STUDIES ON THE FOSSIL FLORA OF NIPANIA (RAJMAHAL SERIES), INDIA — PENTOXYLEAE

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ABSTRACT

The paper describes several new anatomical details regarding the vegetative remains of the Pentoxyleae.

In the genus *Pentoxylon* Srivastava stems possessing more (8-9) or less (3-4) than the usual number of the steles are described. Besides the scalariform pitting, bi- and multiseriate medullary rays — characters not known before — are also described. The genus has been diagnosed for the first time.

The apical region of a dwarf shoot of *Pentoxylon sahnii* is described.

The genus *Nipaniophyllum* Sahni is reinvestigated and consequently the diagnosis of both the genus and the species *N. raoi* Sahni emended. The stomata in the genus are shown to be non-bennettitalean in nature.

The stems of *Nipanioxylon guptai* Sriv. are described.

In the light of new information along with the previously known facts it is shown that the Pentoxyleae is not a synthetic group and belongs to the Cycadophyta. It is the most primitive group amongst the cycadophytes and should rank with the Bennettitales and the Cycadales.

INTRODUCTION

THE Pentoxyleae, a new group of extinct plants, was instituted by the late Professor Sahni in 1948 from the material from the Nipania chert.

A preliminary account of the anatomy of the leaves then known as *Taeniopteris spatulata* was first published by Professor Sahni in 1932. Later Rao (1935, 1943) investigated the anatomy of the leaves of *T. spatulata* which in the year 1948 were assigned a new name *Nipaniophyllum raoi* by Professor Sahni. The two stem genera, *Pentoxylon* and *Nipanioxylon*, were first established by Srivastava (1935, 1937, 1946) who described the anatomy of *Pentoxylon sahnii* Srivastava in details but wrote a brief diagnosis of *Nipanioxylon guptai* Srivastava. Srivastava (loc. cit.) also instituted the genus *Carnoconites* for the seed cones of the group and described two species, *C. compactum* Srivastava and *C. laxum* Srivastava. Professor Sahni (1948) included the above organ genera, e.g. *Nipaniophyllum* Sahni, *Pentoxylon* Srivastava, *Nipanioxylon* Srivastava and *Carnoconites* Srivastava in Pentoxyleae. He also reconstructed the plant *Pentoxylon sahnii* Srivastava which bore leaves known as *Nipaniophyllum raoi* Sahni and the seed cones called *Carnoconites compactum* Srivastava. Professor Sahni also showed that the group Pentoxyleae possesses synthetic affinities (SAHNI, 1948, p. 79) since it shows affinities with conifers on the one hand and Bennettitales on the other.

Further contributions to our knowledge of the genus *Carnoconites* Srivastava were made in 1953 and in the same year the male cones of Pentoxyleae under the name *Sahnia nipaniensis* Vishnu-Mittre were described (VISHNU-MITTRE, 1953, 1953a). The cones were shown to be borne on the dwarf shoots of *P. sahnii* Srivastava. Recently Shukla (1957) has reported another species of *Pentoxylon*, *P. tetraxyloides* Shukla.

The present paper describes some more newly discovered anatomical features in the vegetative remains of the Pentoxyleae.

The observations embodied in this paper were made from the fresh collections of the material of chert from Nipania by the author in 1953 and 1954. The slides and the specimens are preserved in the Museum of Birbal Sahni Institute of Palaeobotany. My thanks are due to Dr. K. R. Surange for kindly going through the manuscript.

DESCRIPTION

A. STEMS

1. Genus *Pentoxylon* Srivastava

Pls. 1, 2, Figs. 1-13; Text-figs. 1-7

So far a single species of the genus *Pentoxylon sahnii* is known which is characterized by five to six eccentric steles arranged in the ground tissue. In 1948 Professor Sahni, while instituting the group Pentoxyleae, mostly depending upon Srivastava's account, further described the species and discussed its affinities. Though the genus has been known since 1935 the diagnosis of neither the genus nor the genotype or the species has been published. The petrified stems of *Pentoxylon*

have also been reported from Amarjola in the Rajmahal Hills by Bose (1952). During a study of recently discovered stems of *Pentoxylon*, some more interesting anatomical details are noted. These new observations are described below.

Size of Pentoxylon Stems — Srivastava's account only gives the diameter of the stems of *Pentoxylon*. Some of my specimens, larger than those of Srivastava, show a great range in diameter which is from 3 to 20 mm. The stems from Amrapara are slightly larger in diameter. In length the specimens measure from a few mm. to 150 mm. The younger stems are ± circular in diameter while the larger stems are slightly flattened or oval in shape — perhaps due to preservation.

Periderm-like Tissue in the Cortex — In some stems the cortex is seen lined internally by a few to several-layered tissue, the short and rectangular cells containing some black deposits of which are seen arranged in radial rows. The whole tissue looks very much like the periderm, but since the preservation is not good nothing definite can be said.

Number of Steles — As the name signifies, typical *Pentoxylon* stems are known to have five equally developed steles (SRIVASTAVA, loc. cit., p. 196). Stems with six steles are also included in the genotype *P. sahnii* Srivastava, but Srivastava (1946) considers such stems as variations from the normal type. Besides the specimens resembling a typical *Pentoxylon* stem, there are some stems in my collection which show a range from three to nine steles. Since all these stems show the eccentric and lop-sided growth of the steles, abundant sclerotid nests in the ground tissue, narrow pith and similar tracheidal pitting as described in *Pentoxylon sahnii* Srivastava, they are all included in the genus *Pentoxylon*.
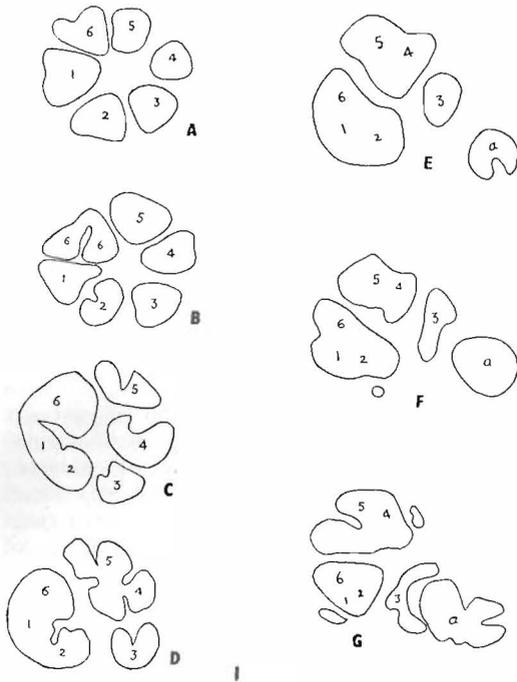
Stems with Five Steles — A stem, about 15 cm. long, 1·8 cm. in diam. at one, probably lower, end and 1·4 cm. in diam. at the other, probably upper, shows five steles. Two of the steles are larger, of more or less equal size as compared to the three small ones. This unequal nature of the five steles is noted throughout the length of this stem and no branching was observed.

Another specimen, about 8 mm. long with five unequal steles, shows three large and two small steles. The specimen is more or less ovoid in shape and measures 4×3 mm. in size.

Stems with Six Steles — They are as described by Srivastava. An interesting case of a stem with six steles measuring about 2 cm. in length showed a range in the number of steles from three to six. At the comparatively narrower end, 0·7 × 0·8 cm., it showed six equally developed steles (TEXT-FIG. 1A). At the broader end, about 1·5 × 1 cm., it showed only three steles (TEXT-FIG. 1G). The change in the number of steles was studied in serial sections.

About 1 cm. below the narrow end showing six equal steles, numbered 1-6 in Text-fig. 1A, the steles 3, 4 and 5 remain normal while the steles 2 and 6 have begun fusing with stele 1 (TEXT-FIG. 1B). During this process of fusion each stele opens at its lenticular region and forms two lobes which meet the corresponding two lobes of the other stele with the result that the ground tissues of the lenticular region of the two steles merge with one another and by further fusion and contraction of the lobes a single lenticular region is produced and the fusing bundles assume the normal form of a single stele. This is clearly demonstrated by the behaviour of the steles 1, 2 and 6 in Text-fig. 1B, C, D.

