IN SUPPORT OF PHYLLORHIZE?

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ABSTRACT

Based on a study of adult and juvenile plants of over a dozen selected taxa of ferns it is shown that the cormophytic plant body is composed mainly of leaves and roots associated with them. Each leaf is associated with a basal root and one or more lateral roots, and the main bulk of the stem consists of leaf bases; no roots other than leaf-associated ones do occur. Vascular differentiation occurs associated with leaves and roots only. Basal regions of vasculature of leaves are interconnected to constitute the stele found in the stem. Protostele of juvenile plants is a product of interconnected bases of simple cylindrical vasculature of juvenile leaves. Transition from protostele to dictyostele is correlated with change to channel-like form of leaf vasculature and not by parenchymatisation of centre of protostele. Axial theory, Stelar concept and Size and Form hypothesis do not explain the characteristic morphology of primitive vascular plants. The present study supports Phyllorhize theory to some extent.

INTRODUCTION

ONE of the enigmas in history of evolution of green plants is how vascular plants came to have a cormophytic plant body (*i.e.* a body composed of three morphologically different parts *viz.* root, stem and leaf). It is accepted that vascular plants are derived from green algae, since these algae are the only group which antedate vascular plants in evolutionary history, are simpler in structure organisation and life history, and at the same time share an array of significant common characters such as chloroplast ultrastructure, complement of chloroplast pigments, process of photosynthesis, basic nature of carbohydrate synthesised, occurrence of 1,4-glucan solely within plastids, capacity to produce sporopollenin, flagella characteristics and presence of cellulose and hydroxyproleine rich protein in cell wall; in addition they possess enzymatic complement similar to lignin-synthesising reaction pathway of vascular plants. However, vascular plants differ from all algae in several distinctive morphological features such as possession of a cormophytic plant body, well organised tissue systems, characteristic cuticular covering (and stomatal mechanism), and distinctive vascular system, the evolutionary history of none of which is known. No intermediary life forms which give a clue to the evolution of these characters are known. Hypotheses which can hardly be verified experimentally, like Axial Theory, Stelar Concept, Size and Form Hypothesis, etc. attempt to give a rational explanation to the morphological peculiarities which distinguish vascular plants from algae.

The popular concept regarding evolution claims that from a heterotrichous algal ancestor evolution of vascular plants took place by reduction and ultimate loss of the creeping system of branches of the plant body and the elaboration of the erect system of branches in such a way that the latter formed an erect axis havhng an apical growing point[1,2]. This upward growing axis (stem) is interpreted by the Axial theory as the principal organ on which leaves and roots are borne as appendages. Based on an extensive study of pteridophyte gametophytes, Nayar[3,4] has shown that at least among the gametophytic generation of this most primitive group of vascular plants, it is the creeping system of branches of the heterotrichous ancestor which got elaborated to form the plant body, and the erect system plays only a minor role. The creeping system during evolution acquired a lateral ring-like meristem (resulting in horizontal growth)

and later an apical meristem (resulting in upward growth) in addition. It is hypothesised that the process of evolution was probably similar in the sporophytic generation also (particularly of ferns), the lateral ring-like meristem giving rise to leaves while the less dominant apical meristem giving rise to the stem. According to this, both the stem and the leaf are primary organs and leaf is not an appendage borne on stem as maintained by Axial theory. In sharp contrast to Axial theory is the Phyllorhize theory[5] of cormophytic construction of body of vascular plants. This theory supports the classical Phytonic concept which maintains that all diverse parts of shoot in vascular plants are metamorphosed leaves, the stem being a construction of 'phytons' or segments of which leaf bases or extensions thereof are the fundamental units. Though it concerns only with fern sporophytes and has never gained popularity, the Phyllorhize theory holds that the plant body is constituted entirely of phyllorhize units consisting of an upward directed leaf and a downward directed root connected together, and maintains that juvenile sporophytes are composed of one or more phyllorhize units and initially have no stem; a stem comes into existence only when fusion of phyllorhizes takes place and arises laterally on the phyllorhize as a bud.

The widely accepted Stelar concept[6] is primarily based on the Axial theory and maintains that vascular tissue which occurs in all regions of plant body (stem, root, leaf) together constitutes one unit and forms an organ, the stele, which has a definite morphology and in which evolutionary changes occur in a predictable manner. Vasculature of the axis or stem constitutes the main part of the stele and gives off vascular connections to leaves and roots[7]. Most morphologists accept the stele as primarily cauline, in that it is developed from the shoot apical meristem[8]. Bower[9,10] proposed the Size and Form hypothesis to explain the different forms in which stelar cylinders occur in the axis of vascular plants, and currently it is accepted that stelar evolution took place as enunciated by this hypothesis. It maintains that the surface exposed by the stelar cylinder to living tissues surrounding it is critical, and it is not posssible for the plant to

function beyond a specific proportion between volume of stele and surface exposed by it. As the size of stele increases either during growth of individual plants or in the course of evolution, its volume increases in geometric proportion while surface area increases in arithmetic proportion only. The hypothesis presumes that the increase in the size of stele would ultimately reach a stage where further increase without increase in the surface area becomes untenable; at this stage a change in the form of the cylindrical shaft-like stele occurs (fluting of surface as in Lycopodidae or development of a central pith as in Filicopsida) whereby surface area is increased considerably. The Phyllorhize theory, mentioned above, offers a totally different interpretation of stele, supporting Hanstein's Leaf-trace concept[11] which currently has several supporters[12-19]. The few detailed studies reported in literature[20,21] on juvenile sporophytes of ferns also appear to support the Phyllorhize concept.

