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SABALOCAULON INTERTRAPPEUM GEN. ET SP. NOV. FROM THE DECCAN INTERTRAPPEAN BEDS OF MADHYA PRADESH, INDIA

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ABSTRACT

Petrified fossil axis belonging to sabaloid palms shows distinct epidermis, hypodermis and central region and is characterized by prominent lacunar ground tissue. Affinities with the known fossils of *Palmocaulon* and with the living members of Palmae have also been discussed in detail. Anatomical details suggest that it shows close affinity with the basal part of the leaf axis of *Sabal* of the family Palmae.

Key-words — Anatomy, *Sabalocaulon*, Petrified axis, Palmae, Eocene, Deccan Intertrappean Series (India).

सारांश

भारत में मध्य प्रदेश के दक्खन अन्तर्ट्रेपी संस्तरों से सेबॅलोकॉलॉन इन्टरट्रेपियम् नव प्रजाति व नव जाति –
भीमशंकर त्रिवेदी एवं छेदालाल वर्मा

सुस्पष्ट रिक्तिका भरण ऊतक से लक्षणित सेबॅलोइड ताड़ का अश्मीभूत अक्ष स्पष्ट बाह्यत्वचा, अधस्त्वचा एवं केन्द्रीय क्षेत्र प्रदर्शित करता है। पाल्मोकोलॉन से ज्ञात काष्ठाश्मों से तथा पाल्मी कुल के वर्तमान सदस्यों से इसकी सजातीयता का विस्तृत विवेचन किया गया है। शारीरीय विवरण से प्रदर्शित होता है कि पाल्मी कुल के सेबॅल के पर्ण-अक्ष के आधारीय भाग से इसकी घनिष्ठ सजातीयता है।

INTRODUCTION

SO FAR, only a few palm petioles are known from the Indian Tertiary deposits. Palm petioles, based on incomplete specimens, have been described by Deshpande (1960), Menon (1964, 1965), Kulkarni and Patil (1977) and a palm peduncle has also been described by Biradar and Bonde (1979). In the present paper a leaf axis, complete in cross section, is described. It shows well-preserved structural details from centre to periphery including both abaxial and adaxial epidermis.

The material was collected from the Deccan Intertrappean beds of Madhya Pradesh exposed at Parapani, a village in Mandla District. So far, only two palm woods, viz., *Palmoxylon parapaniensis* from Parapani and *P. mandlaensis* from Mohgaon have been described from this district by Lakhanpal *et al.* (1979).

OBSERVATIONS

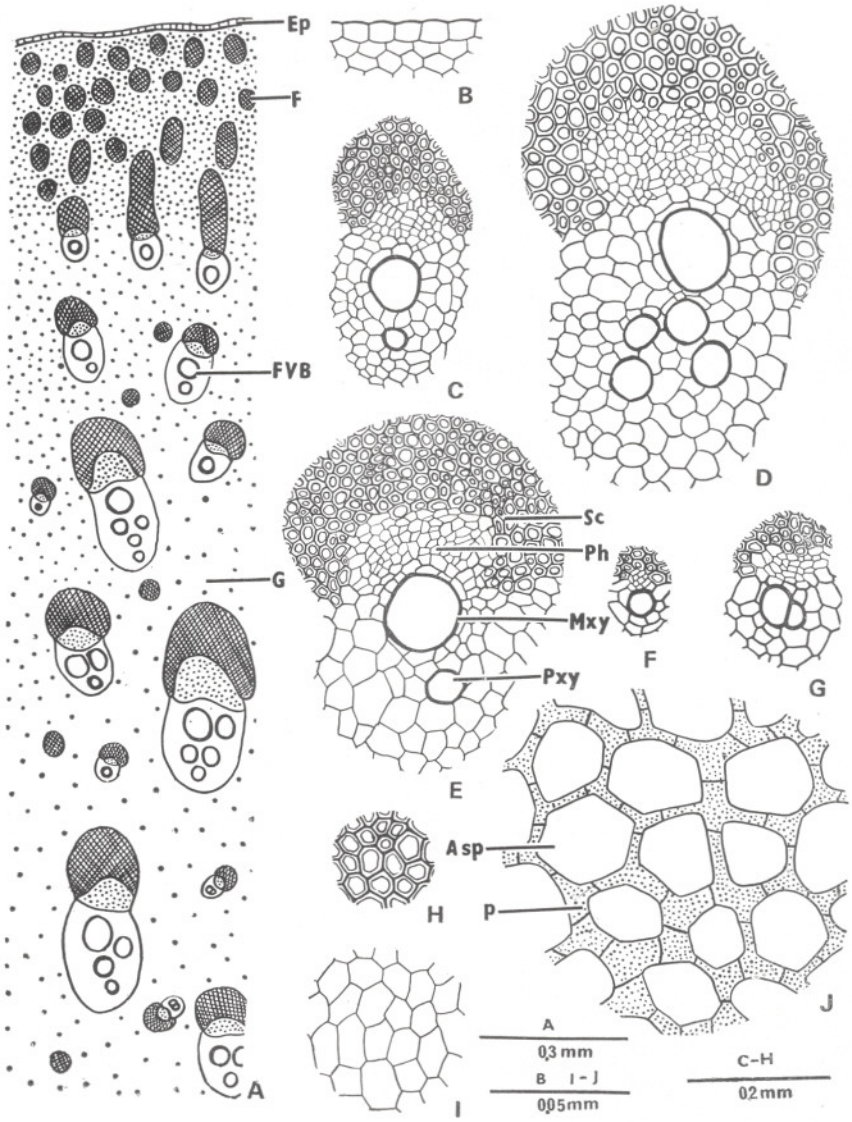
The specimen, about 15 cm long, was embedded in a chert block. The shape of the axis varies somewhat from base to apex (Text-fig. 2C-F). The basal portion is usually flat, broad in the middle, gradually thining towards the margins; the top portion of the axis is concave, broad in the middle with tapering margins.

