RODEITES REINVESTIGATED—III*

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ABSTRACT

The connection between rhizome and petiole with their anatomical transition, structure of leaf and complete reconstruction of the genus *Rodeites* have been given for the first time. A revised diagnosis of the genus *Rodeites* is given along with a key for identification of its species. Its plant size, rhizome, and leaf morphology are discussed in the light of petiole structure, size and shape, length of lamina, etc. which show that the plant was quite large and robust.

INTRODUCTION

The genus *Rodeites* was first described by SAHNI (1943). Further contributions to its knowledge by MAHABALE (1957) and SURANGE (1964) were limited to some characters of sporocarp wall and spores. PARADKAR (1971) and CHITALEY AND PARADKAR (1972, 1973) gave detailed account of the rhizome, petiole and sporocarps with their spatial arrangement, structure of sporocarps wall, arrangement of sori, characters of the two kinds of spores including the gametophytes in them. Rhizome and petiole in organic connection was only surmised on the basis of their close proximity with sporocarps. The findings in this paper are in continuation with previous investigations. The paper describes a connection between the rhizomes, petiole, their anatomical transition, structure of leaf and its attachment on rhizome, and a complete reconstruction of the plant of *Rodeites*.

MATERIAL AND METHOD

The paper is based on the study of four new specimens of *Rodeites* 'plant', from the Mohgaon-Kalan, Chhindwara District, M. P., India, in which rhizomes, petioles, leaves, sporocarps, etc. are found attached to each other, and also separately.

The black rock containing a large petiole and a leaf cut, very near—almost attached to it, is shown in Text-fig. B 3 and 8. This gave good peel sections showing all the internal structure of the leaf (Text-figs. B 1, 2 ; Pl. 1, Figs. 4-6).

The second brown chert containing many rhizomes, petioles, leaves, and sporocarps is shown in Text-fig. A 1-5 ; Pl. 1, Fig. 2. It showed these structures on its surface cut transversely, obliquely, longitudinally and it was studied for surface features and also cut along various planes as shown in Plate 1, Fig. 2. Different surfaces were photographed under low power of microscope. This rock did not give good peel sections and hence the material was studied in incident light under different magnifications.

The entire rock measured 13.5 × 11.2 cm and 5 cm thick and the rhizome measured 4-5 mm broad, petioles measured 4-6 mm broad. Four sporocarps were exposed in surface view and 3 more were exposed on cutting the rock (Text-figs. A 3, 4, 5).

The part of the rock exposed along the cut b-b and subsequent cuts showed the rhizome (Rh), its branches, roots (R) and the petiole (p), (Text-fig. A 6-8 ; Pl. 1, Figs. 1, 3 and 6). The leaf is also seen in this rock. Two more black cherts with petiole and

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leaves were studied for the separating vascular traces entering the leaflets borne at the tip of the petiole. This study has helped in reconstructing the plant in its entire form (Text-fig. B 4).

DESCRIPTION

The rhizome and petioles have already been described in detail (PARADKAR, 1971 and CHITALEY & PARADKAR, 1972, 1973) ; here only the transition zone connecting rhizome with petiole is described along with a general stelar description of rhizome and petiole.

RHIZOME-PETIOLE TRANSITION

The trailing rhizome with erectly borne petioles and adventitious roots at nodes shows dichotomous branching. It is solenostelic, varying in thickness between 6.0-10.0 mm with mid-cortical aerenchyma, and central aerenchymatous pith. The petiole has a horse-shoe-shaped vascular bundle with a number of protoxylem groups.

