Venation patterns in some early Glossopteris

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Glossopterids were the dominant plants in Gondwana during the Late Permian. They characterized the plant assemblages and gave their name to the flora of the time. Although Glossopteris is characterized by anastomosing secondary venation, the oldest known forms placed within this form-genus often have only rare cross connections between adjacent parallel secondary veins or possibly none. At least some of the taxa placed within the form-genus probably evolved from plants that bore leaves with dichotomously branched secondary veins.

Key-words—Glossopteris, Venation pattern, Permian, Gondwana.


THE form-genus Glossopteris was established by Brongniart in 1828 for leaves with a thick midrib and anastomosing veins. The leaves are spatulate, ovate, or linear-lanceolate, ranging in length from 3 to 40 cm (Anderson & Anderson, 1985).

Leaves of similar morphology have been traditionally lumped under a single genus, Glossopteris, but these are now known to have borne a variety of fructifications (Plumstead, 1952; McLaughlin, 1990 and references cited therein). Thus, Glossopteris is not a single genus but a diverse group at a higher taxonomic level (Chandra & Surange, 1979; Archangelsky, 1990). Several authors have suggested separate lineages within the glossopterids (e.g., Surange & Chandra, 1978).

Glossopteris appears suddenly in the Permian over much of Gondwana immediately following widespread southern hemisphere glaciation (Sahni, 1939; and numerous other authors). Several suggestions have been made regarding the origin of Glossopteris. Melville (1969) suggested that Glossopteris evolved from Gangamopteris. This idea was expanded to include Noeggerathiopsis, Rubidgea, Euryphyllum, Palaeovittaria, and Gangamopteris as ancestors (Bernardes de Oliveira, 1978; Srivastava, 1991).

Of these, only Gangamopteris has anastomosing venation, the others have dichotomously branching veins. Palaeovittaria has a few cross connections between veins. Although Palaeovittaria has a midrib in the basal two-thirds, the other leaves lack a midrib. According to the theories on Glossopteris origin cited above, central veins merged to form the midrib common to all Glossopteris.

The almost complete absence of anastomoses in the earliest leaves assigned to Glossopteris (G. wilsonii and G. communis) supports the evolution of Glossopteris as outlined by Bernardes de Oliveira (1978) and Srivastava (1991). In her table 1, Bernardes de Oliveira (1978) shows a possible sequence to Glossopteris with fully anastomosing venation. Srivastava (1991), in his figure 1, shows a similar path of evolution. The author's
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Text-figure 1-A, Cross connections in *Glossopteris wilsonii* consist of brief converging of adjacent veins; B, A short vein segment connecting two adjacent veins; C, Cross connections in *Glossopteris rioaensis* (Drawn from specimen 1789, Instituto de Geociencias, Universidade de Sao Paulo); and D, Venation in *Glossopteris wilsonii* from Chubut Province, Argentina (ISM specimen 118B/Arg. 2)

observations in Argentina and Brazil support these generalizations.

The overall trend of *Glossopteris* evolution (Lele, 1976) from narrow to coarse mesh is consistent with a derivation from an ancestor with open dichotomously branching secondary veins.

Examination of the venation of the oldest known *Glossopteris* leaves provides clues to the origin of this group of plants. Melville (1969) devised a system of appropriate Greek letters to identify various junction forms of *Glossopteris* venation. According to Melville (1969), "The simple dichotomy, gamma, is the most frequent and, on the basis of the fossil record, the most ancient."

Venation patterns in *Glossopteris* from basal Permian strata in South America provide possible evidence regarding the ancestry of at least part of the group. Although *Glossopteris* is characterized by anastomosing venation, the oldest known foliage placed within the genus, for example *G. wilsonii* of Patagonia and *G. communis* of Brazil, has open dichotomously branched secondary veins with few or no cross connections (Archangelsky et al., 1981; Fittipaldi & Rosler, 1985).

Study of the oldest known *Glossopteris* in Argentina reveals an evolutionary pattern of secondary venation. Specimens of *G. wilsonii* from Chubut Province of southern Argentina were studied at the Argentine Museum of Natural History in Buenos Aires. This material is from the basal Permian or uppermost Carboniferous (Stephanian?) (Leary, in press).

Secondary veins depart the midrib at low angles, frequently 10°, and as low as 5°. The veins arch toward the margin, reaching angles of 55° to 65° at mid-arch. Angles at the leaf margin are 55° to 75°. Veins divide dichotomously one to three times. Only on large, well-preserved specimens can rare anastomoses be observed. Anastomoses occur near the midrib (Text-figure 1D), otherwise the secondary veins are parallel for most of their
length as they curve toward the leaf margin. Although true anastomoses are very rare, a limited number of cross connections are sometimes present. Cross-connections are usually in the form of two adjacent veins bending toward one another and touching before separating and curving back to a parallel course (Text-figure 1A).

Examination of a number of specimens of *Glossopteris* from lowermost Permian strata of Brazil supports this interpretation of the developmental pattern of secondary venation. Specimens from the Itare Formation (Early Permian) of the Parana Basin and the slightly younger Rio Bonito Formation were examined at the Geosciences Institute, Federal University of Rio Grande do Sul, Porto Alegre, Brazil. Additional specimens from the Rio do Rasto Formation (Upper Permian) at the Geosciences Institute, University of Sao Paulo were also examined in this study.

Because of the fragmentary nature of many specimens, specific determinations are imprecise. Despite this nomenclatural problem, patterns within the venation are clear.

Secondary veins depart the midrib at low angles: less than 20°, frequently 10°, and even as low as 5°. The veins arch toward the margin, reaching angles of 35° to 70° at mid-arch. Angles at the leaf margin are 45° to 75°. Veins divide dichotomously one to three times. No true anastomoses were observed although a limited number of cross connections are present.

**DISCUSSION**

As Rigby (1984) illustrated, strands within the secondary veins of *Glossopteris* do not interconnect but merely touch and then run adjacent to one another before separating again at the next vein division. This suggests a development from originally parallel, dichotomously branching veins. A later step in the development of true *Glossopteris* anastomosing venation, as evidenced by specimens from South America, is the presence of a short vein segment connecting two adjacent veins (Text-figure 1B).

Simple anastomoses consisting of nearly parallel, dichotomous veins with numerous cross connections, e.g., *Glossopteris rioastensis* (Text-figure 1C) are also present in Early Permian *Glossopteris*. Traditional complex anastomosing venation is present in Argentina and Brazil by Mid-Permian (e.g., *G. tortuosa* and *G. occidentalis*). Seward (1910, p. 508) commented on a specimen from a Permo-Carboniferous sandstone of Vereeniging (Transvaal) that was referred to *Glossopteris angustifolia var. taeniopteroides* "...on account of almost complete absence of any cross-connections" (Seward & Leslie, 1908). Seward (1910) compared the specimen to *Lesleya*, a Permo-Carboniferous leaf with open, dichotomous venation.

Anastomosing venation in other pteridosperms was derived from dichotomously branching veins (e.g., *Lonchopteris/Alethopteris, Linopteris/Paripteris*, and *Reticulopteris/Neuropteris*) (Laveine et al., 1989). Thus, it is conceivable that the characteristic anastomosing veins of *Glossopteris* were derived from leaves with arched, dichotomously branched veins.

**CONCLUSION**

The sequence observed in Argentina and Brazil of increasing cross connections between veins, beginning with mere touching of adjacent, otherwise parallel veins, is consistent with an origin from a leaf with open, dichotomous venation.

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