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# Evolution of a cormophytic plant body in lower vascular plants

B. K. Nayar

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Possession of a cormophytic plant body and stelar system distinguishes vascular plants from thallophytic ancestors. Based on morphology and development of sporophyte and gametophyte of pteridophytes it is argued that current interpretations of morphology and evolution of these features in terms of Axial theory and Stelar theory are untenable in these primitive vascular plants. The leaf, and not the axis/stem, is the primary organ and the first to evolve. The leaf along with its associated root constitutes a Phyllorhize which is the basic unit of construction of the plant body; a succession of phyllorhizes interconnected by the leaf base regions result in the cormophytic plant body. Shoot apical meristem functions only in initiating leaves and branches and what appears as stem is a product of conjoined leaf bases, the shoot meristem contributing little to its construction. Vasculature is developed only in tissues derived from leaf- and root-meristems; no vasculature is developed in tissue derived from the shoot meristem. Stelar cylinder consists of secondarily interconnected basal regions of leaf vasculatures and sometimes also vasculature of leaf-associated roots. The pattern of growth (different in taxa having erect rhizome and plagiotropic rhizome) determines the nature of the stelar cylinder. Evolution apparently followed the same course in gametophytic and sporophytic generations, and evolution of pteridophyte gametophyte indicates that the primitive form was an amorphous cushion-shaped thallus devoid of meristem and vasculature. It is shown how a phyllorhize unit evolved from such a plant body. Morphological, anatomical and ontogenetic evidences are presented in support of the contention that the pteridophyte plant body is formed of conjoined leaf bases and its stele is the product of leaf base vasculatures interconnected in a regular pattern. Also, it is shown that stelar evolution did not follow the sequence suggested by Stelar theory.

**Key-words**—Evolution, Vascular plants, Anatomy, Phyllorhize concept.

B. K. Nayar, Department of Life Sciences, University of Calicut, Kerala, India.

## सारांश

निम्न संवहनी पौधों में कोर्मोफाइटी पादप काय का विकास

बी० के० नायर

कोर्मोफाइटी पादप काय एवं रम्भीय तंत्र के आधार पर संवहनी पौधे अपने थेलोफाइटी पूर्वजों से अलग पहचाने जा सकते हैं। टेरीडोफाइटी पौधों की आकारिकी तथा स्पोरोफाइट एवं गैमीटोफाइट के विकास के आधार पर यह प्रेक्षित किया गया है कि इन आद्य-पौधों में अक्षीय सिद्धान्त एवं रम्भीय सिद्धान्त से सम्बद्ध आकारिकी तथा इन लक्षणों के विकास की आधुनिक व्याख्यायें सर्वमान्य नहीं हैं। पत्ती, न कि अक्ष/तना, प्राथमिक अंग है तथा पहले इसी की उत्पत्ति हुई। जड़ से सहयुक्त पत्ती फिलोराइज का निर्माण करती है जो कि काय की संरचना की मुख्य इकाई है। पत्ती का आधार फिलोराइज के साथ मिलकर कोर्मोफाइटी पादप काय बनाता है। प्ररोह अग्रस्थ विभज्योतक प्रारम्भिक पत्तियों एवं शाखाओं में ही काम करता है। ऊतकों में वाहिनिकाओं का निर्माण भी पत्ती एवं मूल विभज्योतक द्वारा ही होता है तथा प्ररोह विभज्योतक ऊतकों में किसी भी प्रकार की वाहिनिकाओं का निर्माण नहीं करता। रम्भीय बलय में भी वाहिनिकायें मूलतः पत्ती की ही होती हैं। रम्भीय बलय ही वृद्धि का स्वरूप सुनिश्चित करता है। टेरीडोफाइटी गैमीटोफाइट के विकास से प्रदर्शित होता है कि आद्य-प्रारूप विभज्योतक एवं वाहिनिकाओं से विहीन तल्पीय आकार का था। इस शोध-पत्र में यह व्यक्त किया गया है कि एक फिलोराइज इकाई ऐसी पादप काय से कैसे विकसित हुई है। आकारिकीय, शारीरिक एवं वैकसिक प्रमाणों के आधार पर यह प्रदर्शित किया गया है कि टेरीडोफाइटी पादप काय पत्ती के आधारों के पारस्परिक संयोजन से बनी है तथा इसका रम्भ पत्ती के आधार में विद्यमान वाहिनिकाओं के फलस्वरूप विकसित हुआ है। यह भी प्रदर्शित किया गया है कि रम्भीय विकास प्रस्तावित रम्भीय सिद्धान्त के अनुसार नहीं है।

ACCEPTANCE of evolution as causative to the vast diversity of life forms initiated the quest for understanding the process of biological evolution,

and during the past 100 years a vast wealth of information was collected which makes it possible today to circumscribe and characterise the six major groups of plants and also understand the process by which the diversity within each of these groups came about. Currently it is possible to reconstruct with reasonable accuracy the process of evolution within each such group like the bryophytes, peridophytes, gymnosperms and angiosperms, and also to understand the position each occupies in relation to the other groups in terms of evolution. However, when it comes to possible inter-relationships between these major groups, the situation is different; nothing more than intelligent guesswork propagated as hypotheses is available to bridge the gap between the major groups. And the widest gap of all is the one between vascular plants on the one hand and nonvascular plants or thallophytes on the other, though it is accepted that all vascular plants evolved from Chlorophycean ancestors. Morphological differences between thallophytes and vascular plants are so vast that it has not so far been possible to explain how these differences came about. The major distinguishing feature of vascular plants is their cormophytic plant body, i.e., a plant body constructed of stem, leaf and root, each having a characteristic morphology which is basically the same in all and the like of which does not exist in any thallophyte. Another major difference is the vascular system or stele which is universal in vascular plants but totally absent in thallophytes.

