The plants of glossopterids : a reappraisal and review

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New information about the structural features of the plants of *Glossopteris* and related genera is reviewed in the light of advances made on the basis of permineralized fossils of the group mainly those which have been lately discovered in Antarctica. It is pointed out that the permineralized remains have merely confirmed, although far more vividly, the presence of anatomical features which had been inferred earlier by the study of impression and compression (incrustation) fossils of the glossopterids. The author concludes that the study of impression, compression (incrustation) fossils is as important as that of permineralized remains and many a time the former furnish details which are difficult to observe in permineralized remains.

Key- words — Glossopterids, Anatomy, Permineralized fossils, Impressions, Compressions (incrustations).

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सारांश

ग्लॉसॉप्टेरिडी पौधे : एक पुनर्व्याख्या एवं समालोचना

दिव्य दर्शन पन्त

ग्लॉसॉप्टेरिडी तथा सम्बद्ध प्रजातियों के पौधों के संरचनात्मक लक्षणों के बारे में अभी हाल में अंटार्कटिका से एकत्रित इसी समूह के पारखनिजीकृत पादपाश्मों के अध्ययन से उपलब्ध नई जानकारी की समीक्षा की गई है। यह प्रदर्शित किया गया है कि पारखनिजीकृत अवशेषों से केवल शारीरीय लक्षणों की उपस्थिति की ही पुष्टी होती है जैसा कि पहले ग्लॉसॉप्टेरिडी पौधों की छापों एवं संपीडनाश्मों के आधार पर अनुमान लगाया गया था। समीक्षा के आधार पर यह निष्कर्ष निकाला गया है कि छापों एवं संपीडनाश्मों का अध्ययन भी उतना ही महत्वपूर्ण है जितना कि पारखनिजीकृत अवशेषों का बहुधा छापों एवं संपीडनाश्मों से ऐसी विस्तृत जानकारी मिल जाती है जो कि पारखनिजीकृत अवशेषों से बहुत ही मुश्किल से मिल पाती है।

NEARLY twenty years ago I published an account of "The plant of *Glossopteris*" (Pant, 1977) wherein I tried to present a reconstruction of the plant based on studies of impressions and compressions of the different fragments of its vegetative and reproductive organs. A recent article by Pigg and Trevitt (1994) has now triggered the necessary stimulus in me to review my earlier account of the plant which is duly cited by the above authors in their references but, unfortunately, without mentioning that my associates and I had arrived at practically the same conclusions much earlier about the structural features besides additional details of the various organs of the *Glossopteris* plant on the basis of our studies of its different organs in the compressed state. Unfortunately, two papers by Pant and Nautiyal (1965, 1984b) on the compressed seed bearing, fructifications whose permineralized remains are mentioned as "megasporophylls" by Pigg and Trevitt (1994), seem to have been missed in being cited by them. However, their references to Pant (1982, 1987) imply that these authors may have been aware of the work.

IMPRESSIONS AND COMPRESSIONS VERSUS PERMINERALISATIONS

At the outset it is important to say that careful studies of compressed fossils preserved as incrustations, based on observations of parts and counterparts, are often as informative as permineralizations (Whittington & Morris, 1985; Gould, 1991). Organs which became naturally macerated by the plant substance becoming preserved in various states of degradation, during fossilization, are often rendered more or less translucent and they show various details of internal structure under the microscope, particularly when these are pulled out in cellulose acetate and mounted in Canada balsam. When plant parts of sizeable thickness are compressed in rock matrix, e.g., bunches of sporangia which lie in slightly differing planes, above or below the plane of fracture of a hand specimen, they can be carefully excavated out of the matrix or they can be extracted out by carefully dissolving the rock piece in HF, if silicified, or HCl if calcified. Observations of compressions in oil can reveal the presence of hairs or other similarly protruding structures (Pant, 1958). Harris (1938) was able to show that the highly controversial fossils of *Naiadita*, belonged to a bryophyte by studying them in oil.

In fact, sectional views of permineralized remains are often inadequate for a clear understanding of the form and, therefore, some crustaceans (Scourfield, 1926) and cyanobacteria (Croft & George, 1959) had to be observed directly in broken chips of rock by putting them in oil and observing them under an oil immersion objective but without sectioning as is usually the practice for observing permineralized remains. Compressed fossils have often yielded important information about the hidden face of incrustations of compressions by preparing transfers with Walton's transfer technique (Walton, 1923). This was actually done by Pant and Nautiyal (1984) in the case of *Ottokaria*, the female fertiliger of *Glossopteris* where they could observe attached seeds on the usually uneven and therefore firmly rock-attached concave faces of the fructifications.

It is important to mention that even impressions of fossils, when they are well preserved in fine-grained rock matrix, can show features of epidermal cells, stomata, hairs and other superficial structures in the parts and counterparts under oblique lighting or in oil.