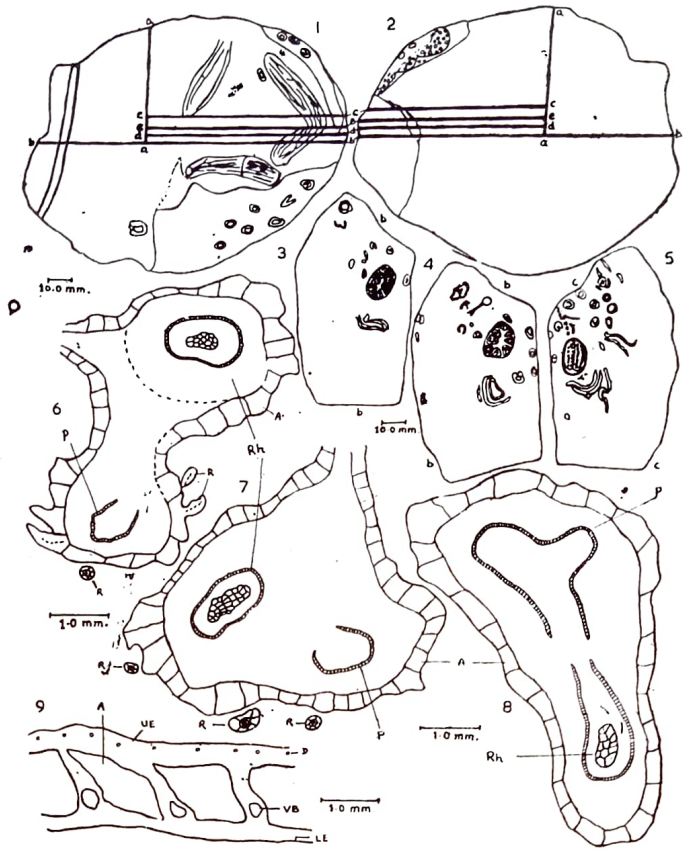
From the rhizome when a petiole trace is to depart the tracheidal cylinder becomes variously stretched out on the side where a petiole is to be formed. The cylindrical shape also becomes modified and broadened (Text-fig. A 8 ; Pl. 1, Fig. 1). The petiole trace gets detached from rhizome stele forming a single gap which is closed a little above it (towards apex). Upto this time it is still enclosed in the common cortical tissue which is continuous round the rhizome (Text-figs. A 6, 7 ; Pl. 1, Fig. 4). Beyond this the petiole and rhizome become separated each showing its own cortex, epidermis, etc. and the leaf-gap in rhizome is closed. The petiole always shows a ventral depression or groove along its length, and the typical shape of its tracheidal tissue helps to distinguish it from rhizome and its branches.

When a rhizome branch dichotomises, there is equal division of the stele of main rhizome so that two similar tracheidal solenosteles are formed by equal division of one (Pl. 1, Fig. 6 Rh). The branching of rhizome stele seen internally and later externally occurs within a distance of 1 cm. Adventitious roots are seen arising from the rhizome and entering surrounding part of chert (Text-figs. A 6 and 7, R). In structure, the roots show an outer epidermis, cortex with aerenchyma and a central diarch stele with two phloem groups (Text-fig. B 6).

LEAF

In this fossil species the petioles are as large (broad) in size as the rhizome ; this is also the case in modern *Marsilea*. The petiole and rhizome size in *Rodeites* varied as in living *Marsilea* species occurring in drier or wetter habitats but the size is still larger than that of the modern genera. The largest (broadest) size of petioles observed in *Rodeites* is 1.0 cm (Text-fig. B 7) which is quite broad. Comparing this with broad petioles of another water fern *Ceratopteris* and its leaf we can assume a large size for the frond of *Rodeites* as it must have had a large leaf-surface for assimilation to provide food for a plant having at least five sporocarps in a row attached to each of its petioles. In fruiting condition many or almost all leaves bear sporocarps so that the number formed must have been quite large and plant itself a large one.

