SOME ASPECTS OF THE MORPHOLOGY OF THE RHIZOME OF *PTERIS WALLICHIANA*

BY SUBHASH CHANDRA AND B. K. NAYAR

(*National Botanic Gardens, Lucknow*)

Received June 14, 1969

(Communicated by T. N. Khoshoo, F.A.SC.)

ABSTRACT

Pteris wallichiana has a short thick ascending rhizome clothed by prominent, spirally arranged, swollen, fleshy, persistent, leaf bases with clusters of roots and paleae between them. A majority of the leaves are reduced, except for their swollen bases which act as storage organs. These are large fleshy ovoid organs, often 3-4 × 1·5-2·5 cm. in size and composed of thin-walled parenchyma cells with dense deposits of starch. A few vestigial leaves are found on the ventral side of the rhizome. All leaves are associated with an abaxial vegetative bud at its base. The prominent lenticels found on the leaf bases are formed by groups of cells of the inner cortex elongating radially and breaking open the peripheral layer of the outer cortex. The vascular cylinder of the rhizome is a solenostele with a ribbon-like medullary strand acting as a compensatory bundle to close the leaf gaps. The leaf traces are Ω-shaped solitary strands. The ground tissue of the rhizome is parenchymatous, except for a cortical intact sclerenchymatous sheath and a similar but thinner sheath surrounding the vascular cylinder. Starch deposits are absent in the cells, except in the inner cortex. In the stipe the vascular bundle is corrugated due to the protoxylem areas being raised as ridges (over 50 per stipe) and each group is associated with a mucilage-containing strand of cells on its inner surface. *P. wallichiana* is probably unique among ferns in having bases of reduced leaves acting as storage organs.

INTRODUCTION

DURING the course of a comparative study of the vascular organization in the homosporous ferns, certain interesting morphological peculiarities of

the rhizome of *Pteris wallichiana* Ag. were noticed. These are recorded in the present communication. Some details regarding the anatomy of the rhizome of *P. wallichiana* are described by Mehra (1944). Some aspects of the vascular organization in some related species are reported by Bower (1928), Gwyne-Vaughan (1903) and Tanseley and Lulham (1904). *P. wallichiana* is a large and graceful fern of the Central and Eastern Himalayan region, occurring abundantly in the hill ranges of N–E. India at *ca.* 1,000 to 2,500 m. altitude. It has a short stout rhizome bearing large leaves, nearly 3 m. tall (stipe up to 2 m.) and with the lamina tripartite, decompound and sub-membraneous. Material for this study was collected from various places in Khasia Hills of Assam, growing in exposed to semi-exposed, well-drained localities on rocky or gravelly soil. Anatomical observations recorded here are based on microtome sections stained with Safranin, Sudan-IV and Iodine. Stelar organization is studied mainly from scale-to-scale reconstructions based on serial microtome sections.

OBSERVATIONS

The rhizome of *P. wallichiana* is short, ascending, hypogeal and covered by chaffy, basally attached paleae at the growing apex and between the leaf bases. In adult plants it is over 2·5 cm. thick, bearing crowded leaf bases and tufts of strong wiry roots between them. The leaf bases are markedly swollen and fleshy, the swollen region being often 3–5 cm. long and 1·5–2·5 or even 3 cm. across. It is slightly tapered towards the base and dorsi-ventrally compressed, with a nearly flat, medianly grooved, adaxial side. This region is sharply demarkated from the rest of the stipe (Fig. 2, *l*) and bears more conspicuous lateral aerating bands. In addition there is an abaxial branch bud (Fig. 2, *b*) borne on the basal half of each leaf base. The larger and more swollen leaf bases bear one or more raised dark brown lenticels (Fig. 2, *n*) on its abaxial surface. A majority of the leaves in *P. wallichiana* are reduced, except for their prominently swollen bases. These leaf bases of reduced leaves (Fig. 2, *rl*) are characteristic in being often larger in size than the bases of normal well-developed leaves, more fleshy and ovoid in shape (with a broader anterior end) but with the adaxial side nearly flat and bearing a conspicuous median groove. A vestigial, circinnately coiled, small hump crowns each and represents the rest of the frond. In addition to these reduced leaves there are occasional highly reduced vestigial leaves (appearing as insignificant humps on the surface of the rhizome) in which even the leaf bases are reduced. Such vestigial leaves are restricted to the ventral surface of the rhizome.