The present communication is a brief account of how far a study of various aspects of the development and morphology of stelar cylinder, in over a dozen selected taxa of leptosporangiate ferns supports the Phyllorhize concept. The study concerned mainly with (i) morphology of stele in adult sporophytes, (ii) progressive changes in stelar morphology as juvenile plants grow to adult condition, and (iii) morphogenesis of leaf, root and vasculature at shoot apex in adult as well as juvenile plants of *Acrostichum aureum, Blechnum orientale, Drynaria mollis, D. quercifolia, Drymoglossum piloselloides, Kaulinia pteropus, Leptochilus decurrens, Microsorium linguaeforme, M. punctatum, M. scolopendria, Nistarika bahupunctika, Pyrrosia lanceolata, P. mollis, Stenochlaena palustris* and *S. tenuifolia,* and tends to show that the classical Axial Theory, Stelar Concept and Size and Form Hypothesis are not applicable to them.

MORPHOGENESIS OF STELE

There is a distinct shoot apical meristem established early during embryogenesis in all the taxa studied, and this meristem contributes tissues which constitute a part of the main axis of

the stem. Leaves are developed on this axis as appendages, in as much as that they develop from single peripheral initial cells close behind the meristem. Early during leaf development, a peripheral cell at the basiscopic base of the leaf differentiates into a root initial cell; by a series of divisions it establishes a root apical cell which by its activity develops into a root associated with the leaf base. Other roots may develop on the acroscopic base of the developing leaf, commonly forming two lateral anterior rows on the leaf base. Initial cells of all roots are peripheral cells derived from the leaf initial cell and constituting the leaf base. No root is developed other than those associated with leaf bases. Vascular tissues are developed associated with leaves and roots only; no vascular differentiation occurs associated with stem apex. Early during ontogeny, vascular differentiation takes place behind the leaf apical meristem in the form of a short channel-shaped strand. As the leaf grows, further vascular differentiation occurs in continuation of both anterior as well as basal ends of the initial vascular tissue; undifferentiated cells of ground tissue next to either end metamorphose into vascular tissue so that the vascular strand extends both acropetally and basipetally. Meanwhile a shaft-like vascular strand is differentiated posterior to the growing apex of the leaf-associated root. As in the case of leaf vasculature, the root vasculature extends basipetally; ultimately it gets connected to leaf vasculature. Vasculature of basiscopic root gets connected to the abaxial surface while vasculatures of the acroscopic lateral roots get connected to the nearest margin of the channel-shaped leaf vasculature. Vasculature of each leaf as it extends basipetally gets connected marginally to vasculature of next two earlier leaves in succession. Such union of leaf vasculatures results in the characteristic stelar cylinder of the stem (figure 1); in many ferns the ultimate form of the stele is determined by vasculatures of leaf-associated roots and the pattern in which they get interconnected among themselves.

Vascular differentiation continually takes place in the region next and behind the leaf apical dome. Provascular tissue forms an intact

channel-shaped strand, the cells of which divide repeatedly by walls parallel to long axis of the leaf. Except isolated ones in strategic positions in the strand, the narrow daughter cells thus formed lose mitotic capacity early and metamorphose into tracheids; isolated daughter cells here and there, however, divide repeatedly by walls perpendicular to the long axis producing a longitudinal row of small isodiametric cells which remain meristematic. At the region where vascular differentiation occurs, rapid expansion in girth of leaf axis takes place by repeated divisions of cells of ground tissue; this induces a shearing stress on the channel-shaped vascular strand, the tracheids constituting which have by then lost mitotic capacity and capacity for radial expansion. Rapid division and expansion of the longitudinal rows of meristematic cells left between tracheids follows making it possible for the vascular strand to expand radially and keeping pace with the increase in girth of leaf axis. This results in the formation of longitudinal rows of parenchyma islands (lacunae) in the channel-shaped leaf vasculature, dissecting it into a reticulum (figure 10). The number of rows of lacunae is characteristic of each taxon and the breadth of lacunae is proportionate to the extent of radial increase in size taking place after tracheid development. Once the increase in girth ceases, the cells constituting lacunae in some taxa like *Microlepia*[22] metamorphose into tracheids so that the dissected leaf vasculature becomes intact again.

