Misinterpretations about the 'Pentoxyleae' - A Mesozoic gymnospermous group of plants

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(Received 13 August 2001; revised version accepted 23 April 2002)

ABSTRACT

Sharma BD 2001. Misinterpretations about the 'Pentoxyleae' - A Mesozoic gymnospermous group of plants. Palaeobotanist 50(2 & 3): 255-265.

Faulty interpretations on the morphology, anatomy and phylogeny of an extinct plant group 'the Pentoxyleae' are pointed out, and correct descriptions based on the study of large number of specimens and slides are included in the present paper. Reviews and reconstructions based on imaginations are challenged.

Key-words-Unique, Extinct plants, Rajmahal Hills, Reviews, Reconstructions.

मीसोज़ोइक युगीन अनावृतबीजी समूह के पौधे 'पेन्टॉक्सीली' के विषय में कुछ भ्रामक विवेचनाएँ बी.डी. शर्मा

सारांश

'पेन्टॉक्सीली' समूह के एक विद्यमान पादप समूह के संरचनाविज्ञान, शारीरविज्ञान तथा जातिवृत्त विज्ञान के विषय में कुछ त्रुटिपूर्ण निष्कर्षों को इंगित करते हुए प्रस्तुत शोध पत्र में अनेक प्रादर्शों एवं स्लाइडों के अध्ययन के पश्चात् यथार्थपूर्ण विवेचन प्रस्तुत किया गया है। कल्पना के आधार पर की गयी समीक्षाओं तथा पूर्नसूर्जनों का खण्डन भी किया गया है।

संकेत शब्द—विशिष्ट, सुस्पष्ट पादप, राजमहल पर्वतश्रेणी, समीक्षाएँ, पुनर्सृजन।

INTRODUCTION

T is after the presentation of a chert piece by Hobson of the Geological Survey of India to Prof. Birbal Sahni that he and his students (Gupta, Rao, etc.) went on an excursion to the Rajmahal Hills, Bihar (now Jharkhand) in 1932 and fortunately they were able to search out the locality (Nipania) from which Hobson probably had collected the chert piece. Sufficient amount of fossiliferous material was collected from Nipania and was given to Rao and Srivastava for investigation (The story narrated by my worthy teacher Late Prof. Gupta, the first research scholar of Prof. Sahni in 1932). Rao (1943a) described in detail the morphology and anatomy of the leaf Taeniopteris spatulata which occurs in abundance in the chert (later on renamed as Nipaniophyllum raoi by Sahni 1948). Rao (1943) was able to photograph a number of isolated sporangia, spores and seeds, seen in thin sections prepared through the chert. While, Srivastava (1944, 1945) gave descriptions of the anatomy of peculiar stems (Pentoxylon sahnii & Nipanioxylon guptai) and seed bearing fructifications (Carnoconites compactum & C. laxum) unfortunately Srivastava expired in 1938 and the manuscript (1945) was completed and published by Prof. Sahni with an obituary note). Sahni (1948) instituted a new group of Jurassic gymnosperms—the Pentoxyleae from the Rajmahal Hills on the basis of following characters noted in its fossil plants :-

- 1. Material permineralised.
- 2. Branching dimorphic; leaves restricted to dwarf shoots.
- 3. Stem polystelic with generally 5 endocentric steles. Primary xylem mesarch.
- 4. Pith and cortex parenchymatous with scattered sclerotic nests.
- Secondary wood compact with growth rings, rays uniseriate and short (1-14 cells high), contiguous uniseriate sometimes biseriate bordered pits on radial walls of tracheids, pits in crossfield large, single per field.
- 6. Leaf trace many with or without secondary xylem.
- 7. Leaves simple *Taeniopteris* type, midrib has 5-9 diploxylic bundles in a saucer, stomata on lower surface and syndetocheilic (?).
- Seeds in globose or elongated infructescence. Orthotropus ovules attached directly to the cone axis. Integument thick heterogeneous nonvascularised. Nucellus free with nucellar pad. Embryo dichotyledonous (?).
- Relationships suggested with medullosan pteridosperms, cycads, Ginkgoales and the conifers.

Mittre (1953) described the male fructification Sahnia nipaniensis bearing a whorl of 12-20, radial simple or branched microsporophylls and large balloon-shaped microsporangia were produced in rows on lateral sides. Spores monocolpate. Mittre (1957) added further to our knowledge about this peculiar group of extinct plants and described stomata haplocheilic (anomocytic).

The author (BDS) and associates were able to collect huge amount of permineralised material of the Pentoxyleae from the original locality Nipania (Sharma, 1975; Suthar & Sharma, 1988; Suthar *et al.*, 1988) and also from other localities like Amarjola (Sharma, 1969, 1973, 1973a, 1974; Sharma *et al.*, 1987) and Sonajori (Sharma & Bohra, 1987). Several hundreds of slides have been prepared of stems, dwarf shoots, leaves and fructifications (both male and seed bearing) and the author has examined each and every slide personally. Many of the figured slides and specimens used in author's publications are deposited now at the Birbal Sahni Institute of Palaeobotany, Lucknow.

Harris (1962) could be able to collect compressions of the pentoxylean seed bearing fructification *Carnoconites cornwelli* from the Jurassic of New Zealand. He correlated it with the *Taeniopteris spatulata* like leaves (Harris, 1982).

Douglas (1969) described from the Jurassic of Victoria (Australia) fertile organs resembling *Carnoconites* and *Salinia* of the Pentoxyleae. He also related *Taeniopteris dintreei* leaves with the short shoot *Pentoxylon*-like stem. White (1981) while working on the Talbragas Fish Bed flora of New South Wales (Australia) identified the leaf *Pentoxylon australica* and correlated it with *Carnoconites australica*. She writes that the Australian material is quite distinct from that of the New Zealand fossils of the Pentoxyleae. The leaf has incised margin and the seed bearing cone is very large in comparison to Indian and New Zealand material. Drinnan and Chambers (1985) reassessed the leaves of *Taeniopteris daintreei* and related them to the Pentoxyleae.