Preservation of the axis is excellent, hence staining was not needed. The specimen in sectional view shows distinct epidermis, peripheral as well as central regions (Pl. 1, fig. 1). The axis is divisible into two parts: outer—peripheral and inner—central (Text-fig. 1A).

Peripheral Zone — This zone consists of epidermis and hypodermis, including fibrous and fibrovascular bundles.

Epidermis — It is very well preserved at places (Pl. 1, fig. 3; Text-fig. 1B), single layered with more or less uniform cells. Cells are small, more or less cubical. A uniform cuticle is also clearly seen over the epidermal cells (Text-fig. 2A). Trichomes have not been observed. Despite good preservation of epidermal cells, stomata could not be observed.

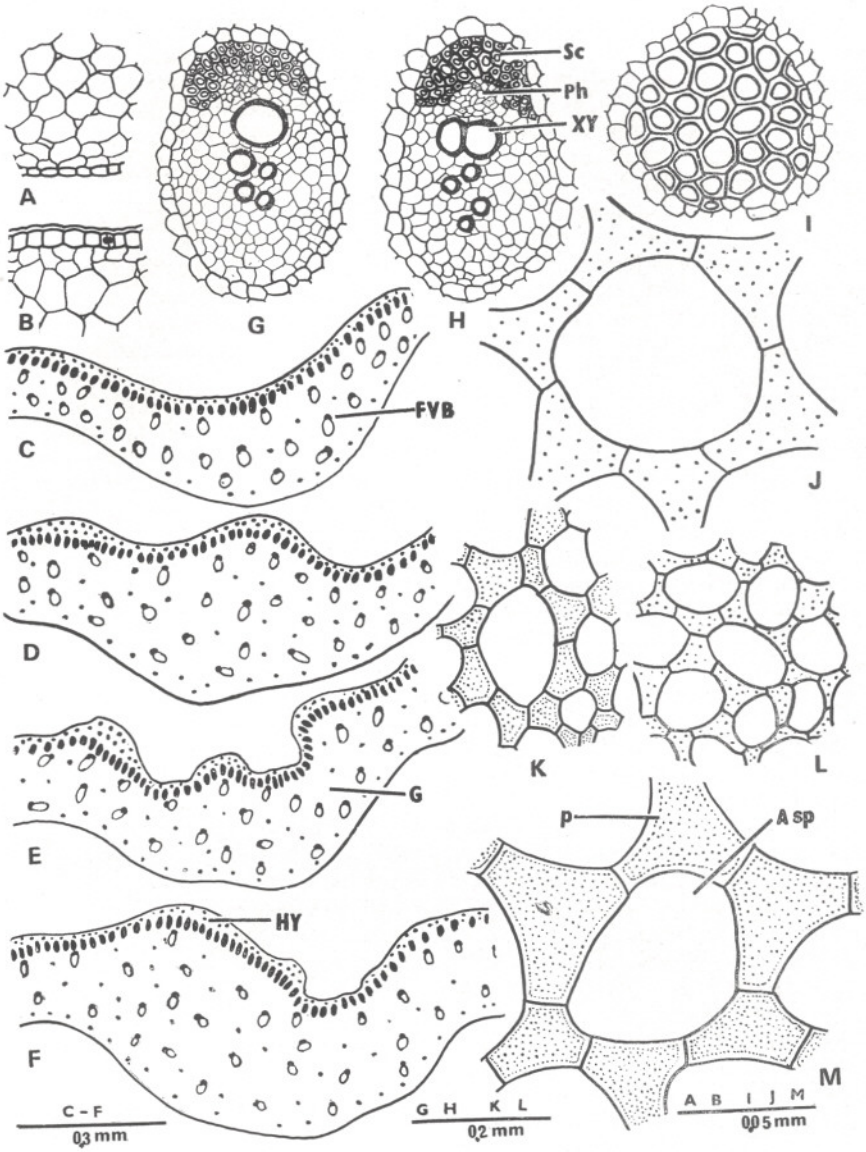
Hypodermis — Two or three layered parenchymatous cells are present just below



