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# Anatomy and ecology of the tree fern *Hemitelia brunoniana* (Wall.) Clarke, with remarks on the phylogeny of Cyatheaceae

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THE earliest record of the occurrence of Cyatheaceae is in the Jurassic Period about 150 million years ago (Ma) in the discovery of *Protopteris witteana* Schenk in Germany and England<sup>1</sup>, which was believed possibly to be of this affinity. In 1877 Feistmantel<sup>2,3</sup> described a fossil, *Protocyathea trichinopoliensis*, from the Upper Cretaceous of Tiruchirapalli in South India, which judging from the highly divided leaf-trace characteristic of Cyatheaceae, almost certainly belonged to this group<sup>4</sup>. There is no detailed account on the living members of Cyatheaceae from India, except for a brief note on the anatomy of *Alsophila glabra*<sup>5</sup>. Eleven species belonging to three genera, *Alsophila*, *Hemitelia* and *Cyathea*, occur in the moist tropical-subtemperate forests of East and South India. Of these, we have investigated five species in some detail with a view to providing data for comparison with any future discovery of cyatheaceous fossils from the country. In this paper the salient features of the anatomy of *Hemitelia brunoniana* are described with emphasis on its ecological adaptation. The genus *Hemitelia* has so far not been investigated anatomically by any of the earlier workers.

Cyatheoids are the tallest amongst the living ferns with dendroid habit, some attaining a height of up to 20 m. *Hemitelia brunoniana*, which incidentally is the only species belonging to the genus occurring in India, is on the average 5–6.5 m tall with usually a single-columnar stem which is covered with persistent leaf-bases and is surmounted at the top by an elegant cluster of decompoundly pinnate fronds. The apex is closely protected by compactly arranged scales or ramenta. The stem may be occasionally forked (Figure 1).

The stelar skeleton of the stem has been extracted with the help of macerating fluid (Figure 2). The leaf-gaps are diamond-shaped in surface view and spirally arranged. A leaf-trace from mature stem is highly divided and composed of up to 50 strands that exhibit a characteristic configuration as a result of the inward



Figure 1. *Hemitelia brunoniana* in its natural habitat in Andheri Khola ravine (Sikkim). Note bifurcating trunk of the specimen, left foreground