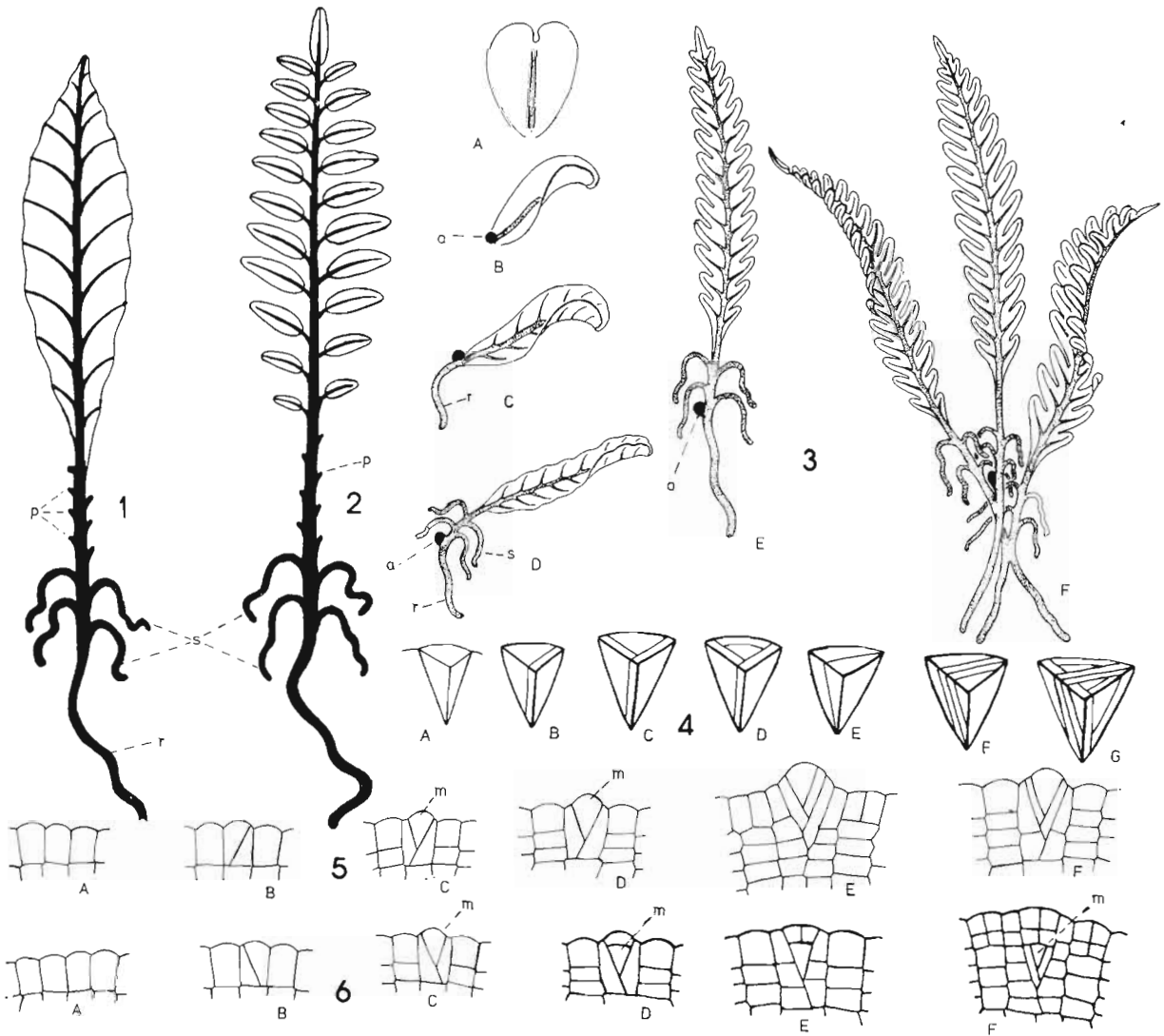
Currently all interpretations of vascular plant morphology are based basically on the Axial theory and Stelar theory, both of which are hypotheses which seek to explain the fundamental nature of the vascular plant body. The former contends that the stem or axis is the most fundamental organ and first to evolve, leaves and roots are but appendages borne on the pre-existent axis. On this basis the evolutionary gap between vascular plants and thallophytes is sought to be bridged by explaining how the axis evolved from a thallose plant body, and several hypotheses have been proposed. But the extensive studies of fossil as well as extant plants have so far failed to provide any tangible evidence in support of the Axial theory. Stelar theory maintains that all vasculature of the plant body together constitutes an organ having a definite morphology which exhibits distinct evolutionary trends from simple to more complex forms. It is based on the Axial theory and attempts to explain vasculature of leaf and root as originating from the axis to supply these organs, the vasculature of the axis being more fundamental. Axis vasculature is presumed to be a

solid central cylinder which during evolution underwent modifications through parenchymatisation of certain of its regions so that a pith, leaf gaps, etc. were formed and the haplostelic protosteles became siphonostelic, dictyostelic, polystelic or eustelic. Bower's (1930) Size and Form hypothesis seeks to provide a rational basis for stelar evolution, maintaining that presumed physiological constraints induced by increase in size resulted in progressive changes in form.

### LEAF AS THE PRIMARY ORGAN

In order to gain an insight into the process through which the cormophytic plant body with its stele evolved, a detailed study of morphology of the gametophyte and sporophyte of pteridophytes was undertaken, and the present account is based on these studies. Pteridophytes are selected because they are among the earliest to possess a cormophytic construction and stelar system. The studies suggest that the pteridophyte plant body is not constructed as explained by Axial theory nor can its vascular system be accepted as an organ. In addition, stelar evolution in pteridophytes does not follow the principles of Stelar theory and Size and Form hypothesis. All evidences indicate that the leaf, instead of the stem, is the primary organ, and that it is the leaf which gave rise to the cormophytic plant body as well as to the stele. The stele is a composite body consisting of interconnected basal regions of vasculatures of successive leaves.

