

# THE *PENTOXYLON* PLANT

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[Plates 1–4]

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The various dispersed organs belonging to the *Pentoxylon* plant viz. *Pentoxylon* (stem), *Nipaniophyllum* (leaf), *Sahnia* (male flower) and *Carnoconites* (female cone) have been studied in detail. Apart from the long shoots (type 1 shoots), the plant bore three different kinds of short shoots: the thick woody short shoots, each with a broadly conical head (type 2 shoots); the slender parenchymatous short shoots (type 3 shoots); and the slightly thicker parenchymatous short shoot (type 4 shoot) terminating in a *Sahnia* flower. In addition to the well known *Nipaniophyllum raoi* leaves a second species, *N. hobsonii* sp. nov., is recognized. In *Sahnia* the sporangiophores were borne on a collar-like structure formed by the raised margin of the receptacle. The broadly conical head of the thick woody short shoot (type 2 shoot) might be the basis of the cone-bearing branchlets of *Carnoconites* fruits. The seeds of *Carnoconites* are spirally arranged rather than being in longitudinal rows as previously suggested.

*Pentoxylon* was probably a shrubby plant which grew beside water. It sent up erect branched leafy shoots which after a few seasons of growth flopped onto the ground or on other stems, making a thicket.

† Died 1 May 1983.

Although the stem, *Pentoxylon*, resembles *Medullosa* and *Rhexoxylon* anatomically, the reproductive parts of the plant, *Sahnia* and *Carnoconites*, are unlike those of any group of gymnosperms. The *Pentoxylon* plant is accordingly regarded as an extinct gymnosperm of unknown affinity.

*Nipanioxylon guptai* has previously been regarded as related to *Pentoxylon*, but its holotype is believed to be a conifer and has nothing to do with the *Pentoxylon* plant.

#### INTRODUCTION

By happy choice, a design based on the *Pentoxylon* plant is the emblem of the Birbal Sahni Institute of Palaeobotany and of *The Palaeobotanist*. We prefer to write informally about the 'Pentoxylon plant' which we feel sure is real even though assembled on circumstantial evidence from separately named organs.

The *Pentoxylon* plant consists of the following parts: the name *Pentoxylon* refers primarily to the long shoots (type 1 shoots) but is extended to include the thick short shoots (type 2 shoots) and the thin ones (type 3 shoots); the male flower is *Sahnia* and its peduncle is a type 4 short shoot; the type 2 short shoot ends by expanding into a conical head which, we believe, bears numerous fruiting branches of *Carnoconites*; the leaves of the *Pentoxylon* plant, if preserved without structure, are included in *Taeniopteris spatulata* but, if petrified and well enough known to be distinguished, are assigned to the genus *Nipaniophyllum*.

*Pentoxylon* was introduced to science in the 22nd Indian Science Congress by Srivastava (1935); however, the first valid record was published by him in 1944. We are deeply impressed by Srivastava's (1946) penetrating research which was published posthumously. In this paper the stem *Pentoxylon* and the female cone *Carnoconites* were described in detail. Rao (1943) described for the first time the petrified specimens believed to be *Taeniopteris spatulata* McCl. and this material was later assigned to a new genus, *Nipaniophyllum*, as a new species, *N. raoi* by Sahni (1948), who pointed out that the stem *Pentoxylon* bore the leaf *Nipaniophyllum* and the female cone *Carnoconites*. Vishnu-Mittre (1953) discovered the male flower of the plant, *Sahnia*.

It will be noticed that the account of the *Pentoxylon* plant is complicated by there being two closely similar species mixed in the same flora and the relation between these species has not yet been fully resolved.

Our observations are based on the available material of earlier authors and a large collection of different organs belonging to the *Pentoxylon* plant made from various localities in the Rajmahal Hills, India, during the last three decades. Although, the types and most of the other figured slides of Srivastava (1944, 1946) are available in the Birbal Sahni Institute, some of his figured slides were found to be missing. We were unable to locate the specimens and slides of *Nipaniophyllum* described by Rao (1943) as *Taeniopteris spatulata* McCl. We have, however, been able to get the holotype of *Sahnia nipaniensis* described by Vishnu-Mittre (1953), though the duplicates are missing.

## SYSTEMATIC DESCRIPTION

Gymnospermae *incertae sedis**Stem**Pentoxylon* Srivastava 1944*Pentoxylon sahnii* Srivastava 1944

(Figures 1–3; figures 10–16, plate 1; figures 17–28, plate 2; figures 29–32, plate 3.)

- 1944 *Pentoxylon sahnii* Srivastava, p. 74; plate 1, figure 11 (brief description and figure).
- 1946 *Pentoxylon sahnii* Srivastava, p. 196; plate 2, figures 7–17; plate 3, figures 18–30; plate 4, figures 31–38; plate 5, figures 39–45 (fuller description, more specimens figured).
- 1948 *Pentoxylon sahnii* Srivastava: Sahni, p. 56; figures 2–12 (review of Srivastava's 1946 account).
- 1953 *Pentoxylon sahnii* Srivastava: Vishnu-Mittre, p. 76; plate 4, figure 5, text-figures 4, 10 (short shoot described and figured, bud attached to a long shoot figured).
- 1958 *Pentoxylon sahnii* Srivastava: Vishnu-Mittre, p. 31; plate 1, figures 1–7; plate 2, figures 8–13; text-figures 1–8 (emended diagnosis of the genus *Pentoxylon* and further information).
- 1969a *Pentoxylon sahnii* Srivastava: Sharma, p. 50; plate 1, figures 1–6; plate 2, figures 7–10, 12; figures 1–3 (specimens from Amarjola described and figured).
- 1969b *Guptioxylon amarjolense* Sharma, p. 20; plate 26, figures 1–7; plate 27, figures 8–12; plate 28, figures 13–18; text-figures 1–5 (conical head of type 2 short shoot described and figured).
- 1972 *Guptioxylon endocentrica* Sharma, p. 114; plate 1, figures 1–4; plate 2, figures 5–8; text-figure 1 (conical head of type 2 short shoot described and figured).
- 1973a *Pentoxylon sahnii* Srivastava: Sharma, p. 215; plate 1, figures 1–9; text-figures 1–7 (further observation on anatomy of long shoot and type 2 short shoot).
- 1973b *Pentoxylon sahnii* Srivastava: Sharma, p. 195; plate 1, figures 1–8; text-figures 1–10 (more information on anatomy of short shoots).
- 1974 *Pentoxylon sahnii* Srivastava: Rao, p. 201; figure 3 (brief review of earlier works).
- 1974 *Pentoxylon sahnii* Srivastava: Sharma, p. 315; plate 1, figures A–K; plate 2, figures L–S; text-figures 1–5 (further information on branching).
- 1975 *Pentoxylon sahnii* Srivastava: Sharma, p. 334; plate 1, figures 2, 3, 4 and 9; text-figure 7 (short shoots from Nipania described).
- 1979 *Pentoxylon sahnii* Srivastava: Sharma, p. 129; plate 1, figures 2, 3 and 5; text-figures 2 and 3 (new specimens of short shoot described and figured).
- 1980 *Pentoxylon sahnii* Srivastava: Sharma, p. 100; plate 1, figures 1–9; text-figures 1 and 2 (anatomy of a branched stem from Amarjola described and figured).
- 1981 *Pentoxylon sahnii* Srivastava: Rao, p. 208 (brief description and discussion).

*Emended diagnosis*

Long shoot at first slender, under 1 cm, bearing leaves on separate cushions, later becoming leafless, usually about 2 cm thick, rarely to 4 cm. Stem with a ring of about five primary vascular bundles, primary tissue forming thin tangentially elongated plates of protoxylem and small parenchyma cells, secondary xylem tracheids laid down on all sides of the primary xylem but,

beyond the first growth ring, more numerous centripetally. Ground tissue comprising a rather small medulla, rather broad rays between the bundles and a broad cortex; cortex and medulla consisting mainly of soft parenchyma but including patches of sclerized parenchyma cells. Small cortical bundles present, ultimately supplying short shoots. Leaf traces small, numerous, running obliquely and directly from protoxylem of primary xylem bundle into leaf base. Wood pycnoxylic, showing narrow growth rings. Tracheids nearly uniform, their radial walls with more or less contiguous uniseriate bordered pits, tangential walls without pits. Ray field showing a single large pit. Rays uniseriate, 1–14 cells high (often 4–7). Xylem parenchyma absent (earlier reports of biseriate tracheid pitting in older wood were not confirmed).

Thick short shoots from less than 1 cm to 2 cm wide, surface covered with persistent leaf base cushions in a crowded helix. Sections at lower level show about five woody bundles and cortical bundles of secondary xylem. In the upper part, the stem increases in diameter and the original bundles divide in an irregular way to give a large number in the outer region of the stem. Small medullary bundles also occur, especially in the lower part. Pith broad, with patches of well preserved sclerotic cells.

Slender parenchymatous short shoots, 5–6 mm wide (rarely 7 mm) and about 2 cm long. All but the shortest abscised at base, apex also often abscised. Surface covered with bulging leaf cushions in a crowded helix. Internally with about five gutter-shaped primary vascular bundles, pith and cortex parenchymatous with nests of sclerotic cells.

Shoot bearing male flower parenchymatous, about 2 cm wide, always abscised at base, surface formed by crowded leaf cushions; grooves between cushions full of hairs. Internally, like slender parenchymatous short shoots, but vascular bundles more massive.

*Holotype.* Slide no. K11/11 of the Birbal Sahni Institute of Palaeobotany, Lucknow (Srivastava 1944, plate 1, figure 11).

*Occurrence.* Nipania and Amarjola, the Rajmahal Hills, Bihar, India

*Description.* We arrange our shoot fragments in four groups or types and then describe each type. We use the terms 'long' and 'short'; the long shoots have widely spaced leaf cushions, but in the short shoots they are in contact. We also use the word 'woody' as opposed to parenchymatous, as seen in transverse section; in the woody long shoots half of the area or more is occupied by five or six (sometimes more) massive strands of xylem. These are the most familiar *Pentoxylon* specimens.

*Type 1 shoots.* These are woody long shoots, 0.5–4.0 cm wide but specimens 1–2 cm wide occur most frequently. The surface when young shows widely spaced leaf cushions but these are later lost by erosion or periderm formation. Specimens of this type are known from sections of Nipania chert and as isolated petrifications from Amarjola. One of these (figure 11, plate 1), about 15 mm thick, shows its surface well. It has broad leaf scars about 3 mm × 1 mm, mostly subtending a round branch scar about 5 mm wide. The leaf scars are well spaced (each has its nearest neighbour at 15–20 mm) and they form an ordinary Fibonacci helix with two and three obvious parastichies. Woody bundles are seen at the broken ends of the main shoot. We imagine that the branch scars belong to short-lived slender parenchymatous branches (type 3 shoots). Srivastava (1946, plate 3, figure 25) showed a parenchymatous short shoot close to a small long shoot from which it is stated to have arisen (in the text, p. 200), but the plate caption leaves this doubtful. The woody long shoots are known to bear moderate sized or large woody branches but as only the bases of these branches are known, their nature is uncertain. They might be smaller woody long shoots or thick short shoots (type 2 shoots). Vishnu-Mittre (1958)

traced the origin of a woody outgrowth, a single bundle from the stem centre, to a point outside the main shoot, but there was nothing to show what kind of branch it became. Sharma (1980, figures 1 and 2) shows what seems to be the origin of a large branch with several bundles, but again the series ends before their fate is clear.

Srivastava (1946), repeated and edited by Sahni (1948), gave our basic knowledge of the structure of woody long shoots, but the preservation of his specimens was only moderate. He was unable to say much about the soft tissues.

Figure 13, plate 1, shows the transverse section of a long shoot with five main bundles well preserved at the end of its first season. The epidermis is nearly smooth and has a cuticle. Under most of the epidermis there is a compact outer cortex of cells with dark contents and without obvious air spaces but at some places there are about three layers of small mechanical cells. The inner cortex has varied cells: much parenchyma, often with dark contents and nests of sclerotic cells, some thick-walled enough to be stone cells. There are also peculiar tangentially elongated cells, each of which shows a brown streak. Similar cells occur between the main bundles and also next to the pith below.

The specimen shows only two cortical bundles. One of these is mostly centrifugal secondary xylem, based on a thin band of 'primary xylem' and there are a few centripetal tracheids beyond this. The other consists of a centripetal secondary xylem; their direction in both bundles is shown by the fan-like spread of the tracheid files.

This specimen is unusual in having its main bundles with feeble centrifugal but strong centripetal secondary xylem. Commonly the two are equal in the first season's growth. The tracheids in the centrifugal xylem are in radial files but this is not always obvious and the innermost are particularly irregular. Inside this is what has been generally described as the band of crushed primary xylem (figure 14, plate 1). But there is no unmistakable crushing and we would not expect it for this position, walled in by layers of secondary xylem should be the safest in the stem, but decay can happen. Most cells look like small or medium sized parenchyma, but at the ends of the band there are small thick-walled cells which do look like protoxylem as others have thought. After this band comes abundant centripetal secondary xylem, beginning abruptly with well formed tracheids. Tracheid files are obvious and spread out as in an open fan but the central files are much longer. Cambium is well preserved; it was active all round, but increasingly so towards the pith. There is little secondary phloem outside the main bundles of xylem. It is at its thickest, 0.3 mm, next to the pith. Many phloem cells have black contents and there are distorted phloem rays but the most characteristic feature is tangential bands of phloem fibres. Some of the phloem cells next to the cambium are small, thin-walled and empty.

The outer region of the pith has several layers of flat cells (but we do not call them crushed) and then a central region of isodiametric parenchyma and some thick-walled cells. The section does not include a layer of sclerotic cells.

Between the large xylem bundles is a thin phloem (with fibres) and then radially elongated narrow cells containing brown streaks are present. But the most impressive view of those cells was observed in a stem with six growth rings; its pith and the tissue between the bundles being well preserved, and unusually large. Both have abundant cells with brown streaks. We saw them again in abundance in a large stem in oblique longitudinal section. Again the cells are narrow, elongated and with brown streaks but though they lie parallel their plane was not obviously tangential to any imagined compressing force. Surely sections of different tissues would not

always catch fusiform cells in longitudinal section. We infer that the cells were originally broad, flat plates oriented across the direction of a compressing force and a section in any plane would show them as fusiform and tangentially placed. We are sure that these cells are among those described earlier as crushed. We suppose they remained alive and grew in a tangential direction and relieved stresses caused by pressure and the movement of bundles past one another by allowing slipping. Their number may have increased but to say this, we would have to look again at the same kind of stem after an interval of growth.

Subepidermal periderm in the woody long shoots is inconstant. We saw it in a section with six growth rings where it is continuous, made up of about four layers of flat cells in radial files situated at the boundary of the outer and inner cortex but other stems with six growth rings showed no such tissue at all. The most impressive periderm surrounds a large wound cavity in the centre of some conical heads terminating the type 2 thick short shoots. In Vishnu-Mittre 1958, text-figure 1, the central pith is necrotic and is surrounded by a thin periderm. A deep periderm is present in the inner cortex of a thin long shoot figured by Sharma (1974, text-figure 5).

In *Pentoxylon* stems the xylem shows growth rings with three to six as common numbers; 16 have been recorded, but when rings are numerous they are thin, obscure and some only doubtfully real. The first six are mostly clear enough and corresponding rings can be recognized in each main bundle of a stem but they are never strongly marked. At best the tracheids of the late wood have an average radial diameter of 15  $\mu\text{m}$  and after the ring boundary an average diameter of 22  $\mu\text{m}$ . Also the walls in the late wood are perceptibly thicker but both size and thickness soon become normal. In other stems there was no measurable difference in either size or wall thickness but the ring was shown by a single layer of flatter tracheids. The ray cells are inconspicuous in transverse section; on our measurements one cell is about as long as four tracheid widths but Srivastava (1946) thought them about equal to one.

Our widest stems, just over 3 cm broad, have main bundles of 10 mm measured radially and about 12 mm measured tangentially. The pith, the rays between the bundles and the cortex are all broad. The uneven surface suggests periderm exfoliation. Details are poorly preserved.

No tracheid has pits on its tangential walls, not even in the late wood and there is no xylem parenchyma. As others have stated, the rays are one cell wide and up to 14 cells high but most have only a few cells (figure 1a). The wide rays figured by Vishnu-Mittre (1958, text-figure 6) are from the disturbed area of a branching bundle as shown by his section (which we were able to examine). In our sections the radial walls of all tracheids showed a single series of crowded bordered pits. We have not observed the biseriate pits reported by various authors, from Srivastava (1946) onwards. Without examining the original slides (which have been lost) we are in no position to dispute their observations. Our account deals exclusively with *Pentoxylon* stems showing five bundles but in the Nipania chert there are many conifer stems, which when decorticated and broken resembled *Pentoxylon* bundles and the larger ones look attractive subjects for study. We are sure that a number of wood sections in the Birbal Sahni Institute of Palaeobotany, labelled *Pentoxylon*, belong to conifers, but have no evidence that these were described. Srivastava (1946, p. 198) notes that his *Pentoxylon* stems had uniseriate pits but 'in older woods' the pitting was biseriate. We are sure that the 'older wood' in his plate 5, figure 39 is from a conifer, no *Pentoxylon* stem has such growth rings. Vishnu-Mittre (1953, text-figure 5) figured a wide tracheid of a dwarf shoot with up to three series of well spaced pits. His slide was available but we failed to recognize the dwarf shoot. But it does contain shreds of xylem

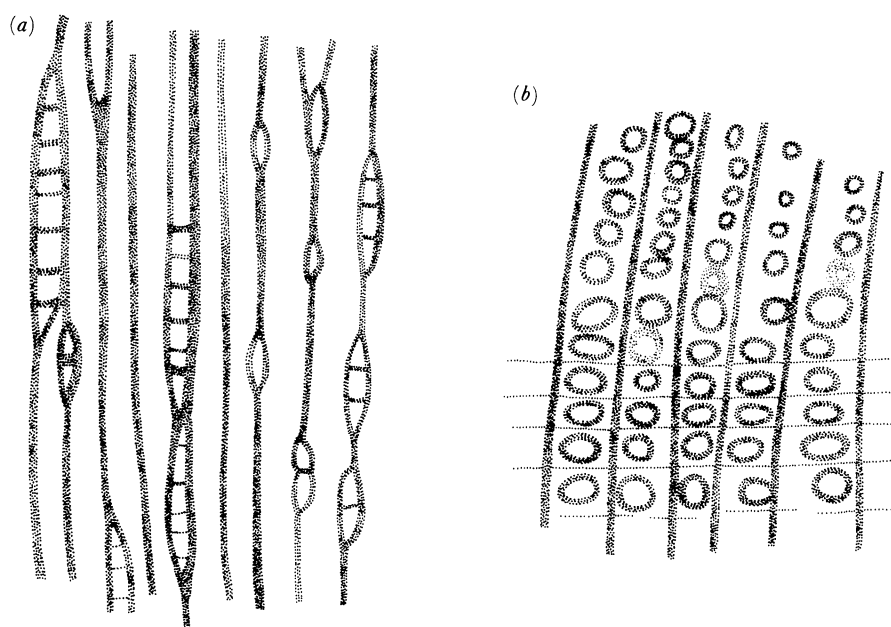


FIGURE 1. *Pentoxylon sahnii* Srivastava. (a) Tangential longitudinal section of secondary xylem redrawn from Srivastava (1946; plate 4, figure 37). Magn.  $\times 200$ . (b) Radial longitudinal section of secondary xylem, redrawn from Srivastava (1946; plate 4, figure 38). Magn.  $\times 300$ .

with various styles of pitting. Our radial sections of short shoots show, as expected, narrow tracheids with uniseriate pitting. We reject this evidence of multiseriate pitting. The biseriate pitting in Vishnu-Mittre's (1953) text-figure 16 from a *Carnoconites* peduncle does not concern us here.

We have not recognized any primary phloem. Secondary phloem in *Pentoxylon* is scarcely known apart from a few words of Srivastava (1946). This is because it is seldom preserved and when well preserved is scanty and not easily recognizable. However, we were helped by a stem which we regard as the base of a fruiting head. Its surface has been lost but it shows five well developed *Pentoxylon* xylem bundles of normal character round an unusually wide and well preserved central region. This consists of ordinary pith, bands of secondary phloem up to 2 mm thick between the pith and the centripetal xylem and minute collateral secondary xylem strands of varied orientation, and often embedded in the secondary phloem. Cambial cells are clear. In the phloem the only cells that show serial files plainly are those of the phloem rays which stand out as dark threads, often distorted. Between them are inconspicuous thin-walled cells which may be sieve cells and very conspicuous tangential sets of phloem fibres (figure 16, plate 1). The oldest secondary phloem (that is, innermost on the centripetal side of the bundle) is mixed with that of other main bundles as well as with pith cells and small medullary xylem bundles but even here the very characteristic phloem fibres and sometimes phloem ray cells can be seen. In this specimen a little tissue outside a main bundle remains and here it can be seen that secondary phloem continues right round it but it is thickest next to the pith. This stem has unusually thick first season's growth rings and outside them about five ill-marked rings. Thus the cells to look for as phloem in a transverse section of an ordinary stem are phloem rays and particularly the tangential bands of phloem fibres. These were recognized in the more scanty phloem of other specimens. In a good longitudinal section we found it difficult to be sure just what part of the phloem we were examining but this was clear

in a nearly longitudinal section which cut the five xylem bundles obliquely. Here, next to the pith we recognized phloem fibres, phloem rays, dark cells and empty-looking cells, but preservation was not good enough to show sieve areas.

