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# Epidermal morphology of Permian Gondwana gymnosperms

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A review of cuticular features of species of the glossopterids reveals that most of the species from Karharbari and Barakar formations are hypostomatic while a few species in the Raniganj Formation are amphistomatic. Lateral walls of cells in species from older horizons are mostly straight, whereas, in Raniganj species they are often sinuous. Similarly, surface walls of cells of species of Karharbari Formation are mostly unspecialised, while those of Barakar and Raniganj formations may be papillate or non-papillate, striated or mottled and sometimes with epidermal hairs. In most species the stomata are anomocytic, irregularly oriented and distributed. Rarely, a regular distribution and a definite orientation is seen. In the older horizons the stomata may be dicyclic or partly amphicyclic besides monocyclic, whereas in Raniganj species they are usually monocyclic. Guard cells are mostly sunken in Karharbari species, normal and usually hyaline in Barakar species and sunken and thickened in the species of Raniganj Formation. Subsidiary cells are usually unspecialised in the species of older horizons, whereas in the Raniganj Formation they are usually papillate, invariably overhanging guard cells. No significant trend is observed in other gymnosperms.

**Key-words**—Epidermal morphology, Gymnosperms, Gondwana, Permian (India).

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## सारांश

### परमी गोंडवाना अनावृतबीजीयों की अधिचर्मिय आकारिकी

रजनी तिवारी

ग्लॉसोप्टेरिड्स की जातियों की उपत्वचा के लक्षणों के पुनरीक्षण से व्यक्त होता है कि करहरबारी एवं बराकार शैल-समूहों की अधिकतर जातियाँ अधोरन्धी हैं, जबकि रानीगंज शैल-समूह में कुछ जातियों में द्विपाश्वरी रन्ध विद्यमान हैं। अधिक आयु के संस्तरों से उपलब्ध जातियों में कोशाओं की पार्श्व भित्तियाँ प्रायः सीधी हैं जबकि रानीगंज से प्राप्त जातियों में सामान्यतः लहरदार हैं। इसी प्रकार करहरबारी शैल-समूह की जातियों की कोशाओं की सतही भित्तियाँ किसी विशेष प्रकार की नहीं हैं, जबकि रानीगंज एवं बराकार शैल-समूहों की पैपिलामय या अपैपिलामय, धारीदार अथवा चित्तीदार और कभी-कभी अधिचर्मियों रोमों से युक्त होती हैं। अधिकतर जातियों में रन्ध एनोमोसाइटी तथा अनियमित रूप से वितरित हैं। अधिक आयु के संस्तरों से उपलब्ध जातियों में रन्ध एकचक्री के अलावा द्विचक्री भी हो सकते हैं, जबकि रानीगंज की जातियों में ये प्रायः एकचक्री होते हैं। करहरबारी से उपलब्ध जातियों में द्वार-कोशायें प्रायः दबी हुई, बराकार जातियों में सामान्य एवं काचाभ तथा रानीगंज शैल-समूह की जातियों में दबी हुई एवं मोटी होती हैं। सहायक कोशायें अधिक आयु के संस्तरों में प्रायः किसी विशेष आकार की नहीं होती जबकि रानीगंज शैल-समूह में ये प्रायः पैपिलामय तथा लटकी हुई द्वार कोशाओं से युक्त होती हैं। अन्य अनावृतबीजीयों में कोई विशेष लक्षण प्रेक्षित नहीं किया गया।

THOUGH during the last three decades a vast amount of data has accrued on the epidermal morphology of gymnospermous leaves recorded from the Permian of India, yet there has been hardly an attempt to trace evolutionary aspects of this feature. Therefore, the available data needs to be collated and organised for proper understanding of the evolutionary significance, if any.

Characters which are considered important for

epidermal morphology are: cuticle hypo-, epi- or amphistomatic; cells differentiated into vein and mesh areas or undifferentiated; anticlinal walls straight, curved, arched, undulate, sinuous, toothed or pitted; surface walls unspecialised, papillate, mottled, striated or with trichomes; orientation and distribution of stomata; guard cells sunken or normal, thickened or hyaline; subsidiary cells unspecialised or papillate.

The three major groups of Permian gymnosperms from India are: glossopterids, cordaites and conifers.

