

PROBLEMS IN THE PENTOXYLEAE

A. R. RAO

Professor of Botany (Retd.),* Lucknow University, Lucknow

ABSTRACT

The morphology, anatomy and affinities of the Pentoxyleae — an incompletely known group of Gymnosperms combining the character of Pteridosperms, Cycadales, Bennettitales and Coniferales are briefly reviewed from certain aspects. The lacunae in our present knowledge of the three petrified plant organ genera which constitute this group are pointed out and discussed. Various suggestions to clear up these lacunae are made for the benefit of the future workers. It is also suggested that a more systematic, well-designed and extensive collection of silicified material from *Nipania* and subsequent objective and purposeful investigations on them would reveal important morphological and anatomical features which would more accurately define the affinities and systematic position of this group of fossil plants.

IT was in 1948 that the late Prof Birbal Sahni instituted a synthetic group — the Pentoxyleae — for the reception of three petrified plant organ genera all recovered from *Nipania* in the Rajmahal Hills, Bihar and which displayed unique and unusual anatomical characters combining those of the Pteridosperms, Cycadales, Bennettitales and Coniferales. Although, it is nearly thirty years since then, the full anatomy and the correct affinities of this group or its constituent genera have not yet been determined, although some work has been done on them, off and on, mostly sporadically, by a few workers, and several important structural features have been brought to light (Rao, 1974 — see this for earlier references). Vishnu-Mittre added a new male cone genus *Sahnia nipaniensis* to this group. As one who has been interested in this group and has also done a little bit of work in it, I have been struck off and on, with several problematical points in this group. I take this opportunity to share them with others — particularly for the benefit of those future workers who may like to investigate the group and its affinities. It seems that the investigation done so far was not made fully, possibly because the study and description of these genera has been made as and when the material was collected, indiscriminately, not with any purpose or design. I will not here describe these genera as they have been repeatedly described. A reference to the review paper by Rao (1974) will give the consolidated

description of these genera and all earlier literature on the subject. I will here refer directly to the problematical points and quote some important papers only, to save space. As it stands, this group is not only a group of convenience but also is incompletely and partly described.

STEM GENUS PENTOXYLON

There are several points which need clarification. The anatomy of this dimorphic stem has been fairly clearly elucidated by Srivastava, Sahni and recently Vishnu-Mittre. The nature and distribution of primary phloem in the stem has not been clarified partly due to imperfect preservation. In the periphery of the long shoot, alternating with the main stem vascular bundles, are five smaller vascular bundles which are composed mostly of secondary wood. These bundles divide radially into two or more bundles. Sharma (1969) reports that these bundles are detached from the lateral sides of the centripetal xylems of the main bundle. As to what part of the plant these bundles traverse further, has yet to be investigated. The anatomy of the short shoot is fairly clear. It was found surrounded by transversely cut petioles bearing unicellular hairs on both sides and containing an arc of seven to eight diploxylic bundles. In some of the transversely cut shoots, four or five tangentially stretched bands of xylem with

*Present address: "Guru Charana", No. 2, XI Main Road, 3rd Block East, Jayanagar, Bangalore 560011, India.

endarch protoxylem were found, with their concavities facing outwards. Vishnu-Mittre figured some similar shoots where the brood pith was surrounded by irregular V or W-shaped loops of xylem. It has still to be established clearly whether this is only a different stage of the earlier described condition or belongs to an entirely different stem. A species of *Pentoxylon* designated *P. tetraxyloides* with four steles was reported by Shukla (1957). No further description of this species was published and even its designation is open to question under the rules of nomenclature. The possibility that this stem is just a form of *P. sahni* with only four bundles (as an unusual occurrence) instead of five, must not be overlooked. It may even be an entirely different genus of stems not at all referable to *Pentoxylon*. So far as I am aware no *Taeniopteris* type of leaves have been mentioned as associated with this stem. This may have some significance.

FEMALE CONE GENUS CARNOCONITES

The anatomy and morphology of *Carnoconites compactum* has been studied fully well by Srivastava (1946), Sahni (1948) and Vishnu-Mittre. A number of correlating features like *Nipaniophyllum raoi*—like leaves surrounding the transversely cut cones and stems, the pentastelic pattern of the stems and the prevailing pentametry in the arrangements of the vascular bundles of the cone have already been elaborated by Sahni. "The five triplets of vascular bundles that supply the usual five pedicels" arise from the main vascular cylinder of the cone in 2/5 phyllotaxis—a phyllotaxis met with in the stem also. These correlating factors leave no doubt that this stem and female cone belong to the same plant. But an organic connection between the two has not yet been found and should be seriously sought for.

The platyspermic, bicarinate and bitegmic seed has a sarcotesta which enlarges at the micropylar end and describes a small chamber. It has yet to be established if this is a pollen chamber or an equivalent of it. The innermost blackish cells of the fleshy layer was regarded by Srivastava as probably secretory in nature. This too,

has to be established clearly. The micropylar part of the sclerotesta becomes thin-walled and bears reticulate pattern thickenings like the *velamen* of some *Aroids* and *Orchids*. This has to be further elucidated. Inside the nucellar cavity occurs a partly preserved, thin-walled tissue regarded as probably the remnants of a female prothallus. This too, has to be demonstrated more convincingly. This means that a very careful, detailed and intensive study has to be done of well-preserved seeds and their finer structural details observed.