The petioles bearing leaf or frond are alternately arising on rhizome (Text-fig. B 4) i.e. two petioles are not seen arising from same node of rhizome. The total length of petiole is unknown as no specimen shows the top end. The longest petiole portions seen were 5 cm and 8 cm. These are not fragments but end where the petiole departs from



Text-fig. A 1-9: 1 and 2. Entire rock from two sides showing the lines along which it was cut for study. a-d indicate successive cuts. Surface features show the rhizome and petioles passing from one end to other and the other axes. In 2 the sporocarps are seen on surface ; 3-5. Rock slabs showing the cut surfaces with rhizomes, petioles, leaves and sporocarps cut transversely ; 6. Transverse section through the nodal region showing rhizome (Rh) with squarish aerenchymatous pith and petiole trace (P) both enclosed in common cortex, but separating by constriction of cortical region and roots (R) ; 7. Transverse section through the nodal region showing closed complete rhizome (Rh), solenostele and petiole trace (P) in common cortex ; 8. Oblique transverse section through nodal region showing stretched rhizome stele (Rh) with gap and separated petiole trace (P). Rhizome stele has aerenchymatous pith, 9. Diagrammatic T. S. leaflet showing upper epidermis (UE), lower epidermis (LE), septa, air chambers (A), vascular bundles (VB) and ducts (D) ;

the block of rock. At the base of petiole just above its connection with rhizome were borne sporocarps generally five in number one above other (*Rodeites polycarpa*). Above this the petiole continued till it reached surface of water or came above it bearing at its tip the leaflets which were quite broad and forming a group of leaflets as in *Marsilea*, the leaflets being formed due to dichotomising of the broader vascular strand at the petiole tip.

A section of the petiole specimen from just below the attachment of lamina is shown in Text-fig. B 5 In this uppermost broader part of petiole with a shallower groove the vascular strand has broken into six parts out of which the two lateral or outermost are smaller. These entered the leaflet bases and further divided to enter the lamina septa as vascular bundles (Text-fig. B 4). There were four large leaflets and two smaller ones were present at the outerside. Presence of lateral small leaflets is inferred because of a small and narrow portion of lamina in transverse section in Text-fig. B 3 and because of smaller lateral vascular traces at the tip of petiole. This compares well with the condition in *Marsilea* where there are four strands at the tip and four leaflets. The lamina of *Rodeites* leaflet was large and entire. Its length and shape of the apex are inferred by comparison with other living ferns with dichotomous palmate type of lamina and the aquatic habit of the plant. Serial sections and cutting of rock transverse to the vertical axis of pinna

indicate that there is no further division of leaflet laminae into pinnules. The orientation of all six leaflets is also inferred by comparison with modern fern fronds. The thickness of leaflet lamina is very unequal in Text-fig. B 3. Transverse sections demonstrate that the leaflet is 3.5-5.0 cm broad showing air spaces and 1.0-1.3 mm thick. Thus it is quite a large leaflet. The upper epidermis has stomata with substomatal cavities. Under this is photosynthetic tissue consisting of about 6 layers of parenchyma cells. Intercellular spaces were not observed. Air spaces are limited by parenchyma bands or septa separating air spaces. It is clear that it has many, almost equal and parallel, veins at about 1 mm apart one to each septum. Each vascular bundle near its lower end has xylem tracheids which can be recognised but sieve tissue could not be seen clearly. No endodermal sheath was observed. The lower epidermis has no stomata but there is photosynthetic tissue. No fibres were observed but mucilage canal-like structures (Ducts D) are seen in lamina and in petiole cortex (Text-fig. A 9 ; B 2 ; Pl. 1, Figs. 5 & 7).

The structure is much like the leaflet of *Marsilea* but on a much larger scale. In the young condition the six leaflets were crumpled together as observed on the cut rock surface and in very young condition may have been circinately coiled. The lamina being quite large their unfolding must have taken some time for their full growth to occur.

Since the sporocarps have been already described in 1971 and 1972 by CHITALEY AND PARADKAR, they are not being redescribed here.