### GLOSSOPTERIDS

Cuticular features are known for the genera *Gangamopteris*, *Glossopteris*, *Palaeovittaria*, *Rhabdotaenia* and *Belemnopteris*. Most of the leaves from the Karharbari Formation are hypostomatic but amphistomatic leaves are also reported, e.g., *Gangamopteris cyclopteroides*, *G. papillosa* and *G. obtusifolia* (Pant & Singh, 1968). Most leaves of Barakar Formation too are hypostomatic except for a few species of *Glossopteris* which are amphistomatic. In the Raniganj Formation, though the hypostomatic cuticle is more common, yet amphistomatic elements are not uncommon, e.g., *Gangamopteris indica*, *Palaeovittaria raniganjensis*, *Glossopteris brongniartii*, *G. formosa*, *G. tortuosa*, *G. varia*, *G. vulgaris* (Srivastava, 1956; Pant & Verma, 1964; Pant & Gupta, 1968). Cells are usually differentiated into midrib, vein and mesh areas with a few exceptions, e.g., *Gangamopteris hispida*, *G. gondwanensis* and *Glossopteris pandurata* (Karharbari); *Glossopteris damudica*, *G. obscura*, *G. intermittens*, *G. rhabdotaenioides*—to name a few (Barakar Formation) and *Gangamopteris flexuosa*, *G. indica*, *Glossopteris arberi*, *G. stenoneura*, *G. conspicua*, *G. contracta*, *G. elongata*, *G. ghusikensis*, *G. gondwanensis*, *G. lanceolatus*, *G. oldhamii*, *G. radiata*, *G. sabnii*, *G. taeniopteroides*, *G. major*, *Belemnopteris sagittifolia*, *B. pellucida* (Raniganj—Srivastava, 1956; Pant & Gupta, 1971; Pant & Singh, 1971; Pant & Choudhury, 1977).

Although the lateral walls of cells are straight in most of the leaves, departures frequently occur, e.g., undulate to sinuous walls in *Glossopteris zeileri* and *G. giridibensis*, pitted in *Gangamopteris cyclopteroides* and *G. hispida* (Karharbari); straight to undulate walls in *Glossopteris pseudocommunis*, *G. cf. leptoneura* and other *Glossopteris* species (Barakar); sinuous walls in *Gangamopteris flexuosa*, *G. cf. hughesi*, *Glossopteris elongata*, *G. gondwanensis*, *G. harrisii*, *G. tenuifolia*, *G. waltonii*, *G. longifolia*, *G. maculata*, *G. oldhamii*, *G. sastrii*, *G. singularis*, *G. subtilis*, *G. transversalis*, *G. nautiyalii* (Pant & Gupta, 1968, 1971; Pant & Singh, 1974), *Rhabdotaenia fibrosa*, *R. daenioides* (Pant & Verma, 1963), *Belemnopteris sagittifolia* and *B. pellucida*; straight to arched walls in *Glossopteris brongniartii*, *G. stenoneura*, *G. petiolata*, *G. searsolensis*, *G. varia*, *G. vulgaris*, and pitted walls in *G. maculata* and laminated in *G. contracta* (Raniganj). Surface walls are usually unspecialised; sometimes papillae are

present which may be numerous, small as in *Glossopteris angusta* or single median as in *G. giridibensis* (Pant & Gupta, 1968) or single, conical or dome-shaped as in *Gangamopteris cyclopteroides*, *G. papillosa*, *G. hispida* and *G. media* (Pant & Singh, 1968—Karharbari Formation). Single hollow, dome-shaped papillae are also present in *Glossopteris ornatus*, *G. intermittens* (Barakar) and in *Gangamopteris flexuosa*, *Glossopteris gondwanensis*, *G. major*, *G. oldhamii*, *G. tortuosa*, *G. vulgaris*, *G. varia*, *Rhabdotaenia fibrosa*, *R. daenioides* and *Palaeovittaria raniganjensis* (Raniganj). In the Raniganj Formation, apart from the single papilla, numerous small papillae are seen in *Glossopteris tenuifolia* and *G. waltonii*. The surface walls are mottled in *Glossopteris harrisii*, *Rhabdotaenia fibrosa*, *Belemnopteris sagittifolia* and *B. pellucida*, striated in *Glossopteris contracta* and *G. rhabdotaenioides* and with circular hair bases in *Glossopteris tenuifolia*.

