



EVOLUTIONARY PATTERN OF THE VASCULATURE IN THE RHIZOME OF POLYPODIACEOUS FERNS*

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I wish to record my sense of appreciation and thankfulness to the Indian Botanical Society and Prof. Chauhan for bestowing upon me the honour for delivering this prestigious Dr. Panigrahi Commemoration lecture, instituted by the society in the year 1994 in the name of this great Botanist who is well known in India and abroad in the botanical world. Science has grown in this country with dedication, vision and support from such people.

It gives me immense pleasure in presenting Dr G. Panigrahi commemoration lecture during 27th annual conference of the Indian Botanical Society. Since Dr. Panigrahi was very much interested in the family Polypodiaceae which is evident from his many publications (1961-1968) I have chosen to speak on the topic connected with the same 'family'. This is a fitting honour to Dr. Panigrahi, the erudite Indian Pteridologist of international repute. It is also my good fortune to be associated with this auspicious occasion in the form of this talk.

Pteridophytes are a group of plants the existence of which extends to as far back as the Devonian-Carboniferous period (some 350 million years ago) in contrast to the meager 75 million years when the angiosperms are presumed to have originated during the cretaceous epoch. Because of their antiquity, pteridophytes hold a special place in any consideration of evolution of vascular plant group.

India represents one of the twelve-mega diversity centres of the world and possesses a rich heritage of pteridophytic flora which constitutes a very fascinating group consisting of more than 1200 species according to the recent census (Dixit, 1984; Chandra, 2000).

In the "good old days", most leptosporangiate

ferns were put onto the family Polypodiaceae. The comprehensive family Polypodiaceae is a large and diversified family of small ferns of the tropics predominantly epiphytic in habit. The family is mostly characterized by the presence of stipe articulated to phyllopodia on the rhizome (T-shaped xylem strand in the stipe) and the leaves are often restricted to two dorsal rows on the creeping rhizome (elongated or short, cylindrical or dorsiventrally compressed, profusely branched), which bears a branch often dormant in a laterally abaxial position (in wide creeping rhizome a branch is often displaced).

The rhizome in the ferns may be erect (short and massive or elongated) or creeping (short or long). The leaves are often spirally arranged all around the rhizome in the case of erect rhizome (Fig. 1) whereas they may be arranged in a spiral or restricted to the dorsal surface in the case of creeping rhizome (Figs. 3, 4). When restricted on the dorsal surface, the leaves may be arranged spirally or in two or more rows. Bower (1923) considered the creeping habit as more adaptable than the massive erect one. The creeping habit according to him led to the climbing habit and finally to the epiphytic one.

Since vascular morphology of the rhizome of ferns is currently well accepted as a conservative feature, which is least affected by the environmental and other edaphic factors, and is uniform due to strictness of genetic control, it is taken as a highly reliable comparative criterion and one of prime significance in taxonomic and phyletic studies of homosporous ferns.

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Figs. 1 - 3. Vascular cylinder of a portion of the adult rhizome. Fig.1. *Polysticum squarrosum* (after Chandra, P. 1969). Fig.2. *Microsorium linquaeforme*. Fig. 3 *Microsorium punctatum*. Fig.4 Hypothetical vascular cylinder showing possible steps through which the highly dissected vascular cylinder of polypodiaceous ferns with its characteristically branched siphonostele as found in *Stromatopteris*. The possible changes in the relationship between branch traces and leaf traces as shown (after Nayar, 1974).

(**B**, branch trace; **BG**, branch gap; **L**, leaf trace; **LG**, leaf gap, **R**, root trace)

Thanks to the pioneering work of Tansley (1907), Bower (1910, 1914, 1915, 1917, 1918) and Hayata (1929), the structure and organization of the vascular system in the fern shoot have long been accepted as valuable guide in taxonomic studies and phylogenetic considerations and the stele is recognized as an organ of high significance in comparative studies. The taxonomic importance of the vascular system of the fern rhizome was also emphasized by Tardieu-Blot (1932), Ogura (1921, 1963, and 1972), Ching (1940), Alston (1956) and

Holttum (1964). In recent years many pteridologists have demonstrated the importance of the structure and organization of the vascular system in phylogeny. The vascular system is now generally accepted as a potentially powerful tool in the understanding of relationships and evolution in ferns.

A relationship between Gleicheniaceae and Polypodiaceae (both have ex indusiate sori and soral morphology) has been suggested (Bower 1923, 1928; Copeland, 1947, Nayar and Chandra, 1965, 1967. Wagner, 1969; Bierhorst, 1971; Holttum, 1973; Lovis, 1977; Gifford and Foster, 1988; Smith, 1995).