Structurally, the rhizome is soft and parenchymatous. The epidermis as well as the ground tissue consists of thin-walled cells. There is a broad cortical sheath consisting of 8–15 layers of narrow, slightly thick-walled, elongated, sclerenchyma cells with dark brown walls. The sclerenchyma sheath separates a narrow outer cortex (composed of 4–10 layers of more compactly arranged parenchyma) from the inner ground tissue. There is a thin, sometimes interrupted, sclerenchymatous sheath (often 4 or 5 cells thick) surrounding the vascular cylinder, but separated from it by a broad band of parenchyma, often 10–12 cells thick. The parenchyma cells of the inner cortex contain starch deposits; starch is absent from the other tissues of the rhizome (including the cells of the pith). Tannin-filled cells occur in small groups, scattered in the ground tissue of the medullary region.

The vascular cylinder of the adult rhizome (Fig. 1) is a radiosymmetric solenostele with a ribbon-like medullary vascular strand (Fig. 1, *mb*) which regularly unites with the vascular cylinder at the region of the leaf gaps. The leaf gaps are small, strictly adaxial to the leaf traces and semi-ovate in outline. They are arranged spirally around the vascular cylinder, and the gaps of successive leaves do not overlap. The leaf traces are large, prominent structures (often larger in diameter than the main stelar cylinder). Vascular connection to each leaf (Fig. 1, *lt*) consists of a large, thin, gutter-shaped bundle with a prominent broad invagination behind either of its margin (so that in a t.s. the leaf trace bundle is Ω-shaped). To produce a leaf trace, the vascular cylinder bulges out as a prominent smooth hollow ridge. The vascular tissue of the bulged region is conspicuously thinner than at other regions of the stele. A deep groove develops on either side of the bulge, at the region where the bulge merges with the rest of the stele. Soon, the bulged region separates as a leaf trace bundle, forming a small adaxial gap. Before the leaf trace separates, it gives off on its abaxial side an irregular transverse row of slender root traces and, a little farther up, a cylindrical siphonostelic branch trace (Fig. 1, *bt*). A branch gap is absent. The medullary vascular strand acts as a compensatory bundle to close the leaf gaps. The medullary strand subtends each leaf gap and towards the anterior end of the gap moves close to the inner surface of the stelar cylinder. The leaf gap is closed by its margins fusing with the outer surface of the medullary strand one after the other or by one of the margins fusing with a margin of the medullary strand and the other fusing with the outer surface close by. In other cases, the medullary strand gives off a thick superficial branch which connects the two margins of the gap and thus closes the gap. Soon after the gap is closed the main medullary strand separates from the vascular cylinder

and proceeds in the direction of the next leaf gap in succession. The medullary strand, thus, has a zig-zag, spiralling course through the medulla of the rhizome. Vascular connection to well-developed leaves as well as the reduced leaves are similar; vascular connection is highly reduced in the case of the vestigial leaves. The latter is nearly similar in shape to the normal leaf trace but markedly smaller in size (Fig. 1, *vl*) and ending blindly in the hump-like vestigial leaf. A small leaf gap subtends these vestigial leaf traces and the medullary strand acts as a compensatory bundle in the case of these gaps also. A hump-like vascular protuberance represents the branch trace on the vascular supply of the vestigial leaf (Fig. 1, *vb*).

The xylem tissue of the vascular cylinder of the rhizome is massive, composed of 4–6 layers of wide scalariform tracheids with xylem parenchyma cells scattered between them. The phloem constitutes a thin layer composed of 3–5 rows of small cells. The peripheral 1–2 layers of the phloem consist of transversely elongated cells; these recall the tangential cells reported in the Cyatheaceae (Holttum and Sen, 1961). The pericycle is two-layered and composed of large cells with dense protoplasmic contents. The endodermis is ill-differentiated.

The leaf bases are fleshy and tuberous. In the well-developed leaves the epidermis and a few layers of hypodermal cells of the leaf bases are thick-walled, the thickening of the walls decreasing progressively in the inner layers. As in the rhizome, there is a distinct cortical sclerenchymatous sheath and a similar sheath surrounding the vascular strand; both are more prominent than in the rhizome. Laterally the cortical sheath is interrupted at the region of the aerating bands. The vascular bundle is solitary, gutter-shaped and with a prominent submarginal invagination on either side. The xylem band of the vascular bundle is corrugated (Fig. 4) with longitudinal, nearly equidistant, smooth ridges on the outer surface. These ridges are more prominent and closely placed on the abaxial half of the xylem (in a normal leaf there are *ca.* 35–40 such ridges on the abaxial half and 10–20 on the adaxial half). These ridges represent the protoxylem areas. At the region of the lateral invagination of the vascular strand protoxylem ridges are few. The metaxylem regions are composed of a single unbroken row of broad scalariform trachieds. On the inner surface of each protoxylem group (except at the extreme margin of the vascular strand) is a cylindrical band of elongated, large, thin-walled, mucilage-containing cells (Figs. 3, 4, *m*). In older stipes these cells often collapse, forming a continuous mucilage canal. As in the rhizome, the phloem forms a thin sheath, the pericycle is 2-layered and the endodermis ill-differentiated. Dense deposits of starch