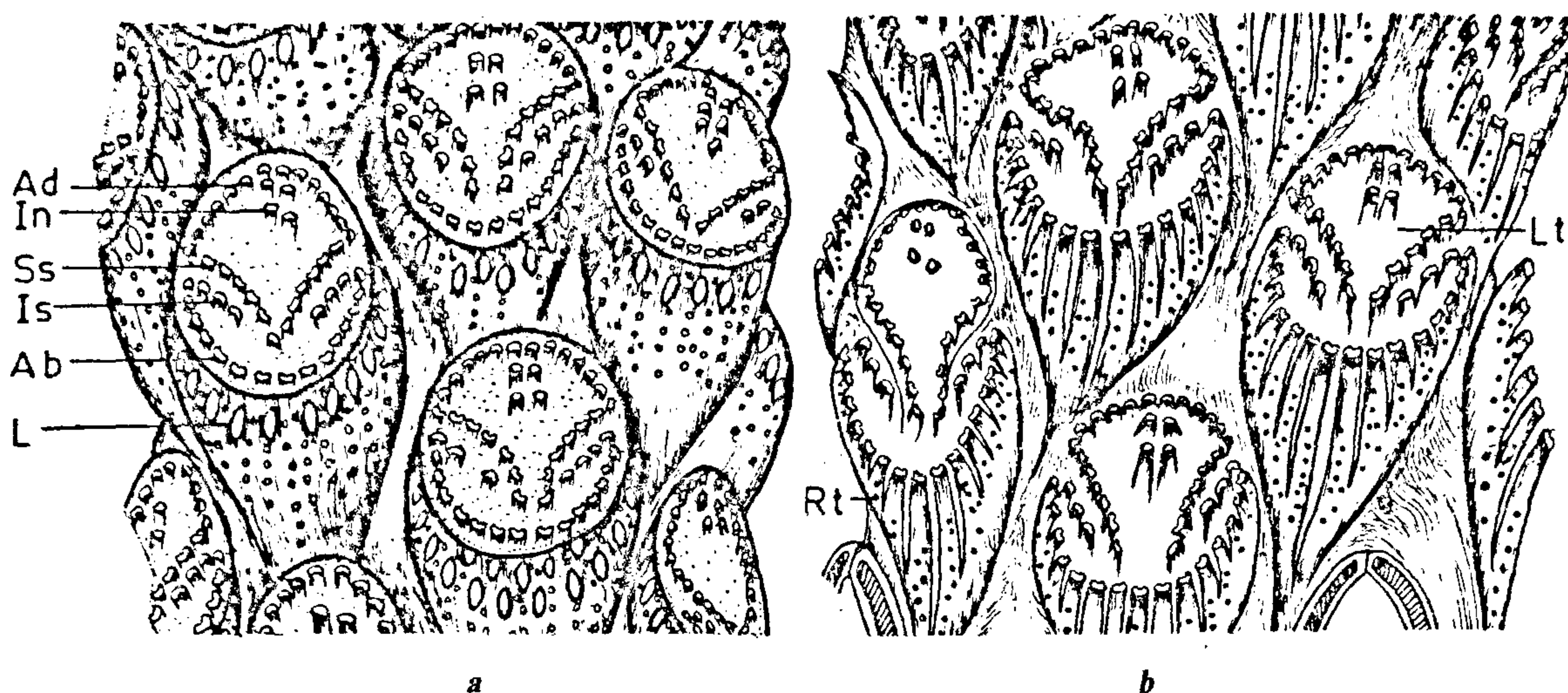


Figure 2. *a*, Tangential section of stem, showing complicated leaf-trace (Lt) and lenticels (L). *b*, Same as *a*, with the leaf-traces exposed. Note the origin of root traces (Rt) from the surface of leaf-trace strands.

and outward invaginations of the meristele from which they are abstricted. The highly convoluted leaf-trace exhibits an abaxial arc of nearly 15 bundles, an inferior and a superior series composed of three and six pairs of bundles respectively, two adaxial arcs each composed of six pairs of bundles with inturned margins of a pair of bundles in each (Figure 2). Such a leaf-trace is characteristic of all the Cyatheoids, with minor variations. The mechanism of increase in the number of leaf-trace strands is clearly an adaptation to facilitate increased supply of water to the massive lamina. In no other fern, not even in the arborescent Dicksoniaceae, is the leaf-trace so highly complicated.

The number of leaf-trace bundles decreases as they ascend the terminal portion of the rachis. They are also fewer in the rachi of the 2nd and 3rd order. The vascular supply to the pinnae, pinnules and leaflets is extra-marginal.

Root-traces arise in profusion from the surface of leaf-trace strands for supplying the bumper crop of adventitious roots, anchoring the columnar stem at the base. Each root-trace becomes diarch on entry into a root.

The mature stem in transection is a dictyostele with commonly six U- or V-shaped meristeles (Mer), exhibiting out-turned margins (Figure 3). The number of meristeles decreases towards the younger basal portion of the stem.