The leaf is essentially a subcylindrical axis with a continual growing apical end (apical meristem) and a root at its basal end in continuation of the leaf axis and with an apical meristem of its own. The leaf axis bears at regular intervals a series of discrete lateral meristems similar to its apical meristem; these form a longitudinal row on either side. In addition, it bears throughout its length a laminar meristem on either side, consisting of a longitudinal row of meristematic cells interconnecting the lateral meristems. Laminar meristem as well as lateral meristems behave differently at different regions of the leaf axis. In the anterior half the lateral meristems grow out as branches similar to the leaf axis and the laminar meristem continues up these branches. In some cases the laminar meristem in the anterior half is uniformly active and this results in a simple leaf lamina with the lateral branches of the axis constituting the main lateral veins (Text-figure 1). In others the activity of the meristem is inhibited except on the lateral branches, resulting in a pinnate lamina (Text-figure 2); the inhibited regions of laminar meristem develop into aerating bands



**Text-figure 1-6—1.** Diagrammatic representation of simplest Phyllorhize unit having simple lamina; **2.** Same having pinnate lamina; **3.** Diagrammatic representation of steps in evolution of a cormophytic plant body from a cordate-thalloid one similar to a fern gametophyte; **4.** The common type of tetrahedral apical meristematic cell of pteridophytes, showing the usual pattern of unequal divisions (**A-D**) and the dichotomous division of shoot apical cell and the unequal divisions in its daughter cells (**E-G**); **5.** Steps in the formation of the meristematic cell of a fern leaf from a peripheral cell of shoot apex, as seen in transections; **6.** Steps in the formation of a meristematic cell of root in Filicopsida from a peripheral initial cell of leaf base, as seen in transections. (**a**, apical meristem; **m**, meristematic cell; **p**, pneumatophores which are reduced pinnae/main lateral veins; **r**, main basal root; **s**, lateral root).

characteristic of all fern leaves. When the process of inhibition of activity of laminar meristem is repeated on the lateral branches of the axis as well, more dissected leaf forms result. Commonly the laminar meristem is inhibited in the posterior half of the leaf axis, developing only an aerating band on either side. At the basal region the lateral meristems also remain dormant or nearly so. This results in a leaf having a naked petiole. However, one or a few lateral meristems close to the basal end of the leaf axis develop into lateral roots. All lateral meristems, as also the meristem from which the basal root

develops, are initiated similarly from solitary peripheral cells of the leaf axis. The initial cell divides by three successive anticlinal walls, each wall being oblique and the three intersecting so that an obpyramidal central daughter cell results, surrounded by sister cells on the lateral and posterior sides and having the peripheral (exposed) wall of the initial cell as its fourth side (Text-figure 4A-D); the central daughter cell constitutes the apical meristematic cell. Except in the case of the few at the basal region of the leaf axis, which develop into roots, the apical meristematic cell cuts



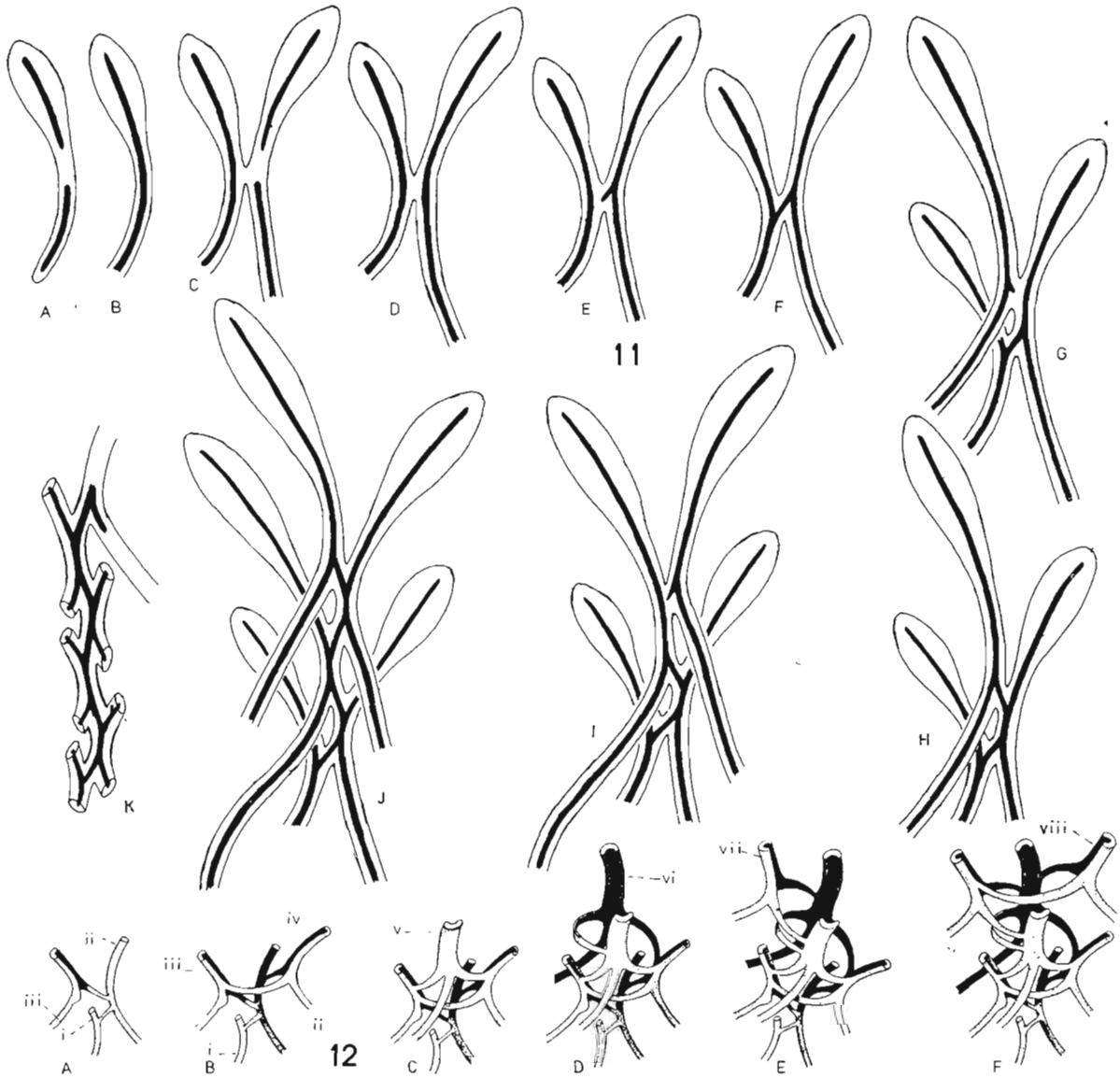
**Text-figure 7-10**—7. Diagrammatic representation of patterns of growth and development at the shoot apex of *Pyrrosia lanceolata*; 8. *Microsorium linguaeforme*; 9. *Stenochlaena palustris*, and 10. *Nistarika babupunctika* (b, dormant branch; d, dormant leaf; g, actively growing branch; l, developed leaf).