Earlier (Nayar & Chandra, 1967; Nayar, 1974) it was suggested that the ancestor of the Polypodiaceae is possibly a genus similar to the modern Gleicheniaceae fern *Stromatopteris*. Nayar (1974) has hypothetically shown the possible steps through which the highly dissected vascular cylinder of polypodiaceous ferns with its characteristic leaf branch association could be derived from characteristically branched siphonostele as found in *Stromatopteris* (Fig.2). The possible changes in the relationship between branch traces and leaf traces are also shown. According to him the modern gleicheniaceae, (*Stromatopteris*) indicates the probable origin of some of the morphological characteristics of the Polypodiaceae. It is suggested that the characteristic vascular organization of the shoot in Polypodiaceae is possibly derived from the Gleicheniaceae fern genera like *Stromatopteris*, which possess a creeping rhizome devoid of leaves but bearing erect dichotomous branches at intervals with the ultimate division of the branches bearing a subapical leaf (with the growing apex of the branch arrested and often pushed aside by the leaf). The polypodiaceous condition, where leaves are borne on phyllopodia associated with branches (often dormant) is suggested as derived by the condensation of the branch system in *Stromatopteris*, leading on to undivided short branches apparently terminated by the leaf. The leaf associated branch of the polypodiaceae is due to displaced growing apex to this branch

Based on evidence from sporangial and

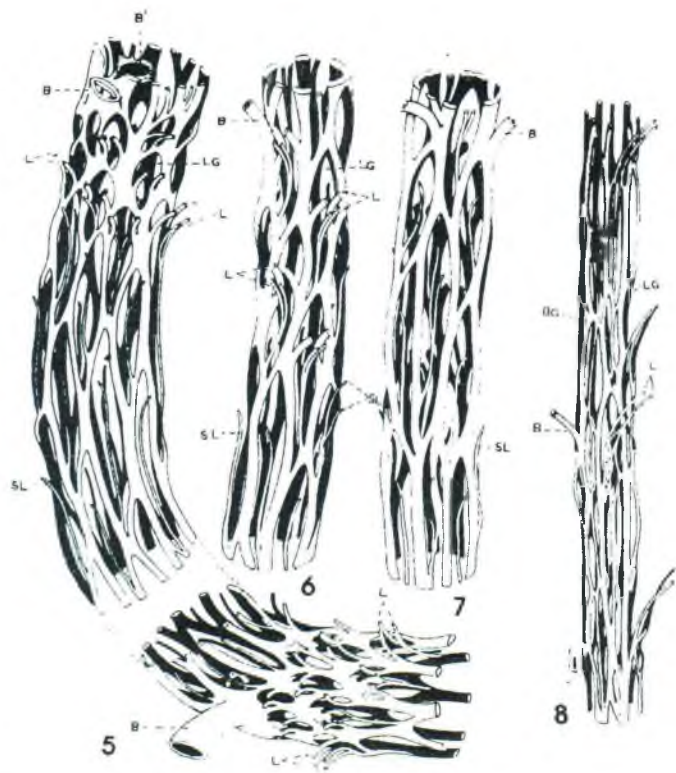
gametophyte structure, Jarrett (1980) refuted a gleichenioid origin of the Polypodiaceae and suggested that the polpods and grammtids are more closely allied to the advanced, indusiate, leptosporangiate ferns (exindusiate condition occurred independently in the polypodioid and gleichenioids).

Among homosporous ferns the evolution of the leaf arrangement is a general progression from the multispiral condition to the alternate two-ranked condition (Fig. 4) and in very few cases to a one-ranked condition (Fig. 3), where all leaves are in one dorsal row on the rhizome (Schaffner, 1938). As to the posture of the rhizome the more primitive condition in ferns is apparently the short erect rhizome bearing crowded spirally arranged leaves; the elongated, wide creeping condition being a derived one. During the course of a comparative study of the vasculature in the rhizome of homosporous ferns, certain interesting and morphological and structural variations of the rhizome have been observed in *Oleandra*, *Araiostegia*, *Davallia*, *Leucostegia* and drynarioid ferns which support the earlier view of Schaffner (1938).

OBSERVATIONS AND RESULTS

The vascular cylinder in the erect rhizome is radio symmetric dictyostele with spirally arranged leaf gaps. This spiral arrangement is maintained in the semi erect and creeping rhizome but the leaf bases on the ventral surface get displaced, more closely adpressed to the rhizome and fused with it for a longer distance. Holttum (1964) also states that the dorsiventral solenostelic rhizome is probably derivative from an ancestral stock with a radial symmetry.