Whether *Pentoxylon* is polystelic or monostelic depends how each of these is defined. It can be settled to some authors' satisfaction by definition; thus, if the stele is defined as all the conducting tissue of a stem, then stems in general are monostelic; but if each strand seen in a transverse section, at least if concentric, is a stele then *Pentoxylon* is polystelic. Some authors call the individual xylem strands of *Pentoxylon* 'steles', others 'bundles' (a morphologically neutral word), while some are not interested, as they use the two words as alternatives without discussion. But two authors have strong views; Stewart (1976) (against polystele) and Sharma (1979) (for it). 'Polystely' has been used in rather varied ways in different plants. Many polypodioid ferns, species of *Selaginella*, *Primula auricula*, etc., have round bundles, each surrounded by an endodermis, which have been called steles. But in all these plants the strands form an organized network and could cooperate under stress. We are impressed by the agreement between *Pentoxylon*, *Medullosa* and *Rhexoxylon* in the way the leaf traces arise (Stewart 1976). These have primary xylem, which is anomalous in relation to most conifers and woody dicotyledons, but the same type of leaf trace origin occurs in *Ginkgo*, a typical 'eustelic' stem. Sharma (1979, p. 134) takes issue with Stewart (1976) but we seem to miss his point. It is to us irrelevant whether the *Pentoxylon* shoot has several bundles or just one at its point of origin and irrelevant also whether at the base of the seedling stem there was one or more strands of xylem. We prefer to call the *Pentoxylon* stem monostelic, because it is a single organized unit.

*Type 2 shoots.* These are thick short shoot, from nearly 1 cm to 2 cm wide. The original length is unknown because they are always broken at the ends. They have persistent leaf base cushions in a crowded helix over the surface. The leaf cushion has raised edges and a rather flat rhomboidal scar at its top. The tissue of the leaf base is apparently much firmer than in type 3 short shoots and resists decay and distortion. In the lower part the pith is broad and there are about five typical *Pentoxylon* bundles which at first have primary xylem flanked by equal amounts of centripetal and centrifugal xylem but later the centripetal xylem is much greater. These bundles give off leaf traces in the ordinary way and also cut off cortical bundles of secondary xylem which are believed to supply type 3 short shoots (of which the scars are to be seen). In the upper part the original five bundles divide in an irregular way to give a large number in the outer region of the stem and these are believed to be the vascular supply of fruiting branches. Small medullary bundles of unknown origin and fate also occur, especially in the lower part. The pith is large, parenchymatous, and at intervals there are the well preserved patches of sclerotic cells some of which are well developed stone cells. These stems are known as isolated petrifications from Amarjola and from the Nipania chert.

A specimen of type 2 short shoot from Nipania was figured by Srivastava (1946, plate 3, figure 28). Sahni (1948) used this short shoot, with much simplified phyllotaxis, in his restoration (figure 45), but we are sure that this was a mistake and he should have used the more slender type 3 short shoot.

Vishnu-Mittre (1953, text-figure 4) illustrated an interesting longitudinal section of a type 2 short shoot tangential to a main xylem strand. It shows the ordinary leaf bases and several cortical bundles which pass upwards and outwards and finally divide just below the surface. Vishnu-Mittre (1953, p. 76) called these leaf traces but we are sure they are the supply to type 3 short shoots as we have seen similar ones enter the bases of such short shoots in our specimens.



True leaf traces arise from the protoxylem and proceed directly as shown in figure 2. Sharma (1973*b*) figured some type 2 short shoots from Amarjola. But the short shoots figured by Sharma (1979) from Nipania are puzzling, because we are unsure which specimens shown in surface view correspond to which in section. We have many specimens that look like some of Sharma's (1979) but which on sectioning proved to be conifers. Certainly the stems in his plate I, figures 2, 3 and 5, show what look like crowded *Pentoxylon* leaf cushions and certainly the sections 1, 2 and 3 in his plate II are *Pentoxylon*. The sections in his text-figures 2 and 3 showing leaf trace origin are also convincing but we do not know which of his type-2 short shoots (shown externally) gave these sections. Sharma's text-figure 1, a smooth stem, looks unlike *Pentoxylon*, and his stems in plate 1, figures 1, 4 and 7, if they are *Pentoxylon*, must have suffered erosion.

Figure 2 shows the longitudinal section of a type 2 dwarf shoot collected from Amarjola. The shoot is 12 mm wide; its surface is wholly covered with rather abraded leaf cushions, and the medulla is 5 mm wide with a continuous vascular bundle on the right but only the base of one on the left. Above, the plane of section has passed between bundles but it touches a cortical bundle. Over much of its length the righthand bundle is divided into two equal parts and in one part it widens into the primary xylem and parenchyma core. This is the division between centripetal and centrifugal xylem, which are equally thick. The bundle on the left shows no such clear division. At several points slender leaf traces cross the cortex and leaf cushions obliquely, and some end at the surface at a point that must be an eroded leaf base.

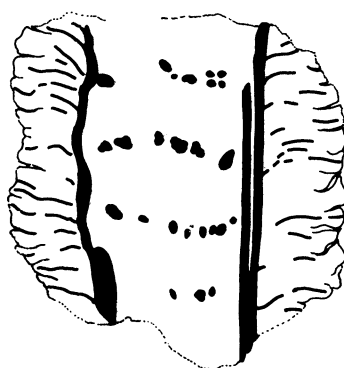


FIGURE 2. *Pentoxylon sahnii* Srivastava. (a) Longitudinal section of type 2 thick short shoot, the xylem bundle on the right shows the primary xylem in the middle, pith shows nests of sclerotic cells, B.S.I.P. Slide no. 8150. Magn.  $\times 4$ .

A well developed type 2 dwarf shoot at its top enlarges into a broadly conical head (the organ described by Sharma 1969*b* as *Guptioxylon*). We have specimens which, at their bases, possess a surface thickly covered with persistent leaf base cushions and internally with about five typical *Pentoxylon* bundles around a slightly enlarged pith; but in their upper part they have been increased in diameter with large number of bundles in the outer region of the stem.

A shoot (specimen number 35681) from the Nipania chert is represented by a series of nine sections, total length estimated at 3 cm, with both the ends terminated by saw cuts. Its width steadily increases from 8 to 11 mm. All sections are nearly round. The lowest section (figure 22, plate 2) in its one half shows three normal *Pentoxylon* bundles (but with rather large and parenchymatous primary xylem) separated by narrow rays. There are three cortical bundles in the outer parts of the rays. The other half shows several collateral or concentric bundles.

The pith is largely normal but includes six minute bundles of xylem. By section 3 (figure 23, plate 2) the three large bundles are becoming less normal. One is receiving an addition from a cortical bundle. At the same time the whole xylem mass is tending to move away from the centre and the number of small bundles is increasing. A group of minute bundles, just like a leaf trace, emerges at the level of section 4. By the level of section 6 (figure 24, plate 2) a hole appears at the centre (but here the base of the hole is seen as two separate pits). In sections 7–9 the hole is broader but periderm formation at the sides and disorganized tissue have reduced the cavity. This hole, described by Sharma (1969*b*) as ‘structure X’, is the feeding burrow of some animal, we cannot say of what kind though we call it a grub, which fed on the central parenchyma at a time when the surrounding tissue was active enough to form a periderm. The burrow contains structureless matter we regard as faecal and small bits of parenchyma and tracheids we regard as frass, chewed off but not swallowed. Such burrows in plant parenchyma are commonly made by various insects, millepedes and slugs; we use the non-committal term ‘grub’. At the level of section 6 (figure 24, plate 2) the xylem bundles are placed further outwards. Although there are still large concentric bundles none of them is precisely the continuation of one of the original *Pentoxylon* bundles. The number of cortical bundles is now large. The minute medullary bundles (seen in sections 1–5) have vanished; this may be due to damage by the grub hole and its surrounding periderm. A typical leaf base is present, supplied by small strands, some emerging through the surface. By the levels of sections 7, 8 and 9 the general outward movement of the xylem strands has continued, most of them becoming collateral not concentric, but there is one fairly large concentric bundle still at the level of section 9. Here a few bundles are becoming organized in groups (figure 25, plate 2).

Specimen number 35682 (made into three serial sections) also shows at its basal end almost normal *Pentoxylon* structure but the pith is slightly enlarged and the cortical bundles are unusually well developed. Higher up the shoot increases in diameter; its centre is again occupied by a grub hole and the bundles increase in number and become collateral.

Specimen number 35683 (represented by two sections) at its basal end agrees well with the top section of specimen number 35682, and appears to be slightly higher than the level of the top section (section 9) of specimen number 35681. Here the grub hole is large, and a lot of bundles are very near the surface. Two groups of medium sized bundles (larger than leaf traces) are leaving the stem and between them there is a round bundle on the surface (figure 26, plate 2) but no large bundle is leaving the stem. A single well-formed lenticel is present.

All of Sharma’s (1969*b*, 1972) type 2 short shoots (described as *Guptioxylon amarjolense* and *G. endocentrica*) are damaged at both ends, just like ours. We suspect that the top was particularly liable to damage by erosion because the broad inner region was of soft parenchyma and the woody tissue was in numerous small bundles at the periphery. However, Sharma’s, (1969*b*) plate 26, figure 1 shows the base of some sort of slender branch and so apparently does our specimen number 35683. We merely imagine that these were the bases of the cone-bearing branchlets of *Carnoconites*. In our view our ignorance of the extremity of the type 2 short shoots is the most serious gap in our knowledge of *Pentoxylon*; the base of the type 2 axis is so like a normal stem that it raises no difficulty. An unusually small type 2 short shoot (figures 19 and 20, plate 2) ended without branching though it is covered with ordinary leaf cushions. The axis narrows and the six bundles at the base narrow, converge and vanish at the apex.

Another shoot fragment (figure 21, plate 2) is 2.3 cm wide and nearly 2 cm between the cut

ends. Its sides show the woody bases of a dozen or more branches. The lower end shows a large pith and typical *Pentoxylon* bundles but above this, they divide into many small strands near the surface (figures 3a–c). The lateral branches are too large and woody to belong to type 3 leafy short shoots, but could form the bases of *Carnoconites*-bearing axes but most of these, as seems likely, would be at the top. If we may regard the ordinary conical head (without side branches) of type 2 short shoots as the axes bearing *Carnoconites compactus* (by dividing at the top, as in our restoration, figure 9), then this specimen with side branches would serve to bear *Carnoconites rajmahalensis*. The xylem strands look about the right size to supply a small group but the large group would seem better placed at the top.

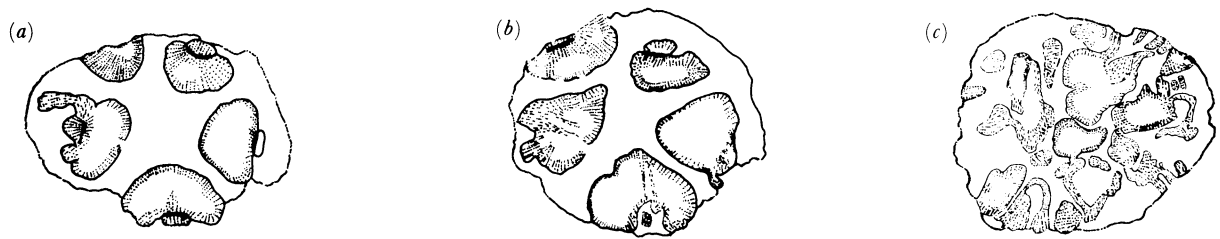


FIGURE 3. *Pentoxylon sahnii* Srivastava selected serial sections of an unusual specimen (figure 21, plate 2) in which branch bases are emerging from the side. (a) Basal section, showing obvious *Pentoxylon* structure but unusually large, both pith and bundles are large, central part of all bundles have been eaten out by a grub and cavities filled with sand, four bundles show primary xylem (in one it is eroded) and from one a strand of centrifugal xylem is running outwards, B.S.I.P. Slide no. 35685-1; magn.  $\times 1.5$ . (b) Middle section just recognizable as *Pentoxylon*, two bundles showing primary xylem and centrifugal xylem, certainly one and possibly more strands of xylem running out, B.S.I.P. slide no. 35685-3; magn.  $\times 1.5$ . (c) Top section, unrecognizable as *Pentoxylon*, xylem strands are much disintegrated and several are running horizontally and possibly five are emerging out of the stem, B.S.I.P. slide no. 35685-5; magn.  $\times 1.5$ .

*Type 3 shoots.* These slender short shoots are all remarkably uniform, 5–6 mm wide (rarely 7 mm) and about 2 cm long unless immature. All but the shortest are abscised at the base and the apex is also often abscised. Their surfaces are covered with bulging leaf cushions in a crowded helix occasionally still bearing bases of *Nipaniophyllum* leaves. Tissues were soft. We think that most of these leafy dwarf shoots were borne in leaf axils on woody long shoots (type 1 shoots) but some on thick dwarf shoots (type 2 shoots), only a few of our specimens show this attachment (figure 23, plate 2) and some of these look as though the base was starting to break. Where a longitudinal section shows the tip of these dwarf shoots, abscission of the apex also may be starting or may be completed. The shoots look delicate but are mostly well preserved. The bulging leaf cushions on the surface are scarcely ever abraded. Small thick-walled cells, about twice as long as broad occur beneath the epidermis of most of the cushions forming a layer of 100  $\mu\text{m}$  thick. Similar-looking cells occur beneath the epidermis of petioles. Where the leaf traces emerge, smaller and thinner-walled cells occur (the abscis layer of Srivastava 1946). The leaf cushion cortex looks spongy as preserved; it may be a photosynthetic parenchyma and extends even between leaf cushions. Beneath this is a more compact cortical parenchyma containing many nests of thick dark-walled cells, the stone cells of some authors, but as the walls are only 5  $\mu\text{m}$  thick and not visibly pitted we prefer to call them 'sclerotic'. They are scarcely elongated in longitudinal section. These short shoots are only known from sections of the *Nipania* chert but there these are more common than type 2 short shoots.

In the youngest stems, that is close to the apical bud (in Vishnu-Mittre's (1958) slide number 918) the stem bundles do not form five plates as they do in older parts but instead consist of tracheid groups separated by small parenchyma cells. Later-formed tracheids link the first ones into gutter-shaped strands and later still a few tracheids are added on the side facing the phloem. We examined many shoots but none had centripetal xylem. Later still the centrifugal tracheids may form files of about 20. Where the longitudinal walls are seen the tracheids have slender scalariform bars or crowded rings. The tracheid file starts at small cells next to the pith and in a well preserved stem some show widely spaced rings as expected in somewhat stretched protoxylem. Not one centripetal secondary tracheid is present. The tissue between the bundles, like the pith, at certain levels, includes many nests of sclerotic cells.

Leaf traces are seen plainly in a radial longitudinal section passing from a stelar bundle into a petiole at an angle of 70–80° to the long axis. In transverse section different traces are seen leaving the edges of bundles and passing through the cortex and out, but as a rule only the metaxylem (scalariform and annular) is recognizable. The phloem is seen as a hole and outside the xylem and phloem is a sheath of rather thick-walled cells, half the width of ordinary sclerotic cells. They are slightly elongated.

We could not settle the organization of the leaf traces in the cortex; whether, as we would expect, the protoxylem was external and whether the metaxylem is truly primary. There are only a few tracheids, and we saw them poorly.

Type 3 short shoots have no epidermal hairs between adjacent leaf cushions, unlike those seen by Vishnu-Mittre (1953) on *Sahnia*-bearing axes.

In good longitudinal section the pith of these short shoots has strongly marked transverse bands of sclerotic cells. As others have pointed out, these bands have no relation to the leaf bases.

A few sections show type 3 short shoots still attached. In some of these the xylem strands are widely separated, these would be the finger-like strands of Vishnu-Mittre (1953, text-figure 4) but in one, possibly because of the plane of section, the xylem seems to form a solid block.

Srivastava (1946, p. 199, plate 3, figures 25, 27 and 29) recognized these short shoots but thought they were covered with scale leaves, as did Vishnu-Mittre (1958, text-figure 8). But we are convinced that they are not scale leaves but the flat bases of foliage leaves (no-one has recognized a *Pentoxylon* scale leaf). Occasionally type 3 short shoots have dilapidated leaf bases higher up, so the statement that no attached leaves of *Pentoxylon* have been seen is a mistake, but they have only been seen poorly.

We note that in a good longitudinal section of these short shoots, the upper and lower leaf bases are more or less equally preserved and we infer that their age is nearly the same. The whole shoot with all its leaves was produced in one growing season, dropped its leaves and then itself dropped off. But we have no evidence whether this was (as shown in our restoration) in the season after the leaves of the long shoot had fallen.

*Type 4 shoots.* These are parenchymatous short shoots about 1 cm in width each ending in a *Sahnia* flower. Their bases are always abscised. Leaf cushions covering the surface are in a crowded helix. This type of short shoot resembles the type 3 short shoot, but is slightly thicker and the grooves between the leaf cushions are full of hairs. Internally it is like the type 3 short shoot but the vascular bundles are more massive. They are known from the *Nipania* chert only.

*Leaf**Nipaniophyllum* Sahni 1948*Type species**N. raoi* Sahni 1948*Emended diagnosis*

Petrified leaf having the form and venation of *Taeniopteris* Brongniart. Vascular bundles of midrib in a row; each bundle having a sclerenchyma sheath and a central protoxylem, a larger centripetal primary metaxylem mass, a small arc of centrifugal xylem and a centrifugal phloem mass. Stomata surrounded by cells without regular relation to position of guard cells (anomocytic), stomatal aperture sunken.

*Discussion*

The chief difference of this diagnosis from that of Sahni (1948) is that he held that subsidiary cell arrangement was 'syndetocheilic', an idea he adopted from Rao (1943); a term more usual today would be 'paracytic' which refers to their mature position rather than their ontogeny. We also avoid phrases which imply affinity, particularly 'diploxylic types, characteristic of modern cycads' (referring to leaf traces) and 'stomata fundamentally of bennettitalean type...'.

Leaves of *Nipaniophyllum* were long and as the rock (which had to be broken with a sledge hammer) did not split well, we have had to use fragments. Even as early as 1948 Sahni had the impression that the broader and the narrower fragments represented two species, an idea supported by Rao (1943), the first to describe leaf anatomy in detail. Others have concurred. The matrix is too hard to degage leaves (where they are buried in large blocks, an hour's labour gave just 1 mm of leaf length), but we hoped that a survey of the dimensions of the exposed parts of leaves in the Birbal Sahni Institute collections might confirm the presence of two species.

We noted that broad and narrow fragments are not evenly distributed. Some blocks have many narrow ones (one had 78 ranging from 3 to 7 mm broad but none at all broader). Other blocks have numerous fragments 8–12 mm broad, but narrow ones also; some of these narrow ones are the bases of broad leaves, some have a broad midrib but others are genuine narrow leaves. We sorted the blocks into ones showing narrow leaves only, and those with leaves of mixed widths and made histograms for each; the narrow give a normal histogram, the mixed give what looks like a somewhat bimodal histogram (figure 4). The narrow ones correspond to the main part of Rao's (1943) description and what Sahni (1948) named *N. raoi*, and we give the broad ones the new name *N. hobsonii*. We cannot yet estimate the length of a normal *N. raoi* leaf. We hoped to sum the length of all fragments and to divide this by the number of leaf apices or leaf bases, but too few of either were seen. We can only suppose the length was great, exceeding 20 cm, but *N. hobsonii* may have been shorter. An original reason for thinking that there should be two leaf species was the presence of two obviously distinct cones but there is still no clear evidence that *N. hobsonii* belongs to *Carnoconites rajmahalensis* though there is a suggestive association. A new locality where just one leaf and cone occurs abundantly should settle it. Another possibility that cannot be ruled out at present is that the two leaf species, *N. raoi* and *N. hobsonii*, are leaves borne on long and short shoots of a single stem species.

In *Nipaniophyllum*, unlike many species of *Taeniopteris*, the veins run straight to the margin and end there without bending forward or merging with a marginal fibre strand.

