The Pentoxyleae : an overview

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The fossil plants of the Group Pentoxyleae collected from the Rajmahal Hills suggest an assemblage of small trees with multimorphic branches, polystelic vasculature and diploxylic bundles in leaves. Microsporophylls are radial, branched and have balloon-shaped microsporangia with monocolpate spores. Ovules originate directly from cone axis. Its relationship has been discussed with different groups of gymnosperms (Medullosales, Cycadales, Bennettitales, Ginkgoales, Coniferales and Gnetales) and angiosperms.

Key-words—Mesozoic, Gymnosperms, Pentoxyleae, Rajmahal Hills.

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साराँश

पेंटाक्सीली : एक पुनर्समीक्षा

बी.डी. शर्मा

राजमहल पहाड़ियों से प्राप्त पेंटाक्सीली समूह के अश्मित पौधों के अवयवों से व्यक्त होता है कि यह समूह पत्तियों में द्विदारु बंडलों एवं बहुरंभी संरचना तथा बहुशाखाओं से युक्त छोटे वृक्षों के रूप में विद्यमान था। सूक्ष्मबीजाणुपर्ण अरीय, शाखायुक्त एवं एक कोष्ठकी बीजाणुओं से युक्त हैं जो गुब्बारे-सदृश बीजाणुधानियों में विद्यमान हैं। इनमें कोन अक्ष से बीजाण्ड उत्पन्न होता है। आवृतबीजीयों एवं अनावृतबीजीयों के विभिन्न समूहों से इस समूह की तुलना भी की गई है।

THE silicified material collected by Professor Sahni and his associates in 1932 from Nipania in the Rajmahal Hills, Bihar was given for study to A.R. Rao and B.P. Srivastava. Rao (1943) described the leaf *Taeniopteris spatulata* in detail while Srivastava (1945) described two new stems: *Pentoxylon sahnii* and *Nipanioxylon guptai* and a new seed bearing fructification *Carnoconites* with two species—*C. compactum* and *C. laxum*. Later, Sahni (1948) described the new group of gymnosperms—the Pentoxyleae. Mittre (1953) described the male fructification *Sahnia nipaniensis* and published further observation on seed-bearing cones and stems (Mittre, 1957). Sharma observes the mode of branching in *Pentoxylon* and anatomical peculiarities in it (Sharma, 1969, 1973, 1973a, 1979; Suthar *et al.*, 1987). Stems with allied anatomy have also been described from the Rajmahal Hills (Sharma, 1969a, 1972, 1972a). Sahni (1948) identified *Taeniopteris spatulata* like fronds collected from Nipania as *Nipaniophyllum raoi* Sahni. The leaf shows wide variation in morphology yet all possess a number of diploxylic bundles in midrib (Sharma & Bohra, 1977). A modification in Mittre's (1953) restoration of the male fructification—*Sahnia* has been suggested by Bose *et al.* (1985) and Suthar and Sharma (1988). The seeds have medullosean characters and also show existence of polyembryony (Sharma, 1989).

The Pentoxyleae has been thought to be related with various groups of plants like Medullosales, Cycadales, Bennettitales, Ginkgoales, Coniferales and angiosperms (Sahni, 1948; Mittre, 1957; Rao, 1974, 1981; Sharma & Bohra, 1980; Sharma *et al.*, 1987; Bose *et al.*, 1985). In the present paper, the present status of this interesting group of extinct plants has been described and discussed.

MATERIAL AND METHODS

The material of Pentoxyleae has been collected from the fossiliferous localities of Nipania, Amarjola and Sonajori in the Rajmahal Hills, Bihar (India). At Nipania and Sonajori the plants are found embedded in silicified chert whereas at Amarjola the stems, dwarf twigs and leaves are found embedded in ferruginous sandy rock. The cherts were cut with the help of diamond edge wheel while the fragile material from Amarjola needs cooking in Canada balsam prior to sectioning with the help of wire bandsaw. Slides were prepared by the usual technique of grinding and polishing and mounted in Canada balsam.

DESCRIPTION

Except roots, all other organs of the plant body are known in the group Pentoxyleae.

Stem

Four genera with five species are represented in the Rajmahal Hills. These are *Pentoxylon sahni, Nipanioxylon guptai, Guptioxylon amarjolense, G. endocentrica* and *Purioxylon jurassica.* Published as well as present observations on them are given below.