A. STELE IN TAXA HAVING ERECT STEM

In taxa like *Acrostichum* and *Blechnum* leaves are spirally arranged on an erect unbranched stem (rhizome); vasculature of stem is dictyostelic, dissected by overlapping leaf gaps. At the anterior end the stelar cylinder is open and continued as the channel-shaped vasculature of the three youngest leaves (figure 1). Vascular differentiation occurs as a channel-shaped strand at the leaf base of the youngest leaf and the strand is initially unconnected to other vascular tissue. A broad ribbon-like vascular bridge is formed interconnecting its basal margin with the
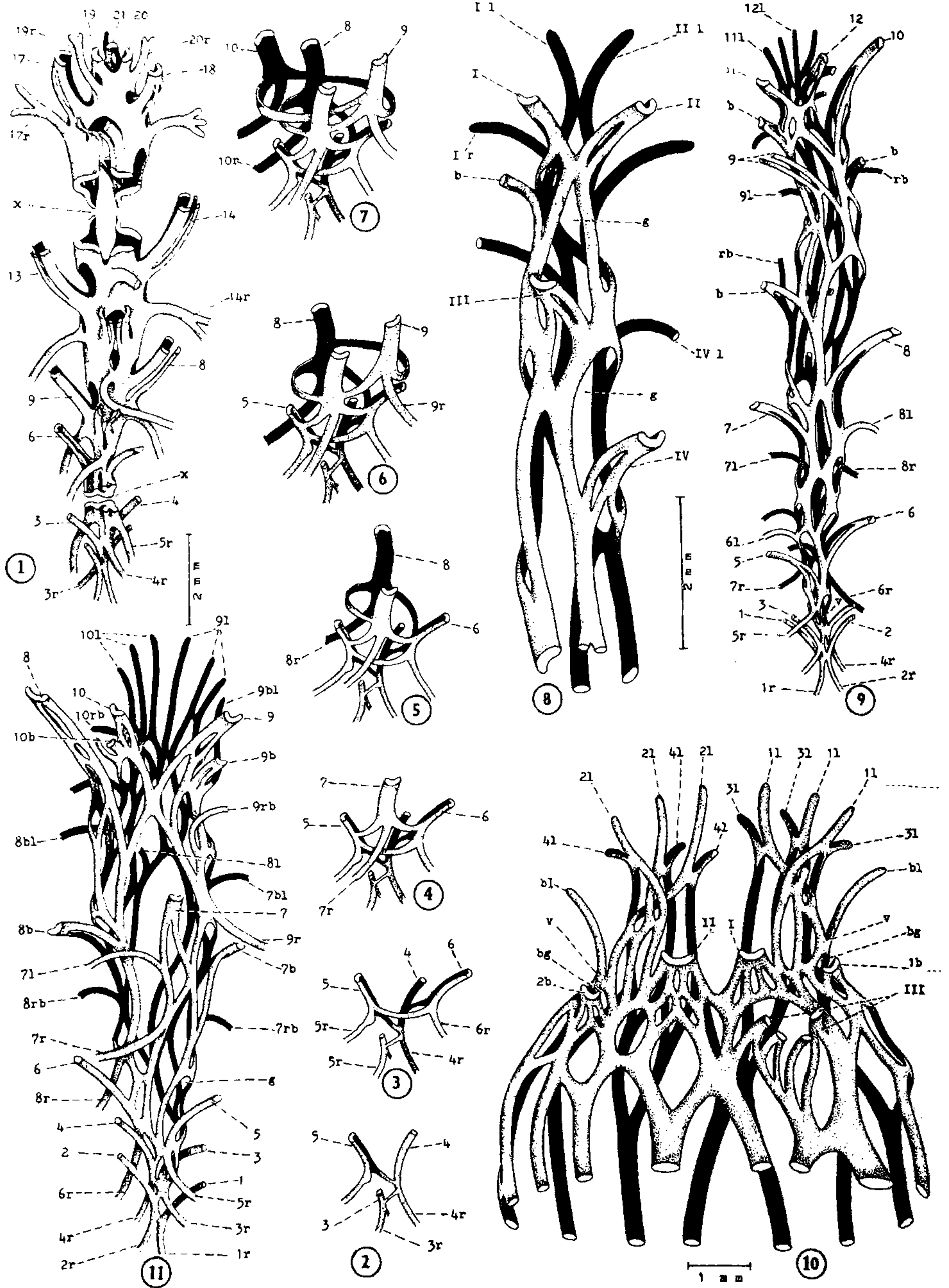
nearest basal margin of vasculature of the next older leaf on one side, and a similar bridge interconnects the opposite margin with the nearest margin of vasculature of the third leaf. Leaves being spirally arranged on the stem, the interconnected basal regions of vasculature of the three successive leaves form a hollow vascular cylinder which constitutes the stele. The vascular bridge between the first and third leaf crosses anterior to vasculature of the next posterior leaf so that a parenchymatous area gets delimited adaxial to the latter, constituting the leaf gap associated with it. As growth continues and further leaves are produced on the stem, the stelar cylinder extends anteriorly by progressive addition of basal regions of vasculature of successive leaves; leaf gaps are formed adaxial to vasculature of each when vasculature is developed associated with the third succeeding leaf. There is a root associated with each leaf at its abaxial base. The intimate relationship between leaf and root as also the role played by leaf vasculature in construction of the stele is more evident in juvenile plants. All juvenile leaves, including the first one, are associated with a solitary basal root (figure 1). As the first juvenile leaf develops, a root is formed basiscopically associated with it, leaf and root growing in opposite directions and root appearing as a downward prolongation of the leaf base. Vascular differentiation takes place early at the leaf base as well as at the root base. Both are in the form of a slender solid cylindrical strand, and

