ON THE STRUCTURE AND AFFINITIES OF *CYCLANTHODENDRON SAHNII* (RODE) SAHNI & SURANGE FROM THE DECCAN INTERTRAPPEAN SERIES*

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INTRODUCTION

IN 1929-30 Rode discovered at Mohgaon Kalan a silicified stem about 17 cm. long and 5 cm. thick with sheathing leaf bases, which he described (1933) as a new species of *Palmoxylon* (*P. Sahnii* Rode). The peculiar form and structure of the fibro-vascular bundles led him to regard this as the axis of a palm inflorescence. Later in 1941 one of us found at the same locality two large clumps of petrified stems of the same species. Each clump was springing from a basal mass of roots. The discovery of this new material revealed an interesting mode of growth and showed that Rode's specimen was not an inflorescence axis but a vegetative stem. Though the root anatomy is palm-like, the clumped habit is not paralleled in any member of this family at present known to the authors. On the other hand, it was thought to be somewhat like that of the related South American family, Cyclanthaceae. We, therefore, published preliminary notes on the plant under a new name *Cyclanthodendron Sahnii* (1943, 1944, 1948, 1950).

Of the family Cyclanthaceae we have hitherto no fossil record. The leaf impressions from the Eocene of Sézanne, which Saporta (1868) referred to a new genus *Ludoviopsis*, may equally probably belong to palms.

The material for the present work, which was collected in 1941, was further supplemented by excursions to Mohgaon Kalan in 1946 and 1950; *Cyclanthodendron* occurs there in abundance. For studying the anatomy thin ground sections were prepared from different stems. A clump was followed from the bottom to the top and also serial ground sections were taken from a stem 27 cm. long to follow the course of the vascular bundles. Peel sections were not successful on this material.

DESCRIPTION

ROOT

Adventitious roots are present in abundance in the rock in which the lower portions of the stems are preserved (TEXT-FIG. 1). They are compressed in all sort of shapes on account of the collapsible cortex and are intermingled with numerous tiny rootlets (FIG. 4). In some specimens roots are seen bursting out of the leaf-sheaths in vertical rows.

Only the lower part of the stem, which presumably remains underground, produces roots in profusion, while the upper part of the stem remains devoid of roots. The roots receive their vascular supply from the peripheral as well as some of the central bundles of the stem and cut across through the leaf-sheaths almost horizontally. The bigger roots measure from 2 to 4 mm. in diameter.

A root (FIG. 7) consists of a small central vascular cylinder and a wide cortex which is pierced by radiating air spaces. The epidermis could not be observed, but generally a thin black strip outlines the root (FIG. 8). Below this comes a zone, about 3 to 5 cells in thickness, of loosely arranged, big, round parenchymatous cells, which appear longer than broad in a longitudinal section. This is followed by a ring of small sclerenchymatous cells, about 2 to 3 cells in width. Abutting on to the inner side of the sclerenchymatous ring and on the outer side of the endodermis are arranged parenchymatous cells, about 2 to 3 cells in thickness. Between these layers of parenchymatous cells are stretched thin cellular partitions, separating the big air chambers,

* Although a joint work on this material was planned in 1943, it had, however, remained in preliminary stage until the sad demise of the senior author. The responsibility for the description and the views expressed here is, therefore, entirely mine. — K.R.S.

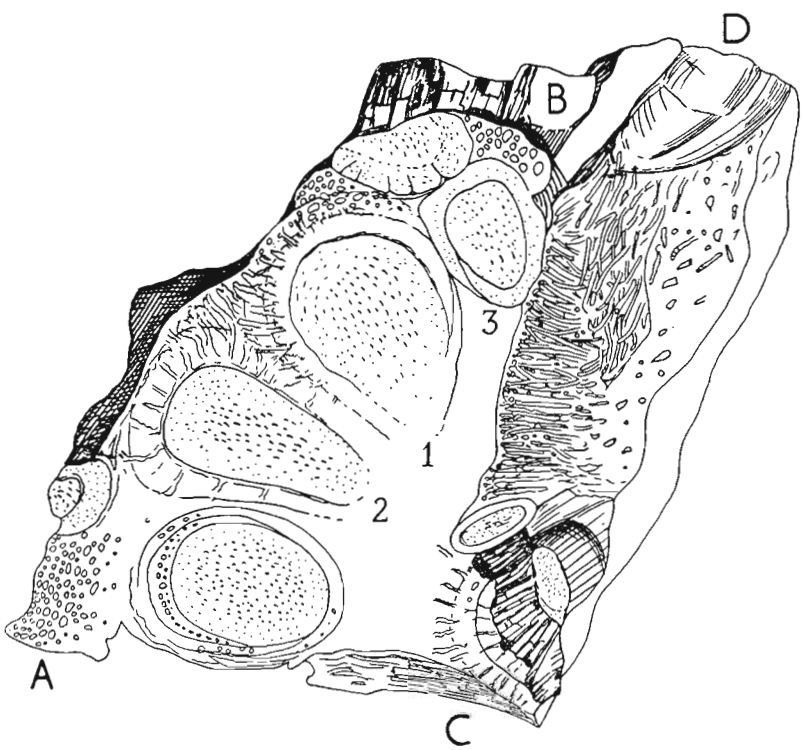
and which occupy the major portion of the cortex. The cellular portions are generally one cell in width, but at some place they may be from 1 to 4 or more cells in width. These cells are generally badly preserved. They are big, oblong to slightly elongated and are arranged end to end.