Pentoxylon sahnii Srivastava

Srivastava (1945), Sahni (1948) and Mittre (1957) described two kinds of shoots: long shoots and dwarf shoots. The leaves are restricted to the dwarf shoots. Sharma (1973) described thick shoots, thin shoots and dwarf shoots.

Leaves were produced on thin shoots and dwarf shoots. Bose *et al.* (1985) described four types of shoots in *Pentoxylon sahnii,* i.e., Type 1 thick and generally with smooth surface; Type 2 thick with persistent leaf cushions in spiral, Type 3 of limited length, comparatively thinner with crowded leaf bases in spiral; type 4 short and ending in a *Sahnia* flower. Suthar *et al.* (1988) described a peculiar type of shoot with irregular surface and interesting anatomy.

The stem has 5 to 9 steles surrounding a distinct pith (Sharma, 1973). Each stele is excentric with secondary growth more on the centripetal side (Text-figure 1A-D). Primary xylem is crushed and not visible. Cortical bundles originate as a result of division and detachment of centrifugal portion of stele (Sharma, 1969) (see Text-figure 1A). In some of the stems an inner periderm layer (Text-figure 1B)) surrounds the stele (Sharma, 1974). The secondary xylem is compact with uniseriate, 1-8 cells high rays and radial walls of tracheids have uniseriate, contiguous bordered pits. Pits in cross field are large, 1-2 in number and circular. Secondary phloem consists of radially arranged rows of sieve cells and phloem parenchyma (Sharma & Bohra, 1977). The ground tissue has a number of patches of sclerenchyma. The peripheral portion of cortex has periderm layer.

Sharma (1974a, 1980) has described the manner of origin of branching in *Pentoxylon* and also the anatomy of its dwarf shoots (Sharma, 1973a, 1979). Primary xylem is preserved in dwarf shoots and cuts off leaf traces from lateral sides. A number of leaf traces enter into a leaf base.

Nipanioxylon guptai Srivastava

The stem has 8-9, more or less concentric steles surrounding a wide pith. The stelar region is protected by an inner periderm, as has been described above in some specimens of *Pentoxylon.* Secondary xylem is compact as in *Pentoxylon.* Sahni (1948). believed that *Nipanioxylon* was a branch of *Pentoxylon* while Mittre (1957) did not agree with Sahni's view and described serial sections of a specimen. Bose *et al.* (1986) did not consider Mittre's specimen as *Nipanioxylon.* Further investigations are required on this genus.

Guptioxylon amarjolense Sharma

Stem surface is without leaf basis. The ground tissue has sclerenchyma patches similar to those found in *Pentoxylon.* There are four concentric to excentric steles (Text-figure 1E) each with a well-developed, compact secondary xylem (Sharma, 1969a). Primary xylem is crushed. There are a number of variously sized medullary and cortical bundles with protoxylem exarch, endarch or mesarch. Radial walls of tracheids have uniseriate, contiguous bordered pits.

G. endocentrica Sharma

There are six excentric steles surrounding a pith. Both medullary and cortical bundles are present