Text-fig. 1C shows a section of the stem 4 mm. below the section shown in Text-fig. 1B. This shows that the steles 4 and 5 have begun to fuse with one another. Stele 5 shows an additional lobe formed towards the stele 6. Steles 1, 2 and 6 complete their fusion about 3 to 4 mm. below this section (TEXT-FIG. 1D) while steles 4 and 5 are still undergoing fusion. About 3 mm. below this region (TEXT-FIG. 1E) steles 1, 2 and 6 are now represented by one stele which is no longer eccentric like a typical *Pentoxylon* stele. Steles 4 and 5 also assume the same form. The stele 3 in this interval has not fused with any of these steles but has changed its orientation and has lost its eccentricity. During this interval one more stele marked ' *a* ' appears in the cortex which about 2 mm. below appears to fuse with stele 3 and becomes concentric (PL. 1, FIG. 1; TEXT-FIG. 1F). The single stele formed by the fusion of steles 1, 2 and 6 becomes three-lobed and ultimately concentric (TEXT-FIG. 1F, G). The concentric stele formed by steles 4 and 5 is first three-lobed and later becomes two-lobed. The change could not be followed beyond this since the material was exhausted. Text-figs. 2, 3 show the reconstructions of the steles in the stem.

TEXT-FIG. 1 — *Pentoxylon sahnii* Srivastava: A, B, C, D, E, F, G, the serial cross-sections of a stem showing six eccentric steles at the narrower (upper) end, A, and three concentric steles at the broader (lower) end, G. *a* = branch trace. × 5.

Stems with Less or More than Five Steles — A section of a small block of chert shows three stems (PL. 2, FIG. 8); 'a' fairly large, incomplete with only three steles preserved, 'c' with eight steles irregularly scattered in the ground tissue and 'b' a small stem with only four more or less unequal steles. This third stem lies between the other two.

The stem 'c' shows two recently divided steles occupying the centre of the stem while the rest are arranged in a ring (PL. 2, FIG. 9). One of the steles shows pith preserved in the lenticular region (PL. 2, FIGS. 11, 12). The cells of the pith are round and moderately thick-walled. The cortex in these stems abounds in the sclerotic nests.

These three stems were discovered on an uneven surface of a small block the counterpart of which was not available. After yielding only one section the material on the block was exhausted.
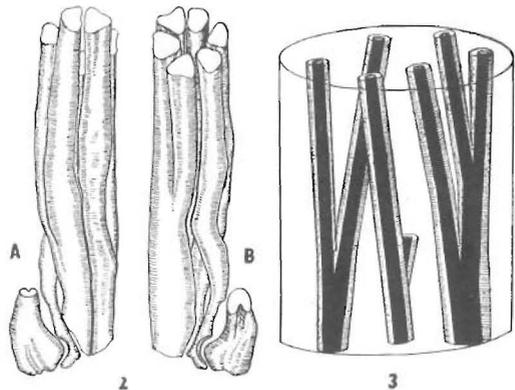
Irregular arrangement of the steles with some occupying medullary position is also noted in another solitary section of a stem

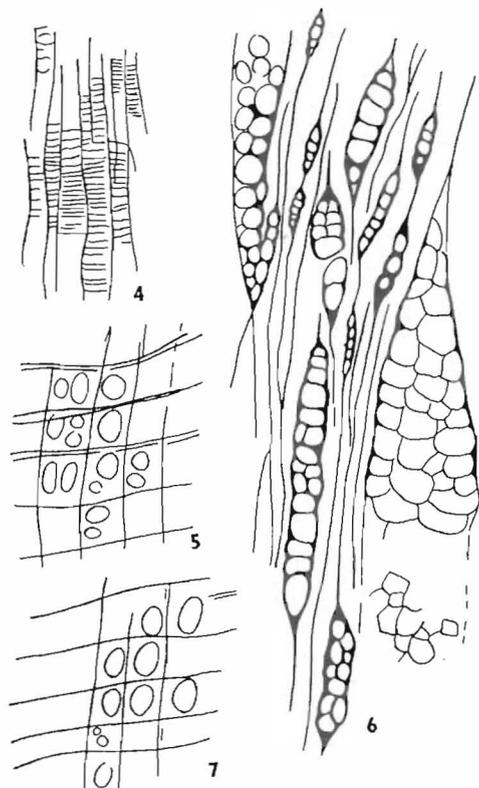shown in Pl. 2, Fig. 13, which shows 10-12 steles in it.

Pitting and the Medullary Rays — Bordered pitting on the longitudinal walls of the tracheids is as described in *P. sahnii* Srivastava but in some stems uniseriate, flattened, contiguous pits are noted in the wider tracheids (PL. 1, FIG. 3). In these stems (PL. 1, FIG. 2) the biseriate pitting is of rare occurrence. The pore in the pits is round. These stems also show tracheids with scalariform pitting — a character not known so far in the stems of *Pentoxylon* (PL. 1, FIGS. 4, 5; TEXT-FIG. 4). These scalariform tracheids seem to belong to the primary xylem and are associated with the tracheids bearing annular and spiral thickenings. In oblique vertical sections of the steles these scalariform tracheids are also noted in the secondary xylem.

Medullary rays in these stems are uniseriate, only 1-5 cells high with 1-3 cells high rays dominant. Field pits are 1-3 and are vertical oblique to horizontal in orientation (TEXT-FIG. 5).

In a branching stem the lenticular region lodging the primary xylem becomes large and shows ground tissue in it and possesses comparatively narrower tracheids in this region. Pitting in these tracheids is not preserved. The medullary rays (PL. 1, FIGS. 6, 7; TEXT-FIG. 6) in this stem are 17 cells high with 5-7 cells high dominant. They are not only uniseriate, but bi- and multiseriate rays are also met with. Field pits are 1-2 (TEXT-FIG. 7).

TEXT-FIGS. 2, 3 — Restoration of the stelar system of the stem shown in serial sections in Text-fig. 1. A and B in Text-fig. 2 show the stem from two views. Text-fig. 3 is semidiagrammatic. × 5.

TEXT-FIGS. 4-7 — 4, *Pentoxylon sahnii* Srivastava. A part of radial longitudinal section of tracheids from another stem showing scalariform pitting. × 380. 5, a part of radial longitudinal section of tracheids showing field pits. × 380. 6, a part of radial tangential section of another stem showing uni- to multiseriate medullary rays. × 200. 7, Field pits from another stem. × 380.

The Pith — In normal stems the steles are arranged in a ring round the pith. The width of the pith is not directly related to the growth of the bundles (TABLE 1) as believed by Srivastava (1946, p. 197).

From Table 1 it is seen that the stems having less number of steles and a few growth rings have comparatively the shortest pith. This observation is quite in contrast to the view held by Srivastava (1946) that in

TABLE 1

No. OF THE GROWTH RINGS IN A STELE	No. OF STELES	DIAMETER OF THE PITH, mm.
Less than 10	4	1·5-2
10-12	5	5 × 3
12-16	5	3 × 3

younger stems the pith "must have been comparatively quite wide ".

The pith in some specimens has a few sclerids while in others numerous sclerotid nests are met with which are irregularly arranged. The numerous sclerotid nests are, however, known in the stems of *P. sahnii* but, in contrast to their irregular arrangement in my specimens, they are described arranged in tiers in *P. sahnii* (SRIVASTAVA, 1946, p. 197).

Genus *Pentoxylon* Srivastava

Diagnosis — Petrified stems with 3-6 or occasionally 7-8 steles closely arranged in a ring round the pith. Stele enclosed partially or completely in a jacket of elongated rectangular cells, probably secondary phloem; stele eccentric or with equally developed secondary wood with first one or two rings complete. Wood picnoxylic, devoid of parenchyma; tracheids with one to many series of circular or flattened bordered pits; field pits 1-3; tracheids with scalariform thickening present. Primary xylem tracheids of annular and spiral thickenings; protoxylem mesarch. Medullary rays one to many cells thick and up to 17 cells high. Sclerotid nests present abundantly in the cortex and few to abundant in the pith.