Bose *et al.* (1985) published a review article 'The *Pentoxylon* plant' on the basis of slides and specimens present at the B.S.I.P., Lucknow. The paper has many erroneous descriptions and misinterpretations. Some of the drawings are poor, unlabelled and show nothing e.g., Fig. 3 page 87 while others, are incorrectly assigned and drawn e.g. Fig. 1b page 83. Srivastava's (1945, pl. 4, fig. 38) photograph of R.L.S. of wood does not show separate unequal bordered pits. There are clear cut uniseriate, equal sized contiguous bordered pits on all tracheids.

There are many other indirect publications on the Pentoyleae which are full of incorrect descriptions and misinterpretations e.g., Stewart (1976), Crane (1985, 1988), Doyle & Donoghue (1986), Stewart & Rothwell (1993), Taylor & Taylor (1993). Probably many of them have neither seen the specimens nor the slides of the pentoxylean fossils from the Rajmahal Hills, India and their faulty descriptions are based on literature and imagination. In taxonomy and morphology one cannot do justice with the description unless and until one examines the specimens (plants growing in nature or herbarium sheet or preserved material) and the slides personally.

Recently, Srivastava and Banerji (2000) have published a very funny review article on the pentoxylean plants with the heading "Pentoxylon plant : A reconstruction and interpretation" in a Journal which publishes mostly articles on plant physiology and cytology. It is full of imaginations and misinterpretation. This is because they have neither examined the specimens nor the slides carefully.

MATERIAL AND METHODS

In addition to the specimens and slides of the pentoxylean plants from Prof. Gupta's collections, the author and associates have also made huge collections of these extinct plants from the well known localities like Nipania, Amarjola and Sonajori. At Amarjola individual fossils are taken out by digging the

PLATE 1

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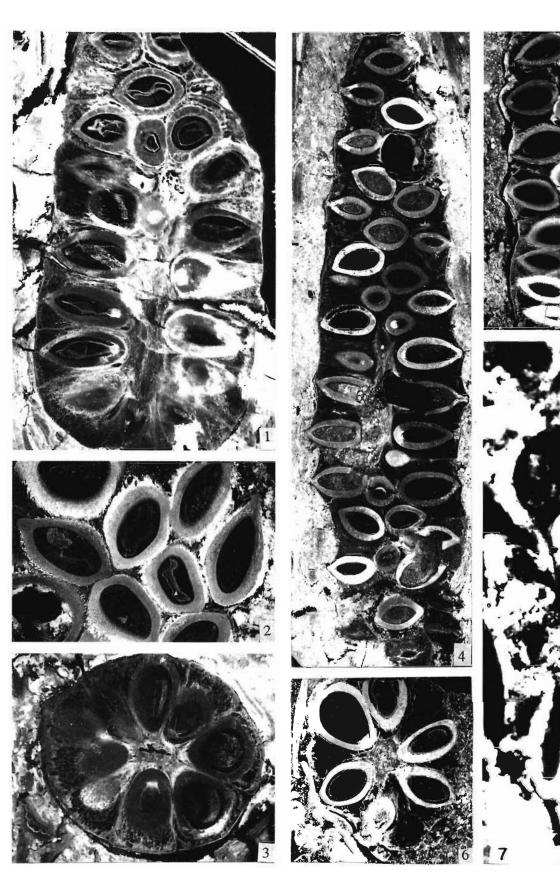
- Carnoconites compactus Longisection seed bearing cone, seeds originate directly from cone axis. X 8.
- 2. Same. Tangential section showing radiospermic nature of seeds. X 8.
- Same. Cross section cone with 8-9 seeds attached to the central axis. X 8.
- 4. C. rajmahalensis (C. laxum) Long cone with many seeds originat-

ing in spiral from the cone axis. X 8.

- 5. Same. Longisection of a portion of cone with radiospermic seeds. X 8.
 - Same, Cross section with 6 seeds around the cone axis. X 8.
 - Salunia nipaniensis. A microsporophyll with balloon-shaped large microsporangia attached on it. X 36 (Fig. 7 from Suthar & Sharma, 1988).

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sandy ferrugenous rock and the specimens are soft and fragile. These are cooked in canada balsam prior to sectioning with a wire bandsaw. Rocks at Sonajori and Nipania are hard and oversilicified. Sections were cut with the help of a diamond edge wheel. Slides were prepared by the usual technique of grinding and polishing methods and mounted in canada balsam. Some of the slides kept unmounted and examined in a water film because sometimes, in silicified cherts, canada balsam makes the section more or less transparent and details of anatomy disappear (Suthar & Sharma, 1988).

OBSERVATION AND DISCUSSION

The organ genera and species now included in the Pentoxyleae are :

Stems

Pentoxylon sahnii Srivastava 1944, 1945 Nipanioxylon guptai Srivastava 1944, 1945 Guptioxylon amarjolense Sharma 1969a G. endocentrica Sharma 1972 Purioxylon jurassica Sharma 1972a

Leaves

Nipaniophyllum raoi Sahni, 1948 N. hirsutum Mittre, 1957 N. anomozamoides Sharma, 1975 N. hobsonii Bose et al. 1985 Taeniopteris spatulata (Harris, 1982) T. draintreei (Dauglas, 1969; Drinnan & Chambers, 1985) Pentoxylon australica (White, 1981)

Male fructifications

Sahnia nipaniensis Mittre, 1953 S. laxiphora (Osborn et al., 1991)

Seed bearing infructiscence

Carnoconites compactum Srivastava (1944, 1945) C. rajmahalensis Bose et al. (1984) (C. laxum Srivastava, 1944, 1945) C. cornwelli Harris 1962 C. australica (White, 1981)