TEXT-FIG. 1 — **A.** A part of the fossil axis in cross section showing epidermis, hypodermis, fibrous and fibrovascular bundles. **B.** Epidermal cells and a few hypodermal cells. **C-E.** An enlarged fibrovascular bundles showing dorsal sclerenchyma, vessels and phloem. **F, G.** Diminutive vascular bundles of the central region showing one or two xylem vessels. **H.** Fibrous bundle enlarged to show the fibre cells. **I.** A few parenchymatous cells just below the hypodermis. **J.** Cells of the ground tissue of the peripheral region — lacunae small with narrow cells. (Abbreviations — **Asp,** air spaces; **Ep,** epidermis; **F,** fibrous bundles; **FVB,** fibrovascular bundles; **G,** ground tissue; **Hy,** hypodermis; **Mxy,** metaxylem; **p,** parenchyma cells; **Ph,** phloem; **Pxy,** protoxylem; **Xy,** xylem).

the epidermis representing a hypodermal region. The cells are polygonal without air spaces (Pl. 2, fig. 3; Text-fig. 1B).

Fibrous bundles are small, numerous, about 60 to 80 μm in diameter, arranged alternately in two or three rows (Text-fig. 1A) and made up of 8 to 20 fibre cells. These bundles are surrounded by small parenchymatous cells. Fibrovascular bundles are large, elongated and are arranged in one row. These bundles at places are oval in shape (Text-fig. 1C) and have a large amount



TEXT-FIG. 2 — **A.** Epidermal cells and parenchymatous cells towards the abaxial side of the axis. **B.** Epidermis showing stomata and a few parenchymatous cells of *Sabal adansonii*. **C-F.** Fossil axis — showing shape from base to top and arrangement of fibrous and fibrovascular bundles. **G, H.** Vascular bundles of *Sabal adansonii* leaf axis showing sclerenchyma, phloem and xylem vessels. **I.** An enlarged fibrous bundle of *Sabal adansonii* showing fibre cells. **J, K.** Ground tissue of the fossil axis showing ' Y '-shaped parenchyma cells and lacunae. **L, M.** Ground tissue of leaf axis of *Sabal adansonii* showing ' Y '-shaped parenchyma cells enclosing large spaces. (Abbreviations— **Asp,** air spaces; **Ep,** epidermis; **F,** fibrous bundles; **FVB,** fibrovascular bundles; **G,** ground tissue; **Hy,** hypodermis; **Mxy,** metaxylem; **p,** parenchyma cells; **Ph,** phloem; **Pxy,** prtoxylem; **XY,** xylem).

of sclerenchyma, a few phloem cells and usually a single large xylem vessel. They are also surrounded by parenchymatous cells. The fibrovascular ratio is 7/1 to 6/1.

Central Zone—This zone is well-preserved and fibrovascular bundles are irregularly distributed in the ground tissue (Pl. 2, fig. 4). The bundles are oriented in various

directions. Three distinct types of bundles have been observed in this zone.