Comparison — The evidence for further speciation of the genus *Pentoxylon* based on fragmentary material described by me and previous workers (SRIVASTAVA, 1946; SAHNI, 1948) is not sufficient. Consequently all the fragmentary stems are provisionally included in the species *Pentoxylon sahnii* Srivastava. These stems show slight anatomical variations which might prove of specific value when larger and better-preserved stems are discovered. No attempt is, therefore, made at present to diagnose even the known species *Pentoxylon sahnii* Srivastava.

The stems described above show that the genus *Pentoxylon*, as the name implies, did not always possess five or six steles which probably were present in the ultimate branches, while in the lower region of the axis not only the number was more or less but also the steles became somewhat concentric in form. Further the anatomical details show a range in pitting, medullary rays, field pits and in the number and arrangement of sclerotid nests in the pith. These observations perhaps indicate that the genus *Pentoxylon* included other species than

P. *sahnii* and the characters of the genus *Pentoxylon* were not so simple as those represented by *P. sahnii*. In order to distinguish the various species of *Pentoxylon* we shall have to wait till more and complete material of *Pentoxylon* stems is discovered.

An attempt has recently been made by Shukla (1957) to differentiate another species of *Pentoxylon, P. tetraxyloides*, merely on the number of steles. In the light of the above knowledge it will be risky to do so. When one stem possesses varying numbers of steles this character does not retain its importance. Secondly it will be against our concepts of nomenclature because the genus *Pentoxylon* is founded on the number of steles, and its species should not be distinguished by the same character.

The stems with five or six steles described above resemble in essential details the stems of *Pentoxylon sahnii* but differ in the tracheidal pitting, the nature of medullary rays, the number of the field pits and the presence of periderm-like layer in the cortex. More work is still required to show whether these stems belonged to other species of *Pentoxylon* or these new characters provide additional information to our knowledge of the stems of *P. sahnii*. The formation of the concentric steles in probably lower region of a stem which shows six steles at the upper narrower end is interesting though its significance cannot be made out at present.

No such fossil stem is known from the Jurassic horizon with which comparisons can be made. From the other horizon in the Mesozoic, the Triassic genus *Rhexoxylon* (BANCROFT, 1913, p. 89) seems to show the irregularly arranged steles, the presence of sclerotic nests in the ground tissue, presence of periderm, mesarch protoxylem, eccentric and centripetal growth of the secondary wood, strictly coniferous picnoxylic type of wood, coniferous pitting, medullary bundles, etc. While comparing *Pentoxylon* with *Rhexoxylon* Professor Sahni (1948) wrote that *Rhexoxylon* is a distinctly older genus whose leaves are not known and further its steles are differently constructed and more complex.

The structure of the stele in *Rhexoxylon africanum* as shown by steles 4 and 9 in section B of *R. africanum*, stele 4 in section A as figured by Bancroft (1913, PL. 11, FIGS. 7, 8) and stele 7 (BANCROFT, 1913, PL. 10, FIG. 5) is not in any way different from those of pentoxylean steles described above. The broken nature with

some pith developed between the two parts of the steles is due to their being fairly large in size. Similar features are noted in some steles of one of the specimens described above (PL. 2, FIGS. 11, 12).

Thus there are several characters of *Pentoxylon* which compare with those of *Rhexoxylon*. It is true that the leaves of *Rhexoxylon* are not known. *Rhexoxylon* is believed to possess medullosean affinities. Regarding the leaves of medullosean stems Seward (1917, p. 86) stated, " there is, however, little doubt that the other forms of leaves such as *Odontopteris* and possibly *Taeniopteris* were borne on medullosean stems ". It is interesting to point out here that *Nipaniophyllum raoi*, the leaves of *Pentoxylon sahnii*, were previously known as *Taeniopteris spatulata*.

Pentoxylon differs from *Rhexoxylon* in age, size, absence of a double ring of steles and the structure of the periderm.

Discussing the comparison of *Pentoxylon* with the Palaeozoic medullosas Professor Sahni (1948) writes that " the band-shaped primary stele, surrounded on all sides by secondary wood is indeed reminiscent of some species of *Medullosa* ". Pointing out the differences of *Medullosa* from *Pentoxylon* Professor Sahni (1948) mentions the large size and the irregular arrangement of the steles which though small in size in *Pentoxylon* do show comparable features with those of the medullosas. In the nature of pitting and medullary rays also *Pentoxylon* compares with *Medullosa*.

The chief point in which medullosas are believed to differ from *Pentoxylon* lies in their uniformly or centrifugally developed steles which in *Pentoxylon* are centripetally developed. Recently Delevoryas (1955) has shown that even centripetally developed xylem is also found in the medullosan stems (DELEVORYAS, 1955; PL. 11; PL. 19, FIG. 36; PL. 20, FIG. 42). Some of the figures given by Delevoryas (1955) remarkably compare with the stems of *Pentoxylon* (DELEVORYAS, 1955; PL. 18; FIG. 31; PL. 19, FIG. 36; PL. 25, FIG. 60). Further in the mode of branching of the stele both *Pentoxylon* and *Medullosa* compare with each other.

It is interesting to note that in this Jurassic genus *Pentoxylon* several common characters with those of the medullosas of the Palaeozoic age are found. The above observations tend to justify to some extent the recent

statement of Stewart & Delevoryas (1956, p. 78) that " the stem anatomy of members of the Pentoxyleae described from the Mesozoic in India by Sahni (1948) has much in common with medullosan stem structure and perhaps some affinity may exist between these two groups ".

Dwarf Shoot of Pentoxylon sahnii — Some leaf bases overlapping one another and grouped together as if representing the terminal apex of dwarf shoot were noted in the cross-section of a slice about 1·5 cm. thick (TEXT-FIG. 8C). These leaf bases surrounded an empty space in the centre where no tissues were seen preserved. Each leaf base showed typical characters of the leaf bases of dwarf shoots of *Pentoxylon sahnii*. After grinding for a distance of about 1 mm. the section, about 1 cm. in diam., showed several vascular bundles arranged more or less in irregular 'v'- or ' u '-shaped loops around the broad pith (TEXT-FIG. 8B). Each vascular bundle is a collateral plate of ˙xylem with protoxylem facing inwards. About a millimetre below this region, as revealed by grinding the slice from the opposite side, the specimen, about 1·2 cm. in diam., showed five band-shaped steles as arranged in a typical dwarf shoot of *P. sahnii* (TEXT-FIG. 8A). Numerous groups of stone cells were found scattered both in the cortex as well as in the pith and unicellular hairs were also seen borne on the leaf bases.
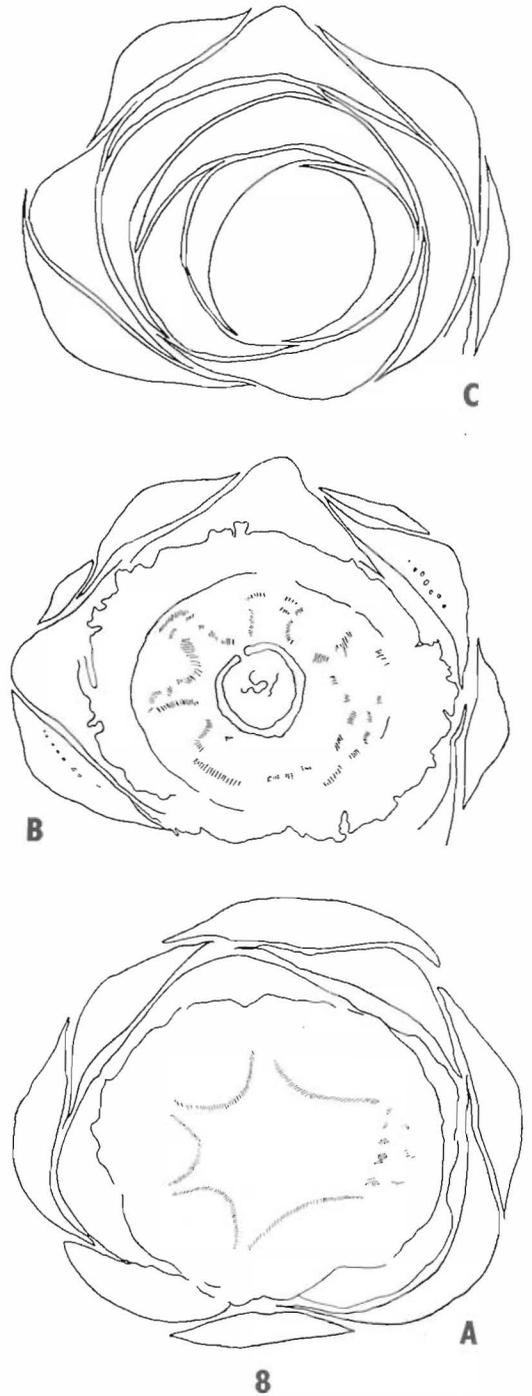
The specimen, about 5-6 mm. long, represents the apical region of the dwarf shoot and shows that each band-shaped stele within a distance of about 2 mm. below the apex disintegrates into 5-7 direct traces which ultimately terminate in the apical leaf bases.