The endodermis can be distinguished clearly. The cells are small, rectangular and perhaps with no thickening. Pericycle could not be observed. The xylem and phloem plates are embedded in sclerenchymatous ground tissue which forms a solid pith. The sclerenchymatous cells are not very much thickened. The number of xylem and phloem plates vary in different roots. They are from 10 to 15 or sometimes more in number. A xylem plate consists of a few xylem vessels arranged in a vertical row, the last vessel towards the pith being always very big. These big vessels are very striking in a cross-section of a root. The phloem plate is small and is situated in between two xylem plates. The details of the phloem tissue could not be observed.

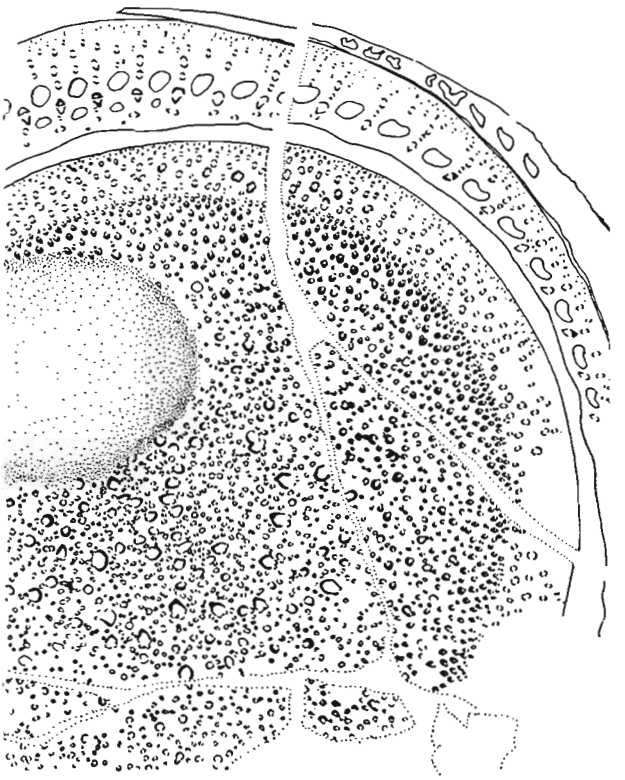
Roots generally branch profusely. In a cross-section of a root sometimes two or three rootlets are seen radiating out. The small rootlets are very simple in structure, consisting of a wide cortex and a small vascular supply in the centre. They very much resemble the rootlets of water plants.

Stem

The clumped habit of the plant is well illustrated by the cut surface of the main specimen (Fig. 1) shown in Text-fig. 1. Three slices, about 2 cm. thick, were cut from the main specimen exposing the surface A B C D and revealing six stems. Of these six stems number one showed branching. Still lower down stem 1 was seen to have first given out stem 2 and then stem 3.



Text-fig. 1 — Main specimen (Sahni coll., 1941). The surface A B C shows six stems with their leaf-sheaths, all cut transversely. The stem is embedded in a mass of adventitious roots, most of them also cut transversely; some roots are seen passing radially out from the stems through the leaf-sheaths. In the stem at the bottom left the leaf-sheaths show a row of air canals. The fractured surface B C D lies at an angle to A B C, and slopes to the right, it shows two small stems near the bottom of the figure; one of these is obliquely cut. At D there is a gutter-shaped depression formed by the leaf-sheath of the stem which is not preserved. Numerous adventitious roots are seen running more or less longitudinally. × *ca.* ½.



TEXT-FIG. 2 — A part of the stem and leaf-sheaths (cf. FIG. 2) magnified to show the arrangement of vascular bundles. In the leaf-sheath mark the row of air canals and vertical arrangement of the bundles in between the air canals. The stem shows a cavity (stippled) which runs through the stem. No trace of any fungus or any destructive agent has been found in the cavity which shows only the broken tissues of the stem. Mark the crowding of the big lobed bundles in the central region of the stem. × *ca.* 2½.

It appears, therefore, that stem 1 is rhizome-like and produced a pair of large buds (stems 2 and 3), which developed into new rhizomes growing right and left of the main stem. This branching habit bears a close resemblance to *Pandanus* (RENDLE, 1930, p. 191).