Compression or telescoping of an organ in different directions can yield information about its shape in different directions, e.g., the platyspermic and radiospermic character of seeds (Pant, 1958; Pant & Nautiyal, 1960) the form of sporangia and annulus (Pant & Khare, 1960) and about internal structures like presence of fibres and vascular strands and nucellar surface and tissues, pollen chambers, megaspore membranes, gametophytic tissues and archegonia and starch grains inside cells of glossopterid seeds have been described in detail by Pant (1958), Pant and Nautiyal (1960), Pant and Srivastava (1964) and Pant *et al.* (1985).

No doubt permineralized fossils can yield indubitable information about the details of internal structure of plant fossils but, as mentioned above, the details of surface and internal features inferred from compressions are in no way less significant. It is actually important to mention that compressions of fossils of several extinct groups of plants which have not been found preserved in permineralized condition have been vividly deciphered from such remains without having a single permineralized fossil. This is also true of many early vascular plants from the Late Silurian and Devonian, numerous Carboniferous, Permian, Triassic, Jurassic, Cretaceous and Cainozoic fossils like those of many Palaeozoic ferns, pteridosperms, the Caytoniales, Corystospermales, Peltaspermales, Pinophytes and Ginkgophytes. Last but even more important are the Cretaceous and Cainozoic flowers (Friis, 1983, 1985, 1990; Friis *et al.*, 1987) which are not usually found permineralized.

Many of the above mentioned plants are known only in the form of impressions and compressions (incrustations) but their structural details are almost as well known as those of permineralized fossils. As is true for almost all fossils, there are many mute points about their growth habits and reconstructions like what is true about the glossopterids, e.g., the growth habit of one of the best known pteridosperms, *Lyginopteris oldhamia- Sphenopteris hoeninghausii-Calymmatotheca-Lagenostoma,* is largely a matter of conjecture. Indeed that is also true about some of the best known Mesozoic pteridosperms like the Caytoniales or Corystospermales. The stems of these two groups are almost unknown although I would like to think that their foliage and fructifications were borne on sizeable trees or climbing shrubs. At least their disaccate pollen grains would suggest that

Caytonanthus and *Pteruchus* microsporangia may have been held high for the wide scatter of such pollen grains through air currents. Pant (1949, 1987, 1992) has suggested the possibilities of pollen rains in forests of Glossopteris flora.

RELATIVE ADVANTAGES OF COMPRESSION FOSSILS OVER PERMINERALIZATIONS

In fact, compressions can many a time vividly indicate and confirm the unclear details of permineralized fossils which can be studied only in almost repetitive sections and thereafter reconstructed. Compressions reveal the entire external form of fossils which permineralized parts may fail to show. A classic example of such studies is furnished by the observations made by Surange (1952) and Chaloner (1958) on *Bensonites fusiformis*, the magasporangium of *Stauropteris burntislandica*. Surange observed *Bensonites* only in sections of permineralized material and could not ascertain the number and the form of the megaspores inside the megasporangia, whereas Chaloner could find the entire megasporangia in macerations of rock matrix and he could also extract them from their permineralized material. He could thus show that the megasporangium of *Bensonites* contained a tetrahedral tetrad of two large megaspores juxtaposed with two small ones and all of them were enclosed in a membrane which he called *Didymosporites*. It is, therefore, important, nay many a time essential for students of permineralized fossils not to overlook the earlier achievements of those who have studied impressions and compressions and found structural details which are confirmed by their studies of permineralized fossils.

Unfortunately, the article by Pigg and Trevitt (1994) while highlighting the details of internal structure revealed by permineralized fossils gives the impression that many of the structural features of glossopterid gymnosperms were discovered for the first time by studies of permineralized fossils. This is far from being true since earlier observations on impression and compression fossils had already revealed many structural details which have no doubt been confirmed vividly by studies of permineralized fossils. I would particularly like to mention that the presence of epidermal hairs, sunken stomata, stomatal pits, subsidiary cells with overarching papillae, polar and lateral lignin lamellae of guard cells, presence of a hypodermis, palisade and spongy mesophyll cells, fibres in vein meshes and along veins, multiple veined midribs, upwardly curved or almost joined veins at the margins, vein and midrib bundle xylem showing scalariform and pitted elements had been observed by the author (Pant, 1958) and his group of workers (Pant & Gupta, 1971; Pant & Singh, 1971, and others).

It must also be mentioned that the difference between leaves of *Glossopteris* and other glossopterids like *Belemnopteris* (Feistmantel, 1976, 1981; Lacey *et al.*, 1974, 1975; Pant & Chowdhury, 1977). *Sagittop- hyllum* (Pant *et al.*, 1984; Pant & Chauhan, 1996) and others would have been difficult to decipher if only permineralized fossils had been available to us.

Our studies of compressions have in fact helped us also in allaying our own doubts about certain features of glossopterid fossils. When Pant (1958) found seeds of *Spermatites crystallinus* showing crystal marks over the outer cuticle, a lurking doubt remained about the crystal marks coming from the rock matrix or belonging to the seed surface. However, when Pant and Nautiyal (1960) found impressions of seeds on the leaf cuticles of *Glossopteris* and these showed cell outlines and crystals only in the region of the impressions of seeds, it became at once clear that the crystals belonged to the seed surface. When leaf cuticle of *Glossopteris* also showed impressions of sporangia of *Arberiella* and also disaccate spores prevailingly shed by sporangia of *Arberiella* it became clear that these were shed over glossopterid leaves due to their being held above the leaves in the life of plants. Thus even though permineralized fossils have their strong points and advantages, over compression and impression fossils, there are also other aspects in which compression fossils are superior to permineralized ones.