off daughter cells against the three lateral oblique sides in regular succession; no daughter cell is cut off against the exposed peripheral wall, with the result that the meristematic cell continues throughout as a superficial cell (Text-figure 3E, F). However, in the case of the root, daughter cells are cut off against all four sides (including the peripheral side) of the apical cell (Text-figure 4A-F). The first daughter cell cut off against the peripheral side behaves like other peripheral cells of the leaf base, dividing anticlinally and periclinally so that the root apical cell becomes deep seated in the cortex of the leaf base. A root cap develops from similar daughter cells cut off later. The leaf with its associated roots constitutes a phyllorhize unit. A

succession of such phyllorhize units builds the cormophytic plant body, the stem being the conjoined basal ends of successive leaves, i.e., a collection of leaf bases.

#### ORIGIN AND EVOLUTION OF THE CORMOPHYTIC PLANT BODY

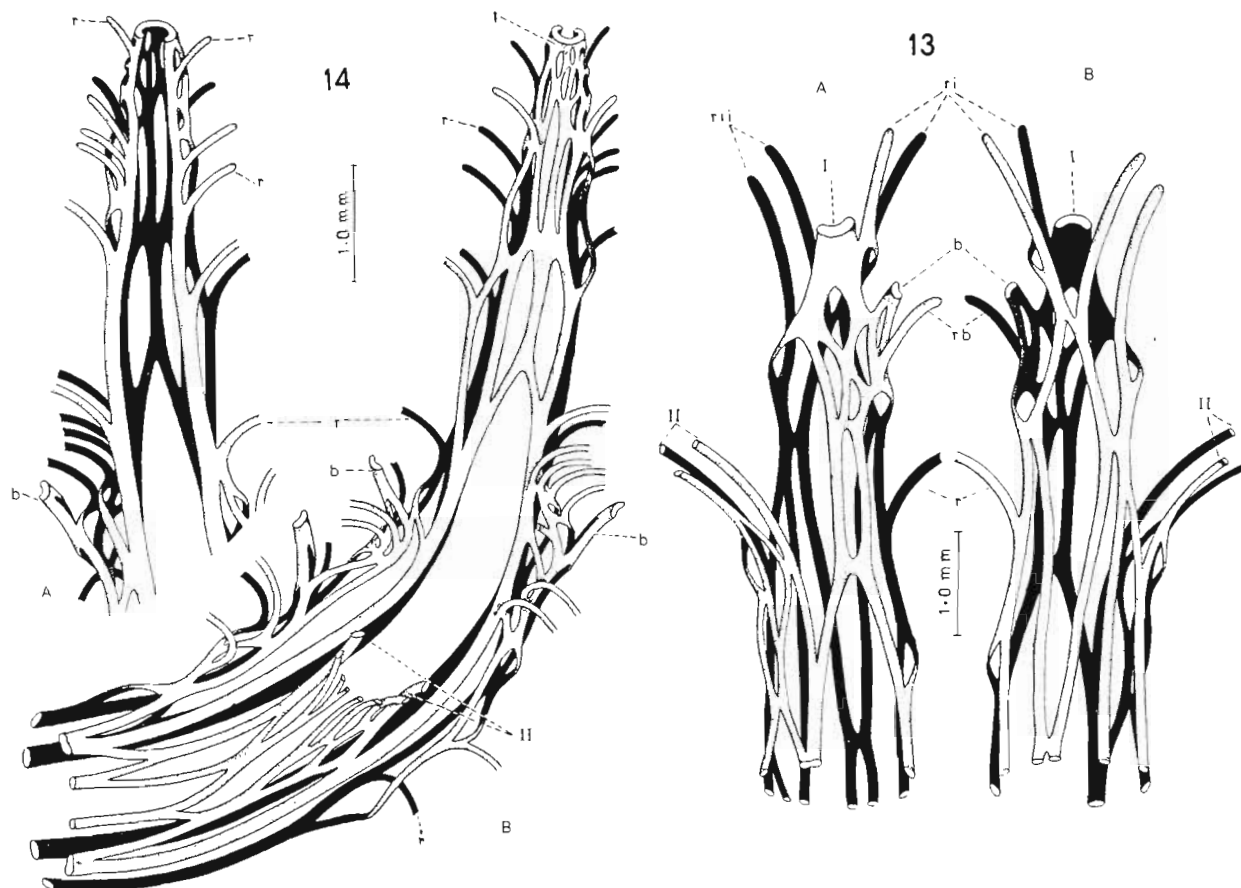
It should logically be presumed that both the gametophytic and the sporophytic generations followed basically the same course in evolution, since both have the same genetic constitution and grow under the same environment. Based on a comparative study of over 3,000 taxa of pteridophytes, I have recently given an account



**Text-figure 11, 12—11.** Juvenile plants of *Drynaria quercifolia* at different stages of development up to the 5-leaved stage, showing vasculature and formation of a haplostelic protosteles; in figure K the leaves and roots are shown cut off at base leaving the conjoined leaf bases which constitute the axis possessing a protosteles; **12.** Hypothetical drawings to explain the formation of protosteles followed by dictyostele, by vascular bridges interconnecting bases of vasculature of successive leaves following the common pattern found among Filicopsida; figure A shows vasculature of the first three leaves, of which **i** and **ii** have cylindrical vasculature and **iii** has a channel-shaped vasculature, all the three interconnected by solitary vascular bridges; figures **B-F** show configuration of vasculature as further leaves are borne one by one (**i, ii, iii**, basal regions of vasculature of successive juvenile leaves alongwith basal region of vasculature of associated roots and vascular commissures interconnecting leaf base vasculatures).