The underground part of the stem is tuberous and thick and bears roots. The stem 1 at the lower end measures 10 cm. in diameter, excluding one leaf-sheath which surrounds it. At a distance of 20 cm. it diminishes to 6 cm. in diameter and is surrounded by three leaf-sheaths. This is the erect part of the stem growing above the ground. What Rode described as *Palmoxylon Sahnii* and many other detached specimens found in abundance at Mohgaon Kalan are the overground stems of *Cyclanthodendron.*

Anatomy — In a cross-section the stem is seen consisting of a narrow cortex and a broad central zone of fibro-vascular bundles (FIGS. 2, 3; TEXT-FIG. 2). The stem is surrounded by a number of leaf-sheaths, the number depending on at what level the section is cut. The organization of the cortex is similar to that of a leaf-sheath, so that if it is traced upwards, it is seen transformed into two leaf-sheaths, situated opposite to each other. It, therefore, appears that the stem bears crowded and overlapping foliage leaves in two ranks. As the number of leaf-sheaths increases, the girth of the stem decreases rapidly.

Since the cortical portion of the stem is just the developing leaf-sheath, its structure depends on what level of the leaf-sheath the section represents. The epidermal cells could not be observed clearly (FIG. 9).

Just beneath the epidermis are situated small, round, oval or slightly elongated fibrous plates, 1 to 4 cells apart. These are followed by two more rows of bigger, elongated fibrous plates, arranged alternately to one another. Some of the fibrous plates may possess a single xylem vessel and perhaps a little of phloem. In the middle of the cortex some irregular cavities (FIG. 8; TEXT-FIG. 2) are seen which develop into air canals in the leaf-sheath. The ground tissue consists of loosely held parenchymatous cells.

The vascular bundles are fairly spaced apart from one another. The bigger bundles are situated in the middle, whereas the smaller bundles are placed in the outer as well as the inner part of the cortex.

A vascular bundle (FIG. 5) consists of a row of xylem vessels, phloem and two massive sclerenchymatous sheaths, the dorsal and the ventral. In a smaller bundle one metaxylem vessel is comparatively very big and the ventral sclerenchymatous sheath is larger than the dorsal. In bigger bundles both the sheaths are equally well developed and there are 2 to 3 large xylem vessels. The two sheaths do not touch each other, but are separated by parenchymatous cells of the ground tissue. Also most of the outermost cells of the sheaths contain a black deposit. These are the stegmata. Sometimes two bundles may fuse by their sides (FIG. 2).

The *central vascular zone* is demarcated from the cortex by the crowding of the small bundles at the margin (FIGS. 2, 9; TEXT-FIG. 2). This crowding is well marked in the marginal region to the extent of about four to five bundles deep. This is the dermal region. These bundles have their long axes parallel to the radial plane and are so arranged that roughly each bundle in the outer row alternates with the bundles in the next row. The outermost bundles are the smallest and the size increases inwards. The bundles are placed from about 3 to 5 cells apart.

The subdermal region is marked by the presence of small and large bundles mixed together (TEXT-FIG. 2). All sizes between the smallest and the largest bundles are met with here. The orientation of the bundles is varied, some are parallel to the radial plane, but others are deviated to the right or left.

In the central region are present the large, lobed bundles and a number of smaller bundles. The bundles also appear to be more crowded here than in the subdermal region. The orientation of the largest bundles is generally parallel to the radial plane, while smaller bundles are irregularly orientated.

A vascular bundle (FIG. 16) in the dermal region is more long than broad and consists of xylem, phloem and two sclerenchymatous sheaths. The ventral sheath which surrounds the xylem is sickle-shaped and consists of thick sclerenchymatous cells with small lumen. The dorsal sheath is a comparatively small crescentic patch of sclerenchymatous cells which surrounds the phloem. The two sheaths are separated from each other by a few parenchymatous cells. But in some of the smaller outermost bundles the two sheaths join together and give an oval outline to the bundle. The xylem consists of one to a few vessels, of which one is the largest and the rest are arranged on either side of it, sometimes assuming a crescentic form. The phloem is not preserved.

In the subdermal region some of the large bundles assume more or less a round shape (FIG. 14). The xylem vessels are arranged in a semicircular manner with the largest vessel in the middle and the xylem ring almost half surrounding the phloem. The dorsal sheath is poorly developed and consists of a small patch on the outer side of the phloem. The ventral sheath is very well developed and it completely surrounds the xylem. Some of these bundles are observed to branch from one side by giving out one or two xylem vessels and a little phloem surrounded by two small sheaths.

The third type of bundle found in the subdermal as well as in the central region is the largest and lobed (FIGS. 11-13). It gives out branches right and left and its lobed appearance in a cross-section is due to the fact that its two branches (small bundles) are seen attached on its either side (FIG. 12). Sometimes three small bundles are seen attached to it (FIG. 11), which is due to the fact that before one small bundle is detached, another is produced by the parent bundle.

The ventral sheath of the bundle is again crescentic and slightly drawn out like a beak in the middle part (FIGS. 11-13). The sclerenchymatous cells are not very much thickened. The xylem vessels are loosely arranged in a semicircular manner, with small parenchymatous cells intervening between the vessels. The protoxylem

vessels, which show spiral thickening, are embedded deep into the ventral sheath with small radiating parenchymatous cells arranged round it, and this gives the protoxylem a characteristic appearance. The phloem is again not well preserved. It is surrounded by a small patch of sclerenchymatous cells.