(i) *Fibrovascular Bundles* — Bundles are large, oval or elongated, 0·30×0·20 to 0·35 × 0·15 mm in size. Frequency of these bundles is 40-50/cm². Little variation has been observed in frequency of these bundles from base to apex of the axis. Bundles have small patch of dorsal sclerenchyma, usually one or sometimes two metaxylem and 1 or 2 protoxylem vessels (Pl. 2, fig. 5; Text-fig. 2D, E). Phloem is in one mass and very well-preserved. Phloem cells are small, thin-walled and of variable shape (Pl. 2, figs 5, 6). F/v ratio is 1/4 to 1/5. Vascular bundles are surrounded by small parenchymatous cells.

(ii) *Diminutive Bundles* — These bundles are irregularly distributed throughout the ground tissue, usually small, 0·08×0·03 mm in diameter. Bundles have only a few sclerenchymatous cells on the dorsal side with one or two small xylem vessels (Text-fig. 1F, G). A few phloem cells can also be seen in these bundles.

(iii) *Leaf Trace Bundles* — These bundles are commonly present in this zone and their frequency is higher than the fibrovascular bundles. Bundles are elongated with usually many xylem vessels (Text-fig. 1D). Phloem is in a single mass and its cells are well-preserved. These bundles are characterized by their protruded tongue-like numerous small vessels.

Fibrous Bundles — Fibrous bundles are scattered throughout the central part of axis in the ground tissue. They are small rounded, about 50 to 80 μm in diameter. These bundles have 8 to 20 fibre cells (Text-fig. 1H). Stegmata, arranged in rows, have been observed in these bundles. The bundles are surrounded by parenchymatous cells.

Ground Tissue — Ground tissue is lacunar throughout the axis. Towards the ventral region of the axis the cells are smaller with small intercellular spaces (Text-fig. 1I). At the peripheral region, below the hypodermis, parenchymatous cells are loosely arranged with large intercellular spaces (Text-fig. 1J). Parenchymatous cells in the fossil axis are 'Y'-shaped. About 4 to 6 individual cells unite together to form oval or circular lacunae (Text-fig. 2L, M). These lacunae are smaller towards the peripheral region but gradually increase in size towards the central region.

In longitudinal sections, metaxylem vessels show multiseriate scalariform thickenings whereas the protoxylem vessels have annular or spiral thickenings (Pl. 2, figs 7, 8).

DISCUSSION AND COMPARISON

Palm axes, so far described from the Tertiary deposits, are placed in the form genus *Palmocaulon* (Menon, 1964). Five known species of *Palmocaulon* are: *P. mohgaoense* Deshpande (1960), *P. raoi* Menon (1964), *P. mahabalei* Menon (1965), *P. monodii* Boureau & Prakash (1968) and *P. costapalmatum* Kulkarni & Patil (1977). Except for *P. monodii* which comes from Eocene of Senegal, all others are from the Deccan Intertrappean Series of India. A palm peduncle has also been described under the name *Palmostroboxylon indicum* (Biradar & Bonde, 1979).

Species of *Palmocaulon* described so far are either incomplete or poorly preserved. Two species of *Palmocaulon*, viz., *P. raoi* and *P. mahabalei* Menon (1964, 1965) are probably the parts of *Cyclanthodendron*. The vascular bundles of the above two species described by Menon (1964, 1965) resemble those of *Cyclanthodendron* described in detail by Trivedi and Verma (1979). Menon (1964, 1965) herself states that bundles are with well-developed ventral sclerenchyma in comparison to dorsal ones, sometimes the two unite to form a continuous sclerenchymatous sheath; type of vascular bundles and the arrangement of xylem in arcs — such bundles according to her are unique and are not reported in any palm stem. This statement is correct. The bundles like those by Menon are, however, characteristic of *Cyclanthodendron*. It is quite likely that *Palmocaulon* described by her might appropriately be a part of *Cyclanthodendron*.

The only described fossil petiole is *Palmocaulon costapalmatum* (Kulkarni & Patil, 1977), but the specimen is incomplete. The present fossil axis has also been compared with *Palmostroboxylon* (Biradar & Bonde, 1979) but differs from the peduncle in the absence of fusion bundles.

AFFINITIES WITH MODERN TAXA

Important characters exhibited by the fossil axis are (i) it has peripheral and central

zone with epidermis and hypodermis, (ii) fibrovascular bundles are irregularly distributed in the ground tissue, (iii) phloem is undivided, (iv) dorsal sclerenchyma is in large amount in peripheral bundles, but a small patch in central bundles, (v) metaxylem vessels are usually 1 or 2 with generally 2 protoxylem vessels, (vi) leaf trace bundles and fibrous bundles are numerous, and (vii) ground tissue is highly lacunar, 'Y'-shaped parenchyma cells enclose large lacunae.