both are separate though close to each other. Soon the intervening parenchyma separating the nearby ends of the two strands metamorphoses into vascular tissue, interconnecting the basal end of the leaf trace with the upper end of the root trace in such a way that they appear as a single strand. As the leaf and root grow out, this vascular strand extends, following the apical meristems of the root and leaf. The second juvenile leaf is formed opposite the first (*i.e.* on opposite side of the shoot apical meristem) and is similar to the first leaf in having a basal root and vascular system developed similarly. Initially there is no interconnection between vasculatures of the two leaves, though at the base both are closely placed. A vascular bridge is soon formed between the two, interconnecting the region where vasculature of each leaf merges with vasculature of its associated root. The bridge is cylindrical and similar to vasculature of the leaf base. The third juvenile leaf is similar to the first two and is borne anterior to the first. A vascular bridge is formed interconnecting its vasculature with vasculature of second leaf, the bridge merging with the latter at the region immediately anterior to the bridge connecting it with vasculature of the first leaf. Succeeding juvenile leaves follow the same pattern so that a series of protostelic leaf-root vasculatures are interconnected by short vascular bridges. The vascular bridges along with the basal regions of leaf vasculatures constitute a protostelic vascular cylinder of the stem.

Figures 1–11. Vascular organisation of shoot axis in ferns. **1.** Vasculature of juvenile rhizome of *Blechnum orientale*. **2–7.** Explanatory diagrams representing successive steps in formation of a cylindrical dictyostele in juvenile rhizome of *Acrostichum aureum*, by paired vascular bridges developed between bases of vasculature of successive leaves. **8.** Dorsal view of vasculature at apex of adult rhizome of *Pyrrosia lanceolata*. **9.** Dorsal view of vasculature of juvenile rhizome of *Microsorium scolopendria*. **10.** Dorsal view of vasculature at apex of adult rhizome of *Drynaria mollis*. **11.** Dorsal view of vasculature of juvenile rhizome of *D. quercifolia*. (1, 2, 3, . . . — Basal region of vasculature of successive juvenile leaves from first onwards; I, II, III, IV—Basal region of vasculature of adult leaves from apex downwards, the last leaf borne on the stem being designated as first from apex; 1b, 2b, . . .—Vasculature of branches associated with 1st, 2nd, etc. leaves; 11, 21, . . . – Vasculature of lateral roots associated with 1st, 2nd, etc. leaves; 1r, 2r, . . . —Vasculature of basal roots associated with 1st, 2nd, etc. leaves; 7rb, 8rb, . . . —Vasculature of roots associated with branches marked seven, eight, etc.; b—Vasculature of branch; bg—Branch gap; bl—Lateral root associated with branch; g—Leaf gap; x—region at which the vascular cylinder is shown cut transversely).

Successive juvenile leaves are progressively larger and the shape of leaf vasculature gradually changes with this increase in size. Instead of being cylindrical the vasculature becomes dorsiventral and ribbon-like at first and then channel-shaped. Vasculature of the leaf-associated root, however, remains cylindrical and slender. Nature of vascular bridges as well as pattern of interconnection between vasculature of successive leaves also change, and consequently the form of the resultant stelar cylinder in the stem. A pair of ribbon-like vascular bridges, one on either side at the base, and as extension of the marginal region, is developed associated with each leaf. One of them gets connected with the nearest basal margin of vasculature of the immediately earlier leaf while the other connects to the basal margin of vasculature of the leaf next older. This results in the formation of a tubular stele in the stem, formed by basal regions of channel-like vasculatures of the three youngest leaves and vascular bridges interconnecting their basal margins. Vasculature of all succeeding leaves are basically similar, being channel-shaped at base and interconnected by marginal vascular bridges with the nearby margin of the vasculature of the next two older leaves as found in adult plants. The transition from protostele to dictyostele is abrupt and usually occurs when the juvenile plant has produced four or five leaves. There occurs no parenchymatisation of the central region of protostele as commonly reported in literature.