When this bundle branches, a few xylem vessels with a little of phloem and a part of ventral and dorsal sheaths are cut off from one end of the arc. After it is detached, it runs straight upwards near the parent bundle for at least some distance.

One stem was traced through 27 cm. to observe the course of lobed bundles. A section in the lower part of the stem (FIG. 2) differs to a certain extent from the one in the upper part (FIG. 3; cf. RODE, 1933, TEXT-FIGS. 1-3). In the lower part of the stem a number of large lobed bundles (with 2 to 3 small bundles attached) are seen crowded in the centre, as if to form a central plexus (TEXT-FIG. 2). Such bundles are absent in the upper part of the stem. These lobed bundles give out branches rapidly and move themselves outwards in their upward course. They become comparatively smaller in size and arrange themselves more regularly on arcs. There is a gradation of size from the inner arc to the outer arc. The bundles on the outer arcs are smaller (FIG. 6) than those on the inner arcs (FIG. 13). These bundles perhaps supply the leaves. Also the number of attached bundles diminishes progressively from 3 to 2 and finally to 1. However, in the upper part of the stem the lobed bundles with 2 or 3 attached bundles are absent. Instead, fusiform bundles with only one attached bundle are present in the subdermal region as described by Rode (1933). It, therefore, appears that a lobed bundle, which looks like the one shown in Figs. 11 and 12 in the lower part of the stem, assumes another appearance as shown in Figs. 6 and 13 in the upper part.

This stem could not be traced downwards, so that we do not know how and where this central plexus of large lobed bundles originated. Their main function appears to be to produce small bundles which crowd the central vascular zone. Is it possible that after diminishing in size they themselves enter into the leaf-sheaths and leaves? The number of lobed bundles being limited, it follows that the plant must have produced a definite number of leaves and perhaps after producing terminal flowering shoot or inflorescence it died as is the case in *Musa*. In the absence of better and more material nothing definite can be said at present.

In a cross-section ground tissue consists of round parenchymatous cells which are loosely arranged and enclose air spaces (FIGS. 6, 9, 13). In a thick section these cells are seen overlapping one another, giving it a characteristic appearance. The cells are slightly elongated and arranged in a radiating manner round the bundles. But this arrangement does not become very conspicuous.

The vessels (FIG. 10) show multiseriate reticulate type of pitting with simple perforation in the end walls. Stegmata are present in abundance round the bundles. Protoxylem vessels are spirally thickened. No pittings are seen on the sclerenchymatous cells of the sheath.

LEAF-SHEATH

The stem is covered by overlapping leaf-sheaths, which rapidly increase in number towards the apex. In one specimen the whole girth is made up of encircling leaf-sheaths with the stem remaining in the centre like a small shaft. This condition is something like *Musa* where an inflorescence axis is surrounded by a number of leaf-sheaths.

In a cross-section of a leaf-sheath (FIG. 2; TEXT-FIG. 2) what strikes the eye at once is a row of air cavities arranged slightly towards the inner side. There are two rows of air cavities in the broad middle part of the leaf-sheath. In between the air cavities are arranged bigger vascular bundles in vertical rows.

Epidermis could not be observed clearly, but just below it a row of closely placed fibrous plates (FIG. 19) is present. These are arranged in 2 to 3 rows placed alternately to one another. A few small fibrous plates are also distributed here and there in the ground tissue. The fibrous plates are followed by rows of vascular bundles also arranged alternately. In between the air canals and in the middle part of the leaf-sheath 4 to 5 bigger vascular bundles are arranged in vertical rows.

The smaller bundles are similar to those described in the cortical region of the stem. The bigger bundles (FIG. 18), however, become more long than broad. The xylem vessels are arranged one below the other in 1 or 2 rows, with a patch of phloem just

outside the metaxylem. The dorsal and ventral sclerenchymatous sheaths are almost equally developed and are separated by a few parenchymatous cells. The bundles are lined by stegmata. The ground tissue consists of round thin-walled cells, many of which are filled with dark contents. It is a prominent character of the leaf-sheath.

Leaf

In one of the later excursions to Mohgaon Kalan a block (Fig. 16) of chert, about 4·5 × 6·5 cm. in size, containing petrified leaves was found. One leaf looked like a fan type of leaf, with elevation and depression on the surface, such as that of *Carludovica*. When a transverse section of the leaf was prepared, the internal structure was very similar to a leaf-sheath of *Cyclanthodendron*. We have, therefore, assigned this leaf to *Cyclanthodendron Sahnii*.

The specimen in Fig. 16 shows a very small part, most likely the lower part, of the leaf. Its surface is divided into furrows and crests which seem to diverge from one another towards the distal end (upper side in Fig. 16). Also furrows and crests tend to fade out towards the margin (right-hand side in the figure).