Rao (1943) observed that just short of the margin, a vein may fork and then the halves rejoin,

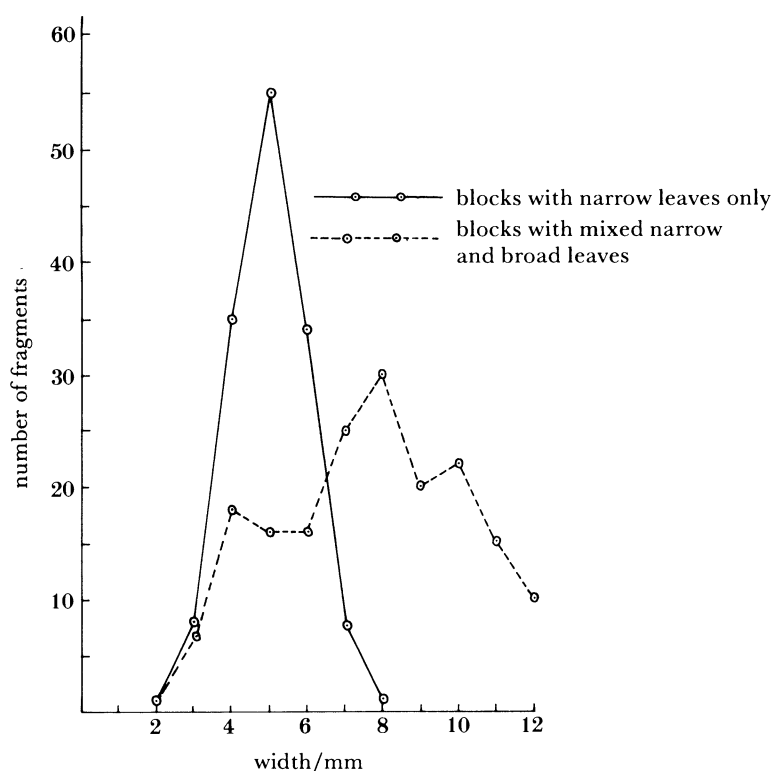


FIGURE 4. Histogram showing the distribution of narrow (*N. raoi*) and broad (*N. hobsonii*) *Nipaniophyllum* leaves on various blocks of Nipania chert.

or they may form a thick tracheidal mass; he suggests a possible secretory function. This behaviour is infrequent and for this reason we have omitted it from our generic diagnosis. The midrib seems to lack assimilatory tissue but its place is taken by somewhat elongated and thick-walled parenchyma. There is no fibre bundle, at least in *N. raoi*.

Rao (1943) gave close attention to the stomata and concluded that subsidiary cells were basically as in the Bennettitales, that is that there was one subsidiary cell alongside each guard cell. But more often there are two and he thought that this might result from later division. Later authors (Vishnu-Mittre 1958; Sharma 1969*a*), however, concluded that there was no regular relation between the subsidiary cells and the guard cells, that is the arrangement is anomocytic (haplocheilic in Florin's terminology). Our own study of the epidermis supports the anomocytic view. The shape of the whole set of cells, stomata and subsidiary cells, seldom suggests origin from a single embryonic cell as it so often does in Bennettitales. In horizontal sections the dorsal lamellae of the guard cells are sometimes visible. The lower layer of mesophyll is compact and the cavity over a stoma is small.

*Nipaniophyllum* has been called 'coriaceous' (Sahni 1948, p. 52), that is leathery, a relative term without defined limits, but we would not use it for either species, particularly not for the more delicate *N. raoi*. Its lamina is only 0.3–0.4 mm thick and has no hypodermal layer apart from a very few cells at the margin. There is some thick-walled parenchyma in the midrib and a single layer round each vein. There are no fibre bundles at all and the cuticle is thin. The other species, *N. hobsonii*, is a little more robust but scarcely coriaceous.

Rao (1943) described the epidermis as 'thick' and this is fair in relation to the rather thin

lamina but its cell walls do not look thick. He does not mention the cuticle but Sahni (1948, p. 52) calls the cuticle 'thick', surely a slip for epidermis. Leaf sections show a very thin dark layer over epidermal surfaces which we take to be the cuticle. Rao (1943) did not succeed in isolating a cuticle. Nor would we describe the stomata as 'deeply sunken' (10–16  $\mu\text{m}$ ). In gymnosperms generally the aperture is at a lower level than the poles, and in *Nipaniophyllum* the poles are on the surface. We would not call the leaf xeromorphic.

We emphasize Sahni's (1948, p. 51) point that *Nipaniophyllum* is only to be used for specimens showing their internal anatomy, particularly the centripetal xylem. Nothing else can justify its use, not, for example, the belief that the leaf belongs to *Pentoxylon*. But a genus within a genus is a difficult concept and *Nipaniophyllum* has already been used wrongly.

No good *Nipaniophyllum* leaf has been found attached to *Pentoxylon* stem but there are buds surrounded by *Nipaniophyllum* leaf bases, which, however, were called scale leaves. It seems that the plant was deciduous and dropped its leaves early. Srivastava's section (1946, plate 3, figure 25) just misses the plane of attachment. Powerful support is given by the agreement of a petiole base (in transverse section) with the leaf cushion (in tangential section). Moreover there is no rival stem for these leaves at Nipania.

*Nipaniophyllum raoi* Sahni 1948

Figures 5a–f; figure 34, plate 3

- 1943     *Taeniopteris spatulata* McClelland: Rao, p. 333; figures in plates 1–12 except plate 10, figure 72; plate 11, figures 73 and 76; plate 12, figure 77, which are probably *Nipaniophyllum hobsonii* (anatomical and epidermal detail, stomata regarded as syndetocheilic).
- 1948     *Nipaniophyllum raoi* Sahni, p. 52; figures 1, 13–17; generalized diagrams in figure 34 are partly like *N. hobsonii* (diagnosis and account based on Rao, 1943).
- 1969a    *Nipaniophyllum raoi* Sahni: Sharma, p. 53 (in part); plate 2, figure 13 (specimen from Amarjola described and figured, stomata regarded as haplocheilic).
- 1974     *Nipaniophyllum raoi* Sahni: Rao, p. 205 (review of earlier works).

*Emended diagnosis*

Mean length of leaf estimated at about 18 cm, lower third tapering to the midrib near point of attachment, upper two thirds parallel sided, often 4–6 mm wide (rarely over 7 mm), leaf tapering gradually near apex or more rapidly to an acute or obtuse point (midrib emerging as a minute mucro). Midrib up to 1.5 mm wide in lower part, longitudinally ribbed, leaf base expanded to about 1.7 mm. Lower part of midrib with a row of about seven bundles, number reduced above. Lower side bearing a few forward-pointing hairs.

Lamina about 0.3–0.4 mm thick, nearly flat or sunken along veins, margin rounded in section, not reflexed.

Vascular bundles of petiole and midrib surrounded by a thin sheath of sclerenchyma cells; midrib region lacking assimilatory tissue but with somewhat elongated and thick-walled parenchyma. Mesophyll of lamina with an upper palisade layer normally continuous over veins and a rather compact lower layer of cells mostly elongated transversely to veins. Substomatal cavities small. No continuous hypodermal layer present but a few cells at leaf margin elongated parallel with margin. Cells of upper epidermis small, isodiametric except over veins, lateral walls broad, nearly straight. Cells of lower epidermis irregularly elongated, seldom forming

conspicuous files, their surface bulging, their lateral walls finely sinuous or with jagged extensions. Stomata confined to strips between veins on lower epidermis, numerous, almost evenly scattered, seldom forming files, orientation random. Guard cell aperture sunken in an oval or rectangular pit but poles at epidermal surface. Subsidiary cells varied in number and position, often about six and of uneven size but sometimes a single cell present opposite a guard cell. Subsidiary cells forming the pit but otherwise unspecialized. Encircling cells absent. (Subsidiary cell arrangement here interpreted as anomocytic). Cuticle very thin.

*Neotype*. Number 35690 of the Birbal Sahni Institute of Palaeobotany, Lucknow.

*Occurrence*. Nipania and Amarjola, the Rajmahal Hills, Bihar, India.

*Discussion*. It is possible that the description of the epidermis relates partly to *N. hobsonii* as the sections we examined show no diagnostic features.

The dimensions we give for the leaf are different from those of Rao (1943). He included broad leaves, in fact the range of *Taeniopteris spatulata*, in his diagnosis. We cannot explain how he decided the length was as little as 7 cm but we are sure it should be much more. We made our estimate by mentally fitting together leaf bases, middle regions and apices (with special regard to midrib width) and this gave about 18 cm although none of our fragments was over 6 cm.

The original figured specimens of Rao (1943) repeated by Sahni (1948) are missing, therefore a specimen from our collection from the type locality (Nipania) has been selected as the neotype of the taxon.

*Nipaniophyllum hobsonii* sp.nov.

Figures 5g–j, figure 33, plate 3

1958 *Nipaniophyllum raoi* Sahni: Vishnu-Mittre, p. 39; plate 3, figures 14 and 15; text-figures 9–12 (but at  $\times 2$ , cf. plate 3, figure 14).

1969a *Nipaniophyllum raoi* Sharma, p. 53 (in part); plate 2, figure 11.

*Diagnosis*

Leaf known to reach 14 cm long, width in upper part typically 10–14 mm, lower third tapering and lamina reduced to a narrow wing ending close to the slightly expanded leaf base, upper two thirds parallel sided but at apex contracted and obtusely pointed or rounded in broader leaves. Midrib 2 mm near leaf base, marked with about eight broad ridges (vascular bundles) narrowed towards apex. Veins typically at about 40 per centimetre and at about 80° to margin, nearly straight, occasionally forked at various levels, often thickened as they approach margin. Leaf margin itself thickened, occasionally depressed.

Structure of leaf similar to *N. raoi* but midrib with some elongated files of parenchyma and in lamina tissue above veins a thick-walled parenchyma rather than palisade mesophyll. Lamina often slightly thicker in section (at least 0.4 mm).

*Holotype*. Number 35695 of the Birbal Sahni Institute of Palaeobotany, Lucknow.

*Occurrence*. Nipania and Amarjola, the Rajmahal Hills, Bihar, India.

*Discussion*. The species is named after G. V. Hobson of the Geological Survey of India, who according to Srivastava, discovered the Nipania chert.

Sahni (1948, p. 52) refers to this leaf. As the leaf is associated with *N. raoi* at Nipania its separation is often uncertain. However, we have taken leaves more than 8 mm wide in their broad upper part and, in particular, leaves over 10 mm wide as *N. hobsonii*. This applies both



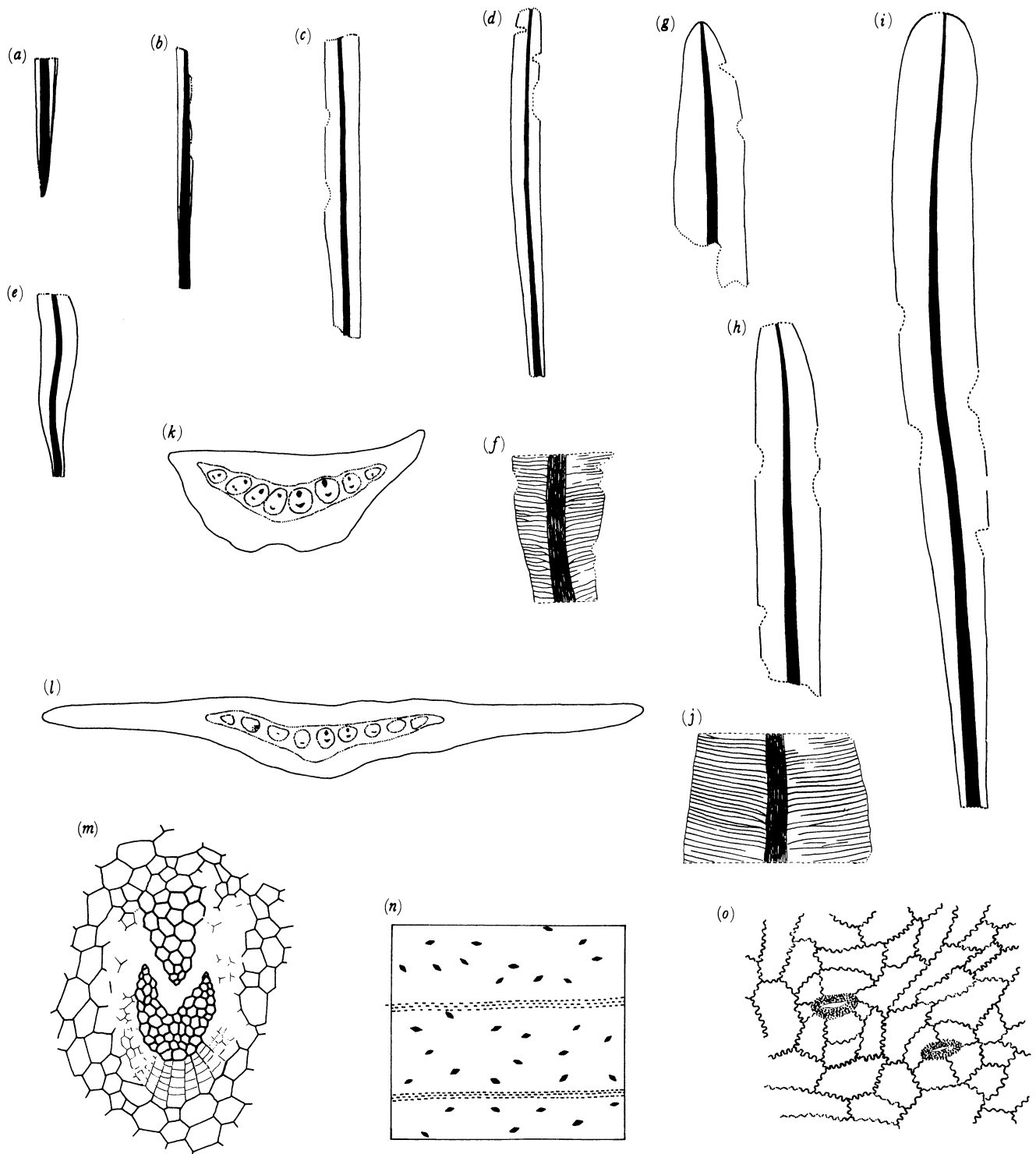


FIGURE 5. (a-f) *Nipaniophyllum raoi* Sahni. (a-e) forms of leaves, B.S.I.P. numbers 35688–35692; all magn.  $\times 1$ . (f) Part of specimen in (e) showing venation; magn.  $\times 2$ . (g-j) *Nipaniophyllum hobsonii* sp. nov. (g-i) Forms of leaves, B.S.I.P. numbers 35693–35695; all magn.  $\times 1$ . (j) Part of specimen in (g) showing venation, magn.  $\times 2$ . (k) Transverse section of petiole of *Nipaniophyllum* sp., redrawn from Rao (1943; plate 5, figure 41); magn.  $\times 25$ . (l) Transverse section of lamina of *Nipaniophyllum* sp., redrawn from Rao (1943; plate 5, figure 39); magn.  $\times 25$ . (m) Transverse section of a vascular bundle of midrib of *Nipaniophyllum* sp., redrawn from Rao (1943; plate 6, figure 45); magn.  $\times 250$ . (n) Distribution of stomata over the surface of *Nipaniophyllum* sp., the two dotted areas represent two veins, B.S.I.P. slide no. 8151; magn.  $\times 30$ . (o) Section of *Nipaniophyllum* sp. cut parallel to the surface, showing two stomata and epidermal cells, B.S.I.P. slide no. 8151; magn.  $\times 250$ .

to leaves seen on weathered surfaces and leaves cut in nearly transverse section. We have not studied any epidermis which we can state is of *N. hobsonii* rather than *N. raoi* but according to Sharma (1969*a*, p. 53) the broad and the narrow leaves have a similar epidermis. It seems that the remarkable thickness of the veins near their ends and the considerable thickening of the margin are characters of *N. hobsonii*, though not seen in all leaves.

The short, but nearly complete leaf from Amarjola figured by Sharma (1969*a*, figure 11) is no doubt *N. hobsonii* though much shorter than our type. It must be remembered that collecting for complete leaves greatly favours short specimens, since the long ones get broken.

A general picture of the material, that is broad leaves with thick midribs near the base, suggests that *N. hobsonii* is probably shorter than *N. raoi*. Apices are met frequently and a statistical estimate (which we abandoned for *N. raoi*) might have been convincing.

#### *Male flower*

*Sahnia* Vishnu-Mittre 1953

#### *Emended diagnosis*

Male flower terminal on a caducous short shoot (peduncle). Receptacle of flower broad, its margin raised as an androecial collar and its centre raised as a broad cone of parenchyma. Androecial collar bearing numerous microsporangiphores at varied levels on its outer surface and edge. Microsporangiphores persistent, erect, mainly composed of fibrous tissue but with a central vascular strand; without any major branches but bearing many short branches on all sides, each short branch bearing several stalked sporangia. Sporangia rounded, wall of one layer of thick-walled elongated cells, opening by a longitudinal split, pollen grains oval.

Peduncle surface covered with crowded broadly rhomboidal leaf cushions. Leaf scar at top of cushion showing a horizontal row of small vascular bundles, each bundle with a sheath and a strand of exarch primary xylem. Peduncle with a broad pith with transverse plates composed of nests of sclerotic cells, and surrounded by about five broad bundles of endarch secondary xylem.

*Sahnia nipaniensis* Vishnu-Mittre 1953

Figures 6*a–e*; figure 35, plate 3

- 1953 *Sahnia nipaniensis* Vishnu-Mittre, p. 76; plate 1, figures 1–4; plate 2, figure 1; plate 3, figures 1–6; text-figures 1, 6–9, 11 (first description and figures).  
 1974 *Sahnia nipaniensis* Vishnu-Mittre: Rao, p. 206 (brief description and discussion, union of microsporangiphores at their bases ruled out).  
 1981 *Sahnia nipaniensis* Vishnu-Mittre: Rao, p. 208 (as Rao 1974).

#### *Emended diagnosis*

Peduncle 10–15 mm wide, enlarging at its top just below the receptacle. Leaf cushions about 5 mm wide, grooves between them packed with unicellular hairs; leaf scar with about nine bundles; pith with layers of nests of sclerotic cells. In a large flower receptacle about 15 mm wide, in small ones barely 10 mm. Receptacle broad, margin raised as an androecial collar, central part raised as a broad cone of parenchyma. Conical top of receptacle about 5 mm broad, up to 3 mm high. Androecial collar 2–3 mm high, 0.5 mm thick, often curving inwards over apex of receptacle. Microsporangiphores numerous, 1.0–2.0 cm long, their lateral branches

about 1 mm long, bearing four to seven stalked pollen sacs. Pollen sacs rounded, 450–700  $\mu\text{m}$  broad, stalk up to 200 by 80  $\mu\text{m}$ . Sporangiphore axis 20  $\mu\text{m}$  thick near its base. Pollen grains often 25 by 20  $\mu\text{m}$  (but poorly known and details of wall not observed).

*Holotype*. Slide number 3226 of the Birbal Sahni Institute of Palaeobotany, Lucknow (Vishnu-Mittre, 1953, plate 1, figure 3).

*Occurrence*. Nipania, the Rajmahal Hills, Bihar, India.

*Discussion*. Vishnu-Mittre (1953, p. 76, plate 1, figure 4) refers to the scars of deciduous bracts round the *Sahnia* receptacle. But the scars and vascular bundles are consistent with well developed *Nipaniophyllum* leaves. We believe the scars below the flower are ordinary leaf scars; there is no evidence that *Pentoxylon* produced bracts anywhere. Vishnu-Mittre (1953) had the microsporangiphores in a simple ring united basally by a membranous sheath about 2 mm high but this was incorrect, as already pointed out by Rao (1974). In fact, the microsporangiphores are borne on a collar-like structure formed by the raised margin of the receptacle. But we cannot tell whether the microsporangiphores are in a true spiral rather than irregular. A good transverse section is needed to show their number but it is certainly more than the estimated 24. Also we could not be sure of the arrangement of the branchlets on the sporangiphores, whether irregular or spiral. We found more pollen sacs on the lateral branches than the two to four that Vishnu-Mittre (1953) gave. We have not recognized any pollen sac attached directly to the sporangiospore, but some may be, especially at its top. Vishnu-Mittre (1953) gave smaller pollen sacs than ours in his diagnosis, but larger in his restoration. The pollen remains ill known, now seemingly worse than Vishnu-Mittre (1953) left it. Intact pollen sacs illuminated from above look beautiful, they gleam a pale cream colour, but under high magnification and transmitted light these or dispersed grains are completely black. What we see is not the wall of a pollen grain but a gas bubble in the chert. It constitutes a strong concave lens. In this the pollen is not unique, as in *Nipaniophyllum* some mesophyll cells are full of gas, and so are occasional cells of sporangiphore axes. Thus the pollen of *Sahnia* is puzzling because it is poorly preserved. Though pollen grains in huge numbers are represented in the sections both free and in intact sacs, they are strictly not preserved at all but are represented by air cavities in the silica matrix replacing the grains. No wall material is preserved and we cannot even say whether they were colpate. The air cavities do have a size range which gives a normal symmetrical histogram, the commonest longitudinal dimension being 25  $\mu\text{m}$  and almost all between 20 and 30  $\mu\text{m}$ . Width is less uniform because the bubbles have angular or distorted shapes but many are about 20  $\mu\text{m}$  across the long axis. This trouble had not been realized in Vishnu-Mittre's (1953) account but explains apparent discrepancies. The pollen of *Sahnia* needs study from differently preserved material.

Vishnu-Mittre (1953, plate 1, figure 3, plate 2, figure 1) had a good longitudinal section which he designated as the holotype, and also other sections which are missing. His plate 1, figure 1, may be a parallel section of the same flower from which the holotype was prepared and also that in plate 2, figure 1, but his plate 1, figure 4 is clearly a different specimen and looks as though it is young and enclosed in leaves, but we have not seen the original slides of his plate 1, figures 1, 2, 4.