Stems

Pentoxylon sahnii Sriv. Hundreds of the pieces of variable sizes (length 1-10 cm and thickness 05-3.5 cm) are present in author's collections, gathered by digging the sandy rock at Amarjola in the Rajmahal Hills. In majority of stems (long shoots) the surface is smooth whereas, close rhomboid leaf bases in helicals (Fig. 5) are present on the dwarf shoots (Sharma, 1973, 1974, 1979). In some of the long shoots distantly placed oval leaf bases (Fig. 9) are present (Sharma, 1973). In an another type of long shoot, a dwarf shoot is seen originating axillary to a decurrent leaf base (Sharma, 1974; pl. 1, figs. C, D). Thick stems may have bases of long shoots on them (Sharma, 1974; pl. 1. figs A, B). Sharma (1996) described various types of shoot systems in Pentoxylon plant and confirmed on the bases of anatomy. These are thick stems with either smooth surfaces or have basis of long shoots; long shoots are of two types, i.e., one may have distantly placed leaf bases and the others produce dwarf shoots axillary to decurrent leaves. Then, the dwarf shoots have close, helical leaf bases and the leaves in majority are produced on them. The fertile shoots are of two types i.e., the male shoot which resembles the vegetative dwarf shoot in general appearance (Fig. 20) but in between leaf bases there are dense growth of hairs (Suthar & Sharma 1988). The seed bearing cones are produced on a peduncle (Figs 14, 15) which in turn is terminal to an another kind of dwarf shoot (Sahni, 1948; Suthar et al., 1988).

Bose *et al.* (1985) also reported the existence of more than dimorphic shoot system in the *Pentoxylon* plant i.e., four types of shoots. However, in support good photographs and camera lucida drawings should have been given. Srivastava and Banerji (2000) in their reconstruction of the *Pentoxylon* plant have shown branches in whorls as well as monopodial, and dichotomy of ultimate branches. Leaves in close spiral are seen on the ultimate dichomotous branches. That is, they did not believe in the origin of vegetative dwarf shoots on lateral sides of the stem and long shoots rather, they considered the dwarf shoots which bear leaves as an extension of long shoots or terminal portion of dichotomised long shoots (Fig. 25). This is not true. Does any body have specimens of dichotomised long or dwarf shoots of *Pentoxylon* ? If yes, how many in number ?

At least this author has neither seen nor has any such specimen in his huge collections of *Pentoxylon* shoots.

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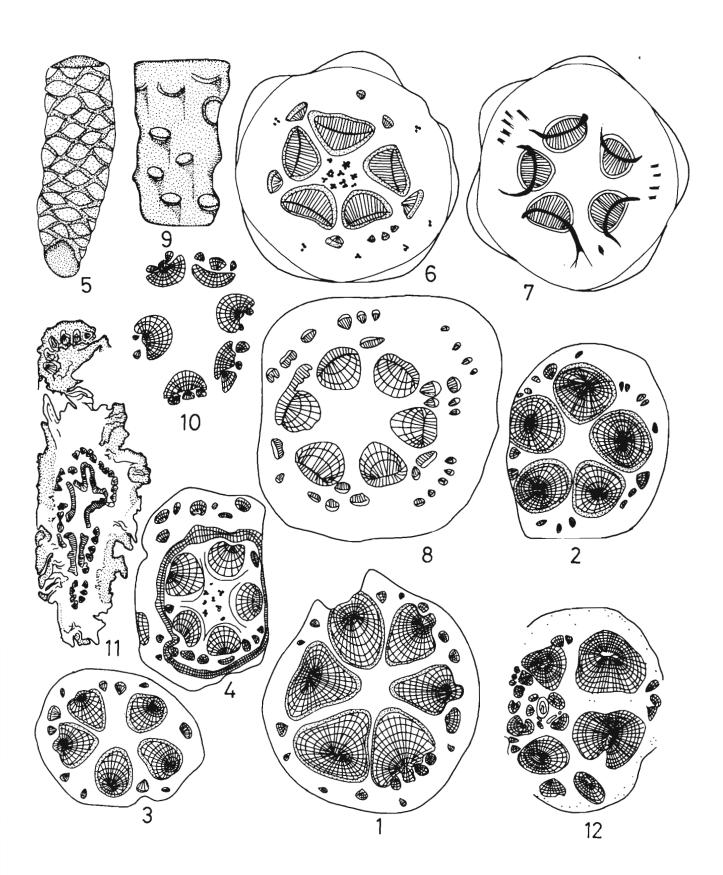
Figs 1-12

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^{1-11.} *Pentoxylon sahnii.* 1-3. Cross sections long shoots of different thickness, note main steles and origin of cortical bundles. X 6. 4. Same. Internal periderm encloses 5 steles. X 6. 5. Dwarf shoot with leaf bases on surface. X 3. 6-8. Cross sections dwarf shoots showing steles and origin of leaf traces from primary xylem. X 8. 9. Thin long shoot with sparse leaf bases on surface. X 3. 10. Cross section fig. 9, cortical bundles (leaf traces) originate from centrifugal portions of steles. X 6. 11. Cross section fertile shoot (peduncle of *Carnoconites*). X 8. 12. *Guptioxylon amarjolense* cross section showing steles, medullary bundles and cortical bundles. X 3.

⁽Figs. 1-3 from Sharma, 1973a; Fig. 4 from Sharma, 1974; Figs 5-7, 9, 10 from Sharma, 1973; Fig. 8 from Sharma, 1979; Fig. 11 from Suthar et al., 1987; Fig. 12 from Sharma, 1969a)

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Stewart and Rothwell (1993) write "An armor of leaf bases also spirally arranged, covers the short shoots and the long shoots as well" (Figs 26-10A). In modified reconstruction both long shoot and dwarf shoots are shown covered with close, helical leaf bases (Figs 13, 14). The modification is wrong. In majority, the stems are smooth surfaced and long shoots which produce dwarf shoots have only a few distantly placed leaf bases.