ACHIEVEMENTS OF STUDIES ON PERMINERALIZED GLOSSOPTERID FOSSILS

In view of the above mentioned facts I am compelled to point out that an otherwise excellent summary of the achievements made by studies of permineralized fossils has unfortunately erred in making it appear that the structural features of the glossopterid gymnosperms were discovered for the first time by studies of permineralized fossils when many of them had been known already on the basis of earlier studies of compressions and impressions. *The credit of the permineralized fossils lies mainly in vividly confirming structural features which had been inferred from impression and compression fossils and we must all admit that is the contribution of paramount importance made by studies of permineralized fossils.*

BLECHNOXYLON IS A *GLOSSOPTERIS*

There are also some other points about the account of Pigg and Trevitt (1994) which need correction. These authors have, for example, mentioned that *Blechnoxylon talbragarense* (Etheridge, 1899) "was recognized as a seed plant by Seward (1910) particularly on the basis of its typically gymnospermous stem as cut in transverse section" but they did not mention that Seward (1910, p. 510) had instead unequivocally stated "Although the leaves of *Blechnoxylon* are much smaller than those of *Glossopteris*, I am now disposed to regard the genus as closely allied or even generically referable to *Glossopteris*. The crowded disposition of leaves is like that in *Glossopteris* ..... The absence of reticulum of anastomosing veins can no longer be considered a fatal objection to the suggestion that the Australian type may be a species of *Glossopteris*". Seward had nowhere suggested that *Blechnoxylon* was a seed plant and the above mentioned statements of Seward were supported by Pant and Singh (1974). Subsequently, Pant and Nautiyal (1984a) re-examined the type material and they supported Seward's ideas on the basis of their having seen a few cross connections between forks of adjacent veins particularly in Museum Slide no. AM 152 (Original No. 6309) and other resemblances between leaves of *Glossopteris talbragarense* and leaves of *Glossopteris*, like those of *G. hispida* (Pant, 1958) in the presence of multicellular hairs. It is necessary to point out that small leaves too are no bar to the reference of *G. talbragarense* to *Glossopteris* since even smaller leaves of that genus have been described by Zeiller (1896) and Pant and Nautiyal (1987).

INTERGRADATION OF PERMINERALIZED AND OTHER KINDS OF FOSSILS

In connection with this discussion on impression, compression (incrustation) and permineralized fossils it is important to point out that these various kinds of fossils intergrade, e.g., a permineralized fossil can be more or less compressed and partially decayed out during preservation. Likewise a compression (incrustation) fossil may also be partially permineralized and infiltrated with mineral matter. This was actually observed in the wood of *Buriadia* by Pant and Nautiyal (1967).

VERTEBRARIA COULD BELONG TO A ROOT OR STEM

It must also be pointed out that attached leaves of *Glossopteris* and other glossopterids have been reported by various workers from time to time. Zeiller (1896), Oldham (1897), Dolianiti (1954) and Pant (1977) found them attached to axes which presented features of *Vertebraria* but others found them attached to axes which lacked typical rectangular areas of *Vertebraria* (Walton & Wilson, 1932). Vascular tissues of *Vertebraria* were first described by Walton and Wilson, (1932) and later by Pant (1956), Pant and Singh (1968) and others. Authors like Schopf (1965), described permineralized axes of *Vertebraria* and thought that their exarch protoxylem indicated that these were roots. But it was pointed out by Pant and Singh (1974) and Pant (1977) that primitive stems were quite like roots in having exarch protoxylem and *Vertebraria* could even be a stem. Indeed Pant (1977) thought that *Vertebraria* axes could represent roots as well as stems. Pant (1958b) also described young roots of *Vertebraria* where he could even see endogenous root primordia slightly behind root apices as they occur in roots. Some of these thin roots were attached to *Vertebraria* axes. *Vertebraria* could indeed be a rhizomorph an organ like stigmarian axes which can neither be termed a root nor stem. These organs clearly suggest that Nature often defies strict definitions.

CONCLUSION

The present reappraisal and review of the work on glossopterids by various workers reminds me of J.G. Saxe's poem.

"It was six men of Indostan"
(or any other country)
"To learning much inclined
Who went to see the elephant
(Though all of them were blind).
....
....
And so these men of Indostan
Disputed loud and long
Each in his own opinion
Exceeding stiff and strong,
Though each was partly in the right,
All were in the wrong"

Like the six men different palaeobotanists either observe impressions, compressions (incrustations) or permineralizations of the fragmented plant bodies. They all obtain only partial views of the original plants, and therefore, it is necessary that they do not remain oblivious of the observations made on other kinds of fossils to correlate and consider their own observations with those made by others to obtain correct ideas about the fossil plants under their investigations.

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