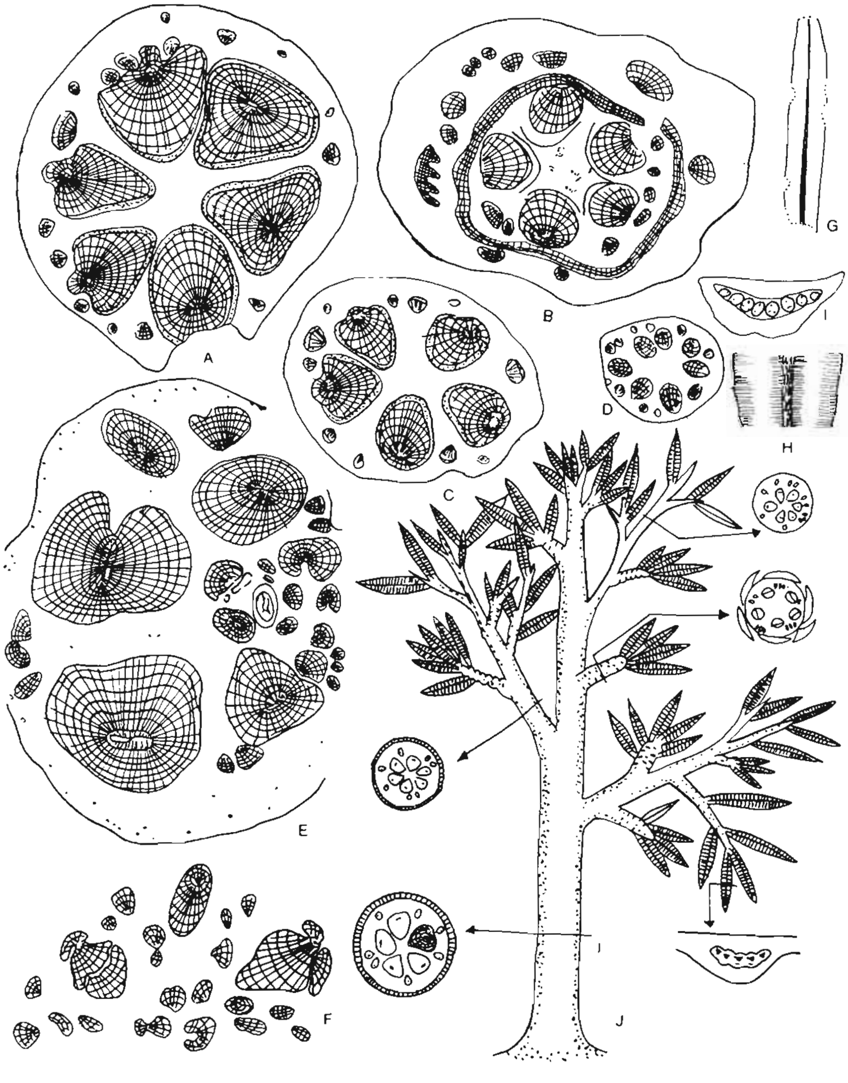
(Text-figure 1F). This taxon resembles *Pentoxylon* in shape and arrangement of steles and in the manner of origin of cortical bundles (Sharma, 1972).

Purioxylon jurassica Sharma

It has a central pith cavity surrounded by a periderm layer (Sharma, 1972a). The vascular zone consists of a number of collateral, conjoint open and endarch bundles. The cortical bundles are of various shapes and sizes, exarch, endarch or mesarch. They possess compact secondary xylem similar to the cortical bundles of *Pentoxylon* stem.

Leaves

Sahni (1948) instituted the genus *Nipaniophyllum* for the petrified leaves found in association with *Pentoxylon* in the Nipania chert. The leaves are *Taeniopteris spatulata* like in external morphology



Text-figure 1A-J—A. T.S. of old shoot of *Pentoxylon sahnii*: cortical bundles originate as a result of detachment of centrifugal portions of the steles X 8. **B.** Same. A stem with an internal layer of periderm which surrounds steles X 8. **C**. Same. A medium thick shoot with 5 excentric bundles. X B. **D**. Same. Thin shoot with 7 steles X **8**. **E**. *Guptioxylon amarjolense* T.S. of stem with 4 main steles with cortical and pith bundles X 4. **F**. *G. endocentrica*, a portion with 3 endocentric steles, cortical and pith bundles X 2. **G.** *Nipaniophyllum hobsonii*, X 1. **H**. Same, a portion with parallel venation X 2. **I.** Same. T.S. through midrib with 8 diploxylic bundles X 25. **J**. Reconstruction of the plant *Pentoxylon sahnii* showing section cut at diferent levels.

(Rao, 1943). Leaves are simple, subpetiolate, narrow or wide with obtuse, acute or round apex; margin smooth (*N. raoi*) or incised (*N. anomozamoides*; Sharma, 1975). On the basis of width and thickness of lamina Bose *et al.* (1985) established a new species, *N. hobsonii* (Text-figure 1G) which resembles *N. raoi* in gross morphology and anatomy but has a comparatively wider (10-14 mm) and thicker (0.4 mm) lamina. Veins are parallel (Text-figure 1H).

Stomata are hypostomatic and syndetocheilic (Srivastava, 1945; Sahni, 1948). While Mittre (1957), Sharma (1969), Sharma *et al.* (1987) and Bose *et al.* (1985) consider the stomata as haplocheilic. Epidermal cells are sinuous and irregular.

The midrib has 5 to 9, diploxylic bundles in a row (Text-figure 1I) each surrounded by a sheath which in turn is covered by the transfusion tissue (Sharma, 1982).