Sharma (1973a) described the anatomy of long shoots, thick and thin and noted that there is no relationship exists between the number of steles (5-8) and the diameter of stem. A thick stem may have 5 and a thin one may have 8 steles. In the majority of steles secondary xylem is more developed towards pith in comparison to that of the centrifugal side (Figs 1, 3). Sometimes, the inner and outer secondary xylem are more or less equally developed (Fig. 2). In dwarf shoots also the number of steles remain constant 5 or 6 throughout the length (Figs 6-8). Stewart and Rothwell (1993, p. 376) write that "The number of vascular segments varies however, from 4 to 10 as a result of branching and anastomosing". Neither in decorted stems nor in serial cross sections cut through many stems could show an anastomosing of steles (vascular segments). There is a definite way of branching of steles in Pentoxylon sahnii (Sharma, 1974, 1979). Segmentation or fission of steles is seen in Guptioxylon amarjolense Sharma (1969a), an extinct pentoxylean taxon but quite distinct from Pentoxylon.

Stewart (1976) described that the vasculature of *Pentoxylon* has originated by fission of an eustele into 5 or more bundles and that is there is no polystelic vasculature in *Pentoxylon*. Has anybody ever seen a eustelic vasculature in any stem or branch of *Pentoxylon*? Why in the majority of stems are there five vascular segments? And each segment has its own secondary growth without disturbing others. Segmentation or fission takes place only in secondary xylem of the centrifugal side (Figs 1, 10) for the formation of cortical bundles (Sharma, 1969, 1974) which later on may become leaf traces or branch traces. In *Pentoxylon* the vasculature is not monostelic (Bose *et al.*, 1985; Stewart & Rothwell, 1993) but distinctly polystelic.

Taylor and Taylor (1993, p. 648) write "Young shoots of *Pentoxylon* less than 1 cm in diameter contain only primary vascular bundle in the pith and cortex". Has any body ever

prepared such a cross section of *Pentoxylon sahnii*? There is one figured by Srivastava and Banerji (2000, Fig. 2.1D) a poor and unlabelled drawing of a c.s. of a type 3 shoot without mentioning any slide No. or source of drawing. All vegetative dwarf shoots ranging 0.5 to 1.6 cm in diameter have identical anatomy and in each secondary xylem (Figs 6-8) is well developed (Sharma, 1973, 1979). *Pentoxylon* is quite close to conifers in an early activity of the cambium. Secondary xylem of centripetal side develops early and fast in comparison to that of the centrifugal side (Sharma *et al.*, 1987). Due to quick development of secondary xylem, the primary xylem in long shoots is generally seen crushed and details of the primary xylem are yet to be studied.

Stewart and Rothwell (1993, p. 376) described the origin of leaf traces "in pair" in *Pentoxylon sahnii*. This is neither true in long shoots (Sharma, 1969, 1973a) nor in dwarf branches (Sharma, 1973, 1979). In the former the cortical bundles originate by fission of secondary xylem of the centrifugal side (Figs 1, 10). While in the latter the primary xylem extends lateraly (Fig. 7) and cuts off series of endarch traces on either side (Sharma, 1973; Text Figs 5-7, 1979; Text Fig. 3). These are without secondary xylem. Five-8 traces enter a leaf base (Figs 7, 8). How and where the leaf trace bundles become diploxylic is yet to be seen ?

Bose *et al.* (1985) described the structure of secondary phloem of *Pentoxylon sahnii* and write "secondary phloem in *Pentoxylon* is scarcely known apart from a few words of Srivastava (1946)". Probably they did not see a paper by Sharma and Bohra (1977) in which the anatomy of secondary phloem of a long shoot of *Pentoxylon sahnii* is described in detail.

The ground tissue (pith and cortex) is parenchymatous with scattered patches of sclerotic cells. In some of the long shoots of *Pentoxylon* an internal periderm surrounding steles is also observed (Fig. 4). Bose *et al.* (1985, pages 83, 84) described the presence of "small medullary bundles of unknown origin and fate" in type 1 shoots and "also occur, especially in the lower part" of "Type 2 shoots'. But neither photograph nor drawing is given of the medullary bundles. In hundreds of slides prepared at random and in serial sections, through long shoots and dwarf shoots of all types (polymorphic shoot system described above), the author has not yet seen the presence of medullary bundles in *Pentoxylon*

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Figs 13-25

^{13-14.} Reconstruction *Pentoxylon salmii* and shoot bearing *Carnoconites* cones. Note closely placed rhomboid leaf bases in spirals on stem as well as branches (Stewart & Rothwell, 1993). 15. *Carnoconites compactus* cross section with seeds, cone axis (ca) and peduncle (pecle) (Sahni, 1948). 16. Reconstruction *C. compactus* infructiscence (Mittre, 1953). 17. Same. Reconstruction with hundreds of cones (Bose *et al.*, 1985). 18. Same. Reconstruction more or less similar to fig. 17 (Crane, 1985). 19. Same. Reconstruction with comparatively lesser number of cones (Srivastava & Banerji, 2000). 20. Sahnia nipaniensis. Reconstruction male flower (Mittre, 1953). 21. Same. Reconstruction with branched microsporangiophores and microsporangia originate on small lateral branches (Bose *et al.*, 1985). 22. Same. Reconstruction with radial microsporophylls and microsporangia terminal in groups on small lateral branches (Taylor, 1988). 23. Same. Reconstruction with cylinderical receptacle bearing microsporophylls in spiral. Microsporangia in lateral rows (Suthar & Sharma, 1988). 24. Same. Dwarf shoot with a terminal male flower (Srivastava & Banerji, 2000). 25. Reconstruction *Pentoxylon* plant (only one side is shown here) bearing dichotomous long shoots which terminate in leaf producing shoots. Male and seed bearing fructifications originate from long shoots (Srivastava & Banerji, 2000).

