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.

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सारॉंश

कुछ प्रारंभिक *ग्लॉसोप्टैरिस* में शिराविन्यासों के प्रतिरूप

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अन्तिम पर्मियन युग के दौरान गोंडवाना क्षेत्र में ग्लॉसोप्टैरिड्स की बहुतायत थी। इन पादपों ने तत्कालीन पादप समुच्चय को अभिलक्षणित करते हुए उस वनस्पतिजात को अपना नाम दिया। यद्यपि *ग्लॉसोप्टैरिस* द्वितीयक शाखा जालित शिराविन्यास द्वारा अभिलक्षणित हुए हैं, इस रूप प्रजाति के अन्तर्गत् प्राप्त प्राचीनतम् ज्ञात रूप संभवतः शिराओं के बीच प्रायः आसन्न समानान्तर द्वितीयक अथवा नगण्य दुर्लभ अनुप्रस्थ सम्बन्ध रखते हैं। इस रूप प्रजाति के अन्तर्गत् कुछ वर्गक सम्भवतः उन पादपों से विकसित हुए हैं, जिनमें द्विभाजक शाखाओं वाली द्वितीयक शिराओं की पत्तियाँ होती थीं।

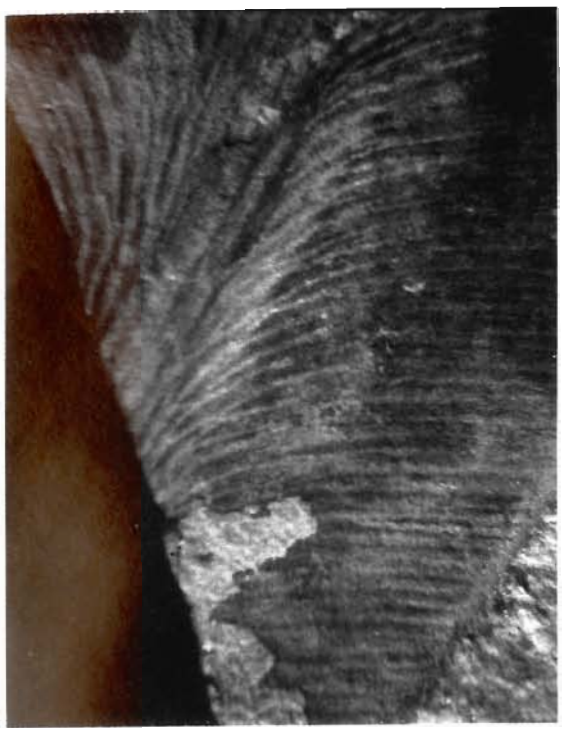
THE form-genus *Glossopteris* was established by Brongniart in 1828 for leaves with a thick midrib and anastomosing veins. The leaves are spatulate, ovate, or linear-lanceolate, ranging in length from 3 to 40 cm (Anderson & Anderson, 1985).

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 Olivera (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



observations in Argentina and Brazil support these generalizations.

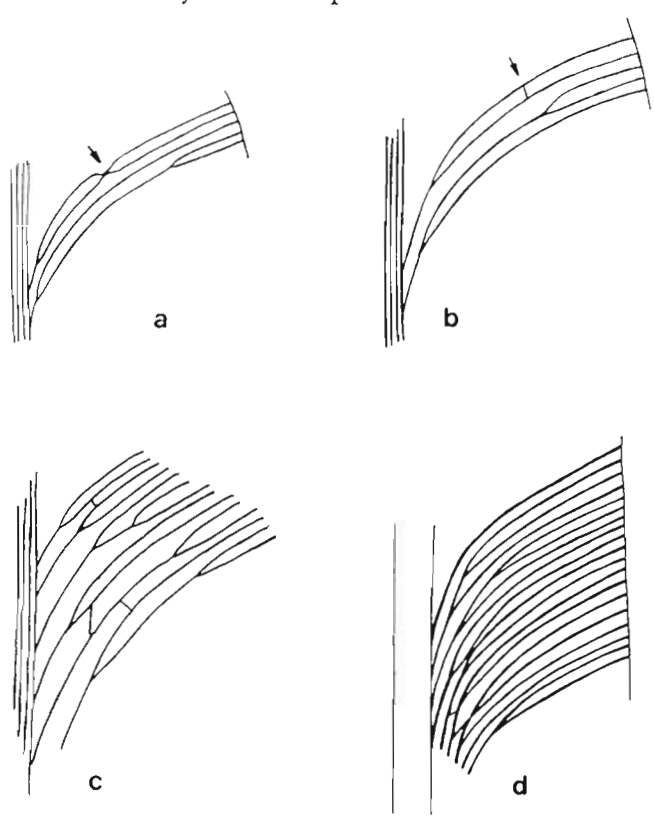
The overall trend of *Glossopteris* evolution (Lele, 1976) from narrow to coarse mesh is consistent with a derivation from an ancestor with open dichotomously branching secondary veins.