The typical structure of fibrovascular bundles of the fossil axis undoubtedly suggests its affinity with palms. Anatomically it could be compared to a young stem, peduncle or leaf axis of a palm. If this axis were a palm stem a clear demarcation into cortical, dermal, subdermal and central zones should be expected. This, however, is not so. In palm peduncles, many fusion bundles occur and their frequency increases from base to apex; since no fusion bundles occur here, the possibility of its being a peduncle is also ruled out. On the other hand, the shape of the fossil axis as seen in transverse section, arrangement of vascular bundles and presence of epidermis and hypodermis clearly indicate that the fossil is a leaf axis of a palm.

Leaf axis of living palms is characterized by (Tomlinson, 1961), viz. (i) differentiation into peripheral and central regions including epidermis and hypodermis, (ii) lesser differentiation of the ground tissue, (iii) peripheral vascular bundles have greater amount of sclerenchyma, (iv) central vascular bundles have less amount of sclerenchyma; phloem is either undivided or divides into 2 or 3 patches, and (v) absence of fusion bundles.

In addition to the above characters the basal portion of the leaf axis is somewhat different and is characterised by (i) presence of large number of leaf trace bundles, (ii) peripheral bundles with massive sclerotic cells, (iii) large number of fibrous bundles in the ground tissue (in some palms), and (iv) the ground tissue sometimes undergoes transverse expansion or forms large lacunae (in a few palms).

The fossil has large number of leaf trace bundles and fibrous bundles and has characteristic ground tissue whose cells undergo late expansion, as seen in section, and form conspicuous lacunae. These characters, however, suggest that it represents the basal part of a leaf axis. Peripheral bundles are more or less homogeneous in living Borassoid and Sabaloid palms. The fossil also shows similar arrangement. Further, the vascular bundles of the central region of the leaf axis are scattered in the ground tissue of the Borassoid and Sabaloid palms (Tomlinson, 1961). Phloem is undivided in Caryotoid, Borassoid, some Sabaloid palms and *Nypa*. Thus homogeneous occurrence of peripheral vascular bundles, scattered nature of central vascular bundles and undivided phloem collectively point out that the fossil axis bears strong resemblance with the basal part of a Borassoid or Sabaloid palm axis.

Absence of compact ground tissue precludes the possibility of the fossil being the petiole of a Borassoid palm. Amongst Sabaloid palms the petiole of *Sabal* has large number of fibrous bundles, leaf trace bundles and highly lacunar ground tissue at the basal region (upper region has no fibrous bundles and the ground tissue is compact), these characters occur in the fossil axis also.

Petioles of *Sabal minor* Pers., *S. mexicana* Mart., *S. major*, *S. adansonii* Guerns., *S. blackburniana* Glazebr., *S. unbraculifera* Mart. and *S. palmelto* Lodd. have also been examined. Because of the presence of fibrous bundles (Text-figs 1H, 2I) in the central region and characteristic ground tissue, the fossil is closely comparable with *S. adansonii* axis. In both, the fossil axis as well as the living petiole, the parenchymatous cells are 'Y'-shaped enclosing large lacunae (Text-fig. 2J-M). Such characters have been observed only in *S. adansonii*. The fossil axis, however, differs from the petiole of *S. adansonii* in having longer elongated peripheral bundles and slightly larger central fibrovascular bundles; also the phloem consists of more cells in the fossil axis (Text-figs 1D-E, 2G, H; Table 1).

FOSSIL RECORD OF *SABAL*

Leaf impressions of *Sabal* have been described by various workers from various Tertiary localities, viz., *Sabal hoeringiana* Unger, *S. major* Unger (Heer, 1876), *Sabal major* (Unger) Heer, and *S. lamanonis* (Schimper, 1870) from Europe; *Sabalites* sp., *Sabalites grayanus* Lesq. (Berry, 1916, 1929), *Sabal miocenica* (Axelrod, 1939) from America; *Sabal nipponica* (Kryshtofovich, 1918) from North Asia; and *Sabalites*