(Nayar, 1981, 1992) of the extent of morphological variation and the evolutionary trends followed by the gametophytic generation, concluding that the most primitive type is a dorsiventrally compressed, amorphous, cushion-shaped thallus as in Equisetales, devoid of any distinct meristem. During evolution two separate growing meristems were acquired by the cushion-shaped gametophyte, one ring-like and lateral along the margin of the cushion and the other median at the centre of the expanded

dorsal side, the former leading to horizontal growth and the latter to vertical growth. The earlier, more dominant and widespread among extant pteridophytes, is the lateral ring-like meristem. The growing meristem of the common cordate-thalloid gametophyte (the most common form among extant pteridophytes) evolved from this lateral ring-like meristem. During evolution, the ring-like meristem became discontinuous, ultimately leaving only up to three active regions as in *Hymenophyllum* and only



**Text-figure 13, 14**—Dorsal (A) and ventral (B) views of vasculature at shoot apex of *Microsorium pteropus* (13) and *M. linguaeforme* (14), showing basal region of vasculatures of the youngest two leaves and their associated roots, vasculature of the dormant leaf on the dormant branch of shoot apex dichotomy and vascular bridges between root vasculatures (**b**, basal region of vasculature of branch; **r**, vasculature of root; **rb**, vasculature associated with branch; **ri**, vasculature of root associated with first leaf; **rii**, vasculature of root associated with second leaf; **I**, **II**, basal regions of vasculature of the first and second leaf from apex).

one in most other taxa. A creeping subcylindrical thallus results when the meristem is active at one point only. Margin to margin fusion of plate-like photosynthetic lobes (of the type found in *Equisetum*) borne on the dorsal side of such a thallus to form one large expanded lobe (wing) on either side of the subcylindrical thallus gave rise to the common cordate-thalloid type of gametophyte. The second meristem acquired by the gametophyte during evolution (i.e., the dorsal median one or the apical meristem which leads to vertical growth) is found only in a few, like some Lycopodiales, among extant pteridophytes. In the Phlegmaria group of *Lycopodium* this meristem is prominent and persistent so that the adult gametophyte is cylindrical and erect-growing with its lateral meristem displaced to form a spiral (instead of a ring) around the thallus. Also, the lateral meristem becomes discontinuous and gives rise to slender, cylindrical, horizontal branches which, on account of the continuous upward growth of the thallus, are

borne at different levels up the erect thallus.

It seems reasonable to presume that the primitive sporophyte would also have been an amorphous cushion-like body similar to the primitive gametophyte. Like the gametophyte it evolved into a cordate-thalloid form (Text-figure 2A, B) but possessed an active apical meristem located at the posterior end of the midrib on the dorsal side. If the midrib of such a thallus were to bear alternate lateral branches with the wings borne laterally on the midrib as well as the branches, and if the posterior end of the midrib were to grow out in the opposite direction as a root (Text-figure 2C), a phyllorhize unit would result except that such a unit would be devoid of any organised mechanical or conductive tissue. Obviously a thallose plant body devoid of mechanical and conductive tissue is considerably handicapped for a terrestrial existence. In the thalloid sporophyte this need is met by the development of vascular tissue and this would have been in the form of a cylindrical central strand in the

midrib. Similar vascular development takes place in the root and the two get interconnected so that the vascular strand is continuous in the leaf and its associated root. Thus the earliest vascular system evolved, permitting the sporophyte to be considerably larger, functionally more effective and better adapted for a terrestrial environment. As in the gametophyte of Phlegmaria group of *Lycopodium*, the apical meristem of the sporophyte is persistent on such a phyllorhize unit and produces a succession of discontinuous lateral meristems in spiral order. Each of these develops into a phyllorhize unit similar to the first one. Though a phyllorhize unit can have an independent existence, it is more advantageous if vascular systems of successive units are interconnected, especially because the root, being a subterranean organ, has a more protected environment as compared to the aerial leaf and therefore could function much longer. If the vasculature of the younger leaves is connected to the vasculature of roots associated with older leaves, the younger leaf can take advantage of the longer life span of the older root even after the leaf associated with it has become dysfunctional. Such interconnection would also provide additional mechanical strength. Because of this, vasculatures of successive phyllorhizes would have become secondarily interconnected by a vascular bridge, the interconnected vasculatures of successive phyllorhizes form the stelar cylinder. Persistent leaf bases with interconnected vasculature constitute the stem.

#### EVIDENCE FROM EXTANT PTERIDOPHYTES

Growth and development in extant pteridophytes provide ample evidence that the cormophytic plant body of Filicopsida evolved along the above lines. The early juvenile plants of all of them consist merely of a single leaf associated with a basal root, with a central cylindrical vascular strand formed independently in the leaf and root and later becoming interconnected. It is of interest to note that in a majority of taxa there initially exists no shoot meristem in juvenile plants. A shoot meristem appears after the first leaf has established itself. Similarly, during apogamous development of the sporophyte, initially only a solitary leaf is produced which later gives rise to a basal root. A shoot apex is established at a much later stage only, commonly after the first two leaves are produced (Nayar & Bajpai, 1964). In all the fern taxa investigated in detail, vascular development takes place independently in the developing leaf and associated

root and this vasculature is unconnected to any other vasculature in the plant body (Nayar, 1985; Nayar & Molly, 1989; Nayar *et al.*, 1980). Undifferentiated cells next to the basal ends of the leaf—and root vasculature later get differentiated into vascular tissue, the process progressively extending until the two are interconnected. Afterwards similar secondary vascular differentiation is initiated next to the basal region of the leaf vasculature and progressively extends posteriorly till a vascular bridge is established with vasculatures of the earlier two leaves and thus getting connected with the anterior end of the stelar cylinder (Nayar & Gopalakrishnan, 1990; Nayar & Molly, 1989).