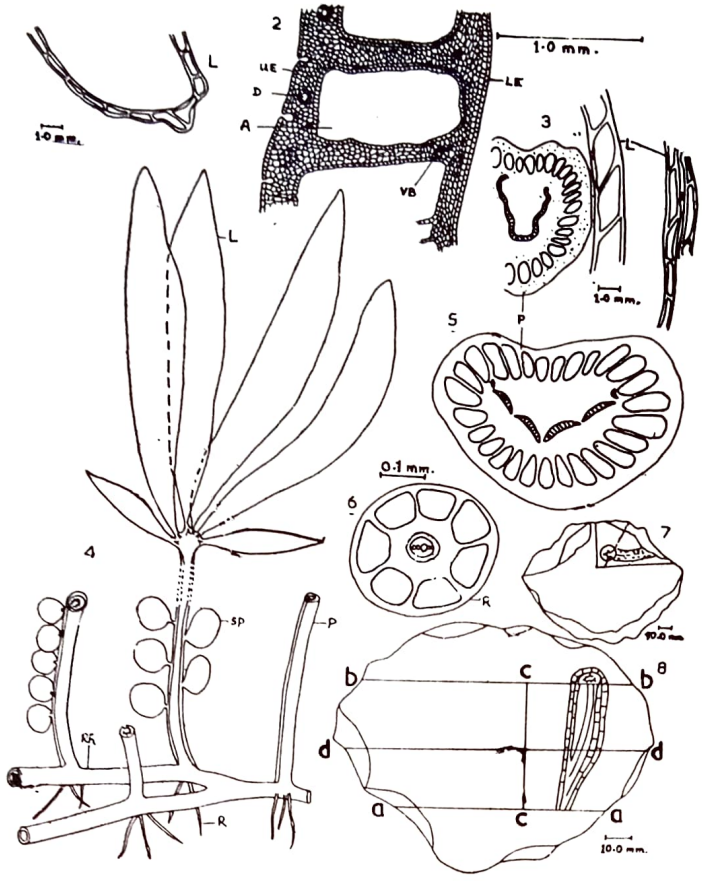
RECONSTRUCTION

We suppose that the whole plant had a thick creeping rhizome in mud under shallow water, and rather long and thick vertical petioles ending in about six unequal leaflets which floated on the water surface. This last idea is based on the distribution of stomata and the large air-spaces. It is also supposed that the sporocarps were near the petiole base because this is their position in *Marsilea*, *Regnellidium* and *Pilularia* but there is, as yet, no direct evidence for *Rodeites*. We know that the sporocarps were produced in large numbers—as over a hundred have been collected. In the reconstruction (Text-fig. B 4) the sporocarps of the leaf on the left are shown in their true position on the adaxial side of the petiole but in the leaf on the right they have been spread out diagrammatically to show the two rows plainly.

Thus, the entire plant looked as shown in Text-fig. B 4 which is a reconstruction achieved after a continuous study of rocks containing the plant material for many years as some links in the plant reconstruction were not available before for study and comparison. Table 1 gives a detailed comparison of the genera of family Marsileaceae.

DISCUSSION

In elucidating the morphology of this fossil fern frond, the views expressed by BOWER (1923) on leaf architecture and ALSOPP and others on experimental work on fern leaves (1953) has been very helpful. According to BOWER (1923) the comparison of juvenile and adult leaves of different genera and comparisons with related fossils reveal their structure. POTONIÉ (1899) has stated that on passing from lower to later geological horizons the size of the leaves increases but the degree of their cutting decreases. This seems to have been partly true in case of Upper Cretaceous *Rodeites* where the leaflets were quite large. In modern genera the size of lamina and leaf is on decrease. *Marsilea*, *Rengellidium* and *Pilularia* show decreasing degree of leaf surface, which seems to be a secondary retrogressive evolution in this group of plants. "The dilatation of stele is closely related to the width of the leaf trace and both stele and trace have followed the demands of an enlarging



Text-fig. B1-8: 1. Diagrammatic T. S. leaflet (L) showing air-spaces and septa. The lamina here shows curved outline ; 2. Detailed structure of T. S. leaflet showing stomata, ducts (D), air chambers (A), undifferentiated mesophyll and vascular bundles (VB) ; 3. Diagrammatic T. S. petiole with associated leaves in T.S. Three sections of leaflets (L) are seen; 4. A complete reconstruction of *Rodeites polyacarpa* Chitaley & Paradkar, showing the plant habit ; 5. Transverse section of petiole at its tip showing splitting of vascular strand into smaller units which enter the leaflet bases. Arenchymatous cortex and broad flattened shape is different from an adaxially grooved normal petiole ; 6. Diagrammatic T. S. root (R) showing aerenchymatous outer cortex and central diarch stele ; 7. Rock specimen showing petiole on its surface. The lines indicate cuts made for study of the rock ; 8. Rock specimen showing another large petiole and the cuts made for study. The specimen after cutting is illustrated and enlarged as in fig. 3.

lamina. Where solenostele is present the leaf trace comes off bodily as a sector of the vascular ring leaving a wide gap (BOWER, 1923)". This is seen very well in the rhizome stele and leaf trace formation in *Rodeites*.