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sahnii. However, these are present in an allied taxon Guptioxylon (G. amarjolense Sharma, 1969a & G. endocentrica Sharma, 1972).

Nipanioxylon guptai Srivastava (1944, 1945) instituted the genus for a stem bearing 8-9 steles (bundles) surrounding a wide pith; each has a well developed compact secondary xylem more or less equally developed on either side i.e., centripetal and centrifugal sides. The ground tissue has scattered nests of sclerotic cells similar to that of *Pentoxylon* sahnii. Sahni (1948) writes in the description of Nipanioxylon Srivastava (page 61) "In any case, there seems no doubt that, if it is a distinct genus, its proper place would be within the group Pentoxyleae". He suspected it a branch system of *Pentoxylon*. Mittre (1957) (based on study of a wrong material probably a conifer stem with anomalous secondary growth) and Sharma (1996) considered Nipanioxylon a distinct stem genus of the Pentoxyleae. Bose *et al.* (1985) believed that it may be a conifer twig. The genus needs further investigations.

Guptioxylon amarjolense Sharma (1969a). The stem is a smooth surfaced nearly 2 cm in diameter and is monopodially branched. Four unequal sized steles, each with well developed, compact secondary xylem are present in the ground tissue (Fig. 12). Unequal fission of bundles and presence of medullary bundles are the characteristics of this taxon (Sharma, 1969a, 1974a). Cortical bundles are of various shapes, sizes and nature (exarch, mesarch, endarch, concentric). Guptioxylon endocentrica Sharma (1972) is a thick stem with a diameter of 5 cm and has 6 endocentric Pentoxylon like steles. Medullary bundles of various size, shape and nature are present. Bose et al. (1985, p. 86) considered both the species of Guptioxylon described above, equivalent to their 'type 2' shoots of Pentoxylon sahnii. They believed (without examination of the type specimens, slides and their mode of preservation) that the specimens "are damaged at both ends like ours" and "imagine that these were the bases of the cone bearing branchlets of Carnoconites". If it is so, then what would be the thickness of the main stem on which these (2 to 5 cm in diameter shoots) were produced ? Secondly their outer surfaces are smooth whereas, 'Type 2 shoots' of Bose et al. (1985, p. 84) "have persistent leaf base cushions in a crowded helix over the surface". No stem or shoot system of Pentoxylon has ever been photographed showing fission of bundles and presence of medullary, and cortical bundles of various shapes, sizes and nature. Guptioxylon is a distinct taxon from Pentoxylon and probably is a link between Medullosa and the Pentoxylon (Sharma, 1972a).

Purioxylon jurassica Sharma (1972a). It is a smooth surfaced Pentoxylon like stem with a fistular pith surrounded by a periderm layer and a ring of collateral, conjoint and endarch bundles. Cortical bundles are of various shapes, sizes and nature, and have compact secondary xylem similar to those of *Guptioxylon* or *Pentoxylon*. Sharma (1972a, 1974a) related it in anatomy to Medullosae on one hand and the cycads the other hand.

Leaves

Sahni (1948) named Nipaniophyllum raoi for the permineralised Taeniopteris spatulata like leaves in which the midrib/rachis has 5-9 diploxylic bundles in a saucer or in a row. Stomata hypostomatic, syndetocheilic (?), scattered irregularly between veins and lower epidermal cells were sinuous. Since then three new species from Nipania in the Rajmahal Hills have been created based on presence of few hairs on lower surface (N. hirsutum Mittre 1957), incised margin of lamina (N. anomozamoides Sharma 1975) and comparatively little broader leaves (N. hobsonii Bose et al. 1985). How valid these parameters are in instituting a new species, needs reconsideration ? Can't these be the different stages of development of the leaves of N. raoi ? (young and old). Similarly, should we include in Pentoxyleae or associate with Pentoxylon the leaves looking like Nipaniophyllum but are found preserved as impressions or compressions, and anatomical details are unknown?

In *Nipaniophyllum* the stomata are definitely anomocytic (haplocheilic) (Mittre, 1957; Sharma, 1969; Sharma *et al.*, 1987; Bose *et al.*, 1985) and not syndetocheilic. Srivastava and Banerji (2000) developed confusion in the positions of centrifugal and centripetal xylem in a diploxylic bundle of leaf midrib and have down an inverted bundle (Fig. 2.1 K).

Male fructification

This material is rare. Mittre (1953) could be able to see longisections through the male fructification and suggested a reconstruction of Sahnia nipaniensis Mittre. He believed that radial microsporophylls (12-20) originated in a whorl, on a dwarf shoot (Fig. 20). Balloon-shaped large microsporangia were produced in rows on lateral sides of microsporophylls. Spores were monocolpate with tuberculate exine. Bose et al. (1985) interpreted differently on the basis of study of longisections of an another specimen of male fructification (Fig. 21). According to them microsporangiophores branched once or twice in the proximal region and then small lateral shoots were produced on them probably spirally. It is on these small branches that 2-5 balloon-shaped (obovate) microsporangia were produced in alternate or opposite arrangements. Suthar and Sharma (1988) published a new reconstruction of Sahnia nipaniensis on the basis of longisections of a male fructification collected from Nipania. According to it simple or branched radial microsporophylls were produced in spiral on a cylinderical receptacle terminal to a dwarf shoot (Fig. 23). Large balloon-shaped microsporangia (Pl. 17) originated directly on the lateral sides of microsporophylls. Spores monocolpate (monosulcate). Influenced by Bose et al. (1985), Taylor (1988) suggested an another reconstruction of Sahnia (probably without making any collection and preparation of slides personally). He has

shown a number of unbranched radial microsporophylls originating in a whorl from the rim-like collar of a receptacle (Fig. 22). "Each stalk gives rise to secondary laterals that terminate in several stalked pollen sacs". Osborn *et al.* (1991) figure *Sahnia laxiphora* and described origin of large balloonshaped solitary microsporangia directly on almost entire length of radial microsporophylls. It supports the reconstruction of *Sahnia nipaniensis* suggested by Mittre (1953) and Suthar and Sharma (1988). Srivastava and Banerji (2000) figure a longisection of male fructification (Fig. 24) and show lateral attachment of sporangia in rows on radial microsporangiophores. Further investigations are required for better understanding the structure of the male fructification of the Pentoxyleae.