2. Genus *Nipanioxylon* Srivastava
Text-figs. 28-31

The genotype *N. guptai* was very briefly described by Srivastava in 1935 and 1937. In 1946 only some photographs showing the anatomy of *N. guptai* were published unaccompanied by any description (SRIVASTAVA, 1946). While describing the salient features of *Nipanioxylon* Srivastava, Professor Sahni (1948, pp. 60-61) expressed his doubt that *N. guptai* might turn out to be a branching stem of *Pentoxylon* cut across the point of forking.

A study of the material on which Srivastava (1946) founded this genus shows

TEXT-FIG. 8 — Showing three serial cross-sections A, B, C, from the apical region of a dwarf shoot of *Pentoxylon sahnii* Srivastava. × 10.

that he had only isolated cross-sections of the stems at his disposal. The present study is made not only from the newly discovered isolated cross-sections of stems but also from a piece of stem about 3·5 cm. long.

The specimens vary in size from 3 × 3 mm. to about 20 × 10 mm. The younger stems are more or less spherical in cross-section while the older ones are compressed and of oval shape.

The single-layered epidermis is followed by more or less loose cortical tissue, which is comparatively narrower than the central ground tissue. Several sclerotic nests are present in the ground tissue.

The steles, 6-9 in number, are arranged in a ring. The stelar region of the ground tissue is demarcated from the cortex and from the pith by a thick band of sclerotic nests. A stele is hardly about 1-2 mm. in diam. The first growth ring is complete while the second and the third are incomplete. The phloem forms a patch towards the cortical side of the bundles. It is not possible to determine the nature of the protoxylem.

Wood is compact. Medullary rays are uniseriate, 1-3 cells high. Tracheids in radial longitudinal section bear the scalariform as well as contiguous and circular uniseriate bordered pits (TEXT-FIGS. 28, 29). Field pits not observed.

A single collateral trace is seen traversing the cortex.

Medullary ground tissue is crushed and deformed. Pith is very wide and its width directly depends upon the diameter of the stem as shown below.

TABLE 2 — RELATION OF THE SIZE OF PITH TO THE DIAMETER OF THE STEM *NIPANIOXYLON*

Stem (diam.), mm.	Pith size, mm.
20 × 10	10 × 4
7 × 5	5 × 2
6 × 4	3 × 2
3 × 3	2 × 1

A very interesting case of a *Nipanioxylon* stem about 3·5 cm. long was obtained in serial sections (TEXT-FIG. 30). At either end the stem is narrow, about 5-6 × 3-4 mm., and shows a single concentric bundle with little pith in the centre (TEXT-FIGS. 30, 31). The stem grows in diameter nearly in the middle region where a cross-section shows

six steles surrounding a very broad pith. Three of the steles in this region fuse and form a single stele thus reducing the number of the steles in the stem to five. A cross-section from this region of the stem is very much similar to the isolated sections described under *Nipanioxylon*. The ground tissue possesses abundant sclerotic nests and the stelar region is demarcated in this swollen part of the stem from the cortex and pith by a thick band of sclerotic nests. This swollen part of the stem is about 6-7 mm. long and beyond this again the steles fuse and the pith becomes fairly narrow and the single stele resulting from it becomes concentric again.

Genus *Nipanioxylon* Srivastava

Diagnosis — Petrified stems with 7-9 very small collateral steles distantly disposed in a ring round a very wide pith. Each stele with growth rings few to none, secondary wood slightly eccentric or more or less equally developed all round. Sclerotic nests few to many. Wood picnoxylic and devoid of any parenchyma.

N. Guptai Srivastava

Diagnosis — Petrified stems up to about 2 × 1 cm. thick with 7-9 small collateral steles. The stelar region limited from cortex by a layer of sclerotic nests and from pith by a parenchymatous layer. Sclerotic cells abundantly present in the ground tissue. Branch trace single. Contiguous, uniseriate, bordered pits in the radial tracheids along with the scalariform thickening. Medullary rays uniseriate, 1-5 cells high.

Comparison — The above observations on *Nipanioxylon* do not confirm the view expressed by Professor Sahni that *Nipanioxylon* represents a branching axis of *Pentoxylon*. The behaviour of the steles studied in serial sections in a piece of stem arouses doubt whether the genus *Nipanioxylon* really belonged to the Pentoxyleae. The polystely and abundance of sclerotic nests in this stem do suggest relationship with the Pentoxyleae. The occurrence of scalariform pitting in these stems further compares with that of *Pentoxylon* stems. Fusion of steles resulting in a concentric stele is also noted in a stem of *Pentoxylon* as described elsewhere.
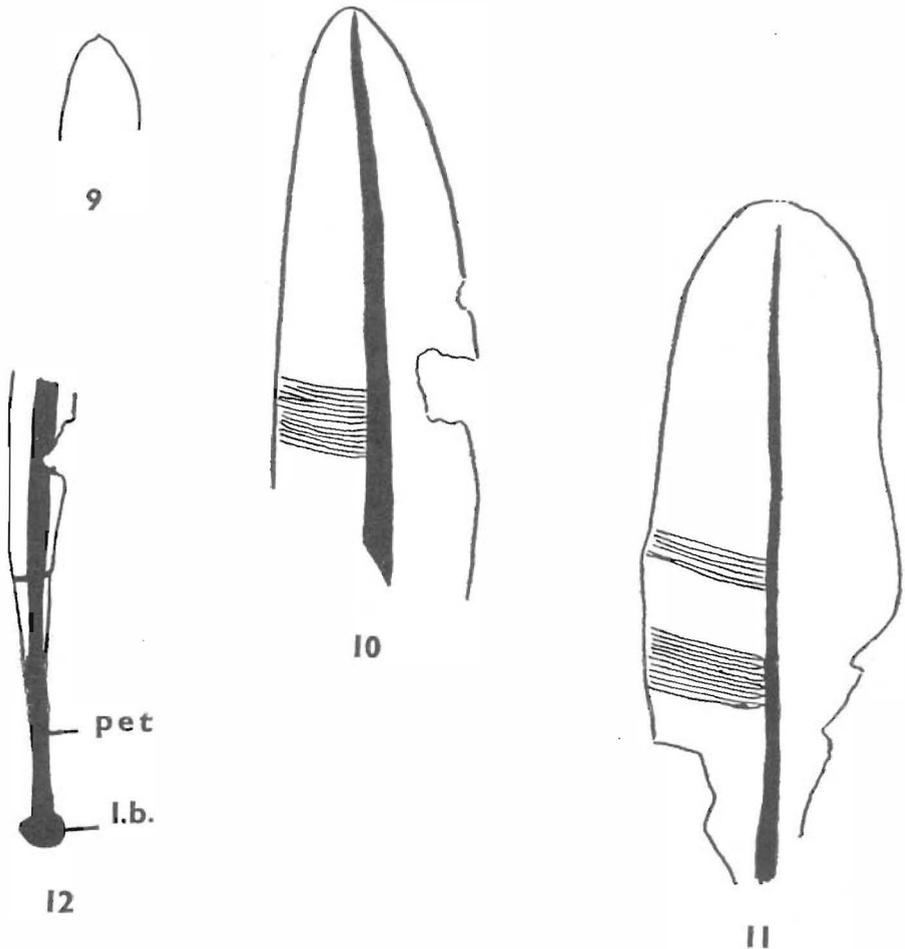
There are several differences between the polystelic stems of *Pentoxylon* and those of *Nipanioxylon*, for instance, the large pith, small and less lop-sided steles, a distinct stelar

region demarcated from the pith and medulla by a thick band of sclerotic nests. These characters show that these stems are distinctly different from those of *Pentoxylon* and Srivastava was justified in instituting a new name *Nipanioxylon* for them.