"Fern leaf being megaphyllous and photosynthesis being its chief function, these impose a demand for conduction roughly proportional to the area of exposed surface so that there is an elaboration of vascular supply of leaf-stalk along with progressive expansion of blade (BOWER, 1923)". This fossil shows an elaborate vascular strand in its petiole which is an indication of its large leaf size. The vascular strand is primitive undivided, adaxially concave and folded into horse-shoe form.

"In a large leaf with large vascular supply the trace expands into a widely arched curve with increased number of protoxylem groups and whole 'horse-shoe' appears to be made up of a number of units linked into a continuous chain. Each unit has a protoxylem group at its centre from which metaxylem extends right and left until the units are linked forming a continuous tract surrounded by phloem, pericycle and endodermis (BOWER, 1923)". The number of conducting units described above also helps to decide the number of leaflets at the tip of petiole. In Text-fig. B 5 there are seen six strands of vascular tissue in T.S. of petiole, two of which at tips are smaller with crowded trancheids and much

Table 1—Comparative study of the four genera of Marsileaceae

Characters	*Marsilea*	*Rodeites*	*Regnellidium*	*Pilularia*
1. Living or fossil	Living 65 spp. and fossil 10 spp.	Fossil 3 spp.	Living 1 species	6 spp. living and 3 spp. fossil
2. Distribution	World wide distribution	Deccan Intertrappean	Restricted South America, Brazil.	
3. Size of plant	Medium to small	Large	Medium to small	Small
4. Structure of rhizome	Amphiphloic solenostelic, pith solid	Amphiphloic solenostele, pith squarish aerenchyma	Amphiphloic solenostele, pith solid	Amphiphloic solenostele, solid pith
5. Structure of petiole xylem trace	V-shaped	Large, horse-shoe shaped with many Px. groups	V-shaped, small trace	V-shaped, a small trace
6. Shape ofleaf frond structure	4 pinnae	6 large leaflets	2 pinnae, not separated completely	No flat lamina, awl shaped-leaf
7. Laticiferous or Mucilage ducts in sporocarps or a plant.	Mucilage ducts	Present, ducts in the sporocarp wall	In entire plant, it is only living fern with laticifers	
8. Sporocarps, size, shape, teeth	Flat, bilateral, raphe present	Bilateral or round, no teeth and raphe	No teeth, rounded raphe present	Spherical, round shape
No. of sori	variable, 3-11,	7-11	7	4 sori only
Attachment of sori, position	On inner lateral walls	On inner lateral walls	On the septa (not on inner walls)	On the wall
9. Position of female sporangium in sorus	At the tip of receptacle	Distribution, position not fixed		At the base of receptacle in a vertical section of sporocarp
10. Structure of megaspores	Aspidote aperture not present. Trilete mark on hemispheric papilla	Aspidote aperture, spirally twisted exine layer	Aspidote aperture, spirally twisted exine layer	
11. Structure of microspores		Trilete mark+	Trilete mark+	Trilete mark+
12. Gametophytes in female spore	At the apex of megaspore only, exosporic	Completely developed, filling entire cavity of megaspore, endosporic.	As in *Marsilea*	As in *Marsilea*
13. Gametophytes in male spore	2 groups of male gametes in 2 antheridia and intrasporic	Same. 2 intrasporic antheridia in male gametophyte	Same	Same
14. Embryo	Present, exosporic	Not observed	Exosporic	Exosporic