Crane (1985), Doyle and Donoghue (1986), Stewart and Rothwell (1993) correlate pentoxylean male fructification with *Cycadeoidea* and the bennettitalean fructification *Weltrichia* on the basis of origin of microsporophylls in a whorl and monocolpate (monosulcate) structure of pollen grains. The author considers this correlation purely hypothetical and imaginative. Bennettitales and Pentoxylales are two distinct groups of Mesozoic plants.

Seed bearing fructifications

Srivastava (1944, 1945) described a peculiar, permineralised seed-bearing fructification Carnoconites with two species C. compactum (Pl. 11-3) and C. laxum (Pl. 14-6). In them othotropus ovules are produced directly from the cone axis. Seeds are arranged either in compact or loose helicals and each has a thick heterogeneous, non-vascularised integument. Nucellus is free and embryo probably was dicotyledonous. Sahni (1948) (Fig. 15), Mittre (1953) and Sharma et al. (1987) have figured a number of sections cut in L.S. and C.S. through these cones and added to our knowledge about them. Bose et al. (1984) suggested a new combination Carnoconites rajmahalensis for C. laxum Srivastava on the basis of homology between an earlier described Specimen No. 4514 present at G.S.I., Calcutta (India) and preserved as an impression of Williamsonia (?) rajmahalensis Wieland (1911). It was collected by Feistmantel (1877) from Mundro in the Rajmahal Hills and had described as a "Cycadeous fructification". They (Bose et al. 1984) also write that similar cones preserved in form of an impression were collected earlier from Onthea and Sakarigalighat by Bose (1959), but no description was published. The author wishes to know whether Wieland (1911) had examined the original Specimen (Holotype No. 4514) or if he gave the name Williamsonia (?) rajmahalensis only on the study of the drawing published by Feistmantel (1877)? There are many records in Palaeobotany literature when different names are given to similar fossils based on their mode of preservation e.g., Trigonocarpus is a cast or impression or compression of a medullosan seed while similar permineralised seeds are described as *Pachytesta* (Taylor & Taylor, 1993; Stewart & Rothwell, 1993). How justified are Bose *et al.* (1984) in suggesting a new combination *C. rajmahalensis* for *C. laxum.* This needs reconsideration ?

Carnoconites compactum is a globose or an oval fructification with compact hexagonal or round ovules in helical arrangement on cone axis (Pl. 1·1-3). Bose *et al.* (1985), Taylor and Taylor (1993), Stewart and Rothwell (1993) and Srivastava and Banerji (2000) have described the seeds/ovules of *Carnoconites* as platyspermic (flat seeds). In majority, the medullosan seeds are radiospermic while in Cordaitales the seeds are designated as platyspermic. In the medullosan seed *Trigonocarpus* or *Pachytesta* the sarcotesta in micropylar portion becomes flat (wing-like) and even then the seed is called radiospermic whereas, in *Carnoconites* only the sclerotesta may become flat (not always) in micropylar region and the seed has been defined as platyspermic. Use of these two terms needs reconsideration. The author considers the seeds of *Carnoconites* to be radiospermic (Pl. 1·1-6).

In *Carnoconites* the vascular supply ends in the basal portion and the nucellus is free with a distinct nucellar pad. Though possible existence of polyembryony has been described in *C. compactum* seeds (Sharma, 1989), yet, the structure of the embryo is not definitely know. It is only a hypothesis that the embryo was dicotyledonous (Srivastava, 1945). No drawing or photograph has ever been published showing a dicotyledonous embryo to be *Carnoconites* seed.

A number of reconstructions have been drawn to show the morphology of infructescence of Carnoconites compactum. Sahni (1948) made 5-6, stalked globose fructifications arising from a peduncle terminal to a dwarf shoot. While Mittre (1953) believed the presence of 15 to 18, stalked globose fructifications in spiral on a peduncle (Fig. 16). However, the attachment of peduncle to stem/branch is not shown. Harris (1962) described Carnoconites cornwelli from New Zealand and suggested the presence of 12, long stalked fructifications in a whorl at the stem apex. Bose et al. (1985) in a reconstruction beyond imagination of an infructescence of Carnoconites compactus (changed from compactum, see Bose et al., 1985) have drawn hundreds of globose, stalked fructifications originating in spiral from nearly 12 naked peduncles (Figs. 11, 17) in a whorl at the top of a dwarf shoot (fertile shoot with raised leaf cushion on surface). No body has ever figured a section through Nipania chert bearing such a large number of cones of C. compactum or stalks on a peduncle. Maximum 9 or 10 cones have been seen in a bunch. Crane (1988) has also published a reconstruction of C. compactum (Fig. 18) resembling more or less that of Bose et al. (1985). Interestingly neither Bose nor Crane ever published any account of Carnoconites specimens or slides prior to their reconstructions given above. Is it not an imagination ? Sahni's reconstruction of Carnoconites compactus is more natural than those of others. Srivastava and Banerji (2000) also suggested a reconstruction of seed bearing infructescence of *C. compactus*. It is similar to that of Bose *et al.* (1985) but with much lesser number of cones on a dwarf shoot (Fig. 19). Leaf bases on dwarf shoot are however shown in whorls, probably this is incorrect.