TABLE 1

CHARACTERS	*Sabalocaulon intertrappeum*	*Sabal adansonii*
Shape	Concave, broad in the middle, gradually narrow towards the margins.	A concave groove in the middle margins but gradually tapers.
Epidermis	Well preserved with more or less cubical cells. Cuticle thick, trichomes and stomata not seen.	More or less cubical cells with cuticle Stomata numerous. Trichomes absent.
Hypodermis	2 to 3 layered, parenchymatous.	2 to 3 layered, parenchymatous, cells somewhat compactly arranged.
Peripheral region	This has elongated bundles, leaf trace bundles and fibrous bundles. Bundles have large amount of sclerenchyma; one xylem vessel and phloem in a single mass.	This is narrow with vascular bundles generally oval and fibrous bundles less in number. Bundles have large amount of sclerenchyma and one xylem vessel.
Central region	Vascular bundles irregularly distributed. Fibrous bundles also distributed throughout the axis.	Vascular bundles as well as fibrous bundles scattered throughout the leaf axis without any order.
(i) Fibrovascular bundles	Bundles have scantily sclerenchyma, 1 to 2 metaxylem vessels, phloem undivided. Size — 0·30×0·20 to 0·35 ×0·15 mm, f/v — 1/4-1/5.	Bundles have little sclerenchyma with usually 1 or 2 metaxylem vessels, phloem small, undivided. Size — 0·18×0·15 mm, f/v — 1/6 to 1/5.
(ii) Diminutive bundles	Small bundles distributed throughout the ground tissue. Size — 0·08 to 0·03 mm.	Small vascular bundles with 1 or 2 vessels scattered throughout the leaf axis. Size — 0·09 to 0·07 mm.
(iii) Leaf trace bundles	Bundles numerous in both the zones. Size — 0·42×0·20 mm.	Common in both the regions. Size — 0·25×0·14 mm.
(iv) Fibrous bundles	Bundles rounded with 8 to 20 fibre cells. Size — 60 to 80 μm.	Bundles small, rounded with 20-30 fibre cells. Bundles surrounded by small parenchyma cells. Size — 50 to 76 μm.
(v) Ground tissue	Highly lacunar, lacunae are formed by 'Y'-shaped parenchyma cells.	It is highly lacunar, lacunae are formed by characteristic 'Y'-shaped parenchymatous cells.

sp., *S. microphyllum* (Feistmantel, 1862; Sahni, 1964) from India. A fossil wood probably belonging to *Sabal*-like palm has been described as *Palmoxylon sabal* by Greguss (1954). From the foregoing discussion it appears that the fossil described here is the first undoubted record of a petrified *Sabal*-like leaf axis.

It is also noteworthy that the fossil appears to have affinities with *Palmoxylon parapaniensis* described from the same locality by Lakhanpal *et al.* (1979). The palm wood and the fossil described here share some characters as the structure of fibrous bundles, leaf trace bundles, diminutive fibrovascular bundles and lacunar ground tissue. However, the fossil axis differs from the wood of *P. parapaniensis* in the presence of epidermis, hypodermis and elongated peripheral fibrovascular bundles typical of palm leaf axis and large mass of undivided phloem. Therefore, the fossil wood described by Lakhanpal *et al.* (1979) might also belong to Sabaloid Group of palms.

Characters enumerated above go a long way to affirm that the fossil represents basal part of the leaf axis of a palm like *Sabal adansonii*. In some characters it, however, differs from *S. adansonii* and hence the name *Sabalocaulon intertrappeum* gen. et sp. nov. is being proposed for it.

DIAGNOSIS

Sabalocaulon gen. nov.

Fossil axis differentiated into peripheral and central regions; epidermis with more or less cubical cells; cuticle thick; epidermal hairs absent; hypodermis 2 to 3 layered; fibrovascular bundles elongated in peripheral region with large amount of sclerenchyma; central fibrovascular bundles scattered with scanty sclerenchyma, xylem vessels 1 or 2, phloem large in one mass; fibrous bundles distributed throughout; high frequency of leaf trace bundles; highly

lacunar ground tissue throughout the axis — parenchyma cells ' Y '-shaped.