The phyletically ambiguous genus *Oleandra* exhibits several characteristic morphological peculiarities. Different species of *Oleandra* exhibit different stages of transition from a erect, radiosymmatric dictyostele to a creeping dorsiventral stele with leaves in two dorsal rows on the upper surface of the rhizome. In *O. pistillaris* (an erect growing sp.) the well developed leaves are in whorls around the rhizome, that at intermittent intervals



Figs. 5-8 Vascular cylinder of a portion of the adult rhizome of *Oleandra*. Fig.5. *O. pistillaris* showing spiral arrangement of leaf gaps. Fig.6. *O. wallichii* dorsal surface of stellar cylinder. showing vascular connection to well developed leaves. Fig.7. *O. wallichii* ventral portion of the same portion as in Fig. 6. Fig.8. *O. distenta* showing two rows of alternate leaf gaps.

(**B**, branch trace; **B'**, base of branch trace on the lower side; **BG**, branch gap; **L**, leaf trace; **LG**, leaf gap; **SL**, vascular strand representing a suppressed leaf).

sometime, far apart. The vascular cylinder of the rhizome is a radiosymmetric dictyostele, dissected into slender cylindrical vascular strands by large crowded leaf gaps arranged in 3 - 4 close spirals (Fig. 5).

A highly interesting feature is the suppression of leaves over extensive regions of the rhizome in the genus, All leaves except small clusters here and there are suppressed; these suppressed leaves are represented by a prominent leaf gap in the stellar cylinder of the rhizome. The characteristic spiral arrangement of the suppressed gaps (small size with blind ending) in the leaf less region in continuation of the spirals of leaf gaps associated with the well developed leaves, leaves no doubt that they are leaf gaps. Leafy and leafless regions alternate thus forming whorl arrangement. The tendency for reduction in

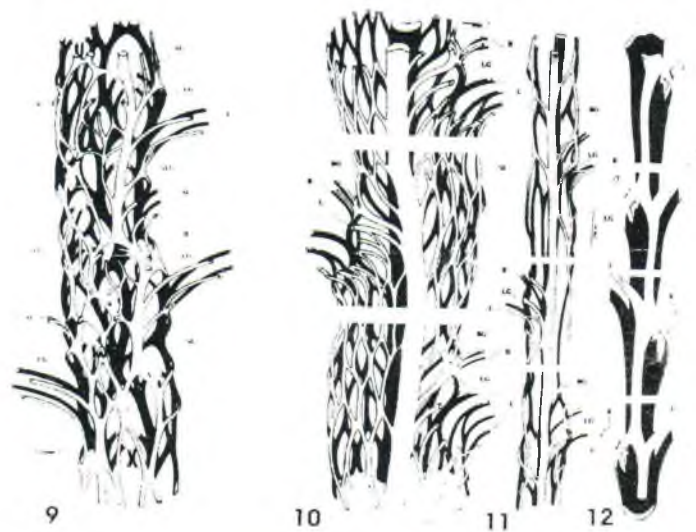
the number of vascular strands constituting leaf trace in *O. pistillaris* apparently represents an intermediate condition leading on to the suppressed leaves.

In *O. wallichii* (creeping sp.) the clusters consist of a few leaves strictly restricted to the dorsal surface; these are dorsally placed leaves in several spirals of leaf gaps in the stellar cylinder (Fig. 6). The leaves on the ventral surface are suppressed and associated with solitary blind ending leaf trace strands (Fig. 7). The presence of occasional vestigial leaves (on leafless portions of the rhizome) supplied by solitary blind-ending vascular structure of some of these gaps, supports this view. In *O. wallichii* suppression of leaves follows a characteristics pattern different from that in *O. pistillaris*. The leaves, except from some of the dorsal side of the rhizome, are suppressed. The characteristics regularities by which the leaves are suppressed on the lower and lateral surface of rhizome, leading on to the possession of well developed leaves only on the dorsal surface, indicates that *O. wallichii* is comparatively more advanced than *O. pistillaris*.

In *O. distenta* (an african species with slender much elongated, prostrate branched rhizome) the vestigial leaf traces associated with the leaf gap of the vascular cylinder fuse back with the vascular cylinder at the anterior end bridging the gap thus forming many lacunae which mask the spiral sequence with only one pair of dorsal rows of developed leaves (Fig. 8) with many lacunae (gaps). This characteristics feature of the vestigial traces indicates that *O. distenta* is possibly more advanced than *O. wallichii*.

Such vascular system if found in a creeping rhizome with two rows of leaves on the dorsal surface, resembles the vascular cylinder in the polypodiaceous ferns.