Male fructification

Mittre (1953) established the taxon *Sahnia nipaniensis* for the male fructification and described the presence of whorled arrangement of radial, simple or branched approximately 24 microsporophylls bearing spirally arranged balloon-shaped microsporangia (Text-figure 2C). Bose *et al.* (1985) also suggest the reconstruction of *S. nipaniensis* with whorled arrangement of radial, branched microsporangiophores surrounding a central conical receptacle (Text-figure 2D). But they showed branching of microsporangiophores in the basal region and origin of a number of lateral branches in spiral, each of which bears 4-7 globose pollen sacs. Suthar and Sharma (1988) suggested another modified reconstruction of the male fructification of the Pentoxyleae (Text-figure 2E). They noticed the origin of radial microsporophylls in spiral on a cylindrical receptacle and dichotomous branching in the distal half of some microsporophylls. They did not observe lateral branching of microsporophylls. The stalked and balloon-shaped microsporangia were produced directly on the microsporophylls. Pollen grains are elliptical or circular and monocolpate with irregular exine. Osborn *et al.* (1991) studied the pollen of *Sahnia laxiphora* Drinnand & Chambers 1985 collected from Australia by SEM and suggested monosulcate nature similar to the pollen of Bennettitales.

Seed-bearing fructifications

Srivastava (1945) described two species of the seed -bearing fructification *Carnoconites* (*C. compactum* and *C. laxum*). The seeds are either closely appressed or little loose, directly attached to the cone axis and micropyles face outward. Integument is thick, heterogeneous and free from nucellus. The vascular supply ends at the base of nucellar pad. Pollen chamber is absent. Female gametophyte may have more than one embryo (Sharma, 1989). Sahni (1948) described *C. compactum* a globose, pedunculate fructification, while in *C. laxum* the peduncle is branched and 2-3 elongated, cylindrical cones are seen in a group (Mittre, 1953). In *C. compactum*, stalked female cones are seen originating from the cone axis (Text-figure 2A); Mittre (1953). Bose *et al.* (1984, 1985) suggested a new name *C. rajmahalensis* (Wieland) for *C. laxum* Srivastava on the basis of their observations that the latter resembles *Williamsonia* (?) *rajmahalensis* Wieland 1911. Bose *et al.* (1984a) make a restoration of the cone *C. compactum* and show hundreds of globose pedicellate cones arising from several peduncles which in turn, originate from the terminal portion of a dwarf shoot (Text-figure 2B).

Harris (1962) reported the occurrence of a new species of *Carnoconites*, *C. cranwelli* from the Lower Cretaceous of New Zealand. A group (12 or more) of small cones with long pedicels were produced terminally at the stem apex. The cones were found in association with *Taeniopteris spatulata*.

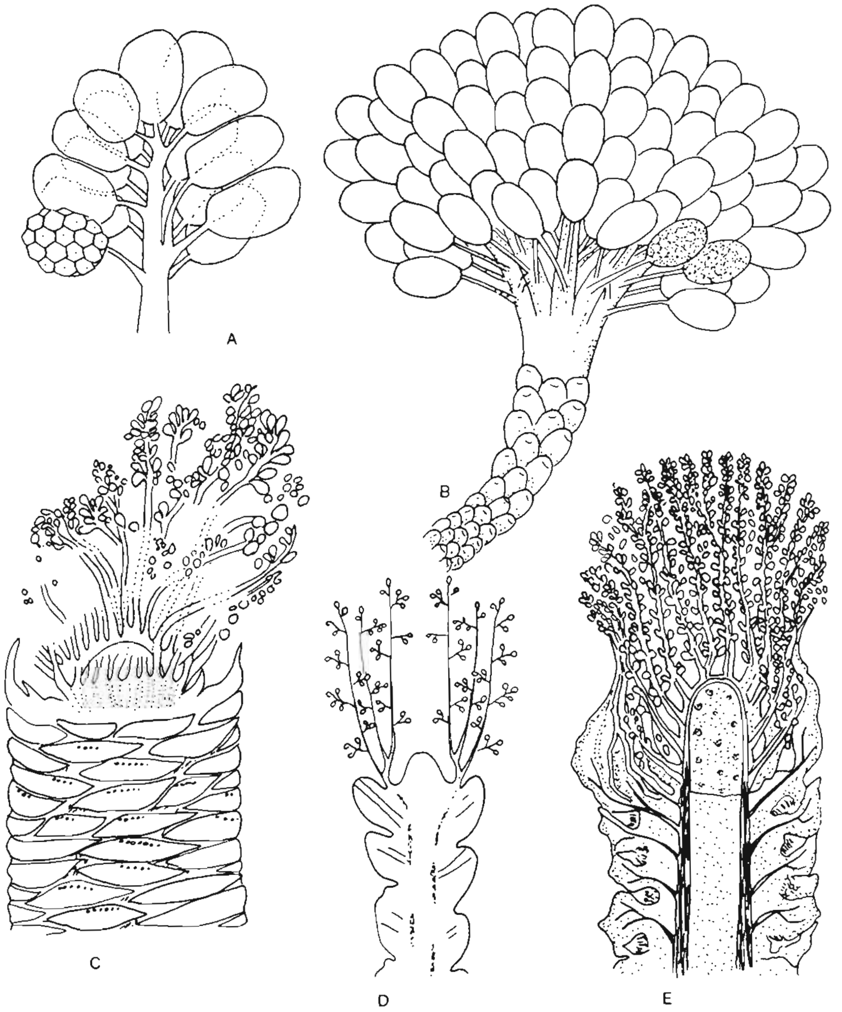
White (1981) described *Pentoxylon australica* sp. nov. and included in it a new seed-bearing pedicellate fructification *Carnoconites australica* from Talbragar fish beds. This fructification is comparatively larger in size and only few seeds are present per cone. Exact structure and attachment of seeds remain unknown for want of better preserved material.