Fig. 20 shows a cross-section of the leaf cut at the lower end of the specimen. Unfortunately we have lost this specimen. Only one transverse section (Figs. 17, 20) and the photograph of the specimen (Fig. 16) have remained with us.

The lower epidermal cells are big, more elongated than broad, with angular inner sides and looking somewhat like prismatic cells of the palisade tissue. Many of these cells are filled with dark contents (Fig. 17). The epidermis is followed by big, somewhat oval cells of the hypodermis. The upper epidermal cells are quadrangular and slightly more broad than long. It is followed by 2 to 3 layers of big transversely elongated cells. Rest of the ground tissue consists of round cells as these in the leaf-sheath. Big air cavities are present in the furrows in only the broader part of the lamina. They are absent in the marginal region. Some of the cells in the ground tissue contain dark contents. Also some big, empty cells are present which may have contained deposits of crystals (raphide bundles).

The vascular bundles are arranged in a single row in the marginal region and more than one row in the broader part of the lamina. Fibrous plates are present, perhaps one in each crest, just below the hypodermis on the lower side of the leaf. They are absent on the upper side. In the broader part of the lamina in each crest two big vascular bundles are arranged one below the other, while in each furrow there is only one big vascular bundle, in addition to one air cavity. Towards the margin there is only a single bundle in the crests as well as the furrows. Small bundles with one or two xylem vessels and two well-developed sheaths are also present on the lower side of the lamina. The structure of the bundle (Fig. 17) is similar to that described in the leaf-sheath.

COMPARISON AND DISCUSSION

From the above description it appears that although this fossil resembles to some extent to palms, it is nevertheless unlike any of the palms known to us.

The other allied family to Palmae to which *Cyclanthodendron* shows some resemblance is Cyclanthaceae.

The structure of the root of *Cyclanthodendron* can be compared with *Cyclanthus* as well as *Carludovica*. The cortical portion of the fossil root is similar to that of *Cyclanthus* (cf. Surange, 1950, Pl. 13, Fig. 1) and the central vascular cylinder is as simple as that of *Carludovica palmata* (cf. Surange, 1950, Pl. 17, Fig. 2). However, air cavities in the fossil root is much more developed than those in the living roots of the Cyclanthaceae.

As regards the stem, the plants of the living Cyclanthaceae are herbaceous with rhizomes and sheathing leaf-bases. In *Cyclanthodendron* the condition is similar, but here the apex of the rhizome grows into an aerial stem which does not bear roots. The vascular bundles of the stem in both are collateral, some concentric with xylem vessels arranged in a crescentic manner and some are compound. It is, in fact, the compound nature of the bundle which is an important feature of the anatomy of the Cyclanthaceae and *Cyclanthodendron* and it is mainly for this fact that this fossil plant was taken out from *Palmoxylon* and referred to the family Cyclanthaceae.

The leaf-sheaths of *Cyclanthodendron* and *Cyclanthus* are again quite similar in appearance (cf. Surange, 1950, Pl. 14, Fig. 6), with a row of big air canals and the bundles arranged in vertical rows between them.

We do not yet know sufficiently about the leaf of *Cyclanthodendron*. But from a part of the leaf which we have found it seems that the fossil leaf had crests and furrows, perhaps, not developed to that extent as in *Carludovica*. The leaf appears to be of the fan type.

In spite of these resemblances in broad outline, there are, however, differences in detail. The fossil root is of a generalized type and cannot be compared tissue by tissue with the roots of any single genus of the Cyclanthaceae. Also as regards the stem since *Cyclanthodendron* stem, unlike that in the living Cyclanthaceae, continues to grow above the ground, differences appear in its general organization. In the living Cyclanthaceae the vascular bundle of the stem either possesses a ventral or a dorsal sheath or no sheath at all, whereas in *Cyclanthodendron* the vascular bundle always possesses both the dorsal and ventral sheaths. Again a compound bundle of the Cyclanthaceae and a lobed bundle of *Cyclanthodendron* differ in the fact that in the Cyclanthaceae a fixed number of distinctly separate bundles join together to form a compound bundle. In *Cyclanthodendron*, however, a big bundle gives out branches to its right and left and these remain attached to the parent bundle for some distance and make the big bundle look like a compound bundle. In *Cyclanthodendron*, therefore, the attached bundles are the branches of the same bundle and not distinctly separate bundles as in the Cyclanthaceae. We have, therefore, called these bundles as lobed bundles.

Cyclanthodendron is, however, still incompletely known. Its flower, fruit, peduncle, petiole and, to a great extent, its leaf are yet to be discovered. It will, therefore, be rather hasty to draw any definite conclusion as regards its affinities only on the anatomical characters of the known parts. It can only be said that *Cyclanthodendron* does not resemble with any single genus of the Cyclanthaceae. It shares to a certain extent the characters of *Cylanthus* and *Carludovica*, the two most important genera and representatives of the two sub-families Cyclantheae and Carludoviceae. But it may be too much to say that *Cyclanthodendron* represents a synthetic genus from which the two sub-families have derived their characters. At the same time the fact that *Cyclanthodendron* may show affinities with certain other monocot families should not be ruled out.