occur in all cells of the ground tissue except those of the sclerenchyma sheath and the peripheral layers of hypodermal cells. The swollen bases of reduced leaves are similar except that sclerenchyma tissues are entirely absent and the vascular bundle is conspicuously thinner. Also, starch deposits are more profuse in the cells. The epidermal cells and 2 or 3 layers of hypodermal cells possess faintly thickened walls and are devoid of any starch deposits. All other cells of the ground tissue are extremely thin-walled and nearly devoid of intercellular spaces. Groups of tannin-containing cells occur scattered in the ground tissue. One or more prominent 'lenticels' occur on each swollen leaf base, mostly restricted to the abaxial surface (Fig. 2, *n*). These are irregularly disposed, oval or circular, raised, dark brown areas where the epidermal and hypodermal (5–7 layers in the developed leaves) layers of cells are broken apart and the cells of the inner cortex protrude out. These protruded specialised cortical cells are devoid of starch deposits and are conscpicuously elongated radially. Thus, the lenticel is composed of a bunch of elongated cells arranged in a palisade-like manner and continuous with the inner cortex. Five or six layers of cells are elongated, and at the free outer surface these cells spread out slightly. The walls of these specialised cells are dark brown in colour and faintly thickened. The outer rows of the cells are devoid of protoplasmic contents.

The stipe is tetragonal, nearly a centimeter thick and with a faint lateral groove (formed by the aerating bands) on either side. Structurally, the stipe is similar to the leaf base, but the sclerenchymatous tissue is better developed and starch deposits are absent. The vascular strand divides towards the apex of the stipe into three equal bundles to supply the three rachises (Figs. 5–10). Before division the lateral invaginated regions of the stipe bundle come together and fuse, making the bundle a hollow cylinder (Fig. 6); the divergent adaxial margins remain as broad flaps attached medianly to the cylinder. Soon the vascular cylinder becomes dorsiventrally compressed and laterally expanded. It becomes constricted into three cylindrical portions (Fig. 7), and later separates as three separate cylinders (Figs. 8, 9). The pair of marginal flaps is attached to the middle one of these cylinders and arch over the lateral ones on either side. Soon a broad ribbon-like strand separates from the marginal flap along its either margin (Figs. 9, 10). Each of these strands gets connected to the branch cylinder nearest to it, the union being by the median abaxial surface of the strand (Fig. 10). The branch cylinder later opens up adaxially by a median slit which splits the fused ribbon-like strand into two (Fig. 11). This results in an Ω-shaped bundle which enters the rachis base. Vascular supply to the branch rachises

originates as cylindrical extramarginal strands and follows the same sequence at origin as the vascular strands to the main rachises (Figs. 12–15).

DISCUSSION

The most characteristic morphological feature of the rhizome of *P. wallichiana* is the presence of special storage organs formed by the reduced leaves. The rhizome itself has no prominent storage tissues; reserve food is stored in the swollen persistent bases of normally developed leaves and the well-developed storage organs formed by the bases of reduced leaves. In ferns the rhizome generally serves as a repository of food material, starch being deposited in the parenchymatous ground tissue. Where the leaf bases are persistent, starch is often deposited in the tissues of the leaf bases also; in some cases the leaf bases may even be slightly swollen. But specialised extra storage organs as found in *P. wallichiana* are very rare; in some like *Nephrolepis cordifolia* the apices of stolons become tuberous and act as storage organs as well as organs of vegetative reproduction. This type of adaptation is uncommon. Even in such cases the rhizome remains as the major storage organ. The characteristic adaptation of *P. wallichiana* thus appears to be unique, in that the function of storage of reserve food is relegated to the bases of reduced leaves and the rhizome scarcely stores any reserve food.

Another interesting feature in the morphology of the rhizome of *P. wallichiana* is the presence of occasional vestigial leaves. Total and partial suppressions of leaves in some regions of the rhizome is reported in *Oleandra* (Nayar and Chandra, 1968) in which in some species like *O. wallichii* and *O. distenta* all leaves on the ventral region of the rhizome are suppressed consequent to the rhizome becoming creeping. The condition in *Oleandra* is taken as an indication that the more primitive condition in the genus is one with an erect dictyostelic rhizome. Possibly the presence of vestigial leaves on the ventral surface of the rhizome of *P. wallichiana* also indicates the same.