Our sections of *Sahnia* flower are inferior to those published by Vishnu-Mittre (1953) in being more tangential and also obliquely longitudinal. Nevertheless, such sections provide information not shown by sections in the best plane.

Figure 6a shows a little of the flower base, the androecial collar stands upon the left (as an

inward-sloping wall 15–20  $\mu\text{m}$  thick). It includes basal branchlets of two sporangiophores (the upper without its base). Below and to the left is a leaf base cushion with strong leaf traces; these suggest a well developed leaf and it seems reasonable to imagine its blade as spreading horizontally when mature, otherwise it would cover the flower. There is a band of xylem immediately below the collar, which we regard as a stem bundle spreading out. It is beginning to disintegrate into longitudinal strands and the closely packed groups of tracheids (15  $\mu\text{m}$  apart and thus doubtfully separate) might be what will supply individual sporangiophores. To the right of the receptacle dome there is an obliquely spreading xylem strand which gives off a leaf trace at its extreme right.

Figure 6*b* is closer to radial longitudinal but is not through the middle of the flower. Here the androecial collar is cut by the plane of section to form a pointed arch over the top of the receptacle dome; the arch is broken on the right but this was caused in preservation. On the left the collar arises from a broad upgrowth which belongs to the top leaf base cushion but it is noteworthy that there is a valley between this and the receptacular dome. This valley is, we suppose, caused by the plane of section intersecting a raised leaf base. But it is noteworthy that four sporangiophores sprout up from near where the collar starts to rise. Their level may not be precisely the same but all must be from near the base of the collar. The section only catches a few in glancing planes higher on the collar. On the right the collar is torn and its base is not separated from the top leaf base by a valley. In this section the vascular supply to leaf bases is clear, but not that to sporangiospheres.

Figures 6*c* and figure 35, plate 3, is like the previous one but the dome formed by the inward-leaning collar is seen as rounded at the top. Sporangiphore bases are clearly attached at all levels. On the left the plane of section has made several sporangiphore bases appear at the same level. Xylem is occasionally visible in the sporangiphores and in the ring or below it, and their tissues, consisting largely of elongated parenchyma, are well seen.

Figure 6*d* the plane of section almost coincides with the inward-sloping collar, so that this is seen as a broad but irregular sheet and the receptacular dome is missed, but some upper leaf bases and the hairs between them are well seen. The view of the collar is unattractive but it shows the bases or vascular bundles of over a dozen sporangiphores. Most of these seem to pass up without branching.

Our sections give some information about the vasculature of *Sahnia*. The peduncle stele has five broad xylem strands and these spread out just above the origin of the traces to the top leaves and run nearly horizontally. We cannot say if they unite into a ring at the base of the collar. They then give off many minute, crowded strands which traverse the collar tissue longitudinally to their point of departure. We saw no instance of division in these bundles. This constitutes a very simple vascular supply.

Some of our *Sahnia* peduncles have been cut off transversely at the base (as are the slender short shoots) and it is interesting that some also have cut off the flower just where the peduncle is expanding into the receptacle but before noticeable changes have begun in the vascular tissue.

The evidence linking *Sahnia* with *Pentoxylon* remains what it was, the association at Nipania and the very close agreement between the *Sahnia* peduncle and a *Pentoxylon* slender dwarf shoot. This agreement as given by Vishnu-Mittre (1953) was mainly in the leaf bases (strikingly similar) and in the nests of sclerotic cells in the peduncle medulla. We can now add the transverse section of the peduncle. This also is just the same except that it is a little wider and

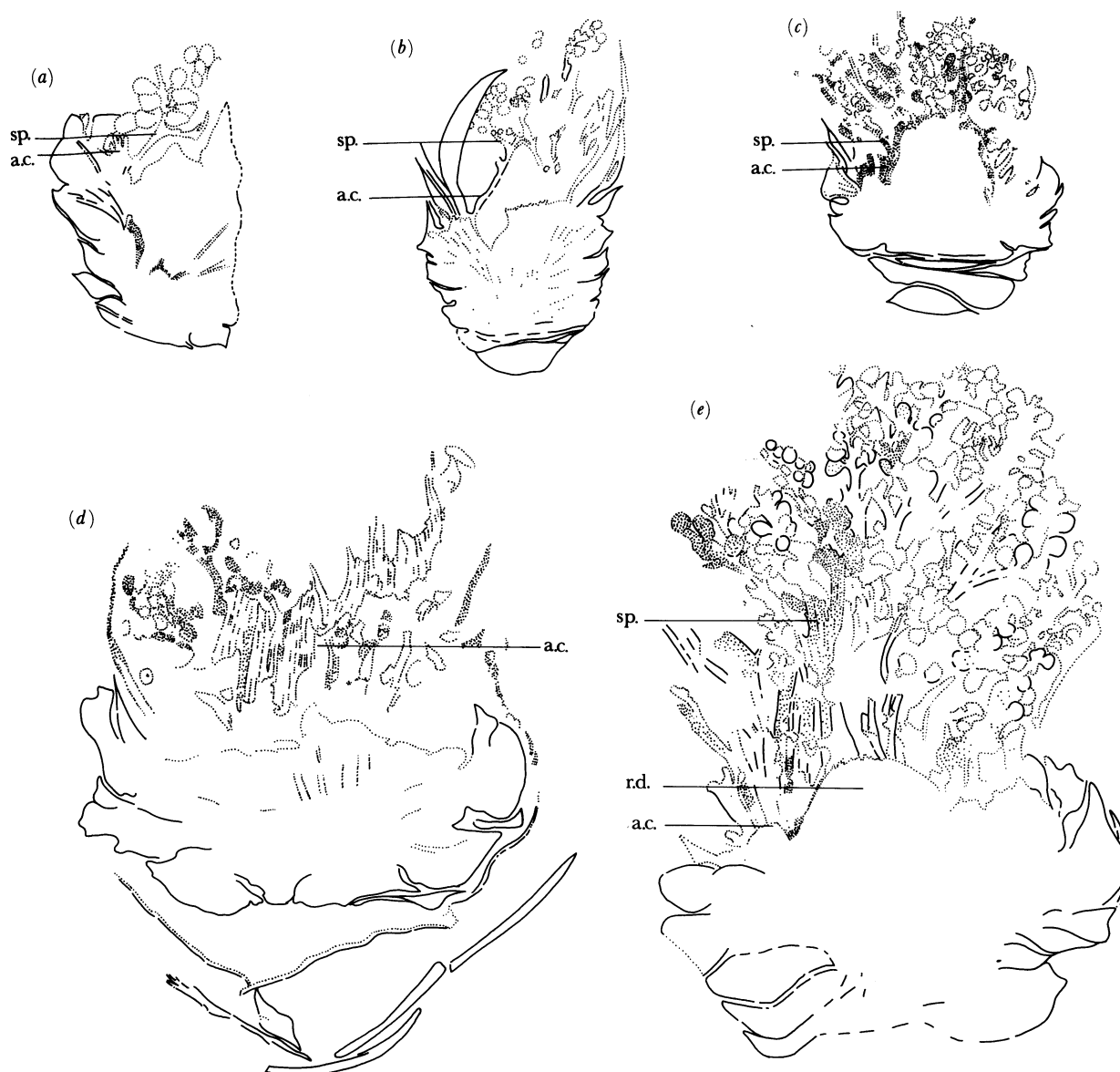


FIGURE 6. *Sahnia nipaniensis* Vishnu-Mittre. (a) Tangential longitudinal section, just including edge of flower and some leaf bases below and to left sporangiospores here arise low on the collar (shown by a dotted line), B.S.I.P. slide no. 8152; magn.  $\times 5$ . (b) Tangential longitudinal section of flower showing the androecial collar as a cone from which sporangiospores arise on its upper part. Three projections on the left of androecium are probably bases of diminutive leaves, B.S.I.P. slide no. 8153; magn.  $\times 5$ . (c) Tangential longitudinal section of flower the androecial collar appears as a rounded dome from which sporangiospores arise at all levels, B.S.I.P. slide no. 8154; magn.  $\times 5$ . (d) Oblique longitudinal section cutting along the collar here seen with ragged edges, nearly parallel androecial vascular bundles traverse the collar, some may branch but this is uncertain, B.S.I.P. slide no. 8155; magn.  $\times 5$ . (e) Drawing of the holotype showing the receptacle as a mound with sporangiospores behind it. B.S.I.P. slide no. 3226; magn.  $\times 5$  (sp., Sporangiospore; a.c., androecial collar; r.d., receptacular dome.)

the thick-walled tissue beneath the epidermis a little better developed. Our sections reveal no unexpected difference. We have no reason to identify *S. nipaniensis* with the *Pentoxylon* plant that bore *Carnoconites compactus* rather than that bearing *C. rajmahalensis*.

*Female cone**Genus*

*Carnoconites* Srivastava 1944.

*Type species*

*C. compactus* Srivastava 1944.

The generic diagnosis (Srivastava 1946) reads 'Strobili bearing several ovules with micropyles pointing outwards. Outer fleshy and stony layer well developed. Nucellus totally free from the integument. Nucellar cone projects into the micropyle. Shrivelled remains of the female prothallus preserved in some cases. Ovular supply consists of a single vascular strand, which pierces the stony layer at the chalazal end and terminates below the base of the nucellus. Few seeds contain the remains of an embryo'.

*Carnoconites compactus* Srivastava 1944

Figure 36, plate 3; figures 37, 42–44, plate 4.

- 1944 *Carnoconites compactum* Srivastava, p. 75; plate 2, figure 12 (brief description and figure).
- 1946 *Carnoconites compactum* Srivastava, p. 203; plate 5, figures 46–54; plate 6, figures 55–64; plate 7, figures 65–71; plate 8, figures 72–74 (fuller description, more specimens figured).
- 1948 *Carnoconites compactum* Srivastava: Sahni, p. 61; figures 35–43, 46 (further discussion, new specimens figured).
- 1953 *Carnoconites compactum* Srivastava: Vishnu-Mittre, p. 82; plate 4, figures 1–4; text-figures 12–16, 16a (more information about the whole fructification, new specimen figured).
- 1974 *Carnoconites compactum* Srivastava: Rao, p. 207 (review of earlier works).

Srivastava's (1946) specific diagnosis gives 'Compact cones about 2 cm × 1 cm, bearing 5 to 6 ovules in each longitudinal row, sometimes very few. Fleshy layer 1–2 mm broad. Cones borne on long stalks which emanate from a central axis; 3–5 mesarch vascular bundles traverse the stalk. Cone axis shows 5–6 mesarch bundles'.

*Holotype*. Number K62/1 of the Birbal Sahni Institute of Palaeobotany, Lucknow (Srivastava 1944; plate 2, figure 12).

*Occurrence*. Nipania, the Rajmahal Hills, Bihar, India.

*Discussion*

The dimensions and figures make this diagnosis adequate but we regard the bundles as endarch. The 'central axis' or peduncle (Vishnu-Mittre 1953) is known to exceed 7 cm in length and is nearly 2–3 mm wide at the base. It bears numerous, mostly rather short cone pedicels. The peduncle has a ring of up to 30 rather curved collateral bundles round a fairly wide pith and from this ring bundles are given off in groups of three to the cone pedicels. The group of three is not radial but the two lateral ones are large and face inwards. Towards the top the peduncle becomes thinner and has fewer bundles. Each bundle has a rather flat group of tracheids and parenchyma. Vishnu-Mittre (1953) describes the bundles as collateral and he states that some of the tracheids are centripetal but this is not obvious in his figures, the tracheids seem scattered among parenchyma.

The cone pedicel (stalk) is rather slender, consisting of a cortex and the core of three bundles,

but at the base of the cone it enlarges, often becoming five-sided and its vascular tissue has not been satisfactorily studied but both Srivastava (1946) and Sahni (1948) recognized a small bundle entering the base of the stone (sclerotesta of the seed) and ending there. There is no suggestion of vascular tissue inside or outside the sclerotesta. The whole fructification was large. In one of our specimens (figure 36, plate 3) there are about nine cones occupying an area of 6 cm × 3 cm and Vishnu-Mittre (1953, plate 4, figure 1) had a longitudinal section of about this size.

The arrangement of seeds on the stalk is spiral, not in longitudinal rows as stated by Srivastava (1946). At their bases adjacent seeds are close, but seldom in contact. At this level the vertical thickness of a seed is about two thirds of the width but further out the seed retains its width but becomes flatter, and finally in the micropylar region becomes a flat plate, almost split into upper and lower halves. In these features *Carnoconites* seeds can be said to be platyspermic. The opening of the micropyle has the form of two broad horizontal lips.

The sarcotesta is a remarkable tissue, seemingly composed of very soft and thin-walled parenchyma pressing against the sarcotesta of the next seed, and forming a smooth surface to the cone. In view of its thin walls it is strange that it is nearly always well preserved, only in the little abortive cones does it look rotten. Occasionally, and mostly in the outer part, the flesh cells are partly or wholly occupied by air (the same filling that created the 'pollen bubbles' in *Sahnia*). Then instead of being faintly visible they stand out starkly, the most obvious cells in the section. We feel sure these are the 'velamen' which Srivastava (1946) referred to; they are not a structure, but a preservational effect.

The sclerotesta is a compact layer of solid isodiametric cells, but the innermost cells are elongated. Outside the sclerotesta the sarcotesta has a layer of cells of very varied aspect, according to their reservation. Srivastava (1946) mentioned them, and Sahni called them 'secretory' (Sahni 1948, p. 63) or 'resinous' (Sahni 1948, p. 73). Most commonly they are totally black (but white when lit from above) because they are full of air, but occasionally they contain brown matter and their form is more visible. No explanation is offered about any original peculiarity that may have led to the filling with air, but it seems characteristic of this species.

Many seeds give a good view of the nucellar membrane attached at the seed base but shrunk away from the interior of the sclerotesta at its top and sides, though its apex may project up into the micropylar canal.

In our best sections the nucellus has an epidermis made conspicuous by the interior of each cell being occupied by air and therefore black by transmitted light, but between cells are broad clear walls. There are several layers of thin-walled parenchyma beneath the epidermis.

In all our seeds the nucellus has shrunk away from the interior of the sclerotesta except at the chalazal end where it is firmly attached. Often the section passes through the pointed nucellar beak and then the broad conical cavity at the base of the micropyle is left empty. We searched this region of many seeds for pollen but saw none, nor could we see any in the nucellar beak.

In most seeds the nucellus is empty but sometimes there is a conspicuous white mass inside it and thin sections were prepared in the hope they might show an embryo. The white matter proved amorphous; no cells at all could be seen in it but it is enclosed in a delicate brown membrane which we regard as the megaspore membrane.

We alter the spelling of the specific epithet to *compactus*, because the generic name ends in *-ites*, a masculine ending (I.C.B.N. Arts 23.5 and 32.5).

*Carnoconites rajmahalensis* (Wieland) Bose *et al.* 1984

Figures 38–41, plate 4.

- 1877 'Inflorescence or fructification of cycadeous plants', Feistmantel, p. 79; plate 39, figures 5, 5a, 5b (a cone impression from Mandro figured).
- 1911 *Williamsonia* (?) *rajmahalensis* Wieland, p. 461; figure 17D (brief account and figure of the specimen of Feistmantel, (1877)).
- 1919 *Haitingeria rajmahalensis* (Wieland) Krasser, pp. 3, 16; figure 10 (description and figure of Feistmantel's 1877 specimen).
- 1928 *Strobilites pascoei* Sahni, p. 42; plate 6, figures 98–100 (specimen of Feistmantel, 1877), described and figured).
- 1944 *Carnoconites laxum* Srivastava, p. 75; plate 2, figure 13 (brief description and figure of petrified specimen from Nipania).
- 1946 *Carnoconites laxum* Srivastava, p. 207; plate 8, figures 75–85 (more specimens from Nipania figured).
- 1948 *Carnoconites laxum* Srivastava: Sahni, p. 73; figures 30–33, 44 (more specimens from Nipania figured and discussed).
- 1953 *Carnoconites laxum* Srivastava: Vishnu-Mittre, p. 83; plate 5, figure 1 (new specimen from Nipania figured).
- 1958 *Carnoconites laxum* Srivastava: Bose, plate 3, figures 8, 9 (two specimens from Sakrigalighat figured).
- 1974 *Carnoconites laxum* Srivastava: Rao, p. 207 (revision of earlier works).
- 1984 *Carnoconites rajmahalensis* (Wieland) Bose *et al.*, p. 368, figures 1, 2 (note on nomenclature, Feistmantel's 1877 specimen and a new specimen from Onthea figured).

*Diagnosis*

Cone pedicels produced in a cluster on separate peduncles. Typical cone up to 25 mm long and 5 mm broad; when in nearly median longitudinal section often showing 20 seeds alongside the axis or in transverse section about five seeds. Cone pedicel nearly 1 mm thick, cone axis fully 1 mm thick, each with a cortex and a vascular cone comprising three bundles. Seeds closely packed; their sclerotesta almost in contact near axis but narrowing and further apart near cone surface. Sclerotesta 2 mm in length from chalazal end to micropyle, almost round below in section, 1.5 mm in diameter near seed base but becoming distinctly flattened in vertical plane near micropyle. Tissue of sarcotesta filling in gaps between the contracted outer ends of seeds and giving the cone a nearly smooth surface, but micropyles slightly prominent.

*Holotype*. Number 4514 of the Geological Survey of India, Calcutta (Feistmantel 1877 plate 39, figure 5).

*Occurrence*. Mandro, Sakrigalighat, Onthea and Nipania of the Rajmahal Hills, Bihar, India.

*Comparison*. Well grown cones of *C. rajmahalensis* are easily distinguished from those of *C. compactus* by their elongated shape, more numerous and smaller seeds and thinner sarcotesta. But apart from these numerical distinctions, the two are similar. In the original Nipania material *C. compactus* was commoner but some later collected blocks have much more *C. rajmahalensis*. We are not prepared to state that *Nipaniophyllum hobsonii* is the leaf associated with *C. rajmahalensis* in the chert. This needs special study. However, the striking block in figure 39, plate 4, *C. rajmahalensis* compressed in clay, shows on other surface fragments of ten



leaves we determine these as *N. hobsonii* with some confidence (as the midribs are broad). There is one fragment near the apex that could equally well be *N. raoi*.

Earlier authors have noted diminutive cones with weakly thickened seed coats among *C. compactus*, and they occur also with *C. rajmahalensis*. We judge that they are abortive, perhaps through failure of nutrition. Vishnu-Mittre (1953, p. 81) gives the fullest data. We judge that these little cones would be unlikely to yield facts that would illuminate ordinary cones.

Others have suggested that *Carnoconites* looks suitable for animals to eat, but we have no evidence that they did, and we could find no stripped cone axes. On the other hand isolated *Carnoconites* seed stones lacking any flesh are frequent in the *Nipania* matrix.

#### FORM OF THE *PENTOXYLON* PLANT

A *Pentoxylon* stem seems deliberately constructed to be weakly flexible. Ordinary land plants have their strong tissues efficiently placed to resist bending and are able to support the foliage. Young stems show this clearly, the strong tissues form a wide tube and the parts of the tube are united and unlikely to slip past one another under stress; later the stem may form a solid column of wood. But *Pentoxylon* has its wood, its only strong tissue, near the centre, not as a

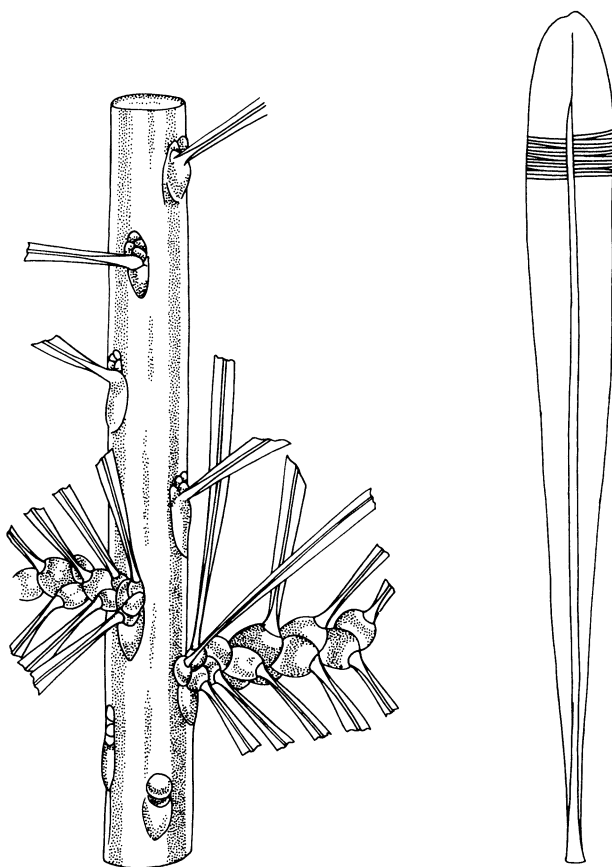


FIGURE 7. Diagram of an upright *Pentoxylon* long shoot in its third year. The upper part has leaf cushions, *Nipaniophyllum* leaves and buds. The middle part has lost its leaves and the buds have grown out as leafy type 3 short shoots with swollen leaf bases. In the lower part the short shoots have fallen leaving round scars in leaf axils at the top of cushions. In a real shoot all three zones would be considerably longer. To the right a typical leaf of *Nipaniophyllum hobsonii*.

tube but as five separate strands and there is evidence that the ray tissue between these strands 'gave' easily. Under lateral stress stiffness would only be offered by the strands individually. We cannot know their stiffness but we note that *Pentoxylon* stems are mostly in short pieces, considerably shorter than associated conifer branches. They may have broken easily.