The examination of Srivastava's slides referred to *N. guptai* consisting of isolated cross-sections of stems numbered K 19/2, K 19/3, K 19/8, K 19/9, K 19/10, K 19/11, K 42/2, and L 42/3 showed that the sections K 19/8 and K 19/10 could not belong to *Nipanioxylon* because these sections represent the oblique vertical sections of the dwarf shoots and their steles are 3-4 mm. in thickness.

In his sections as well as those described by me 1-3 traces as mentioned by Srivastava (1937) are not seen, only a single trace is noted passing through the cortex. Large number of traces are known to pass through the cortex of the dwarf shoots (SAHNI, 1948; VISHNU-MITTRE, 1953a).

The specimen in slide K 19/11 figured by Srivastava (1946; PL. 9, FIGS. 86-93) differs widely from the typical stems of *N. guptai* (SRIVASTAVA, loc. cit.; PL. 9, FIGS. 88-92). The specimen measures 1·7 cm. in length and 0·7 cm. in breadth. The pith is slightly wider than 1 mm., while the cortex is comparatively very wide. There

TEXT-FIGS. 9-12 — 9, *Nipaniophyllum raoi* Sahni showing a pointed acute apex of a leaf. Nat. size. 10, a narrowly acute apex of a leaf. Nat. size. 11, a broadly round apex of a leaf. Nat. size. 12, the proximal region of a leaf. Nat. size. *pet* = petiole; *l.b.* = leaf base.

are eight vascular bundles arranged in a ring. Three of them are very closely placed, two are at a little distance from each other and the next three are again very close to one another. The above characters, however, do not suggest that this section belongs to the genus *Nipanioxylon*. In fairly large size of the steles, their close arrangement and narrow pith the specimen possesses the characters of the genus *Pentoxylon*. Only in the occurrence of eight steles the specimen shows close resemblance to *Nipanioxylon*. The steles, however, differ from those of *Pentoxylon* in having less lop-sided secondary wood and in the absence of the eccentricity of the wood so characteristic of the steles of *Pentoxylon*. *Pentoxylon* stems with five steles exactly similar as in the specimen are not uncommon in the chert. The specimen compares very much with a cross-section of a branching node of *P. sahnii* (VISHNU-MITTRE, 1953a, p. 81; PL. 4, FIG. 5; TEXT-FIG. 10) and is, therefore, believed to belong to a *Pentoxylon* stem.

B. LEAVES

1. Genus *Nipaniophyllum* Sahni

A great variation in size and form of the leaves belonging to the genus *Nipaniophyllum* Sahni has already been pointed out (SAHNI, 1948, p. 52; VISHNU-MITTRE, 1953a, p. 81). Professor Sahni (1948), however, suggested that leaves with a broader lamina and midrib might belong to a species different from *N. raoi* Sahni, the only species known so far of this genus. From his detailed study of various types of leaves then referred to *Taeniopteris spatulata*, Rao in 1943 (RAO, 1943, pp. 337-338) did not distinguish any species.

The results of the re-investigation of the salient features of the *Nipaniophyllum* leaves are given below.

1. The apex is either acute (TEXT-FIGS. 9, 10) or round (TEXT-FIG. 11). Acuminate apex as described by Rao (1943a, p. 337) is not observed in any of my specimens.

2. The venation is either dense or wide. The veins are about 1 mm. apart in some specimens (RAO, 1943, p. 337) while in others their number is 2-3 or 3-5 per mm.

3. The angle of emergence of the lateral veins varies from 60° to 90° to the midrib (RAO, 1943, p. 350). The lateral veins either remain straight and form right angle to the midrib or tend to turn upwards. There are some specimens which show both the straight as well as slightly upturned lateral veins.

4. The margins of a lamina are either almost parallel, straight and tapering gradually (TEXT-FIG. 10) or more or less wavy and abruptly tapering (TEXT-FIG. 11). The leaves with parallel, straight and gradually tapering lamina are narrower in breadth than those with wavy and abruptly tapering lamina.

5. The length of a complete leaf of *N. raoi* has never been known. The descriptions and the reconstructions of the leaves of *Nipaniophyllum raoi* are so far mostly based upon fragmentary leaf impressions showing either the apical, middle or basal regions (RAO, 1943; SAHNI, 1948, p. 78; TEXT-FIGS. 34a, 45). The longest fragment is about 7 cm. (SAHNI, 1948, p. 52) or up to 10 cm. (RAO, 1943, p. 450). The leaves in my collection also show the same range in length.
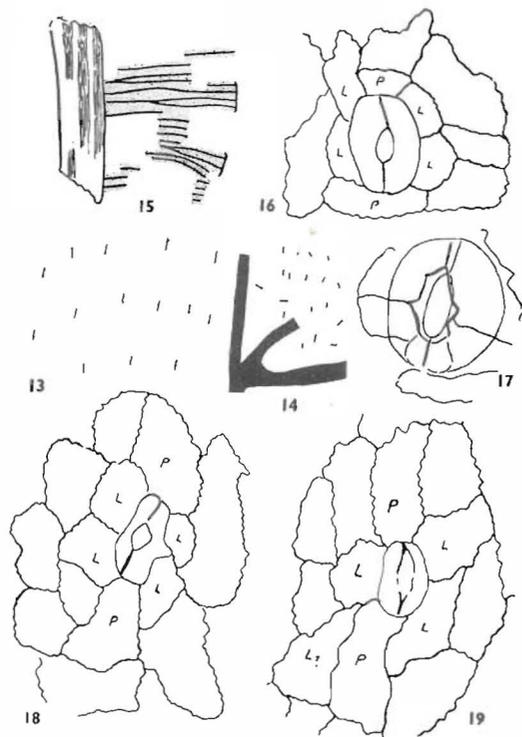
6. In form the leaves are strap-shaped (SAHNI, 1948, p. 51) or spathulate (RAO, 1943, p. 337). There are fragments in my collection showing both the spathulate and the strap-shaped forms.

The recent collection of petrified leaves from Nipania includes fragments of leaves with the proximal region also preserved. One such fragment is figured in Pl. 3, Fig. 14 and Text-fig. 12. The vagina, 2-4 × 1-1·2 mm., is thick and circular. The petiole, 10 × 1 mm., is unwinged. The lamina from the petiole originates gradually or abruptly and then broadens upwards into a strap- or a spathe-like form.

7. In the reconstruction of the shoot of *Pentoxylon sahnii* Professor Sahni (1948, p. 78; FIG. 45) figured a similar proximal region of the *Nipaniophyllum* leaves, though the petiole has been known to be narrowly winged (RAO, 1943, pp. 337-350; SAHNI, 1948, p. 53).

8. *The Epidermal Characters* — The epidermal cells except on the midrib and the lateral veins are not arranged in rows. Hair scars are not noted. The other details of the epidermal cells are as reported by Rao (1943, p. 339).