separated from four other larger strands which are also well away from each other. The outermost enter into two lower smaller leaflets and the rest four into four larger leaflets thus making a total of six leaflets at the tip of the petiole. The condition is similar to that seen in some abnormal specimens of living *Marsilea quadrifolia* (GUPTA, 1962). The six leaflets of *Rodeites* frond represent a primitive condition for this family which is seen as an abnormality in the modern *Marsilea*, a recapitulation of primitive ancestral type. *Marsilea* also shows in its juvenile condition the awl shaped leaf of *Pilularia* and two lobed form as in *Regnellidium*. *Marsilea* is thus derived from *Rodeites* and more related to it, while *Regnellidium* is further away in relationship though in some features it does resemble the extinct fossil genus (see comparative chart of all genera).

It is thus observed that *Rodeites* is an extinct fourth genus of Marsileaceae and its taxonomic position is clear. It is a close ally of *Marsilea* and *Regnellidium*. From *Marsilea* it differs generically in having numerous megasporangia along the sides of each placenta instead of just one row along the top of sorus. In *Rodeites* the microsporangia are mixed with the megasporangia but in *Marsilea* they are below them. In *Marsilea* the top of megaspore is smooth but in *Rodeites* it extends as spirally twisted folds. In *Rodeites* the female prothallus occupies the whole megaspore and not just the top as in *Marsilea*.

From *Regnellidium* it differs in having more leaflets. The sori are not attached to wall but to the septa in *Regnellidium*. The female gametophyte in *Regnellidium* is like that of *Marsilea*. We know rather little of the fossil history of Marsileaceae. What is known is mainly based on megaspores and has already been given by CHITALEY AND PARADKAR (1972, p. 115). The megaspore called *Arcellites* widespread in Lower Cretaceous is like that of *Rodeites*. No fossils which can be accepted as close allies of *Marsilea*, *Pilularia* or *Regnelliduim* are known though they doubtless had a fossil history. Thus we have only one satisfactorily known fossil genus and this is extinct and it seems premature to discuss the evolution of the Marsileaceae. But it appears that *Rodeites* was the most well developed ancestor of this family and it may have diverged later on to give rise to *Marsilea* on one hand and *Regnellidium* on the other by progressive reduction in leaf size, plant size, female gametophyte and by distributing some of its own features in the two modern genera.

Modern *Marsilea*

Sori on inner wall. Female spore not aspidote. Female prothallus small, exosporic. Leaflets 4, abnormally 6.

Modern *Regnellidium*

Sori on septa. Aspidote aperture of female spore. Female prothallus small, exosporic. Leaflets 2. Trilete male spore.

Fossil *Rodeites*, Upper Cretaceous, Sori on inner wall. Aspidote aperture of female spore. Large female prothallus, endosporic. Leaflets 6. Trilete male spore.

In view of the detailed new findings, a revised diagnosis of Marsileaceae and the genus *Rodeites* Sahni as well as the keys for generic and specific identification of *Rodeites* are given.

Diagnosis of family Marsileaceae

Submerged, emerged or marshy water ferns ; trailing rhizome with single leaf and adventitious roots at nodes, rhizome solenostelic ; mucilage or laticiferous ducts present ;

leaf simple, undivided or divided at tip, sporocarps containing both kinds of sporangia in sori ; sori on inner wall or indusial septa ; spores of two kinds ; megaspore single in a sporangium with aspidote aperture or not ; microspores trilete or not ; female prothallus intra- or exosporic ; male prothallus intrasporic.