Pentoxyleae is a synthetic group of Mesozoic gymnosperms which has affinities with the Palaeozoic medullosan pteridosperms in anatomy and structure of seeds. *Guptioxylon amarjolense* and *G. endocentrica* link Medullosales with the Pentoxyleae (Sharma, 1972a). Similar to the medullosan stems, an internal common periderm layer which encircles the steles is also found in many stems and branches of *Pentoxylon* (Sharma, 1974). The seed has thick heterogeneous integument and a free nucellus similar to that of the Medullosae. But the male fertile organs are quite different and distinct in the two groups of extinct plants.

The Triassic stem genus *Rhexoxylon* is close to *Pentoxylon* (Archangelsky & Brett, 1961) in structure of steles and manner of origin of leaf traces. But associated fertile organs of *Rhexoxylon* are yet to be discovered.

The diploxylic bundles of leaf midrib, irregularly oriented anomocytic stomata on lower surface of lamina and monocolpate pollen grains are identical to those of the cycads (Pant & Mehra, 1962). *Purioxylon* Sharma (1972a) is a link in derivation of anatomy of cycads from Medullosae.

On cladistic analyses several palaeobotanists place Pentoxylon close to the Bennettitales i.e., a sister group of the clade that includes flowering plants and the Gnetales (Crane, 1985, 1988; Doyle & Donoghue, 1986). Except orthotropus position of ovules and monosulcate pollen grains, there is no other character which may be used in establishing relationship between Bennettitales and the Pentoxyleae. Taylor and Taylor (1993) write "the platyspermic ovules, thick sclerotesta and ring of pollen bearing structures suggest affinities with the Bennettitales". The author (BDS) has done enough research work on the bennettitalean seed bearing fructification Williamsonia Carruthers but never noticed the platyspermic morphology of ovules and presence of sclerotesta in an integument (Sharma, 1970, 1974, 1980, 1992). Similarly, there is no relationship exists between Sahnia and Weltrichia (Sharma, 1969b). In Sahnia radial microsporophylls are produced in spiral on a cylinderical receptacle (Bose et al., 1985; Suthar & Sharma, 1988) and not in a whorl. Microsporangia in Sahnia are large, solitary and balloonshaped produced directly on microsporophylls. Whereas, in Weltrichia microsynangia originate in two rows on finger-like appendages of flat microsporophylls produced in a whorl at the brim of a circular cup-shaped receptacle (Sharma, 1969b; Sitholey & Bose, 1971; Stewart & Rothwell, 1993).

Pentoxylon resembles *Ginkgo* in morphology of dwarf shoots and origin of leaves on them, compact nature of secondary wood, uniseriate, short wood rays and monosulcate pollen grains. Ovules bearing peduncles on dwarf shoots of *Ginkgo* may be correlated but distantly with the cones producing peduncle terminal to dwarf shoot of *Pentoxylon*.

The secondary wood of Pentoxylean stems is compact and made up of squarish tracheids arranged in radial rows. Xylem parenchyma are absent. Tracheids have bordered pittings uni or biseriate and contiguous resembling Cordaitales, Araucariaceae, etc. of Coniferopsida.

Comparison of the Pentoxylean fossil plants with Gnetales and the flowering plants is not more than an imagination.

Acknowledgements—The author expresses sincere thanks to his pupil Drs DR Bohra, OP Suthar and R Harsh who helped in collection of material from the Rajmahal Hills and also assisted in preparation of slides. For financial assistance thanks are due to the UGC and CSIR, New Delhi.

REFERENCES

- Archangelsky SA & Brett DW 1961. Studies on Triassic fossil plants from Argentina I. *Rhexoxylon* from the Ischigualasto Formation. Philosophical Transactions of Royal Society, London 244: 1-19.
- Bose MN 1959. *Morrisia*, a new genus of cycadophytic fronds from the Rajmahal Hills, Bihar. Palaeobotanist 7 : 21-25.
- Bose MN, Pal PK & Harris TM 1984. *Carnoconites rajmahalensis* (Wieland) comb. nov. from the Jurassic of Rajmahal Hills, India. Palaeobotanist 32 : 368-369.
- Bose MN, Pal PK & Harris TM 1985. The Pentoxylon plant. Philosophical Transactions of Royal Society, London 310 B : 77-108.
- Crane PR 1985. Phylogenetic relationships in seed plants. Cladistics 1: 329-348.
- Crane PR 1988. Major clades and relationships in the "higher" gymnosperms. In . Beck CB (Editor)—Origin and Evolution of Gymnosperms: 218-272. Columbia University Press, New York.
- Douglas JG 1969. The Mesozoic flora of Victoria. Memoir of Geological Survey of Victoria 28 : 1-310.
- Doyle JA & Donoghue MJ 1986. Seed plant phylogeny and the origin of angiosperms. An experimental cladistic approach. Botanical Review 52 : 321-431.
- Drinnan AN & Chambers TC 1985. A reassessment of *Taeniopteris daintreei* from the Victorian Early Cretaceous, a member of the Pentoxyleae and a significant Gondwana plant. Australian Journal of Botany 33 : 89-100.
- Feistmantel O 1877. Jurassic (Liassic) flora of the Rajmahal Group in the Rajmahal Hills. Memoir. Geological Survey of India, Palaeontologica Indica 2: 53-162.
- Harris TM 1962. The occurrence of the fructification Carnoconites in New Zealand. Philosophical Transactions of Royal Society, London 1 : 17-27
- Harris TM 1982. Fossils from New Zealand ascribed in the *Pentoxylon* plant. Phyta-studies on living and fossil plants (Pant Comm. volume) Allahabad : 91-103.
- Mittre V 1953. A male flower of *Pentoxylon* with remarks on the structure of the female cones of the group. Palaeobotanist 2 : 75-84.