We infer that the *Pentoxylon* plant (there is no present evidence that it was more than a shrub) sent up erect branched and leafy shoots but these soon sagged and after two or three seasons flopped onto the ground or among other stems making a thicket. As for its habitat, we know that at Nipania it grew beside a pool or stream of siliceous water, believed to be of volcanic origin. Elsewhere occasional leaves of *Taeniopteris spatulata* are buried in ordinary water-borne sediments. We see no suggestion of a xerophytic habitat either in the sediment or in the organization of the plant or its associates.

We have used *Nipaniophyllum hobsonii* in our restoration; its leaves are shorter, but even so we have trimmed most of them short. We imagine the long shoot producing and dropping leaves in its first growth season and in the next axillary buds producing the flimsy short shoots with their leaves which also drop.

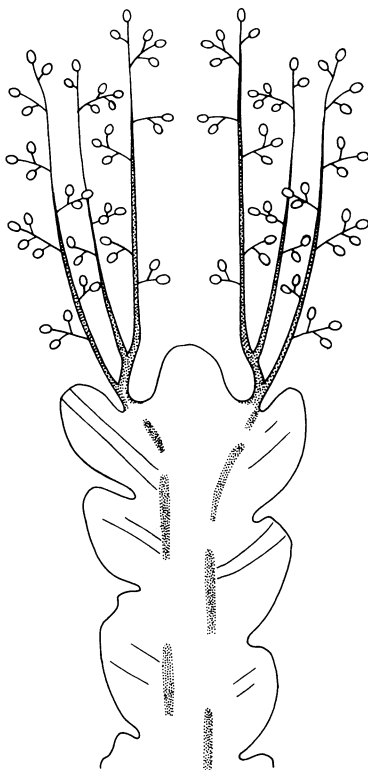


FIGURE 8. Idealized longitudinal section of *Sahnia* flower. The dwarf shoot has dropped its leaves. The androecial collar arches over the central dome of the receptacle, vascular tissue stippled.

We regard the *Sahnia* flower peduncle as a larger form of the ordinary leafy short shoot. *Carnoconites* is difficult; we lack the evidence we need. We rashly place it at the edge of the broadly conical head of the type 2 short shoot. If these suggestions are wrong they call for correction and we hope will receive it.

AFFINITIES OF THE *PENTOXYLON* PLANT

Srivastava knew that he was dealing with very strange plants, and a phrase in the opening paragraph of Sahni's (1948) paper ('a group of plants which defies classification') fits our views. Sahni's mood was more compromising in parts of his paper but what has been learnt since 1948, namely concerning *Sahnia*, has increased isolation of the plant. It is only when workers take individual organs, for instance the leaves, or the wood alone, or just the centripetal secondary xylem, undeniably like that of *Rhexoxylon* and *Medullosa* and then omit from consideration other organs of *Rhexoxylon* or *Medullosa* that they can write warmly about affinities. *Medullosa* bore huge *Alethopteris* or *Neuropteris* leaves and these bore large seeds, *Trigonocarpus* and others singly in cupules. They also bore highly complex pollen capsules, none of these remotely like the male

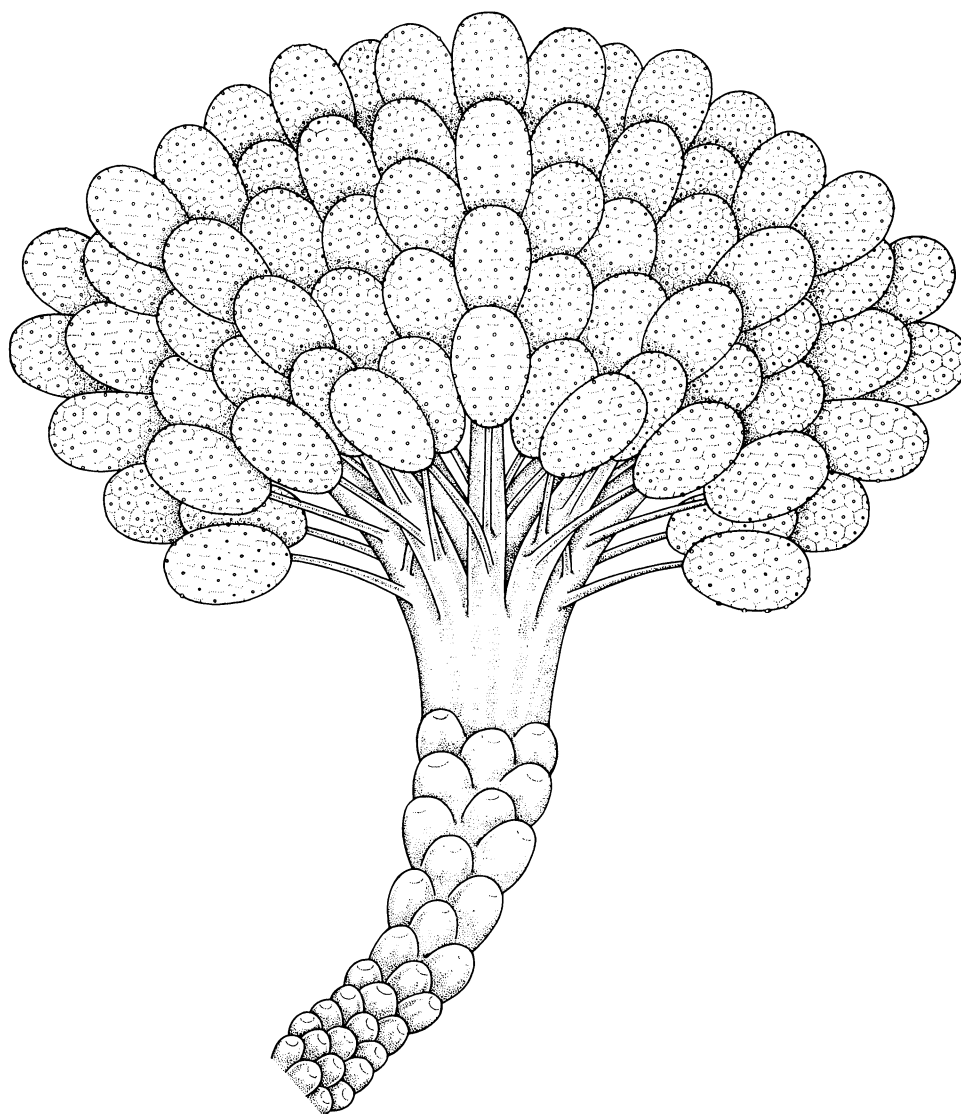


FIGURE 9. Conical head of type 2 short shoot bearing *Carnoconites compactus*. The top of the conical head is supposed to be hollow and its edge divides into six to eight main branches (peduncles) from which the cone pedicels arise.

organ of the *Pentoxylon* plant. *Rhexoxylon* is held to have borne *Dicroidium* leaves, *Pteruchus* microsporophylls and *Umkomasia* and other fruits all of which are again not in the least similar to those of the *Pentoxylon* plant. The natural way to see the agreement in secondary wood is as the result of convergent evolution.

The secondary wood of *Pentoxylon* has been called coniferous in character and we agree, but it is to be remembered also that it is more simply organized than in normal conifers. It has no xylem parenchyma, and as far as we can observe a single type of tracheidal pitting, a single type of ray field pit and no other pits on ray cells. A little variety in tracheid pitting (rarely biseriate) has been claimed and may be real, but we did not notice it in wood taken from stems with five bundles. We did see sections that we feel certain were of coniferous origin among old slides labelled *Pentoxylon*. Certainly if a wood anatomist were offered a block of *Pentoxylon* wood for study as a conifer he would think it unusual.

Sahni (1948) was deeply impressed by the centripetal primary xylem of the vascular bundles of the leaf and petiole and they indeed are like typical cycad leaf bundles. Also, the phloem

#### DESCRIPTION OF PLATE 1

FIGURES 10–16. *Pentoxylon sahnii* Srivastava, long shoots (type 1 shoots).

FIGURES 10 AND 11. Denuded long shoot from Amarjola, the surface shows oval scars of type 3 slender shoots subtended by leaf scars, B.S.I.P. numbers 35678 and 35679; magn.  $\times 1$ .

FIGURE 12. Transverse section of long shoot from Nipania, the specimen retains its cortex, B.S.I.P. slide no. 8156; magn.  $\times 6$ .

FIGURE 13. Transverse section of long shoot from Amarjola, the specimen shows cortex, xylem bundles with centrifugal, primary and centripetal xylem and opposite the pith a layer of phloem and some flat brown cells, B.S.I.P. slide no. 8157; magn.  $\times 6$ .

FIGURE 14. Transverse section showing centrifugal xylem, primary xylem mainly seen as dark flat cells and centripetal xylem, B.S.I.P. slide no. 8157; magn.  $\times 100$ .

FIGURE 15. Secondary wood in transverse section from a specimen in which rays and growth rings are unusually well marked, B.S.I.P. slide no. 8158; magn.  $\times 100$ .

FIGURE 16. Transverse section, at bottom inner edge of centripetal xylem then cambium then secondary phloem showing layers of white fibres, phloem rays form dark streak rising obliquely to left, B.S.I.P. slide no. 8158; magn.  $\times 100$ .

#### DESCRIPTION OF PLATE 2

FIGURES 17–28. *Pentoxylon sahnii* Srivastava, type 2 thick short shoots.

FIGURE 17. Type 2 short shoot from Amarjola, B.S.I.P. no. 35680; magn.  $\times 1$ .

FIGURE 18. Transverse section of specimen in figure 17, B.S.I.P. slide no. 35680–1; magn.  $\times 2$ .

FIGURE 19. Exceptionally small type 2 short shoot with a pointed apex, at no level did it develop the broadly conical head, B.S.I.P. no. 35702; magn.  $\times 1$ .

FIGURE 20. Transverse section of specimen shown in figure 19, B.S.I.P. slide no. 35702–1; magn.  $\times 2$ .

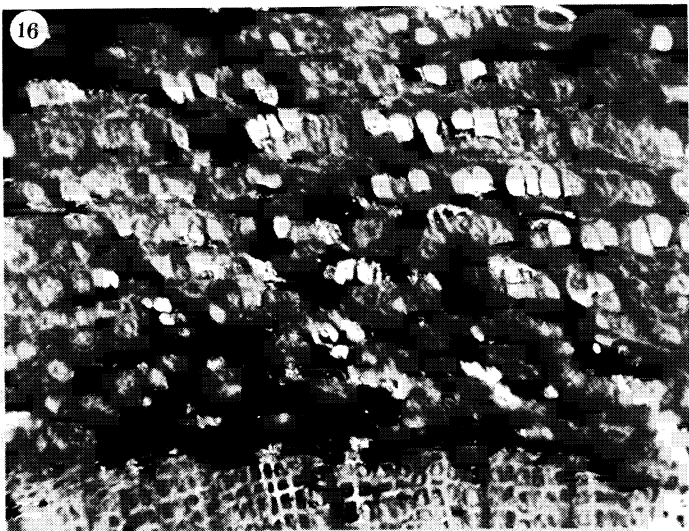
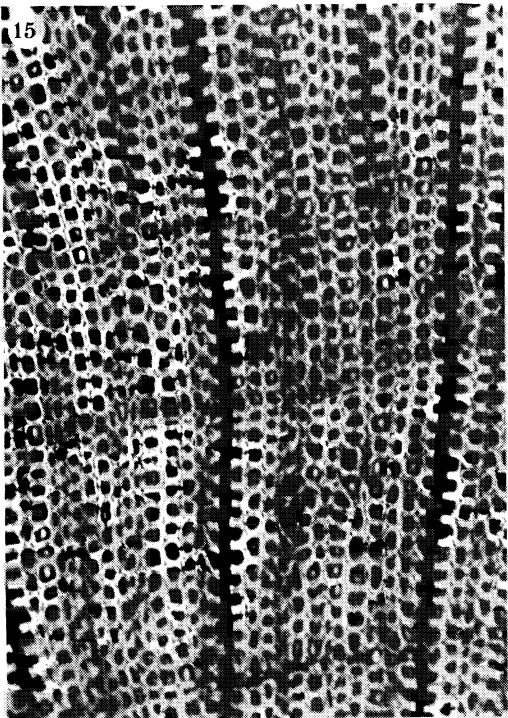
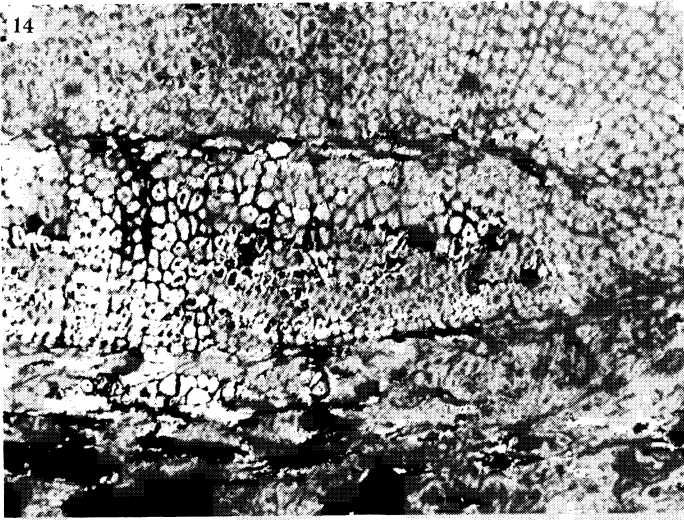
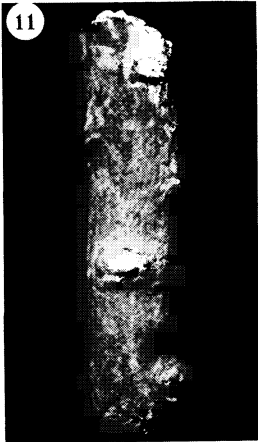
FIGURE 21. Unusual specimen in which branch bases are emerging at the sides (see figure 3 *a–c* for transverse sections), B.S.I.P. no. 35703; magn.  $\times 1$ .

FIGURES 22–25. Selected sections from a specimen from Nipania (no. 35681) cut into nine sections, figure 22 is the lowest (section 1), figure 25 is the highest (section 9) in figures 22 and 23 some typical *Pentoxylon* bundles are clear; figure 24 showing the bottom of the grub hole in the centre; figure 25 showing it as an open cavity lined by periderm, B.S.I.P. slide numbers 35681–1, 35681–3, 35681–6, 35681–9; magn.  $\times 10$ .

FIGURE 26. Transverse section of the top section of a specimen from Nipania (no. 35683) made into two sections, the grub hole is large, two groups of medium sized bundles are leaving out of the stem, between them is a rather large bundle on the surface, B.S.I.P. slide no. 35683–2; magn.  $\times 10$ .

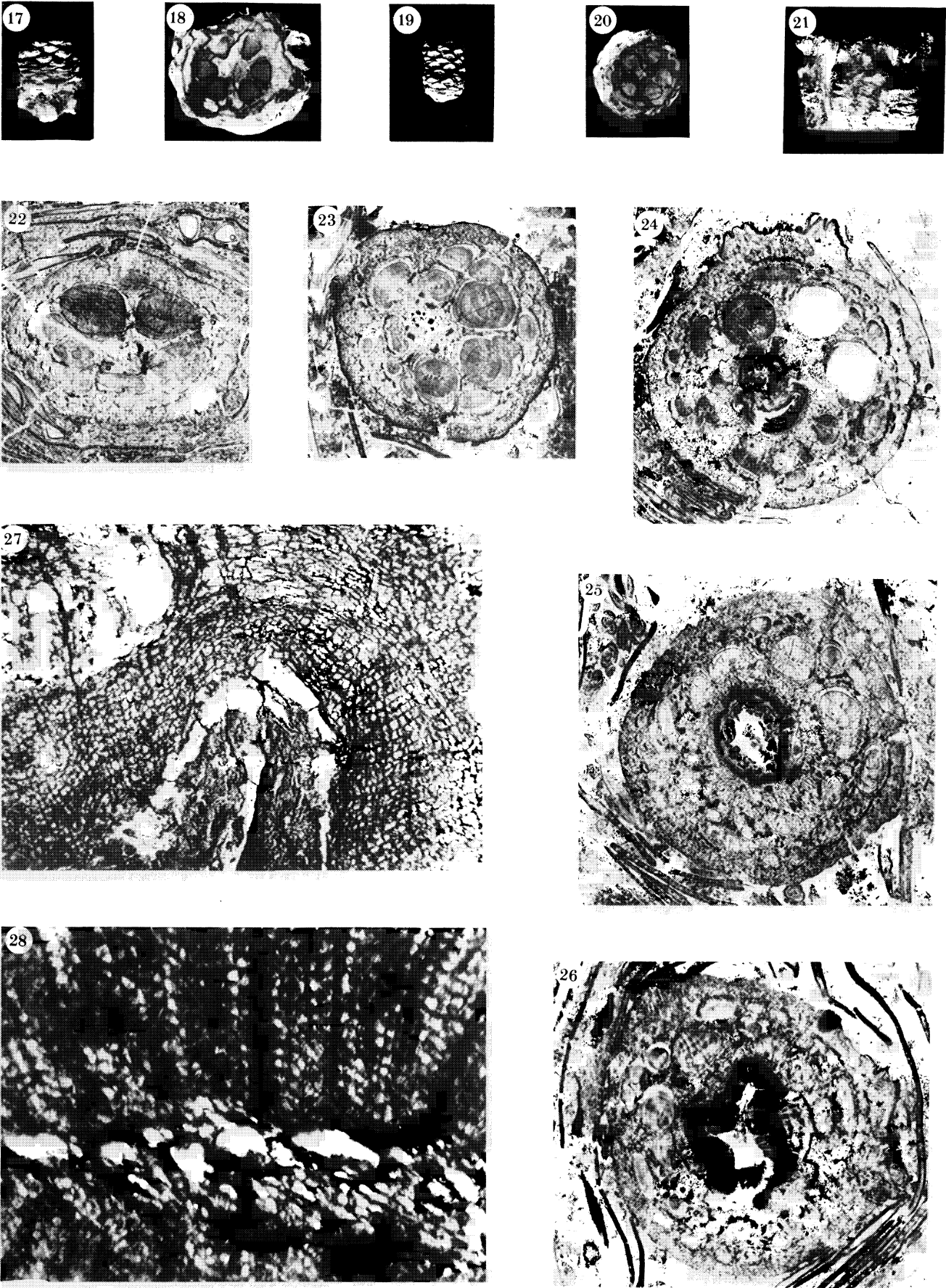
FIGURE 27. Periderm formed round the grub hole, B.S.I.P. slide no. 35682–2; magn.  $\times 50$ .

FIGURE 28. Primary xylem from one of the series of section in figures 22–25, it is broader and more parenchymatous than in the long shoot (plate 1, figure 14), B.S.I.P. slide no. 35681–4; magn.  $\times 100$ .