Carnoconites laxum

A longer, thinner but similarly built cone carrying more seeds than *C. compactum* was described by Srivastava as *C. laxum*. The arrangement of the seeds was by no means lax as suggested by the name. They were quite compactly arranged. The cone certainly resembles *C. compactum* in many respects except that the peduncles are shorter, the cone longer and the pedicels slightly flattened and bearing three vascular bundles. Our knowledge of the anatomy of this cone is very meagre and does not permit comparison with *C. compactum* on all points. The seed structure though generally similar to that of *C. compactum* has yet to be elucidated in several respects. The vasculature of the cone and the seed has also to be traced. In fact, the morphology and anatomy of this cone has still to be studied in detail.

It may not be out of place here to state that impressions of five small seed bearing elongated cones associated with *Taeniopteris* leaves were described from Murrero in the Rajmahal Hills (Feistmantel, 1877). This was later referred to genus *Williamsonia* by Wieland and designated *W. rajmahalensis*. Krasser (1919) placed this under a new genus *Hattingeria rajmahalensis*. This, according to Sahni and Srivastava also, may well be the impression of *Carnoconites laxum* or an allied species. The correlation between the above mentioned impression and petrification is another important line of work that has to be undertaken. A third species of *Carnoconites*, *C. cranwelli* in the form of an incrustation has been described by Harris (1962) from New Zealand. The occurrence of *Taeniopteris* type of leaves in association with all the

above mentioned fructifications is rather suggestive. A more extensive search for the above mentioned impression, incrustation and a very careful detailed comparison between them and the petrifications, in all features, would enlighten us fully on this problem.

MALE CONE GENUS SAHNIA

Vishnu-Mittre (1953) has described the male flower *Sahnia nipaniensis* in detail and the structure is quite clear. But the absence so far of an organic connection between the flower and its parental axis renders it difficult to be emphatic on its attribution to *Pentoxylon Sahnii*, although a number of indirect evidences do suggest this. This problem could be solved finally by searching for this all important organic connection between the stem and flower. The detailed structure of the microsporangia and microspores also needs further clarification.

At this stage, with the evidences already available, it is rather suggestive that *Pentoxylon sahnii*, *Carnoconites compactum*, *Sahnia nipaniensis* and *Nipaniophyllum raoi* are in all probability different parts of the same plant. Infact, though actual organic connections are not available in all these cases, yet indirect evidences and correlative features suggest the above possibility. But a similar correlation between the incompletely described *Nipaniophyllum* and its foliage and relationship, if any, with the seed bearing *Carnoconites laxum* etc., has also to be established.

LEAF GENUS NIPANIOPHYLLUM

The petrified leaves referred to this genus and designated as *Nipaniophyllum raoi* Sahnii were originally known as *Taeniopteris spatulata* McClelland. The anatomy of these leaves was first studied by Sahnii and later in great detail by Rao (1943). The anatomy and morphology of these diploxylic leaves are quite clear. But it is the epidermal features that are most intriguing. The leaves which were associated with *Pentoxylon sahnii* in the original blocks studied by Rao, and Srivastava, showed a Bennettitalean type of epidermis. The general appearance of the stomata suggested

a syndetocheil type of development. The epidermal cells were sinuous-walled, with hair scars in some cells. The two guard cells were surrounded by two subsidiary cells as clearly shown in Rao's photographs. It was even observed in some of these stomata that each of these lateral subsidiary cells further divided later, as in the interseminal scales of *Williamsonia wettsteini* or *W. lignieri* giving the same appearance as a pair of guard cells surrounded by four subsidiary cells. This secondary development would no doubt impart to the stomata seemingly haplocheil type of development. But earlier stages of development showed only two subsidiary cells surrounding the two guard cells. All attempts by Rao to trace a full sequence of developmental stages were unsuccessful. Prof Sahnii who had also examined these epidermal preparations carefully, remarked "thus while the irregular orientation of stomata is a cycadean feature in keeping with the structure of the vascular bundles, the development of the stomata seems to be fundamentally Bennettitalean, the somewhat cycadean appearance of the subsidiary cells being deceptive". Vishnu-Mittre (1957) has figured and described the stomata of some leaves which he regards as *N. raoi*. He notes a number of differences from the observations made by Rao (1943), amongst which are features concerning the stomata. According to him the stomata in *N. raoi* are uniformly haplocheilic. His observations show that each stoma had 4 to 6, sometimes 7, subsidiary cells surrounding the two guard cells. Sharma (1969) also reports that some *Nipaniophyllum*-like leaves collected from Amarjola, also show stomata of the haplocheil type in their lower epidermis. As I have already remarked (1974) this raises two fundamental doubts: (i) whether the *Nipaniophyllum*-like leaves investigated by Vishnu-Mittre and also by Sharma, really belong to the same species as *N. raoi*, (ii) could they be of a species different from *N. raoi*, showing a number of differences in their epidermal characters while generally showing some similar morphological and anatomical features? As one who has studied these *Nipaniophyllum* leaves in some detail, I might mention here that more than one species of leaves seem to have been included under the name *Taeniopteris spatulata* or