The stomata are anomocytic throughout and monocyclic in majority of the leaves. Stomata are sometimes amphicyclic in the Karharbari Formation as in *Gangamopteris cyclopteroides*, *G. hispida*, *Glossopteris giridibensis*, or dicyclic—as in *G. karharbariensis*. In the Barakar Formation no exceptions are found. In the Raniganj Formation amphicyclic (*Glossopteris browniana*, *G. harrisii*, *G. major*, *G. petiolata*) and dicyclic (*Gangamopteris cf. hughesi*, *G. indica*, *Glossopteris formosa*, *G. tortuosa*, *G. cf. divergens*) stomata occur in few cases. Stomata are usually irregularly distributed in the Karharbari species. However, sometimes they are distributed in groups in *G. obscura* (Barakar) or in linear rows in *Gangamopteris cf. hughesi*, *Glossopteris conspicua*, *G. taeniopteroides* and *G. vulgaris* (Raniganj). Orientation of stomata is mostly irregular. However, in some of the members of Karharbari and Raniganj formations the stomata show a definite orientation, e.g., they are oriented longitudinally in *Gangamopteris cyclopteroides* and obliquely in *Gangamopteris papillosa* (Karharbari) and show a longitudinal orientation in *Glossopteris conspicua* and *Palaeovittaria raniganjensis* (Raniganj). Guard cells are sunken and usually thickened in the leaves of Karharbari and Raniganj formations and normal and hyaline in the species of Barakar Formation. However, they are sometimes hyaline in *Gangamopteris hispida* (Karharbari), thickened in *Glossopteris pseudocommunis* (Barakar) and normal in *Glossopteris formosa* (Raniganj).

Subsidiary cells in the leaves of Karharbari and Barakar formations are usually unspecialised, whereas those of the Raniganj Formation are usually

papillate with papillae invariably overhanging the guard cells. However, papillate subsidiary cells are known to occur in *Gangamopteris cyclopteroides* of Karharbari Formation and a few Barakar species of *Glossopteris*. Unspecialised subsidiary cells are present in *Gangamopteris indica*, *G.* cf. *cyclopteroides*, *G.* cf. *hughesii*, *Glossopteris brongniartii*, *G. browniana*, *G. maculata*, *G. bengalensis*, *G. conspicua* and *G. elongata* of Raniganj Formation.

Cells of the cuticle of midrib are usually undifferentiated in most of the members throughout the Lower Gondwana. However, a few species of *Glossopteris* and *Rhabdotaenia fibrosa* show differentiation of cells into striated and non-striated areas corresponding to vein and mesh areas. Anticlinal walls of cells are usually thick and straight. However, straight to sinuous walls have been reported in *G. angusta* (Karharbari); undulate walls are present in *G. rhabdotaenioides*, *G. obscura*, *G. pseudocommunis* (Barakar) and sinuous walls have been reported in *Glossopteris arberi*, *G. contracta*, *G. tenuifolia*, *G. gondwanensis*, *G. ghusikensis*, *G. harrisii* and *Rhabdotaenia daenioides* (Raniganj). Surface walls of cells over the midrib are usually unspecialised though a single hollow, dome-shaped papilla is present in *Glossopteris angusta* (Karharbari), *G. ornatus* (Barakar) and *G. spatulata*, *G. vulgaris*, *G. contracta*, *G. major* (Raniganj). Sometimes, single-celled hair-bases are also present, as in *Glossopteris intermittens* (Barakar) and *G. subtilis* (Raniganj). In the Raniganj Formation other types of variations on cell surfaces also occur, e.g., the walls are mottled in *Glossopteris spatulata* and *Belemnopteris sagittifolia* and striated in *Glossopteris contracta*, *Rhabdotaenia daenioides* and *R. fibrosa*. Stomata, as a rule, are absent from midrib but they have been reported in some species of *Glossopteris* of Raniganj Formation, e.g., *G. varia*, *G. nautiyalii*, *G. subtilis*, *G. tenuifolia*, *G. formosa*, *G. gigas*, *G. petiolata*, *G. spatulata* and *G. waltonii* (Pant & Gupta, 1968, 1971; Pant & Singh, 1971).