B. STELE IN TAXA HAVING PLAGIOTROPIC STEM

In the different polypodiaceous taxa, adult stem (rhizome) is plagiotropic bearing leaves restricted to dorsal surface in two (exceptionally one as in *Microsorium linguaeforme*) rows, and characteristically branched, each leaf base having an abaxially lateral often dormant branch associated with it. Vascular cylinder of adult stem is a dictyostele perforated by lacunae into many slender cylindrical meristeles (figure 10). Leaves are formed in alternate succession behind the shoot apex. After each leaf is initiated the shoot apex divides equally (or nearly so) into two; the daughter apex nearest the leaf becomes dominant and continues growth of the stem while the one away from leaf becomes sluggish and ultimately dormant. The latter gets pushed away to one side and constitutes the characteristic dormant branch which appears associated with the first leaf borne on the dominant daughter apex. A leaf apex is differentiated on each daughter apex on the side facing the other daughter apex. The leaf apex on the sluggish daughter apex is sluggish and ultimately becomes dormant, but the one on the dominant daughter apex continues development and soon grows out as a normal leaf. Each leaf is associated with a basal root (figure 8), a root apex getting differentiated on the abaxial side of the leaf base early. In addition, each leaf is associated with lateral roots borne on the adaxial side of the leaf base. The number of lateral roots varies, some like *Pyrrosia lanceolata* (figure 8) and *Drymoglossum piloselloides* having only one (borne on margin away from dorsal median plane of rhizome), most others (*P. mollis, Microsorium scolopendria, Drynaria quercifolia, D. mollis*) having three (figure 10) and some like *M. linguaeforme* five to seven. Lateral roots are borne in succession on either margin of leaf base and those on opposite margins alternate. Leaf bases are prominent and soon after initiation of leaf the leaf apex becomes meristematically far more active than the shoot apex, producing a prominent leaf base which, as it grows forward, carries the shoot apex up with it so that the extended leaf base constitutes a major portion of the internode, tissue derived from the shoot apical meristem contributing only a minor part.

Vasculature associated with leaf apex is channel-shaped with its concavity facing the shoot apex; vasculature of root is a solid slender cylinder (figures 8, 10). Whereas vasculature of the basal root gets connected superficially on the abaxial surface of the leaf trace, vasculature of lateral roots gets connected to its nearest margin. All roots, especially the lateral ones, grow forward before they curve out towards the substratum. Vasculature of each leaf gets intercon-

nected with vasculature of the next older leaf (borne on the opposite side of stem) by a broad vascular commissure between the dorsal margins of the two. In addition, a ribbon-like vascular bridge is developed on the ventral margin at the base and this extends downward to get connected with the ventral margin of vasculature of the next posterior leaf (third from shoot apex) on the same side of the stem. Since leaves are in two dorsal rows and not spirally disposed as in *Acrostichum*, etc., the composite vasculature formed in the stem by interconnected bases of leaf traces is not tubular but only channel-shaped and restricted to dorsal half of the plagiotropic stem; the channel is open on ventral side and its margins bear the forward-growing root traces of roots associated with ventral margin of each leaf trace. Leaf traces get dissected by up to four longitudinal rows of lacunae, and the rows extend to the extreme base of leaf trace. This results in the channel-shaped vasculature of stem being dissected into a characteristic number of slender meristeles. Vasculature of lateral roots of at least two successive leaves on either side of the stem extend forward beyond the level of the youngest leaf; in many taxa the basal root also is directed forward and runs parallel. Vascular interconnections are developed between nearby root traces borne on the ventral margin; they develop regularly between successive lateral roots of the same leaf (in taxa having more than one lateral root per leaf) and also between roots of successive leaves on the same side of the stem, so that a continuous reticulum is formed consisting of as many slender vascular strands as there are lateral roots associated with each leaf (figures 8, 10). Interconnected basal regions of vasculature of roots associated with successive leaves (one in front of other) constitute each of these strands (meristeles). Interconnections develop regularly between vasculature of the first formed lateral root of each leaf and the corresponding lateral root of the next older leaf (which is on the opposite side of stem) so that the reticulum formed ventrally in either half of stem is regularly interconnected along the ventral median plane. This results in a composite reticulum interconnecting the two margins of the channel-shaped

stele of the internode, and constituting its ventral half; the number of meristeles of the ventral half corresponds to the number of lateral roots involved in the process.

Branching of stem and vasculature developed in association with the dormant leaf on the branch alters the morphology of stele in many taxa. Vasculature of dormant leaf (which constitutes the branch trace) and that of the dominant leaf next to it (*i.e.* the leaf with which the branch is associated) get interconnected at the base. In some (*Drymoglossum, Kaulinia, Pyrrosia, Microsorium linguaeforme, M. punctatum*) they get connected medianly by their abaxial surface so that the branch trace appears as a superficial appendage on leaf trace, and then does not alter the gross morphology of the stele. In some others (*Drynaria, Leptochilus, Nistarika*[23], *M. scolopendria*) the branch trace gets connected by its basal dorsal margin with the ventral margin of the leaf trace posterior to the level at which ventral lateral roots are attached (figure 10). As a result the composite vasculature of stem (formed by marginally interconnected basal regions of vasculatures of the two rows of leaves) gets laterally extended at the region where branch traces occur, the ventral margin of the branch trace constituting the free margin of the composite vasculature of stem at these regions. Lateral roots similar to those of the dominant leaves are commonly found associated with the ventral margin of the branch trace also, and these along with roots of the associated leaf, extend forward through the ventral half of stem (figure 10). These roots develop vascular interconnections among themselves and also with vasculature of the first formed lateral root of the associated leaf so that they constitute part of ventral half of the stelar cylinder. The number of lateral roots borne on ventral margin of branch trace varies with each taxon, but is invariably less as compared to those on ventral margin of the associated leaf. Thus, while there are three lateral roots associated with the dominant leaf in *Drynaria quercifolia, D. mollis* and *M. scolopendria* there is only one associated with the branch trace in *D. mollis* and two in the others. This results in the ventral half of stele of the former

consisting of *ca* 8 meristeles and of the latter of *ca* 10 meristeles.