Nipaniophyllum. To me it appears to be a complex of similar looking leaves with some common gross morphological features but possibly different affinities. If a careful comparative study is made of these *Taeniopteris spatulata* and *Nipaniophyllum* leaves, taking into account the form of the leaf, its apex, dimensions, venation and its prominence, frequency and association with other plant remains, one can certainly establish more than three or four species of leaves. Prof Sahni had already hinted this. And Vishnu-Mittre has also mentioned about this point. It is most unlikely that all the leaves that look like *Nipaniophyllum raoi* really belong to *Pentoxylon sahnii*. I venture to suggest that out of this complex, the ones studied by Rao and also by Sahni and found associated with *Pentoxylon sahnii* are the only ones that belong to this species of *Pentoxylon* and can be regarded as *Nipaniophyllum raoi*, I feel that a careful, exhaustive and comparative study of these *Nipaniophyllum*-like leaves employing if necessary statistical methods would be highly rewarding and useful. This complex of leaves must be resolved into well-defined species that compose it. Their respective affinities would also then become clear. Another important line of study would be to trace the full developmental stages of the stomata in *N. raoi* as well as in the other species that might be sorted out from this complex. This is no easy matter as the highly silicified material becomes brittle in the later stages of grind-

ing and does not lend itself to finer stages of grinding or observation. But careful collection and well selected material may after very cautious and fine grinding, aided by suitable staining technique, show up the really important developmental stages that matter. It must be admitted that the haplocheil or syndetocheil nature of the stoma is conclusively established not by the mere appearance of the adult stoma but by its complete developmental stages. Another structural detail by no means easy to investigate but nevertheless important is the thickenings of the guard cells and subsidiary cells as can be made out in vertical sections. It is needless to say that quite a lot of staining technique will be helpful in this study. It is also surprising that no root remains have been found associated with any of these organs, although the roots are as hard as the stems or cones. A careful search for them has to be made as they might indirectly throw some light on the affinities of this group.

In conclusion it may be pointed out that Meeuse (1961) has suggested "a more or less direct descent of the Pandanaceae and some related monocotyledons from the Pentoxyleae". This aspect has also to be further examined by carefully analysing the morphological and anatomical features of the associated flora. This would throw light on the question whether the synthetic group of Pentoxyleae were a blind line in evolution or gave rise to other groups of plants.

REFERENCES

- FEISTMANTEL, O. (1877). Jurassic (Liassic) flora of the Rajmahal Group in the Rajmahal Hills. The fossil flora of the Gondwana System. *Mem. geol. Surv. India Palaeont. Indica*, Ser. 2, 1: 58-163.
- HARRIS, T. M. (1962). The occurrence of the fructification *Carnocoonites* in New Zealand. *Trans. R. Soc. N.Z.*, 88: 17-27.
- KRASSER, F. (1919). Studien uber die fertile Region der Cycadophyten aus den Lunzer schichten, Makrosporophylle. *Denkschr. Akad. Wiss., Wien*, 97.
- MEEUSE, A. D. J. (1961). The Pentoxylales and the origin of monocotyledons. *Proc. K. ned. Akad. Wet.*, 60: 543-559.
- RAO, A. R. (1943). The structure and affinities of *Taeniopteris spatulata* McCl. *Proc. natn. Acad. Sci. India*, 13: 333-355.
- RAO, A. R. (1974). Pentoxyleae, in: K. R. Surange et al. (Eds): *Aspects & Appraisal of Indian Palaeobotany*. Birbal Sahni Institute of Palaeobotany, Lucknow: 201-209.
- SAHNI, B. (1948). The Pentoxyleae: a new group of Jurassic gymnosperms from the Rajmahal Hills of India. *Bot. Gaz.*, 110: 47-80.
- SHARMA, B. D. (1969). On Pentoxyleae remains from Amarjola in the Rajmahal Hills, India. *Ameghiniana*, 2: 50-56.
- SHUKLA, V. B. (1957). On a new species of *Pentoxylon* with four bundles. *Proc. 44th Indian Sci. Congr.*, 297: Abs.
- SRIVASTAVA, B. P. (1946). Silicified plant remains from the Rajmahal series of India. *Proc. natn. Acad. Sci. India*, 15: 185-211.
- VISHNU-MITTRE (1953). A male flower of the Pentoxyleae with remarks on the structure of the female cones of the group. *Palaeobotanist*, 2: 75-84.
- VISHNU-MITTRE. (1957). Studies on the fossil flora of Nipania (Rajmahal Series), India. Pentoxyleae. *Palaeobotanist*, 6: 31-46.