Irrespective of the adult condition, leaves are borne in spiral order, and the stem is erect-growing and short in the initial stages (i.e., in early juvenile plants) in all the taxa investigated. The shoot apical meristem consists of a conventional obpyramidal apical cell (Bierhorst, 1977) having four triangular sides of which the anterior one is peripheral at the stem apex and the other three lateral but obliquely converged to a point opposite the peripheral side. All divisions in this cell are unequal, one daughter cell being much smaller than the other, plate-like and next to one of the three lateral oblique walls (cutting face of the apical cell) so that the larger daughter cell continues to have the form and function of the apical meristematic cell (Text figure 5 A-D). The smaller plate-like daughter cell by repeated equal divisions forms a plate of small cells which ultimately develop into stem tissue, except one of the peripheral daughter cells which gives origin to a leaf apical cell. This condition persists in many taxa, the activity of the shoot apical meristem continuing unchanged throughout. But in some Polypodiaceae (Nayar, 1985; Nayar & Molly, 1989), Davalliaceae, Lomariopsidaceae, etc. the stem later becomes elongated and creeping (plagiotropic), with leaves borne in two dorsal rows and each leaf associated with an abaxially lateral branch bud at the base. This change is initiated by the shoot apex acquiring the habit of undergoing an equal dichotomous division soon after producing each leaf; commonly this occurs when the juvenile plant has produced 5-10 leaves but in some like *Stenochlaena* and *Microsorium linguaeforme* it occurs only after 15-20 leaves are borne. The shoot apex dichotomises either by the apical meristematic cell dividing to form a pair of daughter meristematic cells (as in most Polypodiaceae) or by the meristematic cell ceasing to function, followed by the formation of a pair of meristematic cells from peripheral cells closeby at the anterior region of the shoot apex (as in *Stenochlaena*). In the former case





**Text-figure 15-17**—15. Dorsal view of vasculature of a portion of the stem of *Stenoclaena palustris* bearing two successive leaves and branches anterior to each; in figure A the outer cortical vasculature is shown cut off to expose the central vascular cylinder; 16, Dorsal (A, B) and ventral (C, D) views of vasculature at shoot apex of *S. palustris*; in figures A and C the outer cortical vasculature is shown cut off to expose the central vascular cylinder; 17. Diagrammatic representation of vasculature at shoot apical region of *S. palustris*, showing successive stages in construction of the central dictyostelic cylinder as successive leaves are added and the shoot apex dichotomises in the characteristic pattern (b, vasculature of branch; f, vasculature of leaf; r, vasculature of root; i-viii, vasculature of successive leaves).



the meristematic cell divides equally by a vertical wall extending from the posterior pointed end of the cell to the middle of its anterior peripheral wall so that a pair of similar tetrahedral daughter cells are formed (Text-figure 4). Each of these functions independently so that the stem dichotomises into two branches. Each daughter apical cell divides unequally so that plate-like daughter cells are cut off in succession against the lateral cutting faces. The first plate-like daughter cell is cut off against the separating wall between the two daughter apical cells. A leaf apical cell is differentiated from one of the daughter cells derived from the first plate-like daughter cell of each of these apical cells and thus the first leaf on the two branches of the dichotomy is on the side facing each other. Where shoot apex dichotomy is initiated by the apical meristematic cell ceasing to function, a periclinal division divides the meristematic cell into an outer and inner daughter cells. A series of anticlinal divisions in the outer (peripheral) daughter cell results in a group of cells which are similar to other peripheral cells at the shoot apex. A peripheral cell next to this group on either side then functions as an initial cell which gives rise to a new tetrahedral meristematic cell by dividing thrice by oblique anticlinal walls. The leaf meristem which is formed first on each of the resultant daughter shoot apices is on the side facing the other. Soon after the shoot apex dichotomises, one branch of the dichotomy, which is away from the subtending developed leaf, becomes sluggish and dormant. The other branch (i.e., the one nearest the subtending leaf) continues growth. The dormant branch ultimately gets pushed aside as the leaf base of the first leaf on the dominant branch grows, and is often carried forward by the developing leaf base, appearing as a branch bud characteristically associated on the abaxial base of each developed leaf (Text-figure 7).

In some like *Stenochlaena* (Text-figure 9) the shoot apex dichotomises only after producing a pair of alternate leaves, but the second leaf becomes sluggish and dormant so that it appears associated with the dormant branch anterior to it. However, it develops an elongated leaf base, with the result that the dormant branch is carried up the internode developed by the first leaf of the dominant branch of the dichotomy. Also, this results in characteristic peculiarities in the architecture of the stelar cylinder. In *Nistarika* (Text-figure 10), though the shoot apical cell dichotomises after each leaf and one of the branches of shoot apex dichotomy remains dormant, the leaf meristem produced by the dormant branch continues to be active, producing a fully developed leaf. This results in the stem bearing

four, instead of two, dorsal rows of leaves, the two lateral rows alone being associated with a branch bud. In *Microsorium linguaeforme* (Text-figure 8) the shoot apex dichotomises as in other Polypodiaceae, after each leaf is developed. But before any leaf meristem is differentiated on the branches of the dichotomy, each branch apex dichotomises again so that four daughter shoot apices result. Of these four, the pair away from the leaf becomes dormant as also the daughter apex nearest the leaf, the medianly placed one of the pair nearest the leaf alone continuing growth. This results in the stem having leaves in one row only and each internode bearing a pair of opposite branch buds of which the one away from the subtending leaf is larger and bears two apices (Text-figure 8).

In all the fern taxa investigated, the shoot apical meristem is sluggish and contributes little to the construction of the plant body except that one of the peripheral cells formed by the repeated division of each plate-like primary daughter cell of the shoot apical cell functions as the leaf initial cell. The leaf meristem is far more active than the shoot meristem and dominates the shoot apex, tissue derived from it constituting the internode subtending the developing leaf. As the internode develops and elongates, it carries the shoot apical meristem forward with it, till the next leaf is initiated from the products of the next plate-like daughter cell of the shoot apical cell and the process is repeated. Thus, the stem which appears to bear the leaves is in fact made up of leaf bases of successive leaves and the vasculature in this stem is the vasculature developed in the leaf base (Nayar & Molly, 1989; Nayar & Gopalakrishnan, 1990). Detailed ontogenetic studies alone reveal this in the case of a majority of taxa, but in some which possess a long creeping stem (i.e., much elongated internodes) such as many Thelypteridaceae, *Hypolepis*, *Stenochlaena*, etc. external morphology also provides clues. The most characteristic feature of all leaves is the possession of a lateral laminar meristem which extends throughout the length of the leaf axis; it develops an expanded lamina in the anterior half of the leaf but on the petiole region it forms only the aerating bands. In all the above taxa aerating bands are prominent and extend down the entire length of the subtending internode also. In the case of *Stenochlaena*, which has pinnate leaves with pinnae alternating on either side in regular succession, highly reduced pinnae in continuation of the two rows of developed pinnae occur down the entire length of the aerating band both on the petiole as well as the subtending internode. Both these clearly

indicate that the internode is part of the leaf base.