Distribution of the Stomata — Except on the midrib where the stomata are more or less vertically orientated, the stomata show irregular distribution and orientation on the lower surface of a leaf (TEXT-FIGS. 13, 14). The other details are as described by Rao (1943).
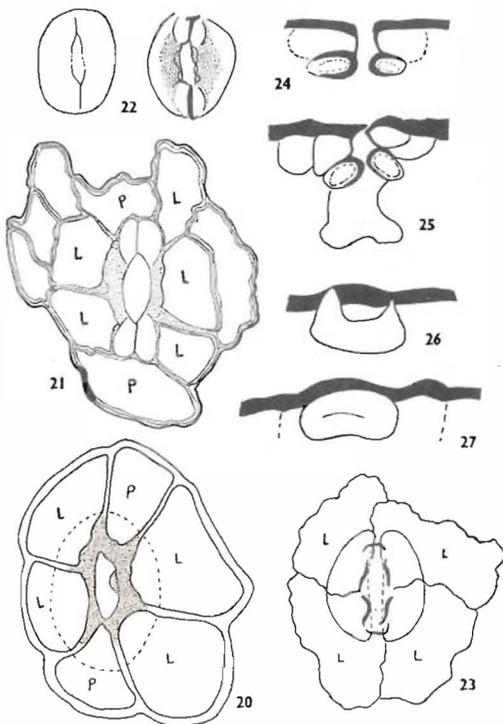
TEXT-FIGS. 13-19 — 13, *Nipaniophyllum raoi* Sahni. Distribution of stomata on a part of a rachis. × 50. 14, distribution of stomata on a part of lamina. × 50. 15, a fragmentary leaf with epidermal characters preserved. × 37. 16, 18, 19, stomatal apparatuses from above leaf showing the haplocheilic nature of the stomata. × 570. *L* = lateral subsidiary cell; *P* = polar subsidiary cell. 17, a stomatal apparatus showing the sunken nature of the guard cells and the over-arching subsidiary cells. × 650.

The Stomata (PL. 3, FIGS. 16-20; TEXT-FIGS. 15-27) — The stomatal apparatus is oval in shape and consists of 4-6, occasionally 7 subsidiary cells, 2 polar and 2-4(5) lateral (TEXT-FIGS. 16-21, 23). The walls of the subsidiary cells are wavy and slightly arch over the aperture. The guard cells in the stomata are sunken in the middle region while the polar regions are slightly raised (PL. 3, FIGS. 17-19; TEXT-FIGS. 20-22, 25). They are heavily cutinized at the polar regions while the thickenings are also noted on the outer, inner and the ventral walls of the guard cells (PL. 3, FIGS. 17-20; TEXT-FIGS. 22-25). Thickenings on the dorsal walls are not seen. Two thin patches are noted at each pole, probably formed due to the raising up of the polar ends of the guard

cells in order to bring them near to the surface at these points (TEXT-FIGS. 21, 22).

Interpretation of the Structure of the Stoma — The structure of the stomata described above shows that the *Nipaniophyllum* leaves had haplocheilic type of the stoma. Rao (1943, p. 350) described the syndetocheilic type of the stoma in *N. raoi* but did not overlook the possibility of their being haplocheilic also. From some of his photographs (RAO, 1943, PL. 15, FIG. 38) the stomata appear to be haplocheilic. My observations tend to show that the stomata are uniformly haplocheilic in the genus *Nipaniophyllum*.

The occurrence of occasionally single subsidiary cell (RAO, 1943, p. 348; PL. 3, FIG. 19; PL. 4, FIG. 22) along with frequent

TEXT-FIGS. 20-27 — 20, 21, another stomatal apparatus showing the sunken nature of the guard cells and the over-arching subsidiary cells. × 650. 22, *Nipaniophyllum raoi* Sahni. A stoma at two different focii. The figure on the left shows two guard cells, the one on the right shows the thickenings on the guard cells. × 570. 23, a stomatal apparatus devoid of the polar cells. × 650. 24, 25, cross-sections of two stomatal apparatuses showing the sunken nature of the guard cells and their thickenings. × 570. 26, 27, vertical sections of two stomatal apparatuses. Text-fig. 26 shows a guard cell with two raised polar areas. × 570.

occurrence of two subsidiary cells on one or both sides of the guard cells led Rao to interpret the stomata as syndetocheilic in nature. The fact that a subsidiary cell in a syndetocheilic type of stoma may undergo division further supported his contention. The occurrence of abnormal and exceptional bennettitalean stomata in *Williamsonia wettsteinii* and *Williamsoniella lignieri* (FLORIN, 1933, pp. 8, 11-12; TEXT-FIGS. 2b, 5a) also lent support to his view.

In a normal course of development of a syndetocheilic stoma, further division of the subsidiary cell takes place by a vertical wall into the lateral cells which instead of really encircling the stomatal apparatus lie entirely at the sides and fit neatly against each other flanking the guard cells dorsally (FLORIN, 1931, p. 515; ARNOLD, 1953, p. 55). Contrary to this fact the division of the sub-

sidiary cells in *N. raoi* is by a transverse wall (RAO, 1943, PL. 4, FIG. 25).

Harris (1932, p. 111) gives certain contrasting features of bennettitalean and non-bennettitalean stomata. In the light of this knowledge such characters of the stomata of *Nipaniophyllum* as the absence of cutinization of the dorsal walls of the guard cells, the irregular orientation of the stomata and epidermal cells (except on the midrib) and the occurrence of a ring of subsidiary cells in the stomatal apparatus, show that the stomata are non-bennettitalean and therefore haplocheilic in nature.

In the occasional occurrence of a single subsidiary cell Rao (1943, p. 348) found support for his syndetocheilic interpretation. The number of the lateral subsidiary cells in a haplocheilic stoma may not necessarily be constant. The cuticles of some recent conifers, viz. *Pherosphaera hokeriana*, *Microcachrys tetragona*, *Podocarpus dacrydioides* and *P. elatus* (FLORIN, 1931; PL. 18, FIGS. 7, 8; PL. 30, FIG. 5), and of some cycads, viz. *Encephalartos* sp., *Zamia* sp., and *Cycas circinalis*, the number of the lateral subsidiary cells on either side of the guard cells is found to vary from 1 to 3.

Assessment of the Characters — Of all the characters discussed above the apex (round or acute), margin (straight or wavy) and form of the leaf (spatulate or strap-shaped) are some of the characters which may help in distinguishing various species of *Nipaniophyllum* from one another. The anatomical characters are more or less uniform.
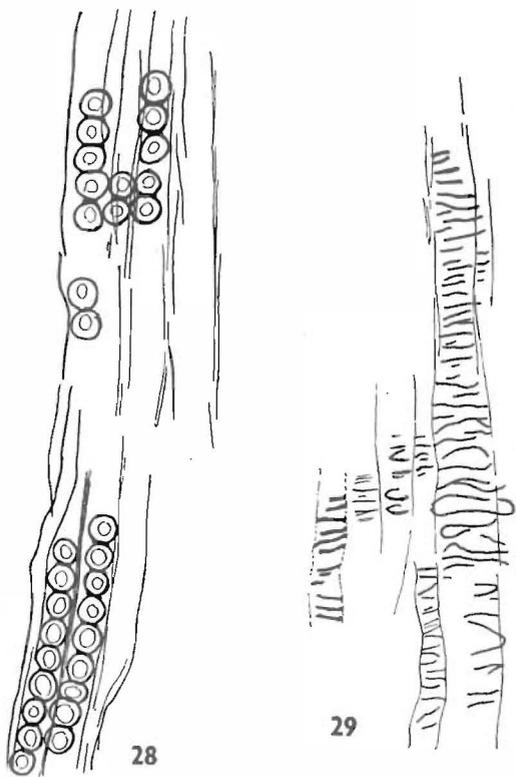
The following two types of the leaves can, however, be easily distinguished from one another on the basis of the shape, margin and apex of lamina.

