidence that ripening of the cones and shedding of the sporangia was achieved by elongation of the laminal sections of scale–fronds. In *S. australis* the reproductive structures are male sporangia of *Arberiella* type (Pant & Nautiyal, 1960). In *S. ampla* they are assumed to be male. A specimen is described as *S. ovulifera.* It bears stalked seeds at junction of scale and lamina". This is an entirely different type of glossopterid fructification. Although complete specimen is not available but there are number of specimens of detached scale leaves in the Gondwana sediments whose affiliation can be correlated with *Squamella*–type fructification.

The male fertile structures of *Glossopteris* are normally described under *Eretmonia* Du Toit and *Glossotheca* Surange and Maheshwari showing branched or unbranched stalk attached with the median portion of fertile scale or bract having bunch of terminal sporangia similar with *Arberiella* type sporangium (Surange & Maheshwari, 1970; Surange & Chandra, 1978). Detached specimens of *Arberiella*–type sporangium are well known in the Gondwana sediments and on maceration they yield large number of disaccate pollen comparable with *Protohaploxypinus*/ *Faunipollenites*–type pollen (Pant & Nautiyal, 1960). *Mohudaea* Banerjee, *Bankolea* Banerjee and *Kendostrobus* Surange and Chandra have also been associated with glossopterid fructification but they need further examination to ascertain their affinity with glossopterid group of plants (Srivastava, 1999).

GENERAL DISCUSSION

Managing, controlling, assigning glossopterid leaves and fructifications to a proper taxonomic level is always a dilemma. During the last 185 years or so glossopterid leaves which were described in simple terms have attained prominence in Gondwana palaeobotany and whosoever worked on this plant fossil, viewed it on their own way. The affiliation and affinity of the group has variously been discussed by many workers ,e.g. lycopsids (Bohlin, 1981), pteridophytes (Feistmantel, 1880–90; Arber, 1905), angiosperms (Melville, 1960, 1983; Retallack & Dilcher, 1981), cycads (Lacey *et al*., 1975; Leary, 1993), Cordaitales and Gnetales (Schopf, 1976), conifers

(Rigby, 1978), Ginkgoales (Meyen, 1987; Pant, 1999) and seed ferns (Arnold, 1948; Surange & Chandra, 1978; Sporne, 1967).

Surange and Chandra (1978) definitely placed the glossopterids under gymnosperms and considered fructifications associated with scale leaf/ bract under the order Pteridospemales and leaf borne multiovulate fertile forms under Glossopteridales. They further classified them under different families, e.g. Parthaceae, Lidgettoniaceae, Denkaneaceae; Cistellaceae, Scutaceae and Hirsutaceae. Meyen (1984) included the order Glossopteridales under Pinophyta and instituted 3 families Arberiaceae, Ottokariaceae and Lidgettoniaceae. Maheshwari (1990) classified the group under two families, viz. Dictyopteridiumaceae and Eretmoniaceae.

A comprehensive study has helped to classify the fructifications under four families of gymnosperms, namely Arberiaceae having large sized ovules mostly situated on the tip of branched flattened axis, Dictyopteridiumaceae consisting of most common type leaf borne multiovulate fructification. Rigbyaceae representing fan–shaped fructifications having seed on distal lobes and Lidgettoniaceae containing scale leaf or bract with cupulate structure having slender axis attached to the median region. However, this categorization needs further improvement to incorporate the different pattern found in *Ottokaria* (Zeiller, 1902) and *Austroglossa* (Holmes, 1973) having ovule bearing structure in attachment with the petiole of *Glossopteris* leaf and S*quamella*–like cone bearing micro and megasporophyll found separately showing progressive modifications from small leaves to scale leaves, aggregated into a cone situated on a foliage bearing branchlets (White, 1978). The examples indicate further variation and complexity in glossopterid fructifications. Recently investigated permineralized specimens of ovule–bearing reproductive organs from Beardmore Glacier region, Antarctica (Taylor *et al.* 2007) demonstrate two basic types of ovulate fructifications as originally demonstrated by Surange and Chandra (1975, 1978).

The leaves of glossopterids also indicate certain categorization on the basis of their morphological structures. Broadly, they are recognizable into reticulate and non reticulate forms. Further, both the groups show successive development of midrib. The appearance of dissected margin and tricostate nature of midvein enhances the intricacy of leaf morphology. Thus, there are five type of leaves, viz. reticulate with midrib (*Glossopteris*), reticulate without midrib (*Gangamopteris)*, reticulate dissected margin (*Gondwanophyllite*s), non reticulate–dissected margin (*Pteronilssonia*) and reticultate with basal tricostate midvein (*Belemnopteris, Surangephyllum*). Occurrence of such leaves at different stratigraphic levels *vis a vis* their alteration are allocated with the developmental pattern of leaf character (Oliviera, 1978; Srivastava, 1991, 1992, 1999, 2004; Maheshwari & Srivastava, 1992). Anatomical study also supports the variation in the nature of glossopterid leaves (Schopf, 1970; Pigg, 1990; Pigg & Taylor, 1993; Pigg & Trivett, 1994).

Although, exact nature of attachment of leaf with stem in glossopterids is not discernible Pigg and Nishida (2006) have found well preserved permineralized specimens of leaves in attachment with stem, root and ovule bearing organs from Antarctica. Interestingly, they observed different types of fertile structures in attachment with different leaves and on the basis of such association they suggested different reconstruction types named after the leaves such as *Glossopteris schopfii* plant, *Glossopteris skaarensis* plant, and *Glossopteris homevalensis* plant. Associated fertile features are not known in *G. schopfii* but leaf and stem are found in attachment.

Earlier workers have proposed different types of reconstruction models, e.g. irregularly branched small herbaceous plant (Seward, 1910), cycad–like (Rigby, 1966), large size branching tree (Plumstead, 1958a, b; Gould & Delevoryas, 1977; Pant, 1962, 1977; Pant & Singh, 1974; Retallack & Dilcher, 1981) and *Ginkgo*–like reconstruction model (Pant, 1999).

Morphology, cuticle, anatomy and gradational characteristics of leaves and fertile forms of glossopterids comprehensively put forward the theory of heterogeneous compassion in glossopterid group of plants as suggested by many workers. Anatomically preserved specimens showing different types of fructifications with different types of leaves strongly support the varied nature of glossopterids. Variety of leaves and fructifications propose that the group in all possibility had multiple choice, and survived and developed adopting different course of morphological, anatomical and reproductive strategies which in all likeness recount the different taxonomic affiliation of glossopterid group of plants.

Acknowledgements—*Sincere thanks are due to the organizers of the Conference for inviting us to deliver a talk and nominating one of us (AKS) as a member of the National Advisory Committee. AKS is also grateful to Prof. Sunil Bajpai, Director, BSIP for logistic support to participate in the Conference. Thanks are due to Dr Rajni Tewari, Organizing Secretary for her kind invitation and necessary arrangements for participation in the Conference and extending help and cooperation.*

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