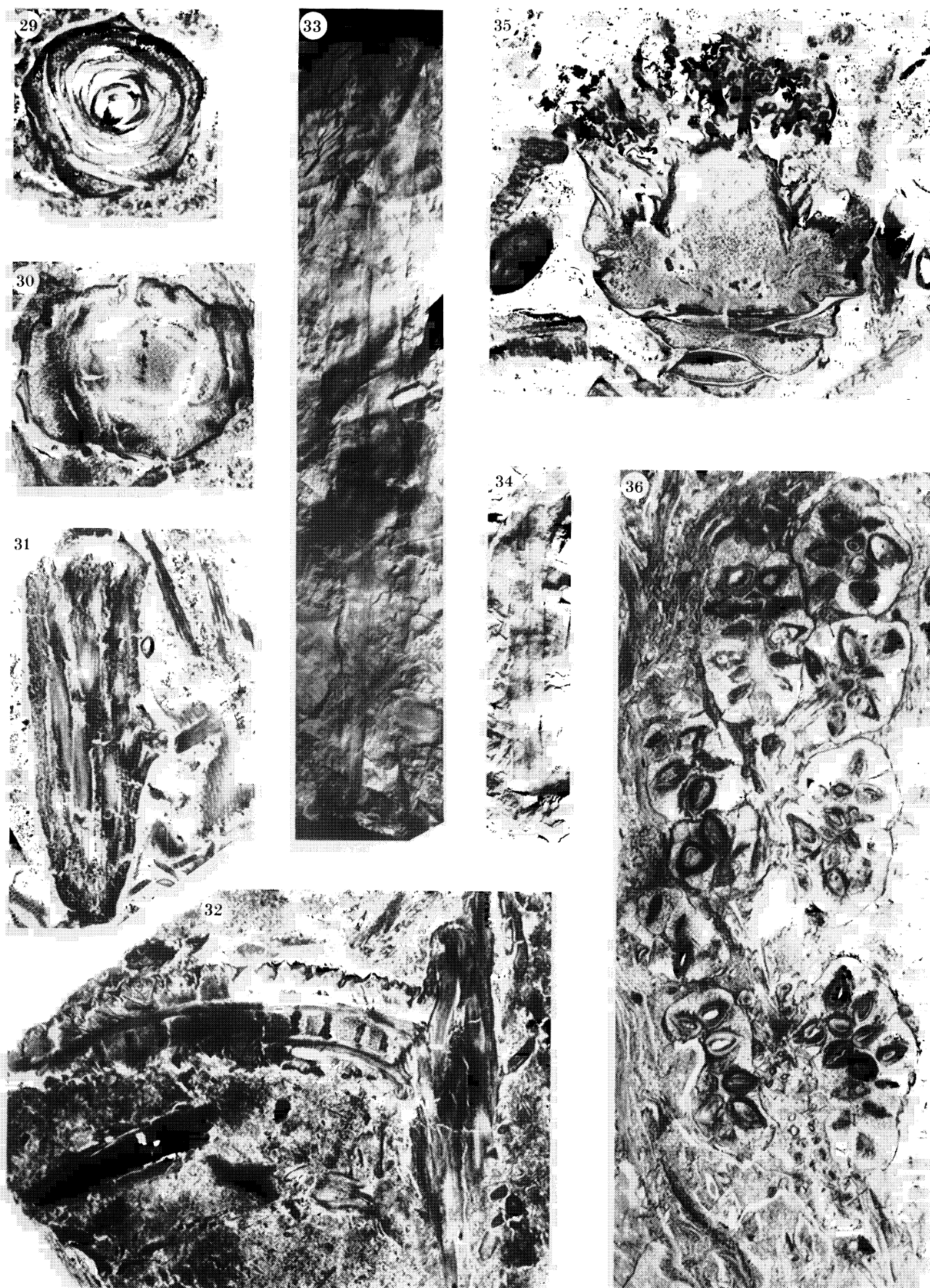
FIGURES 10–16. For description see opposite.

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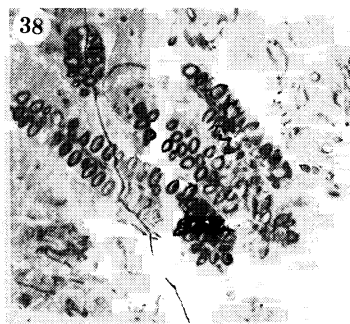


FIGURES 17–26. For description see page 104.





FIGURES 29-36. For description see page 105.



FIGURES 37-43. For description see opposite.



is in the right position for a cycad. On the other hand, he pointed out that the flat plate of bundles in the petiole is not at all cycadean; he might have added that the direct course of the leaf traces in *Pentoxylon* contrasts with the girdling course in cycads. The scalariform tracheids of the petiolar xylem also fit a cycad.

For a time the arrangement of the subsidiary cells was thought to be bennettitalean rather than cycadean (Rao 1943) and this perplexed Sahni, but Vishnu-Mittre (1953) and Sharma (1969a) showed that the arrangement was anomocytic as in most gymnosperms including cycads. Our fresh study confirms this.

The male flower, *Sahnia*, was originally described (Vishnu-Mittre 1953) as having microsporangiophores arranged in a ring and united basally by a membranous sheath and thus looking rather like bennettitalean male flowers (*Weltrichia*, etc.). But the present study has revealed that the sporangiophores of *Sahnia* were borne on a collar-like structure formed by the raised margin of the receptacle. Moreover, unlike the bennettitalean microsporophylls, the sporangiophores of *Sahnia* were stiff, straight (not circinate), branched but not pinnately and bear simple pollen sacs, not compound capsules.

## DESCRIPTION OF PLATE 3

- FIGURE 29. Transverse section of a bud formed by *Nipaniophyllum* petiole bases, B.S.I.P. slide no. 8159; magn.  $\times 10$ .  
 FIGURE 30. Transverse section of a type 3 short shoot of *Pentoxylon sahnii* Srivastava, xylem (all centrifugal) forms flat plates separated by small gaps, B.S.I.P. slide no. 8160; magn.  $\times 8$ .  
 FIGURE 31. *Pentoxylon sahnii* Srivastava, long shoot bearing a bud on its right side, B.S.I.P. slide no. 8161; magn.  $\times 3$ .  
 FIGURE 32. *Pentoxylon sahnii* Srivastava long shoot bearing a type 3 short shoot on its left side, note the bars of sclerotic cells in the pith and the rough surface caused by the leaf base cushions separated by grooves, B.S.I.P. slide no. 8162; magn.  $\times 4$ .  
 FIGURE 33. *Nipaniophyllum hobsonii* sp. nov., holotype, B.S.I.P. no. 35695; magn.  $\times 1$ .  
 FIGURE 34. *N. raoi* Sahni, neotype, B.S.I.P. no. 35690; magn.  $\times 1$ .  
 FIGURE 35. *Sahnia nipaniensis* Vishnu-Mittre, tangential longitudinal section (see also figure 6c) the collar tissue here appears as a rounded dome, B.S.I.P. slide no. 8154; magn.  $\times 8$ .  
 FIGURE 36. *Carnoconites compactus* Srivastava, polished surface of block of chert showing nine cones and some of their stalks at the base, which are attached to the peduncle, the back of this slice shows other cones of this group, B.S.I.P. no. 35696; magn.  $\times 2$ .

## DESCRIPTION OF PLATE 4

- FIGURE 37. *Carnoconites compactus* Srivastava exposed by splitting the chert, B.S.I.P. no. 35697; magn.  $\times 2$ .  
 FIGURE 38. *C. rajmahalensis* (Wieland) Bose *et al.*, section passing longitudinally through four cones of a group, B.S.I.P. no. 35698; magn.  $\times 1$ .  
 FIGURE 39. *C. rajmahalensis* (Wieland) Bose *et al.*, at least eight cones in a radiating group on the fractured surface of a hard clay from Onthea, B.S.I.P. no. 35699; magn.  $\times 1$ .  
 FIGURE 40. *C. rajmahalensis* (Wieland) Bose *et al.*; three short stalked cones, that on the right in radial longitudinal section, the other two in tangential section. The seed arrangement in the middle cone has spiral parastichies, B.S.I.P. no. 35700; magn.  $\times 2$ .  
 FIGURE 41. *C. rajmahalensis* (Wieland) Bose *et al.*, longitudinal section of a cone group, top one is isolated *C. compactus* Srivastava, B.S.I.P. no. 35701; magn.  $\times 2$ .  
 FIGURE 42. *C. compactus* Srivastava, tangential section of two cones attached to the peduncle, section is near the cone axis where seeds are nearly rounded, B.S.I.P. slide no. 8161; magn.  $\times 3$ .  
 FIGURE 43. *C. compactus* Srivastava, two seeds on left in nearly vertical radial section showing micropyle and contracted nucellus (with beak), near middle a seed with white amorphous matter in nucellus, B.S.I.P. slide no. 8164; magn.  $\times 10$ .  
 FIGURE 44. *C. compactus* Srivastava, seed in longitudinal section at top (incompletely shown) with white matter and megaspore membrane, B.S.I.P. slide no. 8165; magn.  $\times 10$ .

*Carnoconites*, the female cone, by itself prevents our linking *Pentoxylon* with any other plant. The specimens are remarkably clear and their study has left almost nothing ambiguous. The features that are still open (attachment of the cone axis, pollination mechanism, and embryo development) would be a welcome addition to knowledge, but whatever they show would leave *Carnoconites* in isolation. Meeuse (1961) has suggested that the sacrotesta may be an aril, which we take to mean a late development round the integument. We searched for evidence that it might have crept up round the integument as it does in *Taxus*, but found no support. The sarcotesta has never been held as a difficulty in placing *Pentoxylon*. *Pentoxylon* is the perfect member of Sahni's class stachyosperms, in all others, even *Taxus*, the ovule is associated with organs that can be considered as leaves.

We regard the reproductive organization of a gymnosperm, rather than any vegetative feature as expressing its fundamental organization, and we know nothing that produces seeds on special otherwise naked axes, and pollen sacs on others.

The family name Pentoxylaceae or names of higher ranks viz. Pentoxylales or Pentoxylopsida presumably include more than *Pentoxylon* but we do not know what. A word often used is Pentoxyleae, but this is not the way a word denoting a class should end; it denotes a 'tribe' an informal division of a family.

If indeed, the rules of nomenclature require that we classify *Pentoxylon* we can only state that it is a fossil gymnosperm of obscure affinity.

Rao has repeatedly, most recently in 1981, tried to assign the *Pentoxylon* plant as isolated synthetic group and with more determination to succeed that we can feel. We refer our readers to his paper.

#### PROBABLE MATERIAL OF THE *PENTOXYLON* PLANT FROM OUTSIDE INDIA

Walkom (1921) described from the Jurassic of New South Wales 'Cone(3)' (p. 16, plate 6, figures 4, 4a) which is like *Carnoconites compactus* Srivastava. This flora also includes broad and narrow leaves of *Taeniopteris spatulata* McCl. (p. 11; frontispiece; plate 2, figure 9; plate 3, figure 1; plate 6, figure 8).

Douglas (1969) described from the Jurassic of Victoria a 'fertile organ bearing microsporangia' (p. 240; plate 45, figures 1 and 2; plate 46, figures 1-6; plate 48, figure 1; plate 51, figure 1; figures 5, 2-6) which is like *Sahnia* Vishnu-Mittre and his 'megasporophyll with seeds-type 1' (p. 242; plate 47, figures 1-5; plate 49, figures 5-6; figures 5, 7-8) is like *Carnoconites compactus* Srivastava. This flora also includes leaves of *Taeniopteris spatulata* group (*Taeniopteris daintreei*, p. 53; figure 1, 1 frontispiece; plate 17, figures 3 and 4; plate 18, figure 3; plate 19, figure 2; figures 1, 51-55; 1, 65). Figure 1, 1 (frontispiece) shows a stem like a *Pentoxylon* short shoot along with the *Taeniopteris daintreei* leaf.

Harris (1962) described *Carnoconites cranwelli* Harris, (p. 20; plates 1-3; text-figures 2 and 3) from the Jurassic of New Zealand.

Harris (1982) described from the New Zealand Jurassic *Taeniopteris spatulata* McCl. (p. 92; plate 1, figures D and E; text-figure 1); stem, cf. *Pentoxylon* sp. (p. 95, plate 1, figures B-D; plate 2, figure A; text-figure 2A, B); possible cone stalks of *Carnoconites cranwelli* (p. 93, plate 1, figure B); isolated seed ?*Carnoconites* sp. (p. 98; plate 1, figure E; plate 2, figures C, D; text-figure 2D, E) and cf. *Sahnia* sp. (p. 99; plate 1, figure E; plate 2, figures E, F; text-figure 2, C) all in association.

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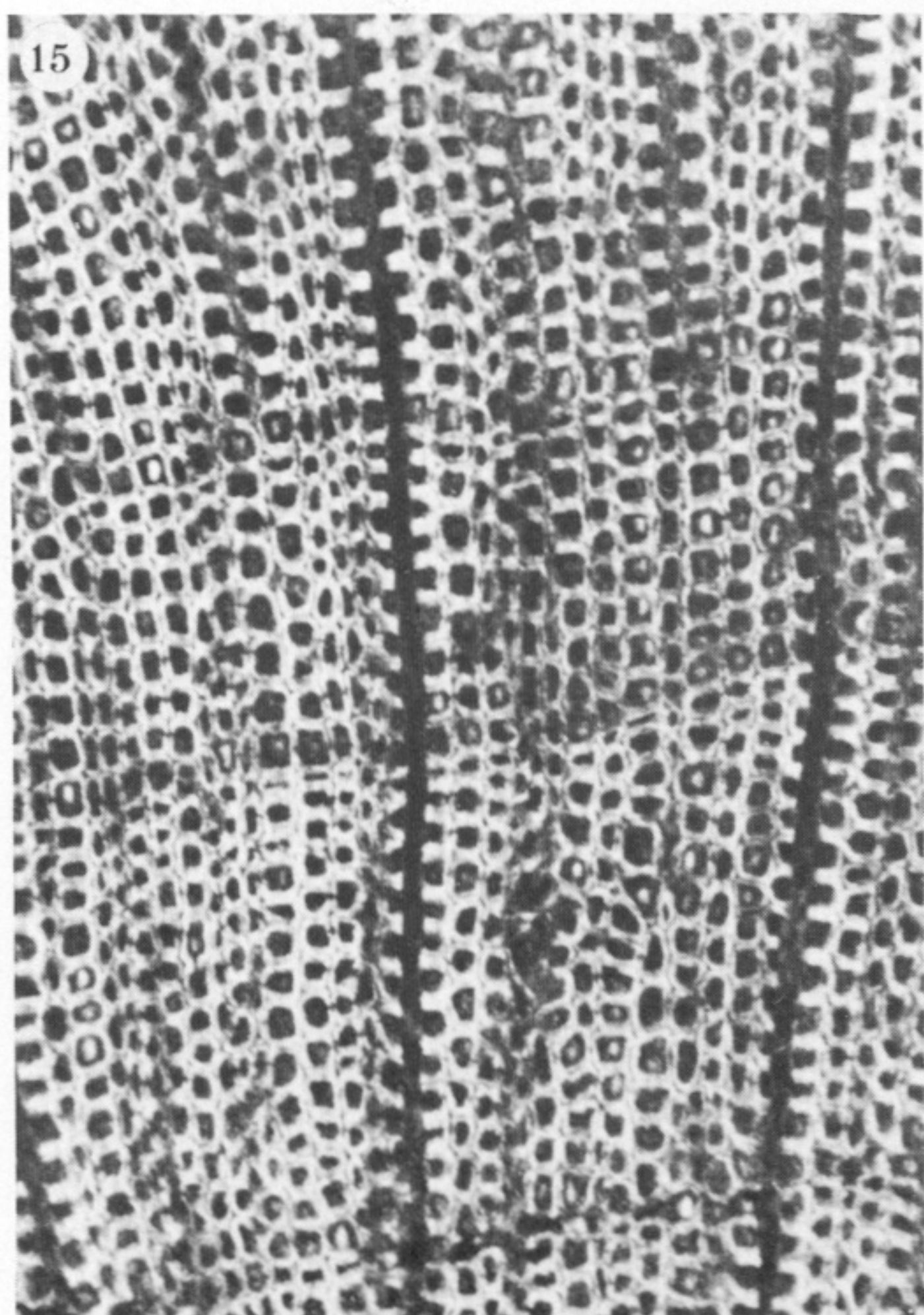
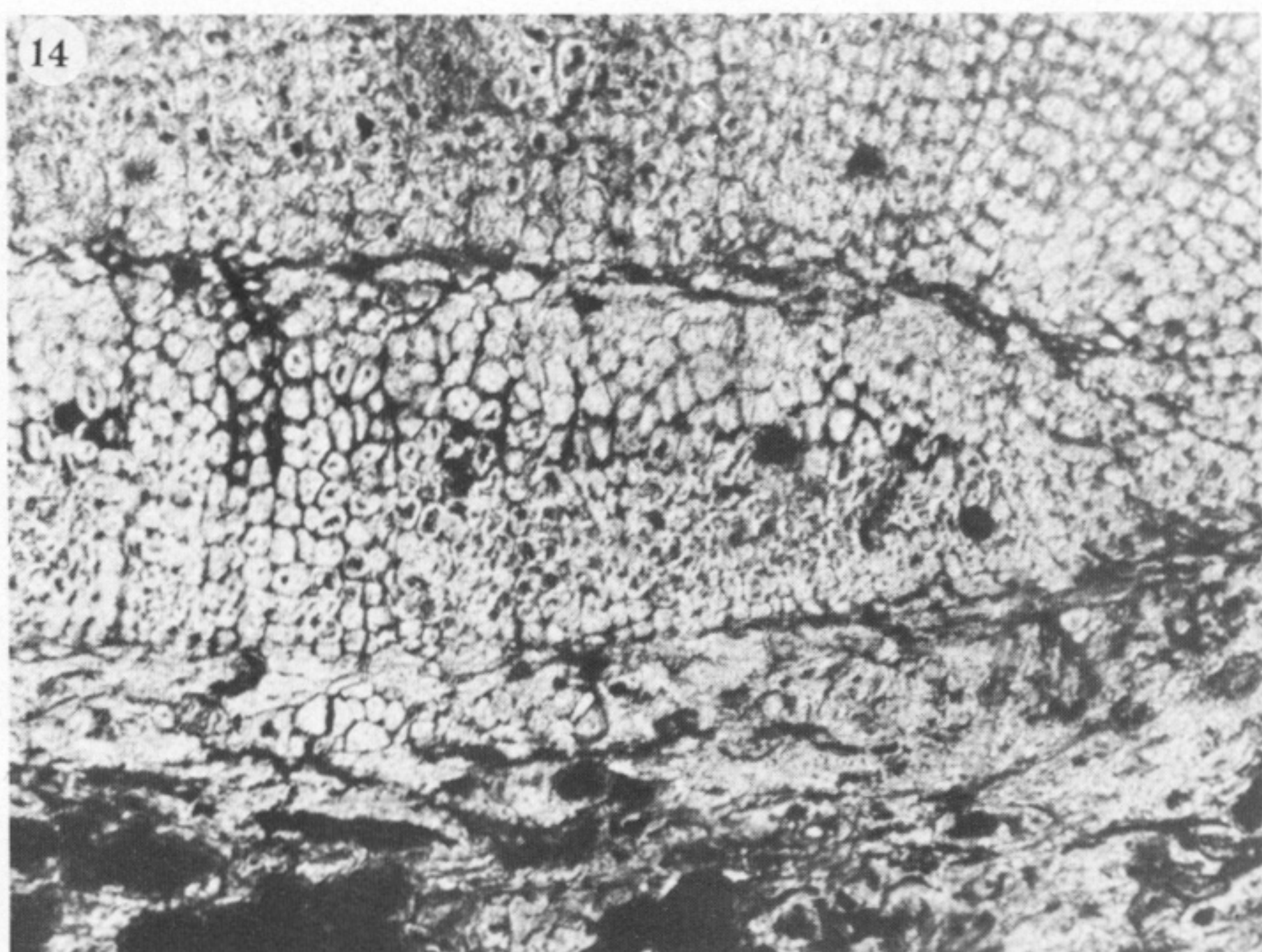
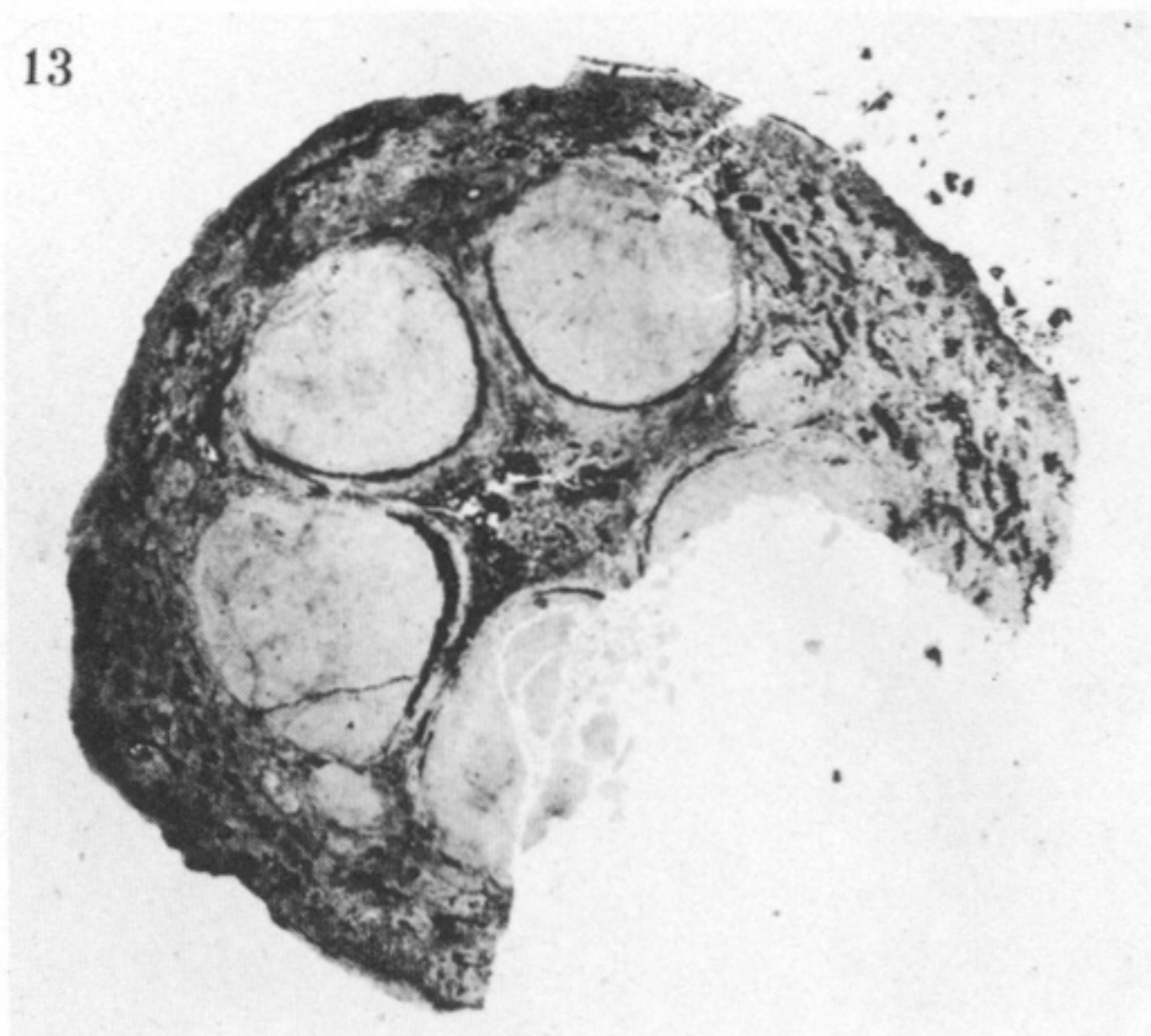
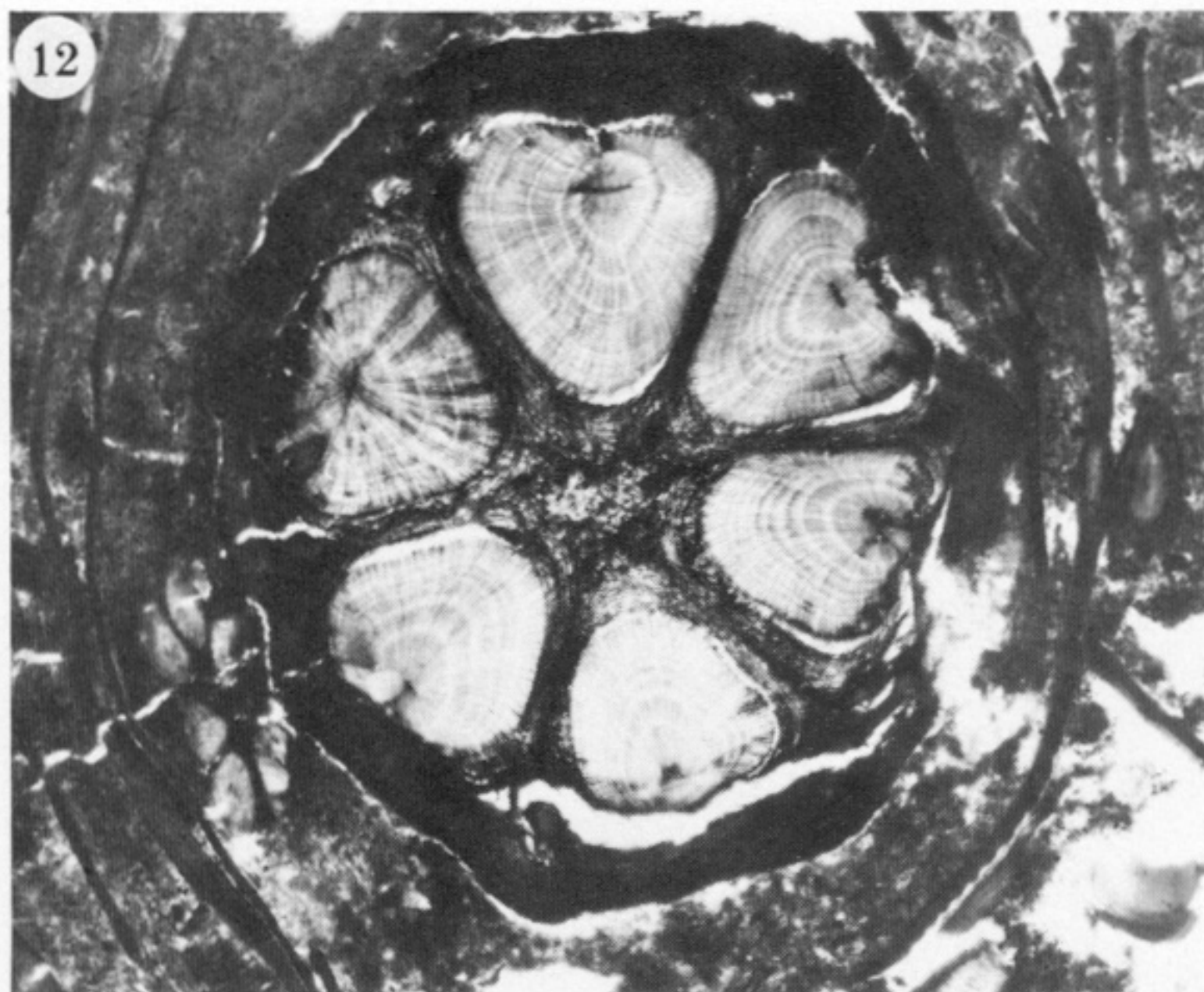
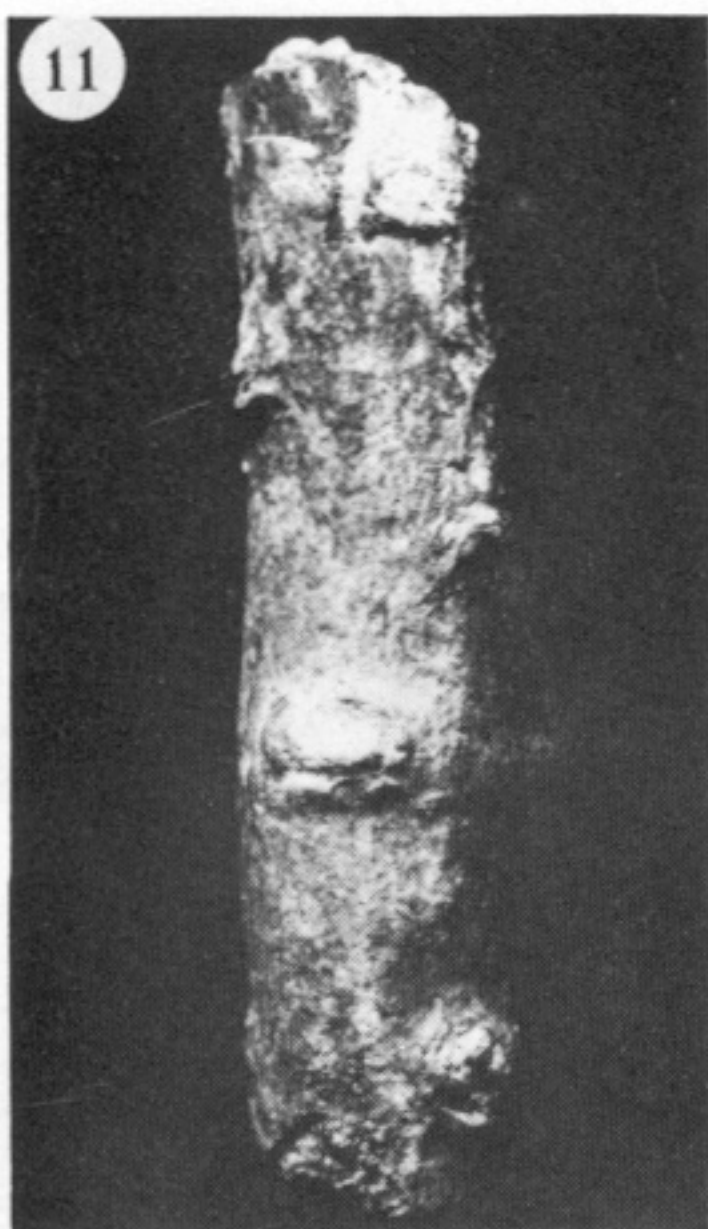
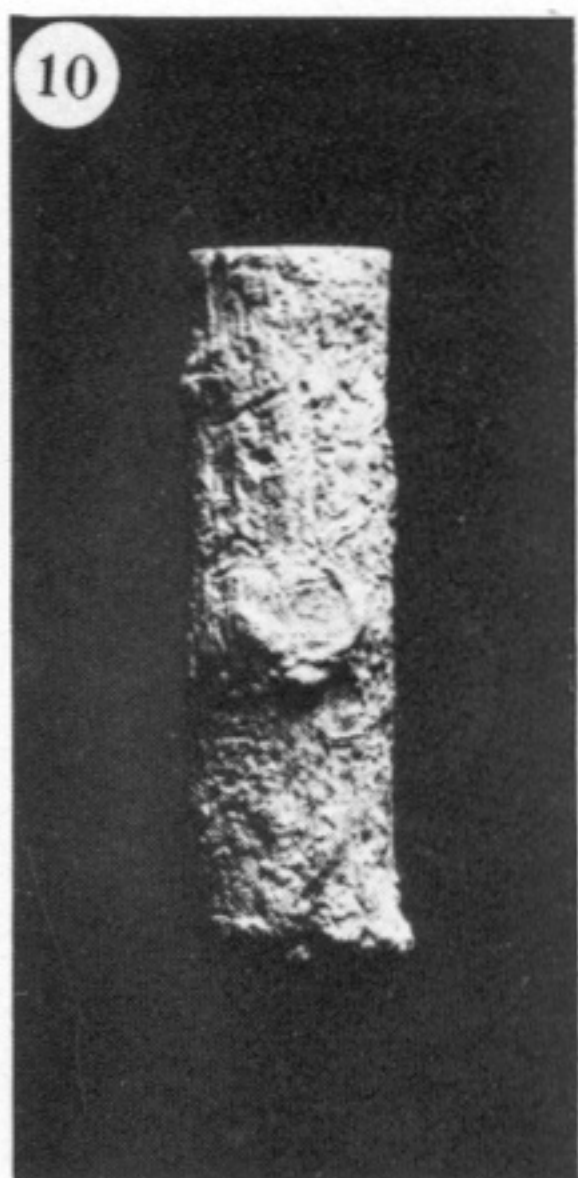
## APPENDIX