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



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 rioastensis*. (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)

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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REFERENCES

Anderson JM & Anderson HM 1985. *Palaeofloras of southern Africa: Prodromus of South African magafloras, Devonian to Lower Cretaceous.* Balkema, Rotterdam.

Archangelsky S 1990. Plant distribution in Gondwana during the Late Paleozoic. *In:* Taylor & Taylor (Editors)—*Antarctic paleobiology: Its role in the reconstruction of Gondwana* : 102-107. Springer-Verlag, New York.

Archangelsky S, Archangelsky A & Cuneo R 1981. Algunos elementos paleofloristicos de las Formaciones Piedra Shotel y Nueva Lubecka, Permico Inferior, Estancia la casilda, Provincia de Chubut. *Ameghiniana* **18** (3/4) : 207-220.

Bernardes-de-Oliveira MEC 1978. Ensaio sobre a utilizacao de caracteres biometricos das Glossopteridofitas em estratigrafia. *Bol. IG. Inst. Geociencias, USP.* 9 : 91-95.

Chandra S & Surange KR 1979. *Revision of the Indian species of Glossopteris. Monograph* 2. Birbal Sahni Institute of Palaeobotany, Lucknow, India.

Fittipaldi FC & Rosler O 1985. A cuticula de *Glossopteris communis* da Formacao Rio Bonito no Estado do Parana. *Eighth Congr. Brasil Paleont. 1983. MME/DNPM, Ser. Geologia 27 Paleont. Estratig.* 2 : 579-595.

Laveine J-P, Shanzhen Zhang & Lemoigne Y 1989. Global palaeobotany, as exemplified by some Upper Carboniferous pteridosperms. *Bull. Soc. belge Geol.* **98**(2) : 115-125.

Leary RL (in press). Comparison of Late Carboniferous Euramerican fossil plant *Lesleya* with the Permian *Glossopteris* of south America. *XII Carboniferous Congress, Buenos Aires, Argentina, 1991.*

Lele KM 1976. Palaeoclimatic implications of Gondwana floras. *Geophytology* 6(2) : 207-229.

McLoughlin S 1990. Some Permian glossopterid fructifications and leaves from the Bowen Basin, Queensland, Australia. *Rev. Palaeobot. Palynol.* **62** : 11-40.

Melville R 1969. Leaf venation patterns and the origin of the angiosperms. *Nature* **224** : 121-125.

Plumstead EP 1952. Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves. *Trans. Geol. Soc. South Africa* **55** : 281-329; 10 pls.

Rigby JF 1984. The origin of the *Glossopteris* Flora-Some thoughts based on macrophyte remains. *Evolutionary Botany and Biostratigraphy, A.K. Ghosh Commem. Vol.* : 19-28. West Bengal Botanical Society, Calcutta.

Sahni B 1939. The relation of the *Glossopteris* flora with the Gondwana glaciation. *Proc. Indian Acad Sci.* 9(1) : 1-6

Seward AC 1910. *Fossil plants.* Cambridge Univ. Press 2, 624pp.

Seward AC & Leslie TN 1908. Permo-Carboniferous plants from Vereeniging. *Quart. Jour. Geol. Soc.* **64** : 109.

Srivastava AK 1991. Evolutionary tendency in the venation pattern of Glossopteridales. *Geobios* **24** (4) : 383-386.

Surange KR & Chandra S 1978. Morphology and affinities of *Glossopteris. Palaeobotanist* **25** : 509-524.