Type 1 — Leaves strap-shaped with acute apex, margins running parallel and straight to the midrib — *N. raoi*.
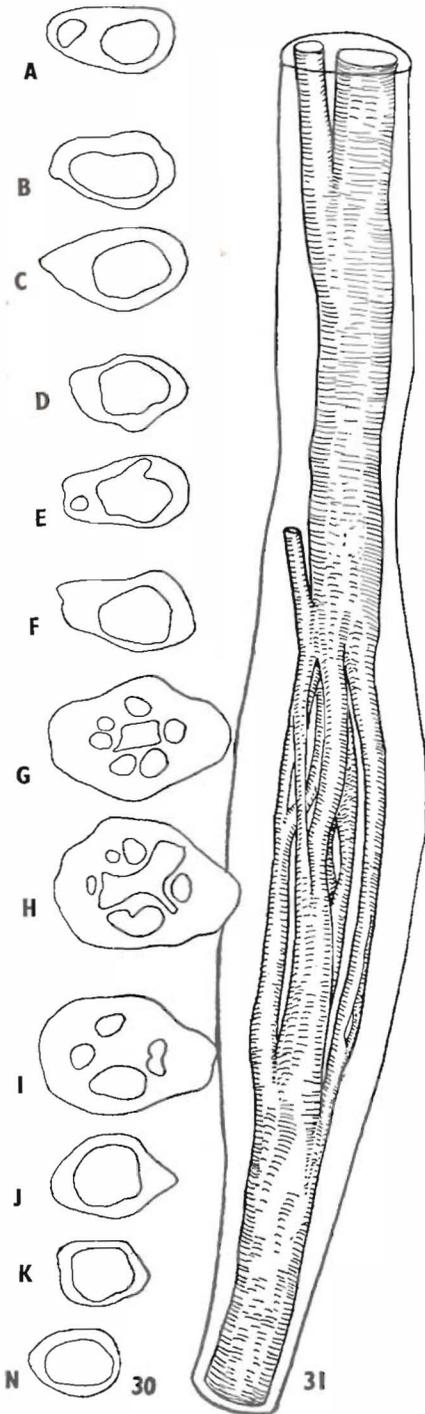
Type 2 — Leaves spathulate with broad apex, margins more or less sinuous and abruptly tapering towards the proximal region — *N.* sp.

The distinction between the above two types is based upon observations made from fragments of leaves. Till complete leaves with more distinguishing data are available, it will not be sound to raise *Nipaniophyllum* type 2 to a specific rank.

In the light of the new information described above the diagnosis of the genus *Nipaniophyllum* is revised as below.

TEXT-FIGS. 28, 29 — 28, *Nipanioxylon guptai* Srivastava. A part of radial longitudinal section of a stem showing uniseriate, contiguous bordered tracheids. × 570. 29, a part of radial longitudinal section showing the scalariform tracheids. × 570.

Genus *Nipaniophyllum* Sahni emend.

Emended Diagnosis — Petrified leaves with
the form and venation of *Taeniopteris* Brong.
Vascular bundles arranged in straight or
slightly curved row, diploxylic. Stomata
haplocheilic, subsidiary cells, 4-6, encircling
the guard cells.

Since a new interpretation of the structure
of the stoma is given the diagnosis of *N. raoi*
needs a revision. As more details are still
required to completely re-diagnose *N. raoi*,
it is apparently suggested that in the diagno-
sis of *N. raoi* as given by Professor Sahni
(1948, p. 52) the later part of the diagnosis
starting ,from the leaf cuticle onwards be re-
placed by the following words:

" Leaf cuticles thick, epidermal cells
sinuous-walled, not confined in rows ex-
cept in midrib and lateral veins; stomata
on lower surface; sunken with the guard
cells raised above, irregularly orientated
except on the midrib, lateral veins devoid
of stomata; guard cells cutinized at the
poles as well as on the ventral inner and
outer walls. Subsidiary cells 4-6, 2 polar
and 2-4 lateral, bulging outwards and
arching over the guard cells."

Comparison — The diploxylic nature of
the bundles of *Nipaniophyllum* was shown
by Professor Sahni (1932) to be cycadean in
character. In the haplocheilic type of the
stomata the nature of the guard cells and
their thickenings the leaves further show
cycadean characters.

In the presence of parallel, very fine and
numerous once-branched veins, presence of
bundle sheath with sclerenchyma wedges
above and below a bundle and the presence
of stomata on lower surface *Nipaniophyllum*
leaves resemble a Mesozoic fragmentary
leaf, *Nipaniophyllum cordaitiforme* Stopes &
Fujii known from the Upper Cretaceous of
Hokkaido in Japan (STOPES & FUJII, 1910).
The occurrence of a midrib and the structural
details of the epidermal cells and the stomata
are not known in this Japanese specimen, so
further comparisons cannot be made.

The chief difference between the two is
noted in the fact that the cross-section of
Nipaniophyllum cordaitiforme corresponds
with the vertical section of *Nipaniophyllum
raoi*. Both these sections show identical
anatomical details. Further difference is
noted in the absence of centrifugal xylem in
N. cordaitiforme. Though the centrifugal
xylem is present in the bundles of midrib of
Nipaniophyllum leaves, it has not been

recognized in the vertical section of these leaves.

DISCUSSION

The Pentoxyleae consist of several organ genera, some of which were shown by Professor Sahni in 1948 to have belonged to a plant named *Pentoxylon sahnii* Srivastava. This plant consisted of stems known as *Pentoxylon sahnii*, bore dwarf shoots which in turn bore the leaves described as *Nipaniophyllum raoi* Sahni and the female infructescence called *Carnoconites compactum* Srivastava. This plant also bore the male cones *Sahnia nipaniensis* Vishnu-Mittre on dwarf shoots. Our knowledge of the plant *Pentoxylon sahnii*, therefore, is fairly complete now though built on direct and indirect evidences.

It is also now clear that the stems of *Nipanioxylon* were distinctly different from *Pentoxylon* stems and were probably borne on a different plant which, as Professor Sahni also believes, bore the broader variety of leaves of *Nipaniophyllum raoi* Sahni and the seed cones of *Carnoconites laxum* Srivastava. It is not possible at present to establish a correlation between the various organ genera making the plant *Nipanioxylon guptai* Srivastava.

Affinities — In the light of additional information regarding the plant *Pentoxylon sahnii*, it will be interesting to see the affinities of the group Pentoxyleae.

(i) *Stems* — The stems of *Pentoxylon sahnii* and also those of *Nipanioxylon guptai* are very different from those of the Bennettitales and the modern cycads in their polystelic character; in nature of steles and their mode of branching they recall characters of the Palaeozoic medullosan stems. Polystely in mature stems of modern cycads is of polycyclic type although that (vestigial polystely) found in the seedling stages of some modern cycads approaches that of *Pentoxylon* stems. The picnoxylic nature of wood and the coniferous type of pitting of the *Pentoxylon* stems are also found in the modern cycads (SIFTON, 1920) and some Palaeozoic medullosan stems. The characters of the nature of wood and pitting should be looked upon as subsidiary characters. In the case of *Pentoxylon* stems the main and the subsidiary characters, therefore, tend to show cycadophytic affinities. The characters of the *Pentoxylon* stems are unique in the whole of the Cycadophyta since they are not shared with any of the known cycadophytic group.

The majority of the characters of the dwarf shoots compare equally with those of the Bennettitales and Cycadales. Characters like the direct leaf traces which bring Pentoxyleae nearer the Bennettitales are also found in the seedlings of *Cycas* and the sporophyll traces of other modern cycads (WORSDELL, 1906, p. 153). The dwarf shoots stand out unique in their polystelic character and the arrangement of the vascular bundles in the leaf base cushions, though the last character is, however, shared by one of the cycads, namely the leaf bases of *Bowenia spectabilis* Hook. which possess 4-7 vascular bundles arranged in an arc (PEARSON, 1898, p. 477).

The characters of the dwarf shoots of *P. sahnii* further confirm the above conclusions, though some characters of the dwarf shoots are common with those of the Bennettitales and the Cycadales.

(ii) *Leaves* — The leaves of *Nipaniophyllum raoi* in general anatomy do show characters common with the Bennettitales, Cordaitales and Cycadales. But their stomatal characters show a remarkable deviation from those of the Bennettitales. The diploxylic nature of the vascular bundles is found in such diverse groups as Bennettitales, Cordaitales, Cycadales, etc., thus indicating the subsidiary nature of this character. The leaves also confirm to the cycadophytic affinities.

(iii) *Male Cones* — The male cones of the Pentoxyleae, though built on the same plan as the bennettitalean male fructifications, differ widely from the Bennettitales in their essential characters, viz. the sporangiophores being erect, radial structures devoid of any sterile portion, spirally branched bearing sac-like unilocular sporangia in contrast to the circinate, dorsiventral pinnate sporophylls of the Bennettitales each with a sterile portion and bearing synangia. The nature of the pollen grains serves here as a subsidiary character since $\pm$ similar pollen grains are found in the Pteridosperms, Bennettitales, Ginkgoales, Cycadales and also some Angiosperms. The male cones are, therefore, unique in their nature and show cycadophytic affinities.