As mentioned above, each leaf is associated with a basal root in all ferns and all leaves, including the first juvenile leaf, bear a basal root. No root other than associated with leaves occur in any taxa. In addition to the basal root, other roots are borne by the leaf base in the majority of ferns. These originate on the adaxial side of the leaf base and are in two alternating rows, occupying the same position as the lateral pinnae (Text-figures 1, 2), i.e., in succession of the pinnae and interrupting the aerating bands. They originate in a similar manner from peripheral cells of the leaf axis. These additional roots are thus modified pinnae. *Nephrolepis*, a taxon having an erect stem and spirally arranged leaves, possesses a unique organ, the stolon, which is root like in being positively geotropic, slender and much elongated, but having a stem like morphology in bearing paleae, lacking a root cap and having an apical meristematic cell which is superficial throughout, i.e., one which does not produce any daughter cell against the anterior peripheral side as occur in the case of root apical cell. Stolons vary in number and are associated with the leaf base. Each leaf bears a succession of adaxial roots in alternate succession along the aerating band as in other taxa and the stolons are in continuation of the two rows but further up the leaf base and in alternate succession. Roots, stolons and pinnae thus constitute an uninterrupted row on either lateral side of the leaf axis, and all of them originate in a similar manner from superficial initial cells along the aerating bands, i.e., interrupting the laminar meristem. Thus, these unique organs are equivalent to the pinnae and roots.

#### ORIGIN AND ARCHITECTURE OF STELE

Initiation and development of vasculature provide further evidence to the phyllorhize concept (Nayar, 1985) presented here. In all taxa investigated, vascular differentiation takes place associated with the growing apices of leaf and root only, tissue derived from the leaf and root meristem alone developing into vascular tissue. No vascular tissue is developed from tissue derived directly from the shoot meristem. A cylindrical vascular strand develops next to the growing apical region of the root early during development. Simultaneously an intact channel-shaped vascular strand is differentiated behind the leaf apical dome. Both are unconnected with any other vascular tissue. As the leaf and its associated root grow, progressive differentiation of tissue derived from the apical meristem of these organs extends the vasculatures,

keeping pace with the growth of the organs. Since the leaf and its associated root grow in opposite directions the basal ends of the two vascular strands face each other though separated by undifferentiated parenchyma tissue of the leaf base. However, secondary differentiation of the intervening parenchyma into vascular tissue takes place, the process starting with cells abutting on the basal end of the two vascular strands and progressively extending. Ultimately the root vasculature gets connected medianly to the basal abaxial (convex) side of the leaf vasculature. Secondary vascular differentiation at the basal end of the leaf vasculature continues, the channel-shaped strand extending down the leaf base and soon splitting medianly into two strap-shaped strands. One of these ultimately gets connected to the nearest margin of the vasculature of the next older leaf while the other gets connected to the nearest margin of the vasculature of the leaf next older. No vascular differentiation takes place other than associated with leaves and roots, i.e., in tissue derived from leaf meristem, and there is no vascular or provascular tissue in the region anterior to the youngest leaf.

Vasculatures of early juvenile leaves and associated roots are slender cylindrical and rod-like. They get interconnected by the intervening parenchyma cells between their basal ends getting differentiated secondarily into vascular tissue. Later, secondary differentiation of vascular tissue next to the basal end of vasculature of the leaf establishes a slender cylindrical vascular bridge with the basal region of vasculature of the next older leaf. The basal regions of vasculature of successive leaves along with the vascular bridges which interconnect them constitutes a haplostelic protostele in the stem (Text-figure 10). Such protostelic condition persists in some taxa such as Hymenophyllaceae which characteristically possess small leaves. In the others, successive juvenile leaves and their vasculature are progressively larger. Increase in size of the leaf vasculature is accompanied by a change in its shape; from cylindrical it becomes progressively strap-shaped and later channel-shaped. Simultaneously the form and pattern of vascular interconnection between successive leaves also change. The vascular bridge which interconnects successive leaves becomes dorsiventral and channel-shaped and later medianly split into a pair of strap-shaped bands; one of the bands gets connected to the nearest margin of vasculature of the next older leaf while the other gets connected to the nearest margin of the older leaf next in succession, the two older leaves being on opposite sides of the youngest leaf (Text-figure 12B). Because successive leaves are initiated from a

daughter cell each of the plate-like primary cells cut off in succession against the three cutting faces of the shoot apical cell, each set of three leaves constitutes a helix of the spiral phyllotaxy (Nayar & Gopalakrishnan, 1990). Thus the vasculature of leaf bases along with the interconnections between them constitute a dissected hollow cylinder (Text-figure 12C, D). The vascular bridge of the youngest leaf which interconnects it with the second older leaf crosses the plane of the fifth older leaf (i.e., 6th leaf from shoot apex) and this results in a leaf gap adaxial to the latter (Text-figure 12E, F). Thus leaf gaps occur associated with the fifth and older leaves only (Nayar, 1985). The resultant dictyostelic vascular cylinder, pierced by leaf gaps, is thus the product of characteristic interconnections developed secondarily between channel-shaped vasculatures of successive leaves and not formed by parenchymatisation of central region of a solid vascular cylinder as maintained by the Stellar theory. The progression from protostele to dictyostele does not occur due to presumed physiological constraints as maintained by the Size and Form hypothesis.