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EXPLANATION OF PLATES

PLATE 1

1. The main specimen which was cut into two parts and showed the stems as shown in Figs. 2 and 3.

2. A cross-section at the lower end of the stem. Mark the leaf-sheath with air canals and roots. The stem itself shows a rotten cavity on the top left side. Big lobed bundles crowd in the centre (*see* TEXT-FIG. 2). Nat. size.

3. A cross-section of the same stem cut at the upper end. Big lobed bundles have disappeared from the centre. Nat. size.

4. A thin section showing a number of roots crowded together with small rootlets crushed between them. × 3.
5. A vascular bundle from the cortical part of the stem. × 60.
6. A small, lobed vascular bundle from the subdermal region of the stem with one bundle attached. × 60.

PLATE 2

7. A root in cross-section. × 20.
8. A part of the same root magnified to show the various tissues in the root. × 52.
9. Cortex, dermal and subdermal region of the stem showing the vascular bundles and the ground tissue. × 13.
10. A vascular bundle and the ground tissue in longitudinal section showing stegmata and the thickenings in the xylem vessels. × 53.

PLATE 3

11. A lobed vascular bundle with three small bundles attached to it. × 50.
12. A lobed vascular bundle with two small bundles attached to it. × 60.
13. A lobed bundle with one small bundle attached to it. × 57.
14. A concentric bundle. × 60.
15. A bundle from the dermal region. × 60.

PLATE 4

16. A block of chert showing a part of the petrified leaf of *Cyclanthodendron*. Nat. size.
17. A cross-section through the leaf magnified to show the upper and lower epidermis, air cavity, ground tissue and the vascular bundles. × 44.
18. A vascular bundle from the leaf-sheath. × 70.
19. A leaf-sheath magnified showing rows of air canals and the arrangement of bundles. × 7.
20. A cross-section through the leaf. × 4.

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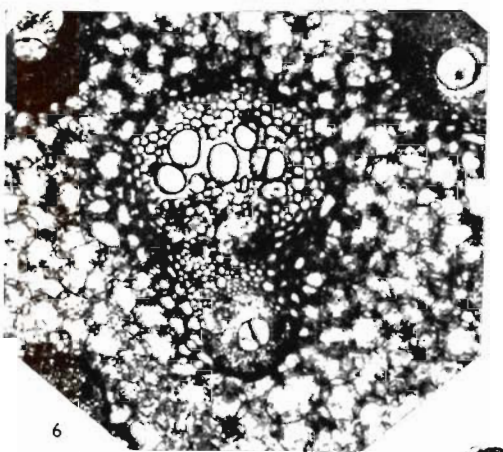

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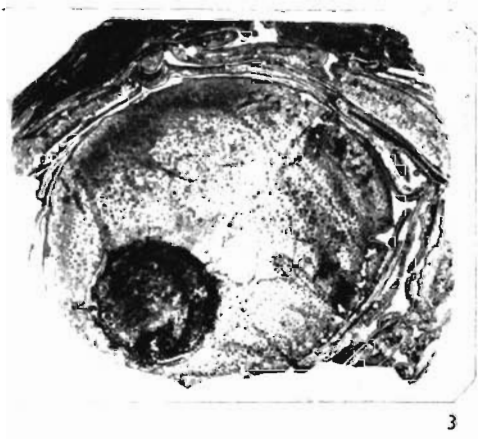

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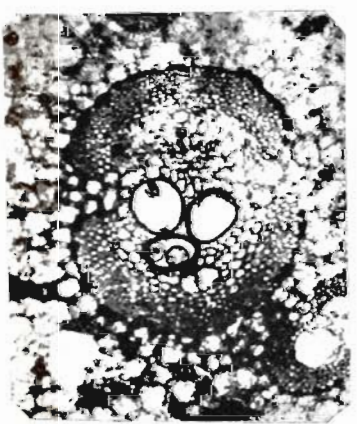

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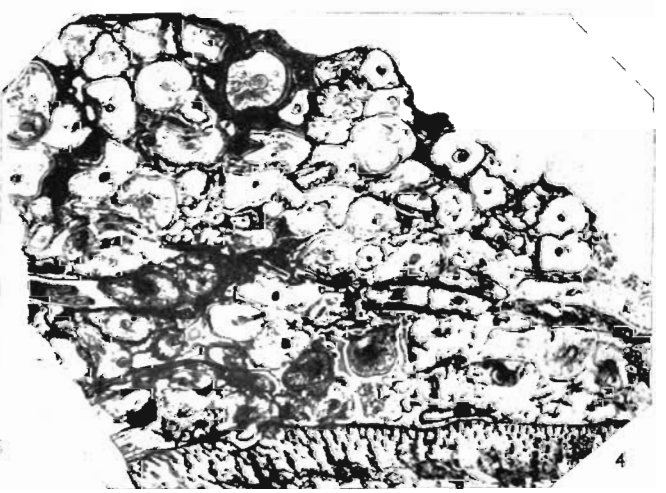