Generic key for identification

I. Sori on inner wall

1. Leaflets six, elongated and entire, with air chambers, septate, floating (at least sometimes) ; petiole with large horse-shoe strand ; rhizome with squarish air spaces in central pith ; sori 7-11 ; mucilage ducts present. — *Rodeites*, fossil
2. Leaflets four ; petiole with V-shaped strand ; solid pith without air-space ; sori variable in number ; mucilage ducts present. — *Marsilea*, fossil and modern
3. Leaf awl shaped ; pith solid ; sori 4 only. .. — *Pilularia*, modern

II. Sori not on inner wall but on septa.

4. Leaflets two ; V-shaped petiole strand ; pith solid ; sori 6-8; laticiferous ducts present. — *Regnellidium*, modern

Revised Generic Diagnosis of **Rodeites** Sahni

Large submerged or emergent or marshy (water) fern, rhizome trailing with single leaf and adventitious roots at a node, rhizome solenostelic with squarish aerenchyma in central pith and aerenchymatous cortex ; leaf trace and petiole trace horse-shoe-shaped, adaxially concave, petiole grooved, large ; leaflets six, two outer smaller, four larger, elongate, lanceolate, entire with air-chambers and septa ; sporocarps large, attached to petiole in linear groups, clusters or isolated ; sporocarps ellipsoid, bilaterally symmetrical or rounded, attached on a small or longer stalk ; wall of sporocarps with epidermis, hypodermis, prismatic palisade layer and inner wall layers with ducts ; stomata in epidermis, vascular bundles 14-16 ; sori 5-7 or 11 ; soral chambers on either side attached to inner wall laterally and vertically, extending to centre of sporocarp, each sorus receptacle traversed by a vascular bundle ; megaspores large, spherical, 650-880 μm in diameter with aspidote aperture 80-100 μm broad, aspis 65-85 μm high, megaspore wall with intine 2 μm, nexine 4 μm, sexine 30 μm and baculae 10-12 μm, perine 2-3 μm, female gametophyte intrasporic, distinguished into apical and basal regions, apical of smaller cells, basal of larger cells ; gametophytic tissue not touching the spore wall except at apex, apical region showing archegonia ; microsporangium 250 μm in diameter ; microspores very numerous spherical, 45-80 μm in diameter with intine 2 μm, exine 7-9 μm thick, baculate to spiny and with a triradiate mark ; some microspores smaller, containing male gametophyte, others empty, dehisced and showing lobed apex.

The three species at present recognised are all based on rock sections. All are not fully known but *Rodeites polycarpa* is the best known having a definite linear row of sporocarps which were almost sessile and flat.

Sporocarps in linear row, bilaterally symmetrical ..	*Rodeites polycarpa* Chitaley & Paradkar
Sporocarps in cluster, bilaterally symmetrical on common branched stalk.	*Rodeites intertrappeana* sp. **nov.** Paradkar & Barlinge
Sporocarps rounded, on curved stalk	*Rodeites dakshini* Sahni

Thus *Rodeites dakshini* var. *intertrappeana* (CHITALEY & PARADKAR, 1972) having a cluster of sporocarps rather than a row is raised to the level of a species and named as *Rodeites intertrappeana* sp. nov. Paradkar & Barlinge. Here the exact attachment of sporocarp cluster to petiole is not known, *R. dakshini* Sahni is known from a single sporocarp with a curved stalk and nothing is known about sporocarp number or attachment to petiole. The sporocarp is rounded in longitudinal section but its shape in T. S. is unknown.

Holotype—As given in CHITALEY AND PARADKAR, 1972.

Locality—Mohgaon-Kalan, Chhindwara District, Madhya Pradesh, India.

Horizon—Deccan Intertrappean Series of India.

Age—? Lower part of Deccan Intertrappean Series by some regarded as Lower Eocene (Palaeocene) but by some as Uppermost Cretaceous.