In taxa having a plagiotropic stem (Davalliaceae, Lomariopsidaceae, Polypodiaceae) the shoot apical meristem dichotomises after each leaf and only one of the branches of the dichotomy continues growth (Nayar & Molly, 1989). Consequently the leaves are borne in two rows only (Text-figure 7). Each leaf is associated with one or more adaxial roots. The shoot meristem is very sluggish while the developing leaf apex is markedly active. As a result the latter dominates the apical region, pushing aside the shoot apex away from the median position and often carrying it forward as a lateral appendage on the elongating leaf base. The prominent, elongated leaf base becomes the youngest internode of the stem. Thus, the stem is formed entirely from the activity of successive leaf meristems. Origin and development of vasculature are as in taxa having an erect stem, but the adaxial roots of each leaf, particularly those on the ventral margin, grow forward through the internode formed by the same leaf, often extending into one or two anterior internodes as well, before emerging from the anterior end ventral to the shoot meristem. Vasculature of these roots run in the internodes parallel to the channel-shaped vasculature of the leaf base, with their basal ends connected to the margin of the channel-shaped leaf vasculature (Text-figure 13). The pair of vascular bridges developed as posterior extensions of each leaf vasculature interconnect the leaf vasculature with the nearest margins of the vasculatures of the next two older leaves. But since leaves are restricted to two dorsal

rows, such interconnection does not result in a cylindrical dictyostele but only to a channel-shaped one with its free margins facing ventrally. Vasculatures of forward running roots of two to four successive leaves, however, run between and parallel to the margins. Vascular bridges develop secondarily between nearby root vasculatures so that a loose reticulum is formed by the root vasculatures bridging the free margins of the channel-shaped stele and making it a reticulate cylinder (Text-figure 13B). Thus, the dorsal half of the resultant dictyostele is made up of interconnected leaf vasculatures while the ventral half is made up of interconnected root vasculatures (Nayar, 1985; Nayar & Molly, 1989). In Davalliaceae and Lomariopsidaceae secondary differentiation of intervening parenchyma between the basal regions of root vasculatures ultimately results in an intact broad ventral vascular strand which in Lomariopsidaceae is channel-shaped and large.

Variations from this basic pattern, induced by characteristic differences in the cyclic activity of shoot apical meristem in some taxa, provide additional evidence for the explanation given here for the construction of the stele and cormophytic plant body. Thus, in *Microsorium linguaeforme*, which bears only a single dorsal row of leaves, vasculatures of successive leaves are interconnected by strap-shaped basal extensions, each of the two extensions associated with every leaf becoming connected to the nearest margin of vasculature of the next older leaf. The interconnected vasculature thus is channel-shaped and open on the ventral side (Text-figure 14). Each leaf bears up to 14 adaxial roots, the roots growing forward through the leaf base of the anterior two leaves. Vasculatures of these roots run parallel to the free margins of the channel-shaped vasculature, and get secondarily interconnected to form a reticulum bridging the margins. Though vasculatures of roots borne on the same side of the leaf base establish interconnections early, no such interconnection is formed between roots of opposite sides so that the stele remains channel-shaped up to the level of the 5th or 6th (from shoot apex) internode where vascular bridges between them develop. However, such bridges are less frequent so that the median row of lacunae in the resultant dictyostelic vascular cylinder is conspicuously longer and broader (Nayar & Molly, 1989).

*Stenochlaena* has a polycyclic dictyostele, a central cylinder of about six stout meristemes and an outer cylinder of many slender meristemes (Text-figure 15). The two cylinders are connected by the basal regions of the vasculatures of leaves and roots.

The shoot apex dichotomises after producing two leaves (Text-figure 9). As the channel-shaped vasculature developed by the leaves extends posteriorly it splits into three (instead of two as in other taxa) strap-shaped bands. The median one of these gets connected medianly to the concave adaxial surface of the vasculature of the next older leaf while the two lateral ones unite with the nearest margin of the vasculature of the same leaf (Text-figure 17). This results in a cylindrical tube-like stele in the subtending internode, but since the younger one of the two leaves becomes dormant and remains associated with the dormant branch of the shoot apex dichotomy (Text-figure 9), it gets pushed away to one side and its vasculature (which by then gets interconnected with vasculature of the first leaf on the dormant branch) appears as vasculature of the branch (Text-figure 17D). The tube-like vasculature of the branch is attached to the main vasculature of the internode without any associated gap. Also, there are no leaf gaps on the main cylinder because of the characteristic median vascular bridge between successive leaves (Text-figures 16, 17). In contrast to other ferns having a plagiotropic stem, root vasculatures do not contribute to the construction of the main vascular cylinder of the stem (Text-figure 17). Root vasculatures pass obliquely through the cortex of the leaf base. Secondary differentiation of vascular tissue occurs in the developing leaf after the main vasculature has developed and established interconnections. Undifferentiated tissue at isolated regions next to the abaxial convex surface of the channel-shaped leaf vasculature gets differentiated into vascular tissue resulting in a row of slender cylindrical vascular strands which extend parallel to the main vasculature of the leaf base. These get connected with the margin of vasculature of the next posterior leaf on the same side (Text-figure 16B). Similar secondary differentiation of vascular tissue occurs associated with root vasculatures also, interconnecting the basal regions of successive roots on the same side (Text-figure 16D). Occasional vascular bridges interconnect nearby vascular strands associated both with the leaves and roots, and thus a loose cylindrical reticulum is formed; this constitutes the outer cylinder of the polycyclic stelar cylinder (Text-figure 16B, D). In juvenile plants such secondary development of vasculature does not occur and the juvenile stem has a simple dictyostele and is erect with spirally arranged leaves as in other ferns. A plagiotropic stem and characteristic stelar architecture follows when the shoot apex acquires

the habit of regular dichotomy, and this happens when the juvenile plant has produced more than 20 leaves.

Leaf vasculature is undissected at origin in all the taxa studied, and gets differentiated next to the leaf apical dome before the leaf axis increases in girth (Text-figures 13, 14, 16). Increase in girth is abrupt and occurs by repeated division of all undifferentiated cells. This stretches the channel-shaped intact vascular strand and in response parenchymatous lacunae are developed, dissecting the strand into a reticulum. The extent of dissection depends on the level at which vascular differentiation takes place behind the leaf apex and the extent of increase in the girth of the leaf axis. In some like *Microlepidia* (Nayar *et al.*, 1980) the parenchyma constituting the lacunae later gets secondarily differentiated into vascular tissue, with the result that the leaf as well as stem vasculature becomes undissected at maturity.

Thus, the three classical hypotheses, Axial theory, Stelar theory and Size and Form hypothesis, which are the cornerstones for all considerations of taxonomy, phylogeny, etc. of lower vascular plants may have to be rejected and replaced by the Phyllorhize Theory outlined here.

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