In *Microsorium linguaeforme* leaves are in a single dorsal row and each is abaxially associated with a pair of opposite branches[24]. As in other Polypodiaceae the shoot apex divides equally into two after producing each leaf, but in contrast to others the resultant daughter apices repeat the process so that four sister daughter shoot apices are produced; leaf formation on the daughter apices is initiated only after the four apical domes are established. Of the two pairs of daughter apices one becomes sluggish and ultimately dormant, constituting the first branch found at each node; the leaf primordia on this pair also become dormant. The other pair of apices continues growth but soon the daughter apex away from the dormant pair becomes dormant, constituting the second branch at the node. The median daughter apex continues growth, the leaf born on it ultimately developing into the next leaf on the main stem. Vascular differentiation takes place associated with all four leaf primordia borne on the four daughter shoot apices; all leaves are associated with lateral roots, the dominant leaf having three or four lateral roots on each margin. Vasculature of dominant leaf is strongly channel-shaped and gets dissected by five rows of lacunae; at the base it splits medianly into two ribbon-like dissected strands which get connected to either margin of vasculature of the immediately older leaf so that the vasculature of young internodes (interconnected bases of successive dominant leaves) is channel-shaped. Vascular bridges between root traces on opposite margins (to form the reticulate ventral half of stele) develop rather late. Vasculatures of the pair of dormant leaves on the first branch at the node get interconnected at base by their abaxial surfaces; their free margins get connected to the lateral abaxial surface of vasculature of the dominant leaf. Vasculature of dormant leaf of the second branch also gets connected superficially by its abaxial base with the opposite lateral abaxial surface of vasculature of the dominant leaf. Thus, both branch traces appear as superficial appendages on the channel-shaped vasculature of the dominant leaf.

As in the other ferns, juvenile plants of Polypodiaceae possess a short protostelic unbranched rhizome bearing small leaves associated with a basal root each and having a slender cylindrical vascular supply; the protostele is formed by successive leaf-root vasculatures getting interconnected by short cylindrical vascular bridges (figures 9, 11) as in *Acrostichum*. As larger leaves are borne, their vasculature progressively becomes channel-shaped. Additional lateral roots are produced associated with each leaf, and this brings about the transition to a hollow tubular dictyostele, interconnection between vasculature of lateral roots of successive as well as opposite leaves constituting the ventral half. The characteristic branching habit is acquired in most taxa simultaneous with occurrence of lateral roots associated with leaves. The pattern of branching is similar to that of adult plants, except in *M. linguaeforme* which has a branching similar to other taxa in the early stages. The change in pattern of interconnection between bases of vasculature of successive juvenile leaves consequent to their becoming channel-shapped is different from that in *Acrostichum*. Instead of bearing a pair of ribbon-like vascular bridges (one on either margin) the leaf traces of Polypodiaceae bear only one in the early stages of the transition and this interconnects the dorsal margins of successive leaf traces so that a broad channel-shaped vasculature is formed in the stem, located in the dorsal half and with concavity facing the ventral side. With further increase in the size of juvenile leaves and their vasculature a vascular bridge is developed on the ventral margin also, extending backward and merging with the ventral margin of vasculature of the next posterior leaf on the same side of the stem. The stele which results is still channel-shaped and open on the ventral side (on account of the fact that leaves are not spirally arranged and there is no vascular bridge between the ventral margin of vasculatures of the two opposite rows of leaves). Later the channel-shaped stele acquires the form of a hollow cylinder

(dictyostele) by vascular bridges developing between vasculatures of leaf-associated lateral roots. Commonly lateral roots associated with leaf bases occur from the 6th to 8th juvenile leaf onwards but in some (*Kaulinia pteropus, M. punctatum*) they are not produced till 15–20 leaves are borne. In many taxa acquisition of branching habit and possession of lateral roots are simultaneous, but in some like *M. scolopendria* in which branching occurs only after the 9th leaf, lateral roots (consequently tubular form of stele) are found from 6th juvenile leaf onwards, while in others like *K. pteropus* and *M. punctatum*, in which branching occurs from the 5th or 6th leaf onwards, lateral roots are found only from the 15th–20th leaf onwards. Thus, it is not branching habit but possession of leaf-associated lateral roots which results in a tubular dictyostele in the stem.