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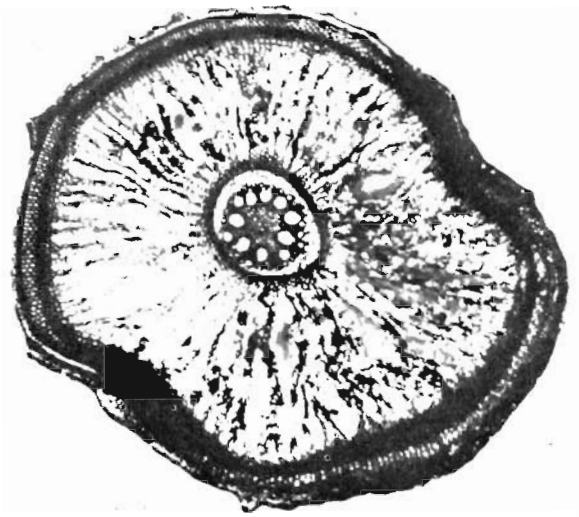

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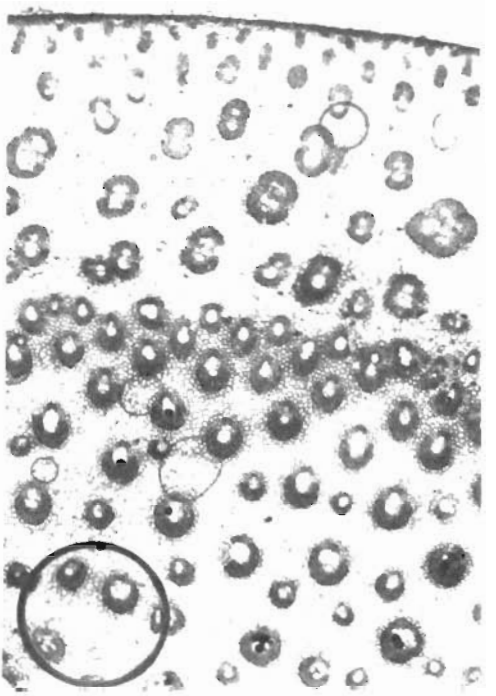

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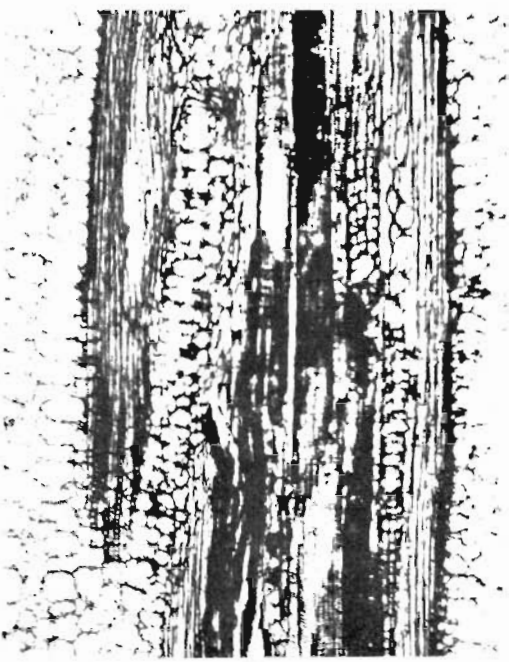

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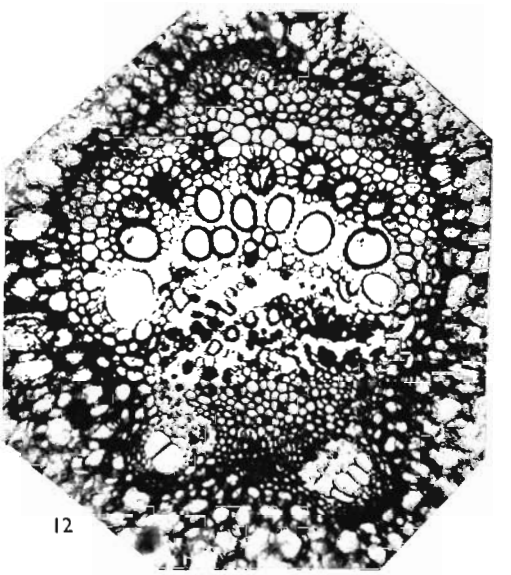

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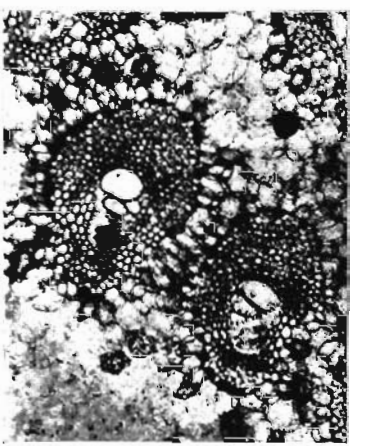