DISCUSSION

The Pentoxyleae originally collected from Nipania do not occur at many places in the Rajmahal Hills. It has been reported from two more localities:

Amarjola and Sonajori (Sharma, 1969; Bohra, 1979). It suggests that the plants of this group were not widely distributed. However, the reports of occurrence of the Pentoxyleae in New Zealand (Harris, 1962, 1982) and Australia (White, 1981) do not favour the hypothesis of restricted distribution of the group. The Australian material of *Carnoconites australica* White is very different from the New Zealand specimens of *C. cranwelli* Harris in size as well as morphology (White, 1981). Similarly, the *Sahnia* fructification shown by Osborn *et al.* (1991) does not match with the original material of *Sahnia nipaniensis.*

The anatomy of the stem of *Pentoxylon* has been derived from *Medullosa* through *Guptioxylon amarjolense* Sharma and *G. endocentrica* Sharma. In *Guptioxylon,* the medullary bundles identical to those of medullosan plants are present whereas, the main steles specially of *G. endocentrica* are similar to that of *Pentoxylon sahnii* Sharma 1972. Bose *et al.* (1985) suggest *Guptioxylon amarjolense* as an enlarged top portion of the dwarf shoot type 2. The specimen of *G. amarjolense* itself shows branching and the existence of medullary bundles is a constant feature throughout the length of the specimen measuring 7.2 x 1.9 cm in length. Two more specimens of *G. amarjolense* (B.2G/Raj. A and B. 3G/Raj. A) are present in



Text-figure 2A-E—A. *Carnoconites compactum.* Reconstruction suggested by Mittre (1953); **B.** Same. Reconstruction suggested by Bose *et al.* (1985); **C.** *Sahnia nipaniensis.* Reconstruction suggested by Mittre (1953); **D.** Same. Reconstruction suggested by Bose *et al.* (1985); **E.** Same. Reconstruction suggested by Suthar and Sharma (1988).

author's collection and none shows the branch top character, i.e., broadly conical head. *Guptioxylon* is a distinct genus of the Pentoxyleae. However, its associated organs are yet to be discovered. Similarly, the cycadean stem anatomy may be derived from *Medullosa* through *Purioxylon* which has a number of collateral, conjoint and endarch bundles. The cortical bundles have compact secondary wood and are identical to the cortical bundles of *Pentoxylon* and *Guptioxylon* (Sharma, 1972).

Whether *Nipanioxylon guptai* Srivastava is a distinct taxon or a branch system of *Pentoxylon sahnii* needs more material and reinvestigations. The author agrees with Bose *et al.* (1984a) that Mittre's (1957) specimen of *Nipanioxylon* does not resemble *N. guptai* described by Srivastava (1945).

The leaves of *Nipaniophyllum raoi* which resemble *Taeniopteris spatulata* in external morphology (anatomy of *T. spatulata* not known) show wide variations in shape and size.