### CORDAITES

Epidermal morphology is known only for the Karharbari species of the genus *Noeggerathopsis* (Lele & Maithy, 1964; Pant & Verma, 1964). The cuticle, though usually hypostomatic, is amphistomatic in *N. bunburyana* and *N. indica*. The cells of lower surface of all the species are differentiated into vein and mesh areas whereas, those of upper surface are undifferentiated. The cell walls are straight except in *N. zeilleri* where

they are flexuous and toothed. Whereas the upper surface has unspecialised cells the lower surface often has dome-shaped papillae (Pant & Verma, 1964). The stomata are anomocytic, usually monocyclic, rarely amphicyclic as in *N. fibrosa*, oriented longitudinally and distributed in longitudinal rows except in *N. gondwanensis* and *N. zeilleri* (Lele & Maithy, 1964) where they are irregularly arranged. The guard cells are sunken, usually thickened, sometimes hyaline, e.g., *N. indica*, *N. gondwanensis* and *N. zeilleri*. The subsidiary cells may be papillate (*N. papillosa*, *N. indica*, *N. gondwanensis*) or non-papillate (*N. bunburyana*, *N. fibrosa*, *N. zeilleri*) and are usually heavily cutinised.

### CONIFERS

Of the four conifer genera known, *Paranocladus* (Talchir) is amphistomatic, *Buriadia* (Karharbari) and *Walkomiella* (Barakar) are epistomatic and *Searsolia* (Raniganj; Pant & Bhatnagar, 1975) is ?hypostomatic. Anticlinal walls of cells are straight and pitted in *Buriadia* (Pant & Nautiyal, 1967) and sinuous and toothed in *Walkomiella* (Surange & Singh, 1957). In rest of the genera, they are straight. Surface walls of either one surface (*Paranocladus*, *Buriadia*, *Searsolia*) or both the surfaces (*Walkomiella*) show papillae. Sometimes epidermal hairs are present as in *Buriadia* and *Walkomiella*. Stomata in all the genera are monocyclic, sometimes incompletely amphicyclic in *Paranocladus*, usually longitudinally oriented except in *Walkomiella* where they are irregularly oriented. The stomata are distributed in wide bands in *Buriadia* and *Searsolia*. Guard cells are sunken and thickened and subsidiary cells are papillate in all the genera with papillae overhanging guard cells.

### CONCLUSIONS

The data available is insufficient to critically evaluate the evolutionary pattern in epidermal morphology of Gondwana gymnosperms. The hypostomatic cuticle, differentiated cells of laminar region, straight anticlinal walls, unspecialised surface walls, monocyclic stomata, their irregular distribution and orientation, sunken and thickened guard cells, unspecialised subsidiary cells are dominant characters and are present throughout, however, exceptions are not uncommon. Amongst the exceptions, normal and hyaline guard cells dominate over the sunken and thickened ones in the

Barakar Formation and papillate subsidiary cells are more frequent than the unspecialised ones in Raniganj Formation. Among the exceptional characters it is observed that their occurrence in older horizons, viz., Karharbari and Barakar formations, is lesser as compared to in the Raniganj Formation. This may be due to the fact that cuticular features of a larger number of genera and species are known in the Raniganj Formation. However, as an overview, it can be said that cuticle tends to be hypostomatic although a few amphistomatic species occur in Karharbari and Barakar formations, their number being larger in the Raniganj Formation. Lateral walls of cells in species from older horizons are mostly straight whereas in Raniganj they are often sinuous and pitted. Similarly, surface walls of cells of species of Karharbari Formation are mostly unspecialised (with the exception of *Noeggerathiopsis* and *Buriadia*), while those of Barakar and Raniganj formations show variations and may be papillate or non-papillate, laminated, striated, mottled and sometimes with epidermal hairs. In most species, except for those of *Noeggerathiopsis* the stomata are irregularly distributed and oriented. The leaves of Karharbari and Raniganj formations apart from monocyclic may also have dicyclic and amphicyclic stomata. The species of Barakar Formation are always monocyclic with one exception, viz., *Walkomiella* where they are partly amphicyclic. Guard cells are mostly sunken in Karharbari species, normal and hyaline in Barakar species and again sunken and thickened in the species of Raniganj Formation. The above overview clearly shows that more data is needed on epidermal morphology of Gondwana gymnosperms for tracing evolutionary tendencies.

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