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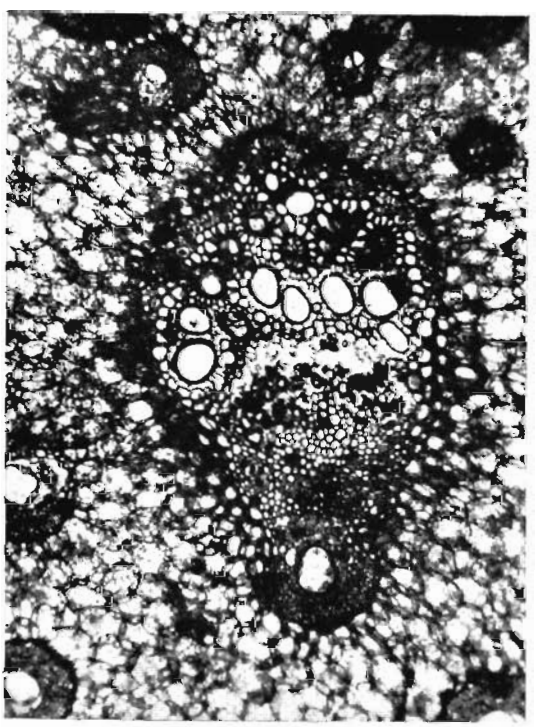

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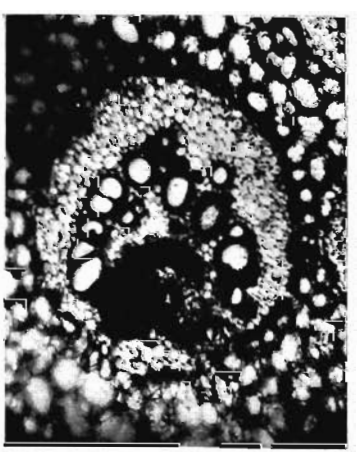

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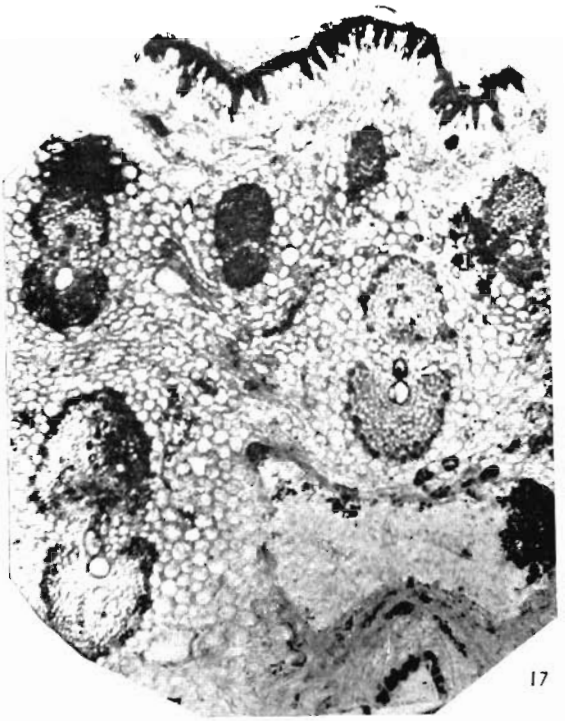

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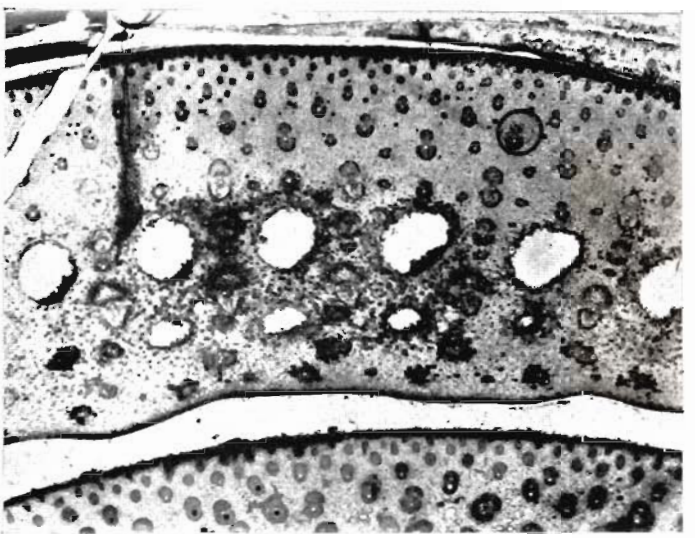

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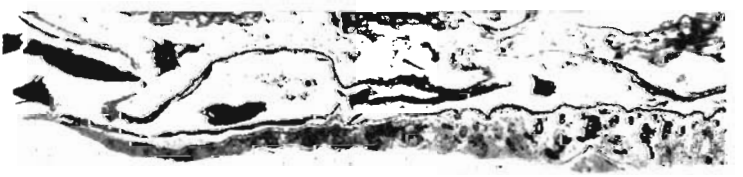

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