*Nipanioxylon guptai* Srivastava

*Nipanioxylon guptai* was described by Srivastava (1944, p. 75; plate 2, figure 14) from the Nipania chert, the figure is of a very poorly preserved specimen which leaves its nature open. Subsequently, by Srivastava in 1946 (after his death and the paper edited by Sahni) two plates of photos (9 and 10) were published with the caption *Nipanioxylon guptai* gen. et sp.nov. but no related manuscript was found. Sahni queried the determination of many of the photos, including the one which Srivastava (1944) made his type, but accepted others as firm. In our view figures 86, 87 and 93 are certainly *Pentoxylon* (figure 93 being an enlargement of the middle bundle of figure 86 and figure 87 but inverted). While we cannot be sure about Srivastava's type figure (Srivastava 1944, plate 2, figure 14; 1946, plate 9, figure 92), we think it might be a young conifer stem with a broad pith surrounded by eight collateral bundles. It has nothing to do with *Pentoxylon*. We have seen similar poorly preserved shoots labelled '*Nipanioxylon*' in the Sahni Institute slide collection, and these bear twigs with minute conifer leaves. Other figures on the plates are obscure, particularly the longitudinal sections unrelated to anything in transverse view. Plainly the specimens of these two plates are a mixed lot and it does no honour to Srivastava to perpetuate the name *Nipanioxylon*. Many authors have however considered *Nipanioxylon* to be related to the genus *Pentoxylon* and some (without evidence) have regarded it as the stem of one of the two *Carnoconites* species.

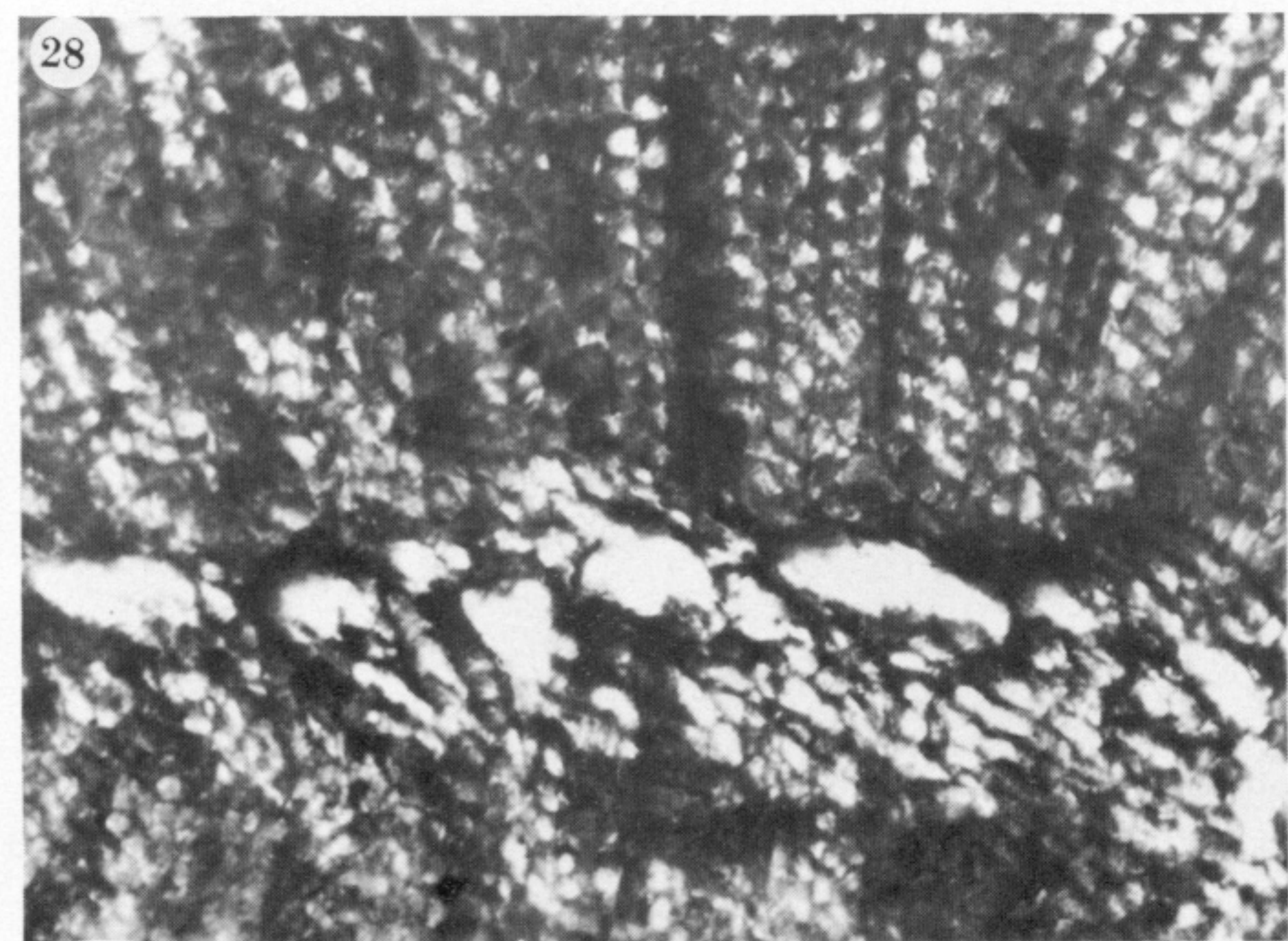
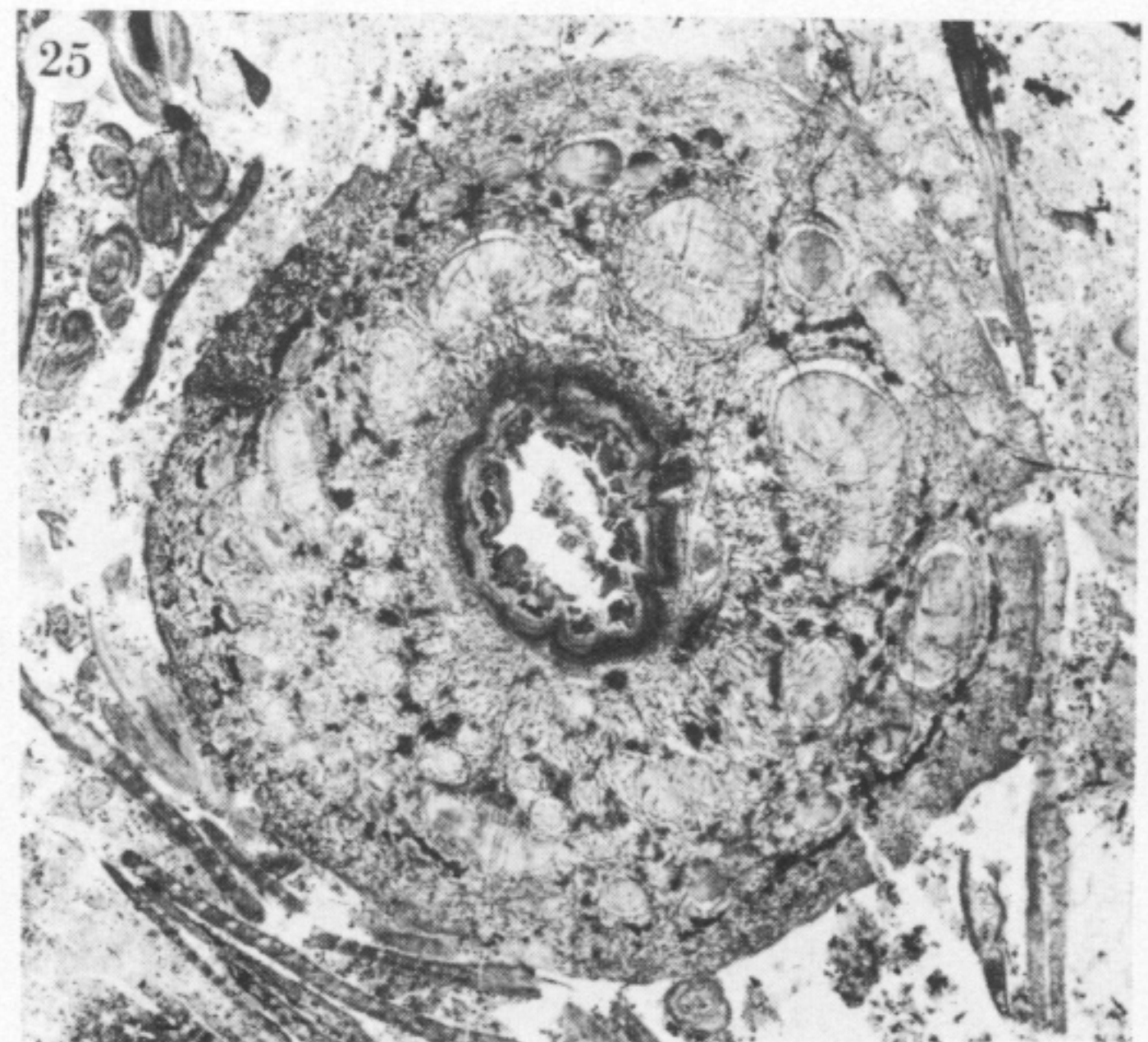
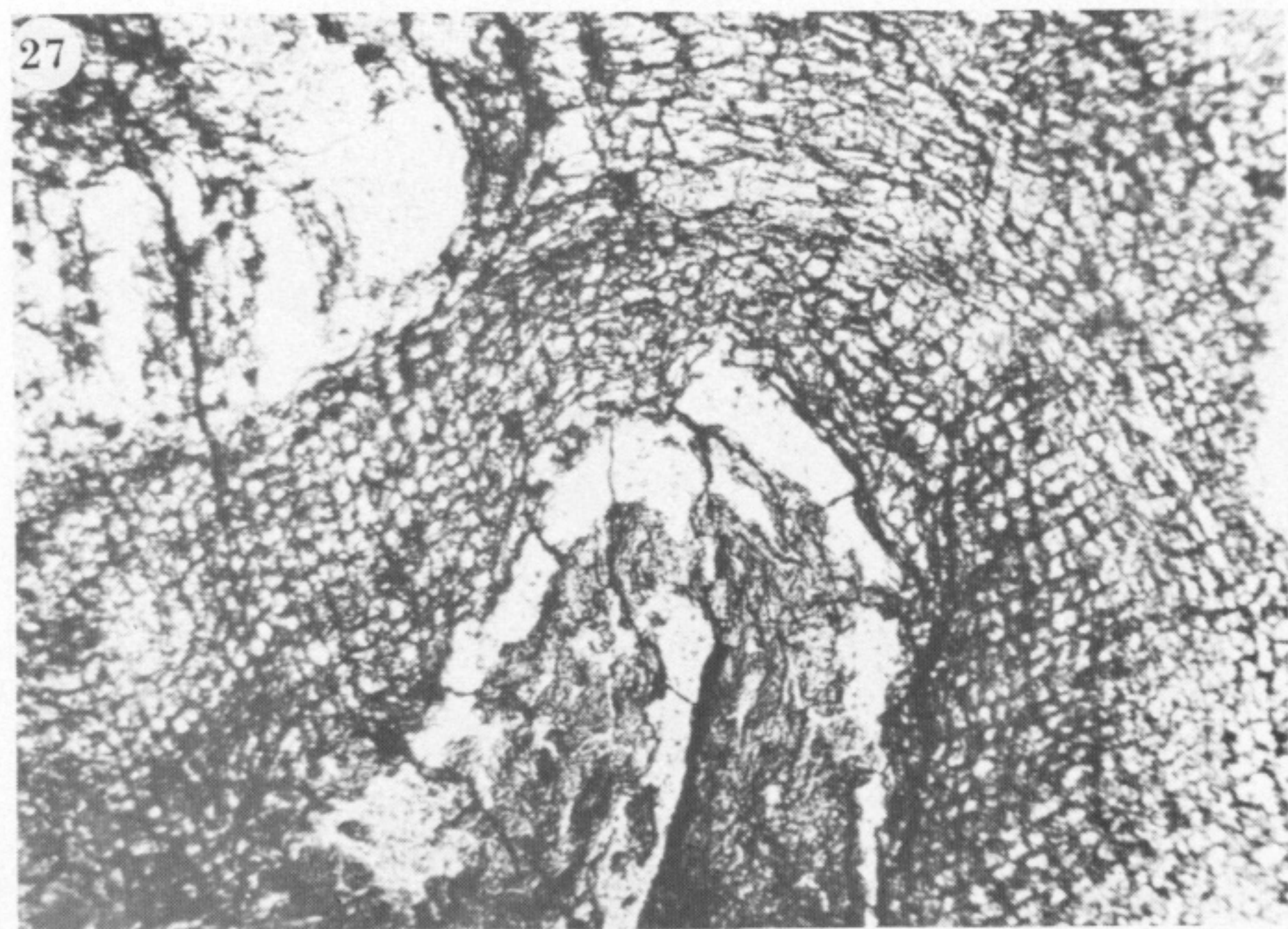
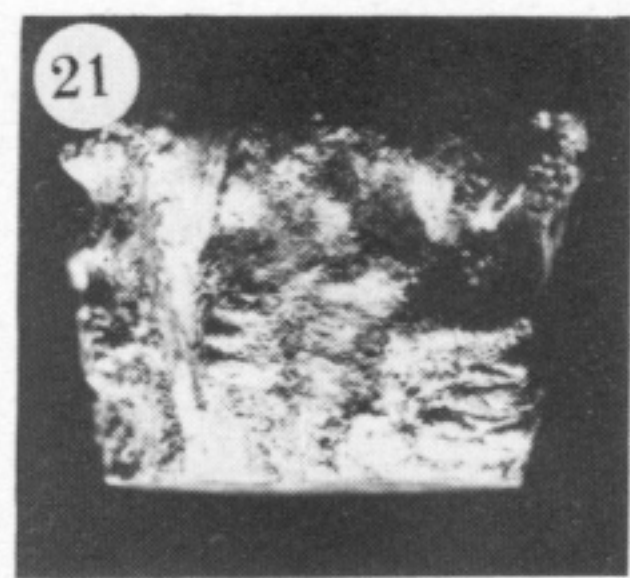
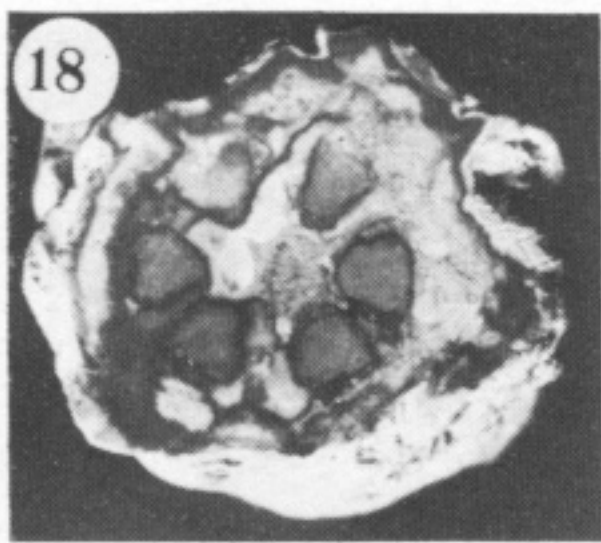
The work of Vishnu-Mittre (1958) is, however, different. He recognized that Srivastava's (1946) material was heterogeneous but does not seem to have considered his 1944 type description and figure. He gave a wholly new diagnosis of the genus and species and then described a remarkable stem as *Nipanioxylon guptai* with the help of serial sections. We have seen nothing like it but Vishnu-Mittre's (1958) stem deserves further study and under a name that is valid.