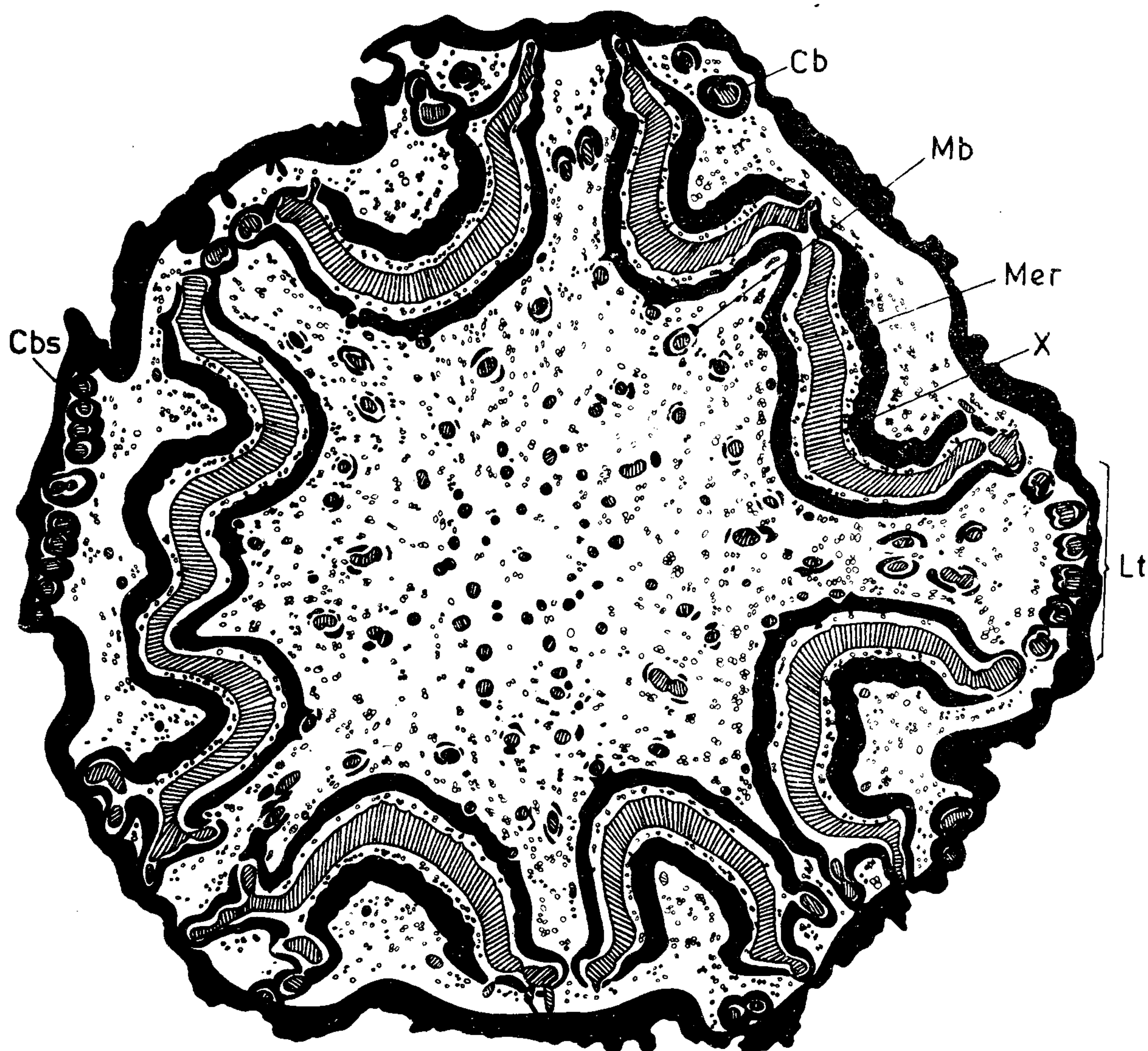
The stem at the periphery shows a thick sclerotic mantle formed of highly thickened fibres. This mantle is pierced by numerous lenticels for aeration (Figure 2, *a*). The cortex is narrow, parenchymatous and studded with numerous mucilage sacs. A few cortical bundles

are also present which occasionally may be joined together to form a sort of a sheath (Cbs). Each meristele is enclosed by a thick covering of sclerenchymatous fibres both on the inside and on the outside, except at the margins. The pith is massive with many medullary bundles traversing through the medullary parenchyma. Each bundle may be protostelic or siphonostelic and is completely or incompletely surrounded by its own sclerenchymatous coat. Interspersed in the ground parenchyma are present mucilage sacs in vast numbers.

The mode of origin of mucilage sacs has not been investigated earlier in any of the Cyatheoids. Our observations reveal that they originate as schizogenous cavities in the ground parenchyma, broaden, become filled up with mucilage and assume a rounded form (Figure 4, *a*). They do not run longitudinally as ducts.

The outer part of a meristele in transection is shown in Figure 4, *b*, but without the sclerenchymatous sheath. Endodermal cells (E) possess the usual casparian thickenings. A conspicuous feature within the endodermal ring is the presence of mucilage cells (M) adjoining the protophloem (P) and rather broad sieve elements (S), which in maceration reveal numerous sieve plates along the radial and lateral walls (Figure 4, *c*). Xylem (X) is constituted of tracheids with quite broad lumen and sclariform pittings, and is interspersed with conjunctive parenchyma (C). The average length of tracheids is 10.11 mm. (In *Cyathea spinulosa* the average length is 18.75 mm. These tracheids, however, are far short of 45-50 mm long tracheids in the climbing fern *Stenochlaena palustris*, even though the cyatheoids are tree ferns necessitating transport of water to great heights.)