CONCLUSIONS

The close interrelationship between leaves and roots and the dominant role played by them in the construction of the plant body, particularly in the construction and architecture of the stele, in all taxa of ferns investigated, contradicts the classical concept that roots of pteridophytes are adventitious having no correlation with leaves or any fixed position on the shoot[25], and play no role in determining stelar morphology. The fact that in all taxa, all the roots are leaf-associated and each leaf has a root system of its own, consisting of a basal abaxial root and often one or more adaxial lateral ones, suggests that the leaf-root combination (phyllorhize) constitutes a basic unit in construction of the plant body. This is all the more so since the major bulk of tissues which constitutes stem is derived from leaf apical meristem, and in those taxa possessing an elongated plagiotropic stem the internodes are formed mainly by the leaf bases. But however insignificant it is, the shoot apex contributes tissues to the internodes and it is not phyllorhize units alone that make up the shoot system as maintained by the Phyllorhize theory[5]. Also, the possession of a dominant shoot apical meristem

from which the leaf apical meristem is ultimately derived, refutes the Phytonic concept of organisation of the cormophytic plant body. At least in respect of ferns, the cormophytic body seems best explained in terms of phyllorhize units but accepting also the dominant role played by the shoot apex in morphogenesis.

It seems apparent that stele cannot be accepted as a morphological unit as held by Stelar Theory[6,7]; nor is it a part of the cauline system in that it is not developed from tissues directly derived from the shoot apex. Vascular cylinder (stele) of the fern stem is made up of bases of leaf vasculatures interconnected by vascular bridges in a regular fashion in taxa possessing erect stem and crowded spirally arranged leaves (*Acrostichum, Blechnum*); in others like Polypodiaceae possessing elongated plagiotropic stem, bearing leaves in longitudinal rows restricted to one (dorsal) side only, it consists of interconnected bases of leaf vasculatures (dorsal half) as well as interconnected vasculatures of leaf-associated roots (ventral half). Thus the stele is a composite structure, and at best only the vascular bridges which interconnect leaf traces and root traces are derived from cauline tissue. Also, stelar ontogeny and progression from protostele to dictyostele do not conform to the widely accepted Size and Form hypothesis[9,10] in any of the taxa studied. A tubular stele is not initiated as a solid cauline cylinder in which potential vascular tissue gets parenchymatised to form medulla and gaps. Similarly, transition from protostele to siphonostele or dictyostele in juvenile plants is not by medullation of central region of stele as currently believed[8]. Change in the shape of leaf vasculature (cylindrical to channel-shaped) and change in pattern of vascular interconnection between successive leaf traces (solitary median to paired marginal) concomitant with increase in size result in tubular form of the stele; in the polypodiaceous taxa, characteristic forward growing lateral roots and vascular interconnections regularly formed between them contribute to the process. At the region where the change in form from protostele to siphonostele occurs in juvenile stem the cortex as well as pith together

constitute an uninterrupted mass of parenchymatous ground tissue. The marginal interconnections between vasculatures of the youngest leaves develop by metamorphosis of a few cells of the ground tissue which separate the leaf vasculatures. In taxa having spiral phyllotaxy this process results in the central region of ground tissue getting encircled by vascular tissue, and in transections appears as a pith unconnected to ground tissue surrounding the vascular cylinder (cortex). In taxa having leaves restricted to dorsal half of stem, this process results only in a channel-shaped stele; vasculatures of roots borne on ventral margin of the leaf base form a reticulum which interconnects the two margins of the channel, so that no distinct pith is ever formed. Thus the perforations found in the ventral half of the stelar cylinder of stem are merely a portion of the ground tissue through which root traces have developed and got interconnected. In contrast the perforations which dissect the dorsal half are parenchyma islands developed from provascular tissue of leaf traces; as mentioned already these lacunae form longitudinal rows which are continous throughout the length of the leaf vasculature.

The progressive increase in thickness of stem as juvenile plants grow does not seem to play any role in progression from protostele to dissected dictyostele as maintained by Size and Form hypothesis. However, as regards leaf vasculature there is a correlation between the extent of dissection and the extent of increase in girth of leaf axis occurring after vascular differentiation has taken place. The more the leaf axis increases in thickness (especially by division of cells in the central region) the more and larger the lacunae. At initiation (next behind leaf apical dome) the leaf vasculature is an intact band and provascular cells metamorphose into xylen tracheids which soon lose their mitotic capacity as well as the capacity for radial expansion. Solitary cells at strategic positions in the band, however, fail to metamorphose into tracheids, remaining meristematic. As leaf axis increases in thickness by division of central cells, there occurs a shearing stress on the vascular strand. Rapid division of the meristematic cells left here and there com-

pensates for the lack of capacity of the developing xylem tissue to expand radially, and results in expanding spindle-shaped parenchyma islands which dissect the intact leaf vasculature. This process of lacuna formation and dissection occurs in all taxa studied, the extent of dissection being least marked in *Drymoglossum* in which the extent of increase in thickness of leaf axis posterior to region of tracheid differentiation is least while it is most marked in *Acrostichum*, *Blechnum*, *Drynaria* and *Microsorium* in which increase in thickness of leaf axis is high. Once increase in thickness of leaf axis ceases, parenchyma of the lacunae may get differentiated into vascular tissue, obliterating the lacunae in some taxa like *Microlepia*[22].