(iv) *Seed Cones* — The seed cones of the genus *Carnoconites* are unique in character although in the structure of their seeds and that of the peduncles they show cycadean characters, though the mode of attachment of the seed in pentoxylean female

fructifications is fundamentally different from those of modern cycads. The seeds are distinctly stem-borne in Pentoxyleae as contrasted from the leaf-borne seeds of the cycads. It is interesting to note that the seeds in the Bennettitales are also stem-borne though the synangia are leaf-borne. The true morphological nature of the seed-bearing stalks of the Bennettitales is not known and so is the case with the seed-bearing organs of the Pentoxyleae. Apparently in both the cases the seeds are borne on the axis (stem). In terms of stachyospermy and phyllospermy the Bennettitales are partially stachyospermous and partially phyllospermous while the Pentoxyleae are wholly stachyospermous. The Coniferales are likewise partially stachyospermous and partially phyllospermous (LAM, 1948, pp. 131-135; 1950, p. 522). Florin (1951, p. 386) also believes that the microsporophylls of the true conifers though derived from radial, repeatedly dichotomized and undifferentiated sporangial trusses with terminal erect sporangia are dorsiventral and hyposporangiate in nature. The more vegetative development in them shows their greater transformation.

The stachyospermy and phyllospermy (stachyospory and phyllospory of Lam) should, therefore, be looked upon as representing the stages of evolution from the most primitive stage of the radial repeatedly dichotomized and undifferentiated sporangial trusses bearing terminal and erect sporangia to the highly advanced stage where the sporangia are borne on the dorsiventral organs with a great amount of vegetative development appearing leafy in nature. It is an admitted fact that all the organs of a plant or of an animal are not evolving at the same rate of evolution. The male and female organs in the gymnosperms which, to begin with, were merely dichotomized sporangial trusses have attained the present-day forms — the stachyospermous or phyllospermous — due to their evolution at different rates. To attach any importance to this purely evolutionary phenomenon for tracing affinities and the interrelationships will not be in accordance with our present knowledge of evolution and the morphological interpretations. Therefore, the coniferous relationship of Pentoxyleae based on the stachyospermous nature of the seed-bearing organs in both the Coniferales and the Pentoxyleae is not borne out by the facts.

Summing up the affinities of the individual genera discussed above it appears that the group Pentoxyleae is purely a cycadophytic group and its synthetic nature showing affinities with the Coniferophyta on the one hand and Cycadophyta on the other is not proved by the facts which are now available.

Systematic Position — Amongst the cycadophyta the Pentoxyleae show some relation with the Bennettitales and some with the Cycadales and possess at the same time some unique features of their own. The Pentoxyleae should thus be given an equal rank amongst the Bennettitales and the Cycadales and because of their most primitive reproductive organs they should lead the list Pentoxyleae, Bennettitales and Cycadales. The reduction of the division Pentoxyleae to Pentoxylales (LAM, 1952, p. 75) seems to be justified in the light of the systematic position discussed above.

The Application of Telome Theory to the Pentoxyleae — The structural organization of various members of the Pentoxyleae appears to be simple and less advanced when the telome theory of Zimmerman (1930, 1949) is applied to it.

The stems, dwarf shoots and the leaves are all characterized by repeatedly dichotomizing cylinders within a fused axis. In the stems the individual steles are seen to branch, the branches overtop with the result that the number 5 or 6 or 5-6 or 3-6 is maintained. In a *Nipanioxylon* stem (TEXT-FIGS. 30, 31), in approximately the middle region the single concentric stele repeatedly branches off and gives rise to 5-7 individual steles, the ultimate branches of which meet again and the concentric cylinder is formed again.

The origin of the leaf traces is further based upon dichotomous branching. In the leaf due to planation and webbing the dorsiventrality has been attained, but the individual bundles are still retained in the midrib from which the lateral veins showing the simple dichotomy are given off.

The reproductive organs are further interesting. The peduncle has several bundles arranged in a ring in its proximal region, but towards its distal region the number of the bundles goes on reducing due to the reduction process. The pedicel trace to begin with is originated as a single bundle which divides into two by simple dichotomy and one of these by unequal dichotomy gives rise to a third smaller bundle, thus there are three in

the pedicel, occasionally four. The number of five or six vascular bundles in the cone-axis is also obtained by dichotomization.

In their radial symmetry the male and female sporangiophores (the term sporo-phyll or cone as previously applied to them is a misnomer) are typical and represent wholly fertile syntelomes (sporangial trusses). In the male sporangiophores the wholly fertile telomes bear spirally arranged, occasionally branched, weaker appendages which carry sporangia terminally. In con-trast to the female sporangiophores, the weaker appendages are missing due to fur-ther reduction resulting in the sessile nature of the seeds. In neither case the sporangio-phore is terminated by a sterile appendage. The female sporangiophores are spirally arranged on the peduncle while a whorled arrangement is noted in the male.

Both kinds of the sporangiophores are built on the same plan and are, therefore, homologous organs. The leaves are also built on the same structural plan as the sporangiophores with the difference that they have further evolved due to planation and webbing into dorsiventral structures. The female sporangiophores seem to be the most primitive in the group because of spiral arrangement, but in the reduction of the weaker appendages resulting in sessile seeds they are advanced.

Structurally, therefore, the group seems to be very primitive in possessing stems with polystely showing repeated dichotomy of steles and having radiosymmetric simple sporangiophores. The group does not seem to show any evolutionary tendencies in contrast to its contemporaries the Jurassic conifers which had evolved tremendously from their ancestors. The retention of very primitive characters by the Pentoxyleae in the Jurassic period probably accounts for the extinction of the group.

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EXPLANATION OF PLATES

PLATE 1

Pentoxylon sahnii Srivastava

1. A cross-section of a stem shown in Text-fig. 1F showing the three-lobed single stele formed by the fusion of steles 1, 2 and 6; steles 4 and 5 in the final stage of fusion. Steles 3 and 'a' approaching each other. × 8.

2. An oblique cross-section of a stem. × 9.

3. A part of the radial longitudinal section of the tracheids from above stem showing uniseriate contiguous bordered pits both in the summer and autumn tracheids. × 540.

4. A part of the radial longitudinal section of the tracheids from stem in Fig. 2 above showing scalariform pitting. × 200.

5. A part of above shown enlarged. × 540.

6, 7. Parts of radial tangential sections from a branching stem showing uni-, bi- and multiseriate medullary rays. × 100.

PLATE 2

Pentoxylon sahnii Srivastava

8. A part of a slice of chert showing cross-sections of three stems, a, b, c, 'a' is a part of fairly large stem, 'b' is the smallest of the three with only four steles, 'c' shows 7-8 steles. × 35.

9. Stem 'c' from above (enlarged) showing the irregular arrangement of the steles with two medullary steles. × 35.

10. Stem 'b' from Fig. 8 above (enlarged) showing four steles; two of the steles on the right-hand side of the figure seem to have just divided from a single stele. × 10.

11. One of the steles from stem 'c' with pith in the lenticular region. × 35.

12. Pith region in above enlarged. × 90.

13. Cross-section of another stem showing 9-10 irregularly arranged steles in the stem. × 14.

PLATE 3

Nipaniophyllum raoi Sahni emend.

14. The proximal region of a leaf. Nat. size.

15. A fragment of a leaf showing the gradually tapering lamina with more or less parallel sides. Nat. size.

16. A part of cuticule showing the orientation and distribution of the stomata and the nature of the epidermal cells. × 150.

17-19. A part of above (enlarged) showing the haplocheilic nature of the stomatal apparatus. Figs. 17, 18 show the same stomatal apparatus at two different focii. p.r. = polar region, g.c. = guard cells, s.c. = subsidiary cells. × 450.

20. A stomatal appratus from another leaf showing a ring of subsidiary cells with the thickenings on the ventral and outer walls of the guard cells. × 850.