**Figure 3.** Transection of mature stem, showing leaf-gaps with outgoing leaf-trace strands (Lt), cortical bundles (Cb), medullary bundles (Mb) and cortical bundle sheath (Cbs). Note the massive pith and narrow cortex studded with mucilage sacs. Sclerenchymatous sheaths on the outer and inner side of meristele (Mer) are shown in solid black.

### *Adaptive ecological features*

- i. The cyatheoids are dendroid in habit and lack secondary growth, which is a genetic feature characterizing all the true ferns. The peripheral outer cortical sclerenchymatous cylinder, the two similar coaxial sclerenchymatous cylinders one external and another internal enveloping the dictyostele, together with the vascular stele itself, compensate for the lack of secondary growth for giving adequate strength to the denroid columnar stem with its crown of massive leaves.
- ii. No vessel elements are present but tracheids have a quite broad lumen.
- iii. Sieve elements are also rather broad with numerous sieve areas on radial and lateral walls for conduction of

food material.

- iv. There is copious formation of schizogenously developed mucilage sacs in the ground tissue. These in addition to the mucilage cells present adjacent to proto-phloem in the meristeles, together have abundant supply of mucilage which helps the plant to retain water to tide over periodic unfavourable desiccating climatic conditions.
- v. A bumper crop of adventitious roots serves as a reasonably efficient mechanism for binding the plant to the soil in a protected environment not tossed by high winds.
- vi. The highly complicated leaf-trace facilitates the conduction of water to the massive lamina.

Ecologically, thus, the cyatheoids are well adapted to their habitat. Evolutionarily, the cyatheoids are a blind