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1. Fritsch, F. E., *New Phytol.*, 1916, **15**, 233.
2. Fritsch, F. E., *Ann. Bot. N.S.*, 1945, **9**, 1.
3. Nayar, B. K., In: *Current trends in botanical research* (ed) M. Nagaraj and C. P. Malik, Kalyan Publ., New Delhi, 1981, p. 247.
4. Nayar, B. K., *Curr. Sci.*, 1982, **51**, 717.
5. Chauveaud, G., *La constitution des plantes vasculaires revele par ontogenie*, Payot et Cie, Paris, 1921.
6. van Tieghem, P. and Douliot, H., *Ann. Sci. Nat. Bot. Ser.*, 7, 1886, **3**, 275.
7. Beck, C. B., Schmid, R. and Rothwell, G. W., *Bot. Rev.*, 1982, **48**, 691.
8. Wardlaw, C. W., *Phylogeny and morphogenesis*, Macmillan, London, 1952.
9. Bower, F. O., *The origin of a land flora*, Macmillan, London, 1908.
10. Bower, F. O., *Proc. R. Soc. Edin.*, 1923, **83**, 117.
11. Hanstein, J., *Jahrb. Wiss. Bot.*, 1858, **1**, 233.
12. Cuenod, A., *Soc. Sci. Nat. Tunisie Bull.*, 1951, **4**, 3.
13. Galinat, W. C., *Bot. Mus. Leaflet, Harward Univ.*, 1959, **19**, 1.
14. Mitra, G. C. and Majumdar, G. P., *Palaeobotanist*, 1952, **1**, 351.
15. Nayar, B. K., In: *Companion to R. H. Beddome's Ferns of British India*, B. K. Nayar and S. Kaur, Chronica Botanica, New Delhi, 1974, p. 111.
16. Nayar, B. K., In: *Recent advances in botany* (ed) P. Kachroo, Bishen Singh Mahendrapal Singh, Dehra Dun, 1976, p. 145.
17. Nayar, B. K., In: *Aspects of plant sciences III* (ed)

S. S. Bir, Today and Tomorrows Print. Publ., New Delhi, 1980, p. 1.

18. Priestly, J. H., Schott, L. I. and Gillett, E. C., *Ann. Bot.*, 1935, **49**, 161.
19. Wetmore, R. H., *Torreya*, 1941, **43**, 127.
20. Campbell, D. H., *Am. J. Bot.*, 1921, **8**, 303.
21. Nozu, J., *Jpn. J. Bot.*, 1956, **15**, 208.
22. Nayar, B. K. and Molly, M. J , *Proc. Indian Acad.*

Sci. (Pl. Sci.), 1980, **B80**, 381.
23. Nayar, B. K., Molly, M. J. and Madhusoodanan, P. V., *Brit. Fern Gaz.*, 1985, **13**, 33.
24. Nayar, B. K. and Madhusoodanan, P. V., *Bot. J. Linn. Soc.*, 1977, **75**, 283.
25. Ogura, Y., *Comparative anatomy of vegetative organs of the pteridophytes*, Gebruder Borntraeger, Berlin, 1972.

ANNOUNCEMENTS

SEVENTEENTH NATIONAL SEMINAR ON CRYSTALLOGRAPHY

The Seventeenth National Seminar on Crystallography (XVII-NSC) is being organised by the Department of Crystallography and Biophysics, University of Madras and by the Department of Physics, Indian Institute of Technology, Madras from **20–22 December 1985** and will be held in the campus of the I.I.T. Madras. It is sponsored by the National Committee for Crystallography, of the Indian National Science Academy, which is affiliated to the International Union of Crystallography.

For further details please contact Dr E. Subramanian, Convener, XVII-NSC, Department of Crystollography & Biophysics, University of Madras, Madras 600 025.

INTERNATIONAL UNION OF PURE AND APPLIED CHEMISTRY

Prof. C. N. R. Rao, Director, Indian Institute of Science and President of Current Science Association, has taken over as the President of the International Union of Pure and Applied Chemistry (IUPAC), the oldest and the largest scientific union. Prof. Rao, inaugurated the IUPAC Congress in Manchester last month. He is the first Indian chemist to occupy the position.

We wish Prof. C. N. R. Rao all success.

MEDICAL TELEVISION

A Medical Television Project, the first of its kind in India and perhaps amongst the developing countries, has been introduced with the approval of the Government of India, by Dr J. K. Jain, a Delhi based Surgeon who is president of Jain Medical Centre and a former president of Delhi Medical Association. This Project aims at producing video films on Medicine, Health and Family Planning for the National Television Network and for use by professional institutions for under-graduate, post-graduate and continuing medical and allied professional education. Organisations like ICMR, MCI and IMA have all shown interest in the Project and assured their co-operation. Collaboration of leading international concerns engaged in the production of medical and health films, has also been an encouraging factor.

To produce these programmes, a professionally equipped and staffed Television Studio – Jain Studios – has been set up in South Delhi. Some of the equipment installed in the studio is available for the first time in India and enables recording through an endoscope or a microscope. Video technology is of course eminently suited to medical education especially in a country like ours where many institutions do not have adequate facilities or resources.

Further particulars may be had from Dr J. K. Jain, President, Jain Medical Centre, A-39 New Delhi, South Extension Part II, New Delhi 110 049.