It seems that the creation of a new species *N. hobsonii* Bose *et al.* (1985) for little wider and thicker fronds is not justified. The variations suggested from *N. raoi* are not many and even in a single plant the younger leaves and older leaves, and lower leaves and upper leaves show morphological variations. *N. anomozamoides* Sharma also resembles *N. raoi* in shape and size but the former has deeply incised margin similar to the bennettitalean taxon *Anomozamoides* Schimper. Anatomy of *N. anomozamoides* remains unknown for want of better preserved material.

Harris (1962) reported the occurrence of leaves of *Taeniopteris spatulata* from New Zealand and related them to Pentoxyleae as these were collected in association with the seed-bearing fructification *Carnoconites cranwelli*. However, comparison with *Nipaniophyllum* remains incomplete for want of preservation of anatomical details. Similarly, the leaves figured and described by White (1981) under the name *Pentoxylon australica* resemble *T. spatulata* and do not preserve anatomical structures.

The male fructification *Sahnia* occurs rarely in comparison to the seed-bearing fructifications. Mittre's (1953) reconstruction of the fructification was modified by Bose *et al.* (1985) and suggested the origin of 4-7 globose microsporangia per lateral thin branch of the branched microsporangiophores. How such thin branches could bear and support the weight of so many large sporangia? In this reconstruction (Bose *et al.*, 1985, p. 102, fig. 8), the dwarf shoot which bears *Sahnia* does not match with any of the figures of *Sahnia* given on page 97, fig. 6(a-e) and the termination of entire vascular supply of the shoot into microsporangiophores is not correct. The central dome also has vascular supply. Suthar and Sharma (1988) suggested another reconstruction of the male fructification, *Sahnia nipaniensis* which shows a cylindrical receptacle with spirally arranged radial microsporophylls. The balloon-shaped stalked microsporangia are produced directly on microsporophylls, i.e., without lateral branches on microsporophylls. The spores are typical cycads-like, i.e., monocolpate. There is no extinct or extant plant known as yet which can be correlated with *Sahnia* in morphology.

Sahni (1948) suggested a reconstruction of the seed-bearing fructification *Carnoconites compactum* Srivastava and showed only 5-6 globose, stalked fructifications arising from a peduncle which borne terminally on a dwarf shoot. In a reconstruction of *C. compactum*, Mittre (1953) has shown 15-18, stalked globose fructifications originating in spiral on a peduncle (axis). The attachment of peduncle is not shown. In *C. cranwelli*, Harris (1962) described nearly 12, long, stalked fructifications in a whorl at the stem apex. Bose *et al.* (1985) have drawn a reconstruction of *C. compactum* in which hundreds of globose, stalked fructifications are seen originating from nearly twelve peduncles in a whorl at the top of a dwarf shoot. This reconstruction is not at all correct. None of the sections or polished surfaced blocks from Nipania could show more than 9 or 10 cones of *C. compactum* in a bunch. It is beyond imagination that a dwarf shoot approximately 1.00 cm in diameter and consisting of mostly parenchyma could produce hundreds of globose fructifications at its top.

The dwarf shoots have generally laterally elliptical or rhomboid leaf bases in Pentoxyleae (Sharma, 1973, 1975) and not oval-shaped as shown by Bose *et al.* (1985, p. 103, fig. 9). From the phyllotaxy point also the drawing of the leaf bases on the dwarf shoot is incorrect. Sahni's reconstruction is more natural than those of others.

The Pentoxyleae has been treated as a synthetic group for its relationship with various plant groups (Sahni, 1948; Meeuse, 1961; Rao, 1981; Suthar *et al.*, 1987). In the anatomy of stem and seed structure the Pentoxyleae has been related with Medulloseae while presence of diploxylic bundles in midrib and haplocheilic stomata are comparable to cycads. Crowded leaves on dwarf shoots and terminal position of fructifications on the dwarf shoots suggest relationship with Ginkgoales. The compact wood with small uniseriate rays and contiguous bordered pits on tracheids are similar to conifers. Meeuse (1961) derived monocotyledons from the Pentoxyleae. He correlates the anatomy of *Pentoxylon* with the extant genus *Pandanus*.

The anatomy and seed structure of Pentoxyleae may be derived from Medulloseae but the attachment of seeds directly to cone axis and construction of male fructification are unique. Similarly, the occurrence of a number of diploxylic bundles in the midrib can not be related with any known extinct or extant groups of plants. Indubitably, it is an interesting group of extinct plants and still needs more investigations.

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