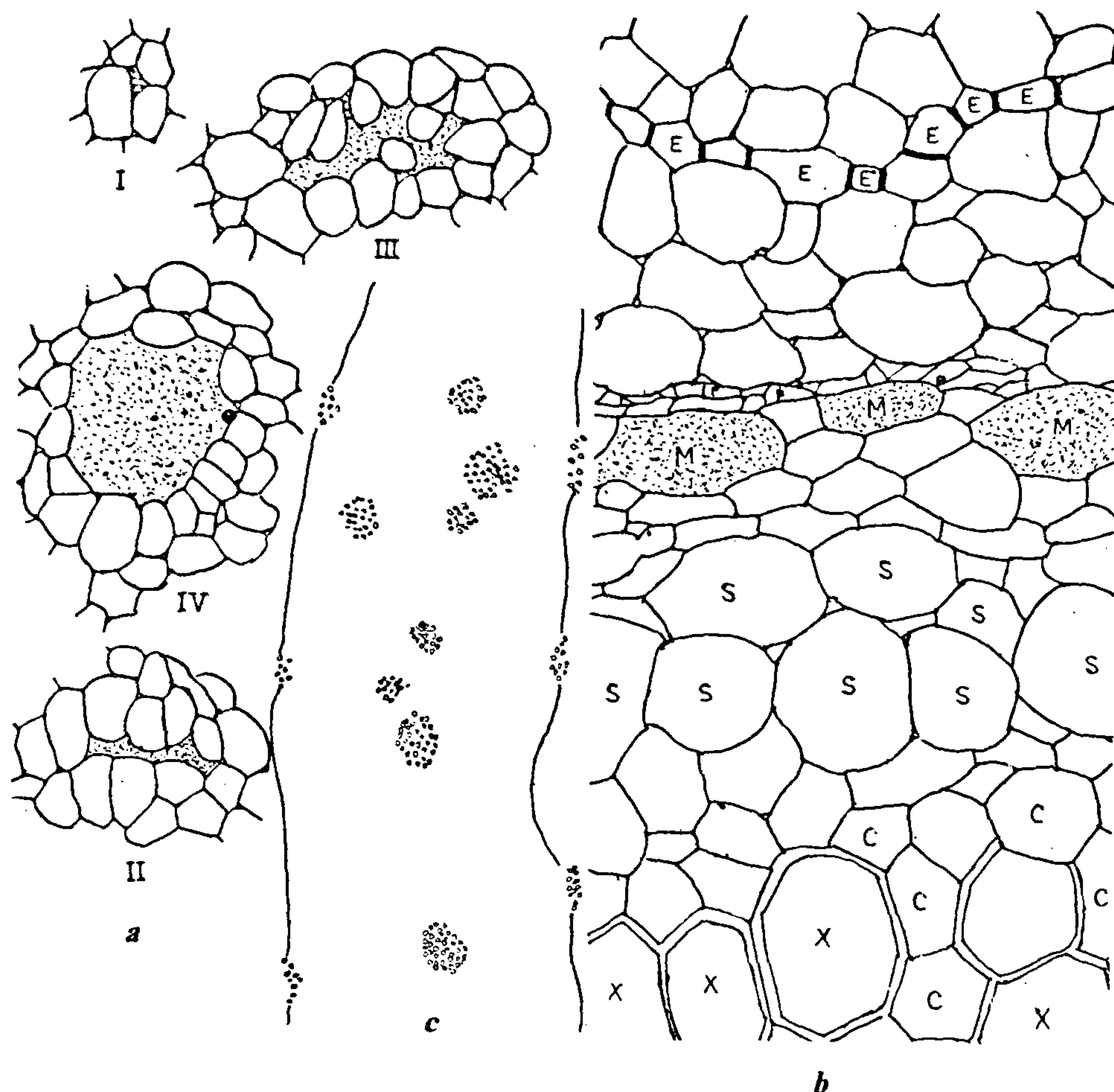


Fig. 4. *a*, Stages (i-iv) in the schizogenous development of mucilage sacs in the ground parenchyma of pith. *b*, Peripheral region in transection. Outer section, cyma sheath, is not shown. C, Conjunctive parenchyma; E, endodermis; M, mucilage cell; S, sieve tube; X, tracheid. *c*, A sieve tube in maceration, exhibiting broad lumen with sieve areas on tangential and radial walls.

attened with extinction because of the destruction of their natural habitats, augmented further by exploitation by man for their horticultural value.

### Phylogenetic relationships

These facts are worthy of consideration. First, whether Cyathea is phylogenetically related to Dicksonia or descended from it<sup>6,7</sup> or if they should be regarded as belonging to the Superficiales and related, or, alternatively, to Gleicheniaceae, and immediately to Cyathea as Bower<sup>8</sup> speculated. The first view<sup>6</sup> i.e. that Cyathea is related to Dicksonia, has been demolished earlier<sup>9</sup> (cf. Mehra and Bawa<sup>9</sup>). Stokey<sup>10</sup> supported Bower's concept on the basis of occurrence of scales in Gleicheniaceae and Cyathea and their emergence from a specialized

basal cell in both the gametophytes (the gametophytes of Dicksoniaceae are naked and there are no emergences of any kind). The fallacy in regard to the similarity in the ontogenetic development of sorus of Cyathea and Dicksoniaceae has been elaborated elsewhere<sup>9</sup>. And now my attention has been focused on a paper<sup>11</sup> (previously overlooked) where the authors have conclusively demonstrated that the origin of the indusium in *Cyathea fulva* is initiated superficially from protoderm cells near the vein which bears the sorus and is in no way marginal in origin as in the Dicksoniaceae. This sets at rest the first point I wanted to elaborate.

The second point is whether Cyathea is immediately phylogenetically related to Woodsia as Bower<sup>8</sup> assumed. I entirely disagree with it on the basis of cytological and anatomical evidences. The Woodsiaceae are all based on  $x=41$  chromosomes, and do

not possess accessory medullary or cortical bundle system in the stem which is characteristic of the Cyatheaceae. Furthermore, the uniform occurrence of  $x = 69$  chromosomes in all the members of Cyatheaceae has no relation whatsoever to the basic chromosome number  $x = 41$  found in the Woodsiaceae. There is in my view a beautiful series, starting from Gleicheniaceae with prostrate dorsiventral rhizome to a similar one in *Alsophila acaulis* and *A. formosana*<sup>12</sup>, both of which are unmistakably cyatheaceous in their vascular anatomy and in possessing medullary and cortical system of bundles. The transition from this to the typically dendroid habit of the majority of Cyatheaceae is perfectly conceivable. In the matter of soral organization the series should be read from *Alsophila* with the sorus non-indusiate, circular and superficial on the vein as in *Gleichenia*, to *Hemitelia* with a scale-like indusium partially covering the sorus and superficially seated on the vein, to *Cyathea* with well-developed indusium completely covering the sorus which too is dorsal on the vein.

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