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- Mittre V 1957. Studies on the fossil flora of Nipania (Rajmahal Series), India—Pentoxyleae. Palaeobotanist 6 · 31-46
- Osborn JM, Taylor TN & Crane PR 1991. The ultra-structure of *Sahnia* pollen (Pentoxyleae). American Journal of Botany 78 : 1560-1569.
- Pant DD & Mehra B 1962. Studies in gymnospermous plants *Cycas*. Central Book Depot., Allahabad, India.
- Rao AR 1943. Jurassic spores and sporangia from the Rajmahal Hills, Bihar. Proceedings of National Academic Science India 13 : 181-197.
- Rao AR 1943 a. The structure and affinities of *Taeniopteris spatulata* McCl. Proceedings of National Academic Science India 13: 333-355.
- Sahni B 1948. The Pentoxyleae : a new group of Jurassic gymnosperms from the Rajmahal Hills of India. Botanical Gazette 110 : 47-80.
- Sharma BD 1969. On the Pentoxyleae remains from Amarjola in the Rajmahal Hills, India. Ameghiniana 6 : 50-56.
- Sharma BD 1969a. *Guptioxylon amarjolense* gen. et sp. nov. from Amarjola in the Rajmahal Hills, India. Palaeontographica 126 B : 145-153.
- Sharma BD 1969b. Further observations on *Williamsonia santalensis* Sitholey & Bose with description of a new species. Palaeontographica 125 B : 93-103.
- Sharma BD 1970. On the structure of the seed of Williamsonia collected from Amarjola in the Rajmahal Hills, India. Annals of Botany 34 : 1071-1077.
- Sharma BD 1972. *Guptioxylon endocentrica* sp. nov. du Jurassique D' amarjola daus les Rajmahal Hills (Inde) Extrait, du Bulletin Mensuel de la Societe Linneenne de Lyon 21 : 114-120.
- Sharma BD 1972a. *Purioxylon jurassica* gen. et sp. nov. from Amarjola in the Rajmahal Hills, India. Adv. Pl. Morph. (Puri comm. vol.) : 233-242. Sarita Parkashan, Meerut (India).
- Sharma BD 1973. On the anatomy of dwarf shoots of *Pentoxylon sahnii* Sriv. collected from Amarjola, Rajmahal Hills, India. Acta Palaeobotanica 14. 195-206.
- Sharma BD 1973a. Further observations on *Pentoxylon sahnii* Sriv. from the Jurassic of Amarjola in the Rajmahal Hills, India. Palaeobotanist 20 : 216-220.
- Sharma BD 1974. Observations on branching in *Pentoxylon sahnii* Srivastava. Bulletin of National Science Museum of Tokyo 17 : 315-324.
- Sharma BD 1974a. *Pentoxylon* and allied fossil woods from Amarjola in the Rajmahal Hills, India. Bulletin of National Science Museum of Tokyo 17 : 75-86.
- Sharma BD 1975. Further observations on the fossil flora of Nipania in the Rajmahal Hills, India. Ameghiniana 12 : 329-336.
- Sharma BD 1979. Further observations on the dwarf shoots of *Pentoxylon sahnii* Sriv. collected from the Jurassic of Rajmahal Hills, India. Acta Palaeobotanica 20: 129-136.

- Sharma BD 1980. Micropyle in *Williamsonia* carr. (Bennettitales). Annals of Botany 45 : 191-195.
- Sharma BD 1989. Possible occurrence of polyembryony in Pentoxyleae. Phytomorphology 39 : 199-201.
- Sharma BD 1992. Indian Williamsoniaceae an overview. Palaeobotanist 40 : 260-265.
- Sharma BD 1996. The Pentoxyleae an overview. Palaeobotanist 45 : 50-56.
- Sharma BD & Bohra DR 1977. Structure of phloem in some plants of Bennettitales and Pentoxylales collected from the Rajmahal Hills, India. Geophytology 7 : 214-216.
- Sharma BD & Bohra DR 1987. The fossil flora of the Rajmahal Hills, recent investigations with critical remarks. Geological Survey of India Special Publication No. 11 vol. 1 : 253-260.
- Sharma BD, Bohra DR & Suthar OP 1987. The phylogeny of Pentoxyleae. Facena 7 : 5-14.
- Sitholey RV & Bose MN 1971. *Weltrichia santalensis* (Sitholey & Bose) and other bennettitalean male fructifications from India. Palaeontographica 131 B : 151-159.
- Srivastava BP 1944. Silicified plant remains from the Rajmahal Hills. Palaeobotany in India 5. Proceedings of National Academic Science India 14 : 73-76.
- Srivastava BP 1945. Silicified plant remains from the Rajmahal Hills, India. Proceedings of National Academic Science India 15 : 185-211.
- Srivastava SC & Banerji J 2000. Pentoxylon Plant. a reconstruction and interpretations. Plant Cell Biology & Development 13 : 11-18.
- Stewart WN 1976. Polystely, Primary xylem and the Pteropsida. Birbal Sahni Institute of Palaeobotany, Lucknow, India. 21st Sir AC Seward Memorial Lecture : 1-13.
- Stewart WN & Rothwell GW 1993. Palaeobotany and the Evolution of plants. Cambridge University Press, New York.
- Suthar OP & Sharma BD 1988. A new interpretation on the structure of *Sahnia nipaniensis* Mittre from the Rajmahal Hills, India. Palaeobotanist 37 : 90-93.
- Suthar OP, Sharma BD & Bohra DR 1988. Record of an additional shoot system in *Pentoxylon sahnii* Srivastava from the Rajmahal Hills, India. Journal of Earth Science 15: 75-78.
- Taylor TN 1988. Pollen and Pollen organs of fossil gymnosperms : Phylogeny and reproductive biology. *In*: Beck CB(Editor)— *Origin and Evolution of Gymnosperms*. Columbia University Press, New York.
- Taylor TN & Taylor EL 1993. *The Biology and Evolution of Fossil plants*. Prentice Hall Inc., New York.
- White ME 1981. Revision of the Talbragar Fish Bed flora (Jurassic) of New South Wales. Records of Australian Museum 33 : 695-721.
- Wieland GR 1911. On the Williamsonia tribe. American Journal of Science Ser. 4. 32: 433-466.