S. intertrappeum sp. nov.

Fossil axis differentiated into peripheral and central zones; epidermis with more or less cubical cells, trichomes absent, stomata not observed, hypodermis parenchymatous, 2 to 3 layered; peripheral fibrovascular bundles in one row, elongated with large amount of sclerenchyma cells, usually one vessel, phloem undivided, f/v ratio 7/1 to 6/1; fibrous bundles in 2 to 4 rows, rounded; leaf trace bundles common. Central fibrovascular bundles scattered, 40-50/cm², 0·30 × 0·20 to 0·35 × 0·15 mm in size, f/v ratio 1/4 to 1/5; dorsal sclerenchyma less developed, xylem vessels usually 1 or 2 with 2 protoxylem vessels, phloem in a large mass, undivided, small parenchymatous cells round the bundles; diminutive fibrovascular bundles scattered in ground tissue, small with a few sclerenchyma cells, 1 or 2 small vessels; leaf trace bundles numerous; fibrous bundles scattered, 50 to 80 μm in diameter with 8 to 20 fibre cells; ground tissue highly lacunar throughout axis, composed of ' Y '-shaped parenchyma cells.

Holotype — P-M/103, Botany Department, Lucknow University, Lucknow, India.

Locality — Parapani Village in Mandla District, Madhya Pradesh, India.

Horizon — Deccan Intertrappean Series.

Age — Eocene (Tertiary).

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EXPLANATION OF PLATES

PLATE 1

1. Cross section of the specimen showing one complete axis and other incomplete axes. ca. × 2.
2. Cross section of the outer portion of the axis magnified to show the arrangement of fibrovascular bundles. × 8.

PLATE 2

3. Cross section of outer portion of the axis magnified to show the epidermal cells and fibrous bundles. × 40.
4. Cross section of the central part of axis showing fibrovascular bundles in the lacunar ground tissue. × 25.
5. An enlarged fibrovascular bundle of the central region showing phloem cells in one mass and one large metaxylem vessel. × 40.
6. A few phloem cells highly enlarged. × 90.
7. Longitudinal section of the axis showing thickening in the vessels. × 25.
8. Longitudinal section of the axis showing annular and spiral thickening in protoxylem vessel. × 90.