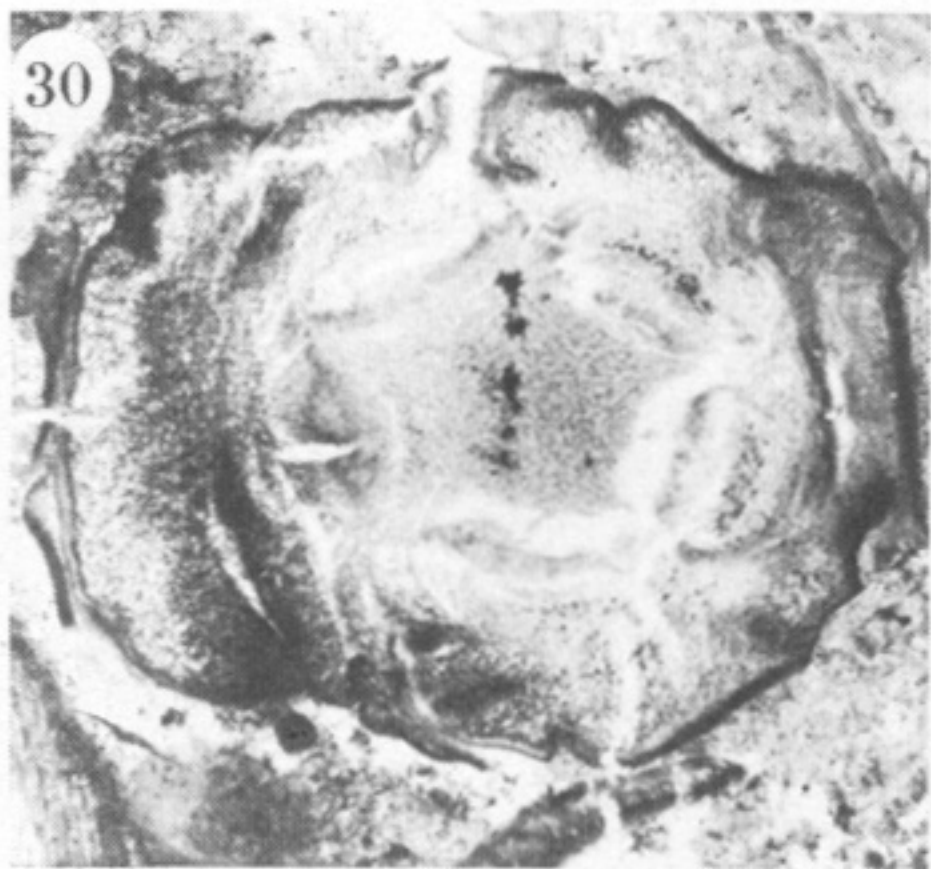
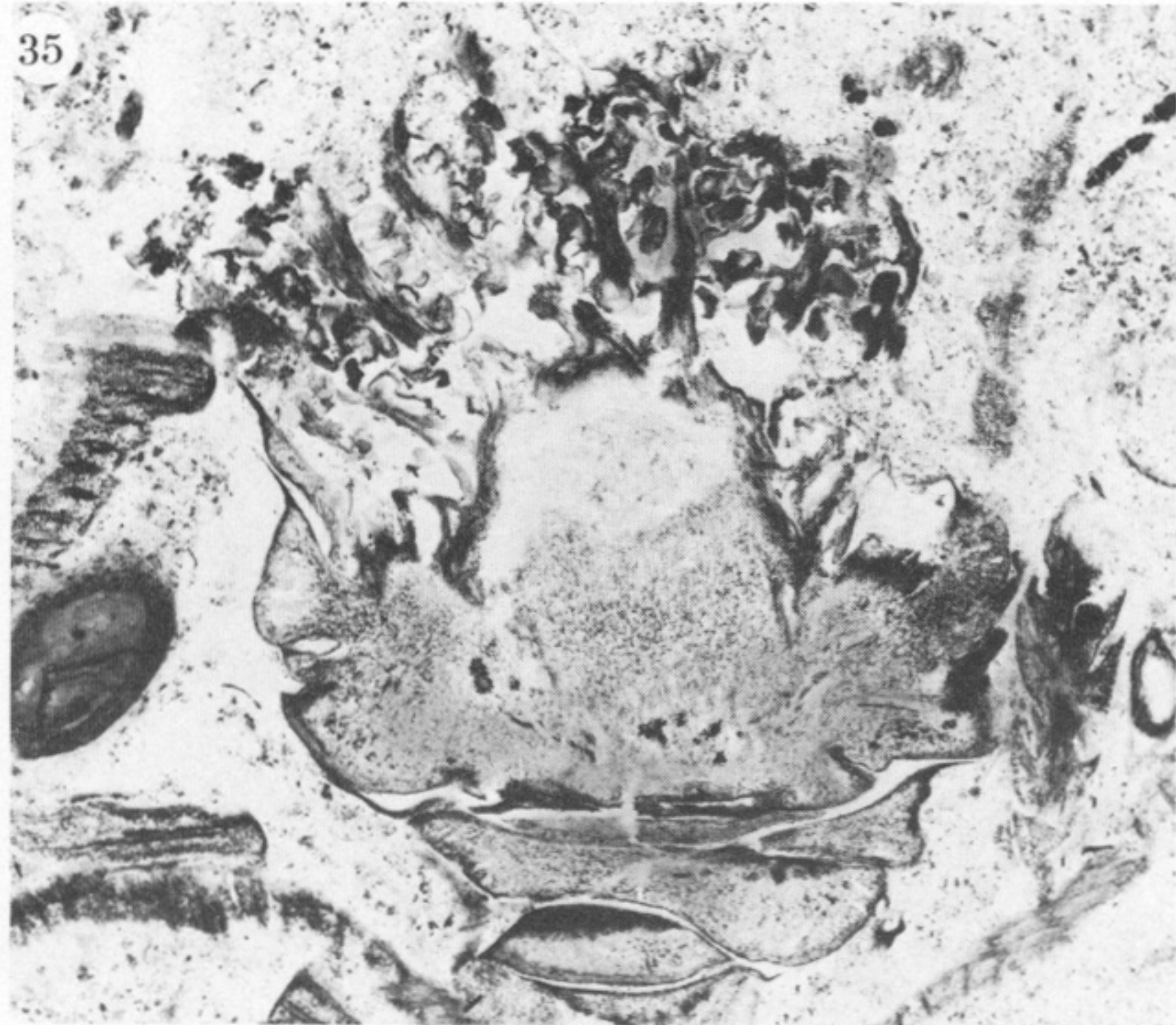
FIGURES 10-16. For description see opposite.





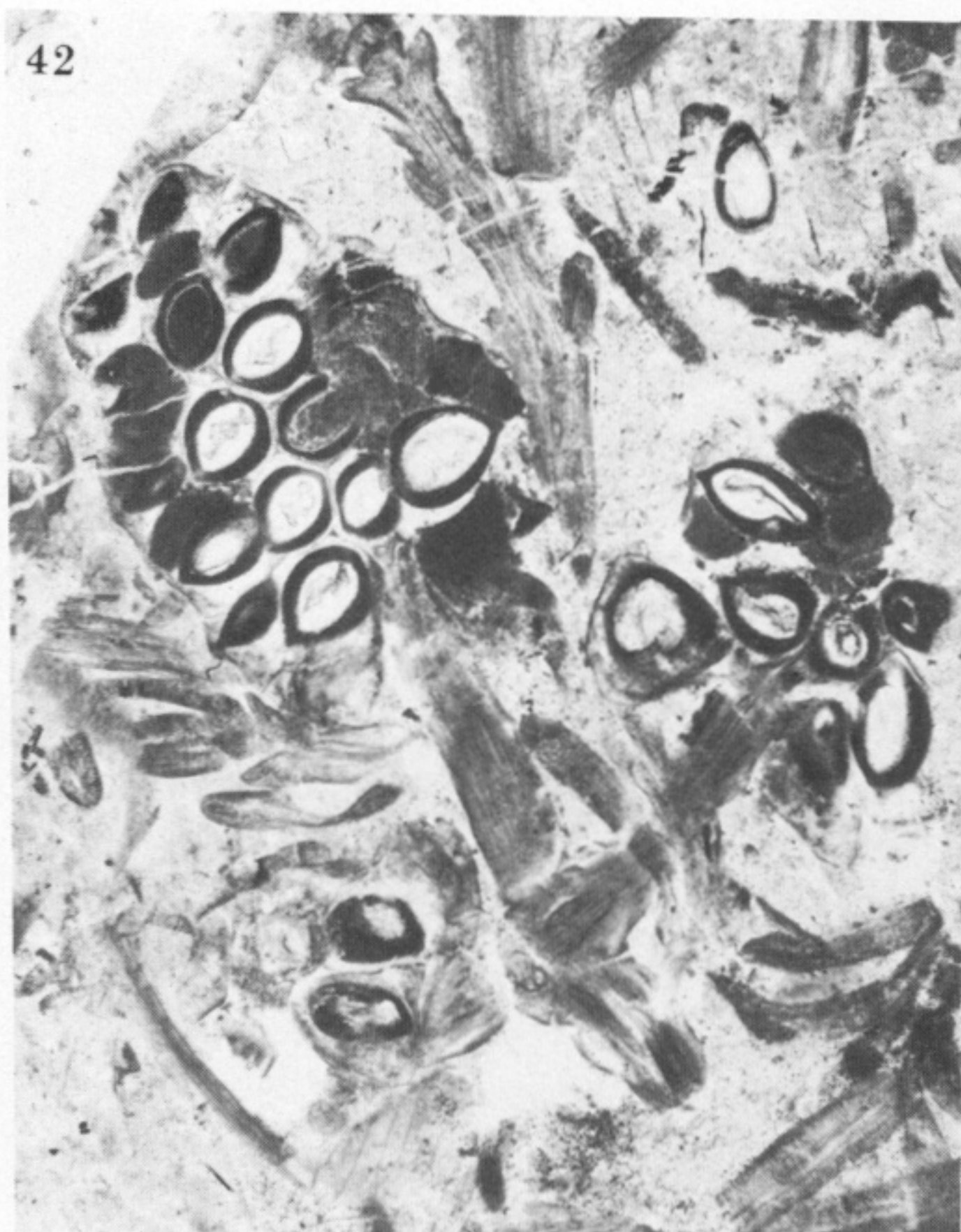
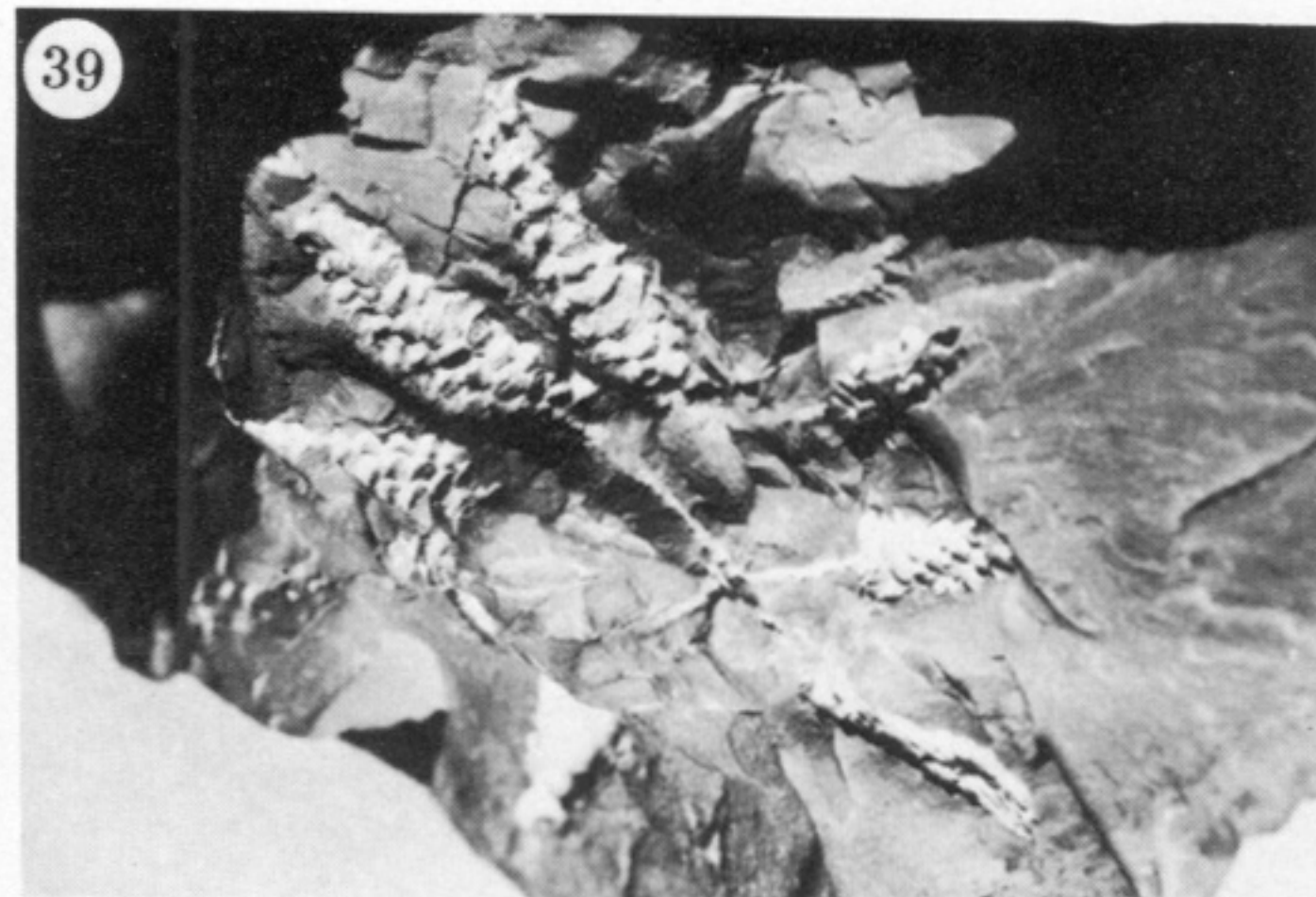
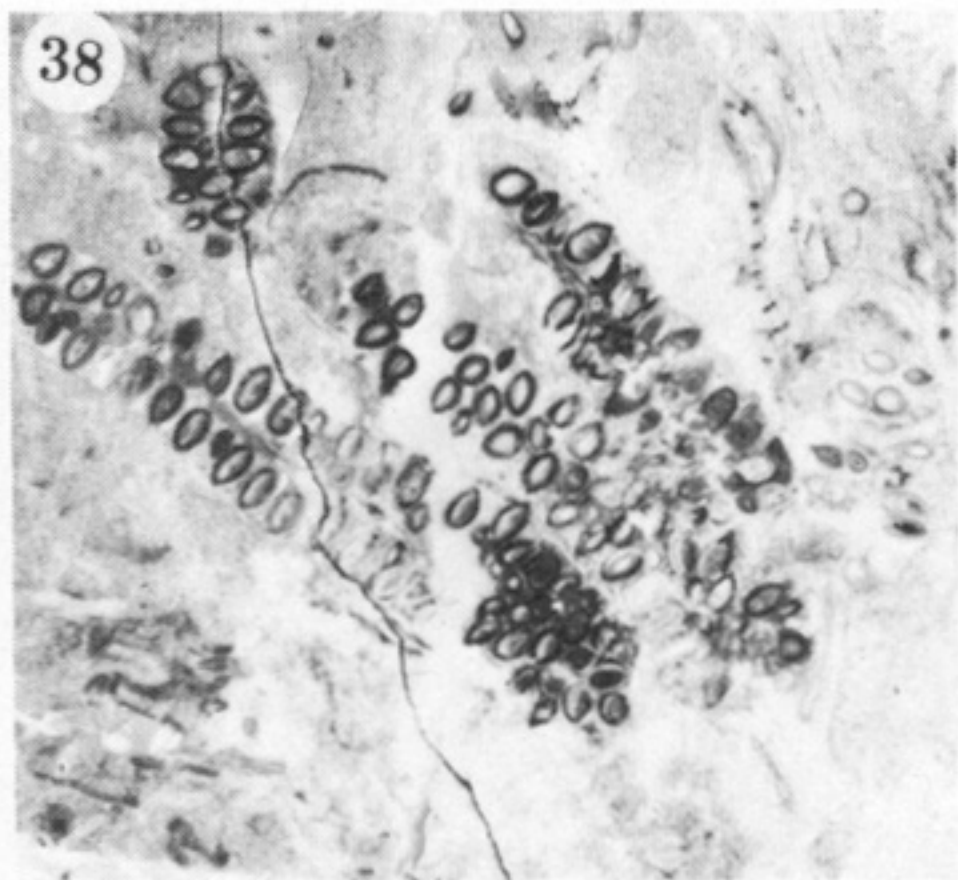
FIGURES 17-26. For description see page 104.





FIGURES 29-36. For description see page 105.





FIGURES 37-43. For description see opposite.