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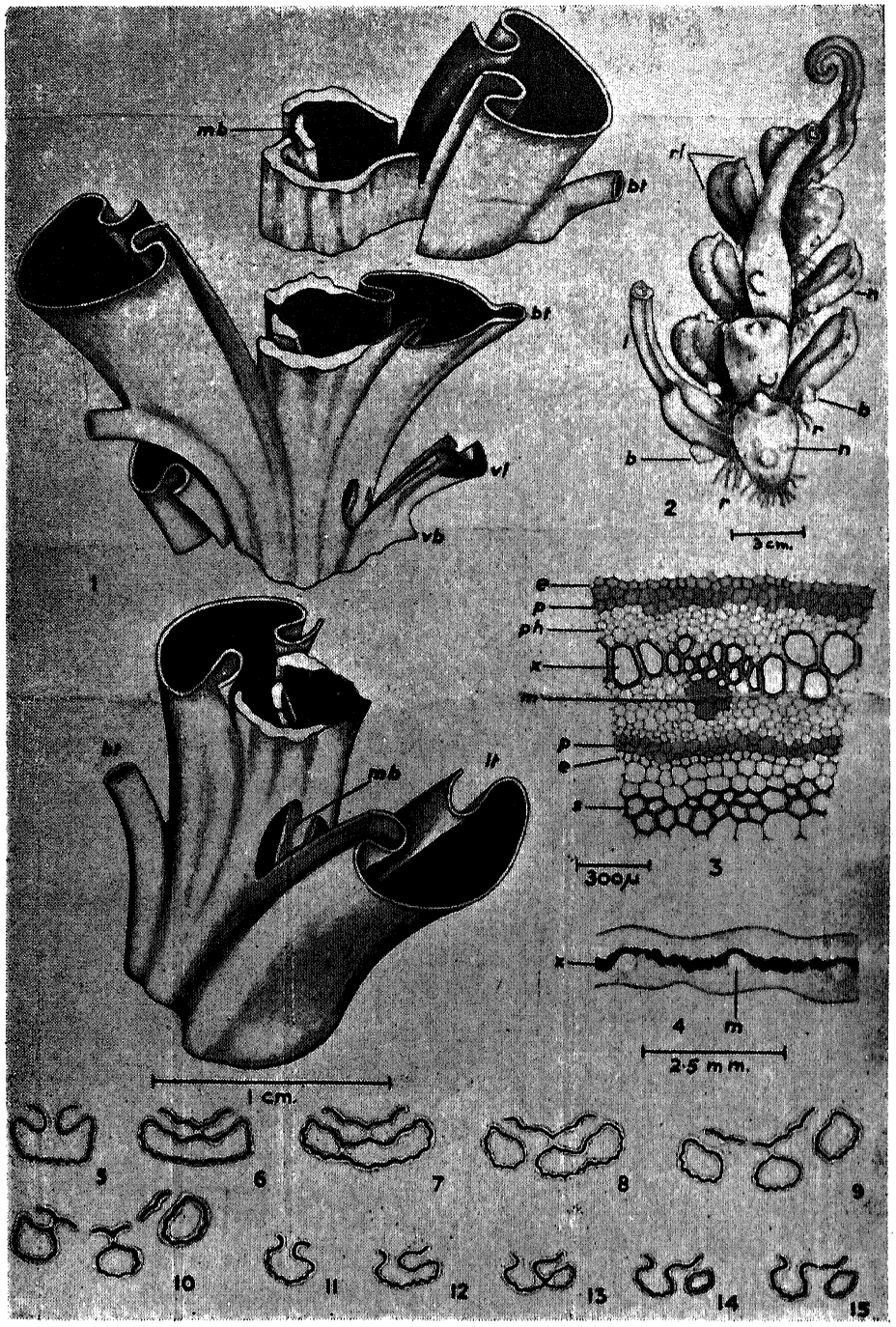

FIG. 1. Stelar cylinder of a portion of the rhizome of *P. wallichiana* (shown in pieces to explain the organization).

FIG. 2. Dorsal view of the rhizome of an adult plant, showing the swollen bases of normal as well as reduced leaves.

FIG. 3. Cellular organization of a portion of the vascular strand of the stipe.

FIG. 4. T.s. of a portion of the vascular strand of the stipe showing distribution of mucilage strands.

FIGS. 5–10. Configuration of the vascular strand at successive heights (base upwards) of the stipe showing branching.

FIGS. 11–15. Configuration of the vascular strand of one of the primary rachises at successive heights from the base showing origin of pinna trace (on the right).

(*b*, branch bud; *bt*, branch trace; *e*, endodermis; *l*, base of normal leaf; *lt*, leaf trace; *m*, mucilage-containing cells; *mb*, medullary vescular strand; *n*, lenticel; *r*, root; *rl*, reduced leaf; *s*, sclerenchyma; *p*, pericycle, *ph*, phloem; *x*, xylem; *vb*, vascular hump representing reduced branch; *vl*, vascular connection to the vestigial leaf.)

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