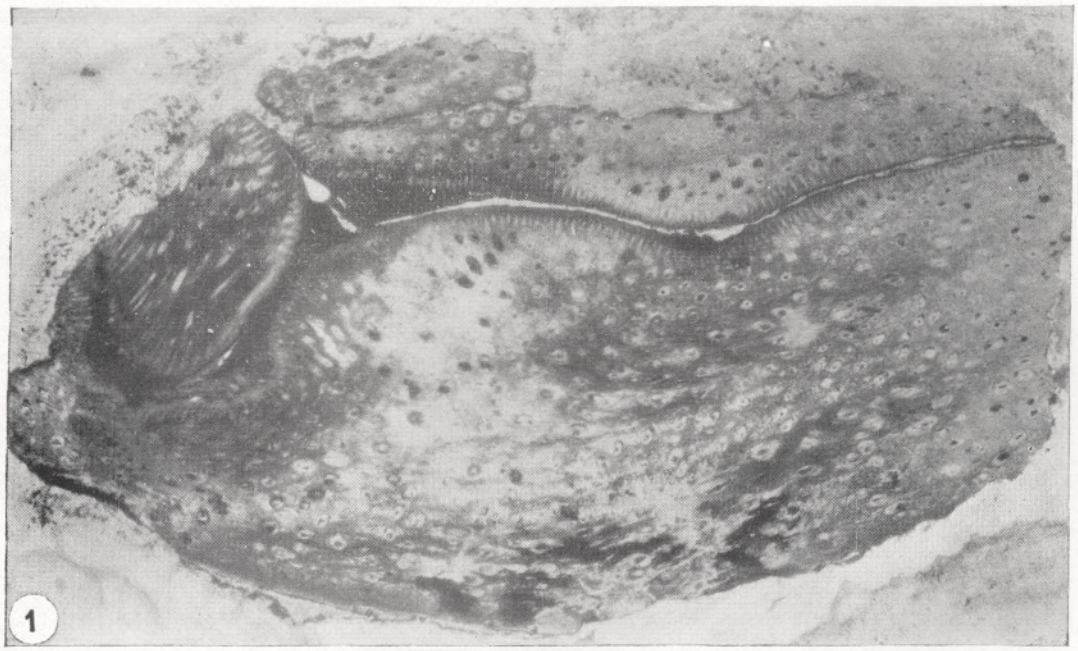
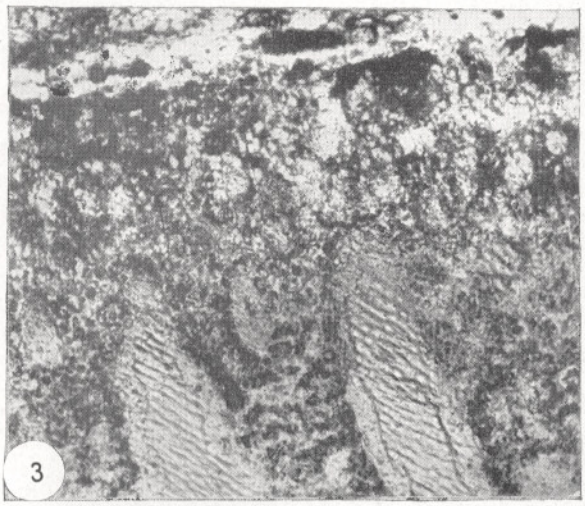
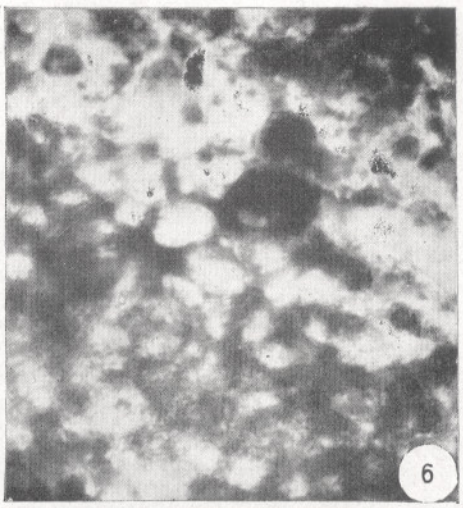
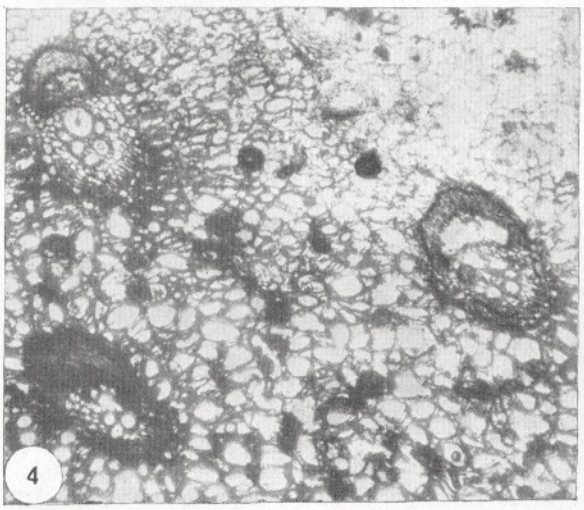
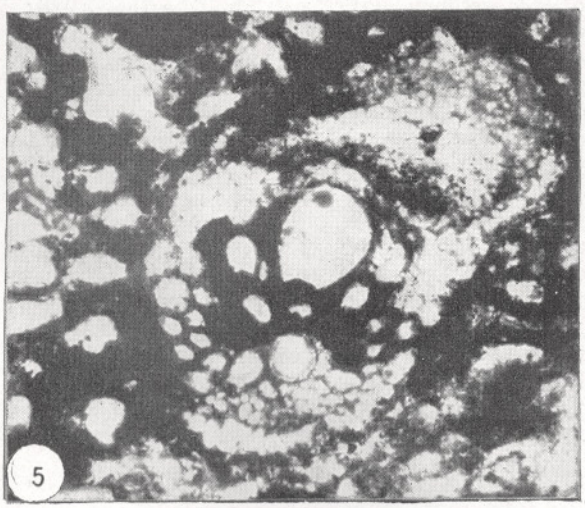


PLATE 1









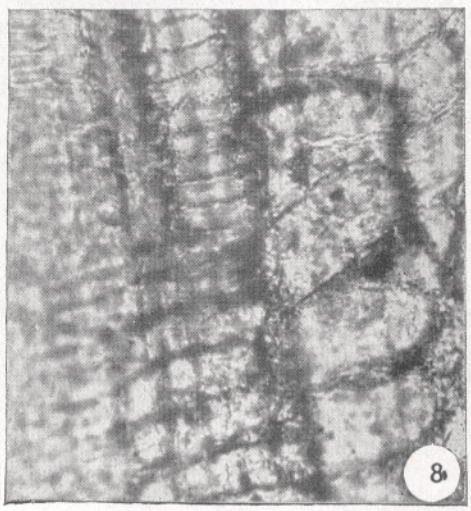


PLATE 2