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EXPLANATION OF PLATE 1

1. Oblique T. S. through a nodal region showing stretched rhizome stele with gap and separated petiole trace. ×40.

2. Rock showing the lines along which it was cut. ×¾.

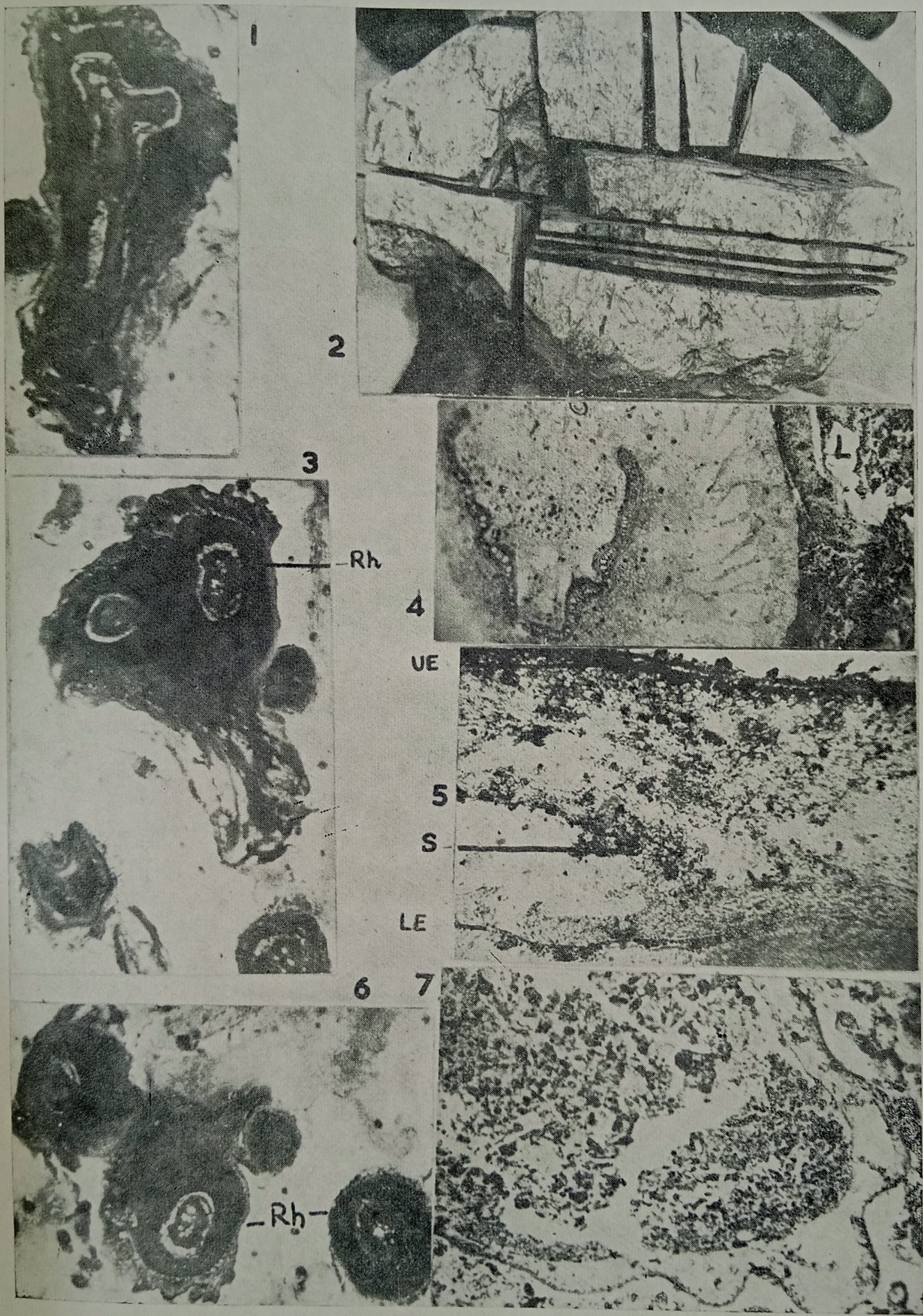
3. Transverse section through nodal region with rhizome stele and petiole trace (rhizome on right side with darker cortex). ×40.

4. T. S. *Rodeites* petiole showing splitting of vascular strand into parts. Ducts in outer cortex, air spaces, septa and portion of leaflet (L) on its right. ×50.

5. T. S. part of leaflet enlarged to show details of epidermis, air-chambers, oblique septum with vascular bundle. ×250 (UE—upper epidermis, VB—Vas, bundle, S—septum, LE—Lower epidermis).

6. Transverse section through nodal region showing rhizome and petiole separating ×40.

7. T. S. Leaflet *Rodeites*, with air-spaces and septa ×50.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