This indicates how during evolutionary progression the form of erect (primitive) dictyostelic vascular cylinder with spiral leaf gaps may change (by suppression of leaves and bridging of the leaf gaps thus loosing the spiral sequence) into creeping vascular cylinder with only one pair of dorsal rows



Figs. 9-12. Vascular cylinder of a portion of the adult rhizome Fig. 9. *Araiostegia dareiformis* showing developed and suppressed leaves (after Bajpai, 1972) Fig. 10. *Davallia bullata* (after Bajpai, 1972) Fig. 11. *D. denticulata* (after Bajpai, 1972) Fig. 12. *Leucostegia immersa* (after Bajpai, 1972).

(**B**, branch trace; **BG**, branch gap; **L**, leaf trace; **LG**, leaf gap; **SL**, vascular strands of suppressed leaves, **SLG**, leaf gap of suppressed leaf).

of leaf gaps and dissected by many lacunae characteristic of the Polypodiaceae (the highest evolved condition) (spiral whorl-2 ranked).

The stellar organization of the rhizome of *O. distenta* is explained throwing light on the interpretation of the characteristic vascular organization of the polypodiaceous ferns as well as some of the Davalliaceae (one pair of dorsal rows of leaf gap and is dissected by lacunae (gaps) around the cylinder). Thus, The stellar organization in *Oleandra* is interpreted as indicating that an erect habit with close spirals of leaves is more primitive and a creeping habit with leaves in two dorsal rows on the rhizome are apparently derived features (cf. Holttum, 1964).

A condition closely parallel to that of *Oleandra* is found in *Araiostegia dareiformis* (closely placed overlapping spirally arranged leaf gaps). There is an extensive suppression of leaves all over the rhizome, well developed leaves being in two lateral rows on the rhizome (Fig.9). Leaf traces end blindly and also fuse back with the rhizome bridging the leaf gap as

in *O distenta*.

Such reticulation of the leaf trace strands and the tendency for them to bridge the posterior half of the leaf gap is characteristic of the well developed leaves of *Araiostegia dareiformis* as well as most of the davallioid ferns. Apparently the characteristic solenostelic vascular cylinder of *Davallia* is derived by suppression of dorsal and ventral leaf from a radiosymmetric dictyostele vascular cylinder as found in *Araiostegia* & *Oleandra* except the laterally placed ones as seen in *D bullata* (Fig. 10) and *D denticulata* (Fig. 11, vestigial strands associated with small gaps towards the dorsal as well as on ventral side of the vascular cylinder). In *Leucostegia* (Fig. 12) leaves are in two lateral rows but oriented more onwards the dorsal median plane than towards the ventral side, branch traces are reduced structures (solitary) without branch gaps, associated with the leaf gaps. Thus showing advancement over *Davallia*.

Alston (1956), however, suggested the relationship of Davalliaceae and Oleandraceae to the Polypodiaceae. Later Holttum (1973,74) also doubtfully suggested that Polypodiaceae sensu stricto (excluding grammitidaceae) could be related to Davalliaceae on the basis of the similarities of epiphytic habit, stipe articulation, occurrence of peltate scales, vasculature of the rhizome, spore structure and soral morphology. Ching (1978) in his new classification of Filicales has also kept polypodiaceous ferns after Davalliaceae which further gives an idea that probably the polypodiaceous ferns are closely related to Davalliaceae as suggested earlier.

Based on the studies on vascular organization of the rhizome in *Oleandra*, *Davallia*, *Araiostegia*, *Humata*, *Leucostegia* and other polypodiaceous genera the possibility of similarity in the vascular organization of the rhizome of polypodiaceous ferns with that of Davalliaceae is suggested.

CONCLUSIONS

The vasculature of the rhizome in *Oleandra* is interpreted as indicating that an erect habit with

close spirals of leaves is more primitive and a creeping habit with leaves in two dorsal rows on the rhizome is apparently a derived condition, resembling the vasculature of the rhizome in polypodiaceous ferns. The vasculature of the rhizome in *Oleandra* is interpreted as indicating that an erect habit with close spirals of leaves is more primitive and a creeping habit with leaves in two dorsal rows on the rhizome is apparently a derived condition, resembling the vasculature of the rhizome in polypodiaceous ferns. Thus, a possible evolution of the dissected dictyostele of the creeping rhizome of polypodiaceous ferns from a typical dictyostele by a process of reduction is evident.

A condition closely parallel to that of *Oleandra* is found in most of the davallioid ferns (*Araiostegia dareiformis*, *Davallia*, *Humata*, *Leucostegia*). However, based on the vasculature of these taxa, it is here suggested that there is a possibility of similarity in the vasculature of the rhizome of polypodiaceous ferns with that of Davalliaceae (both share many other morphological characters).

Findings based on molecular studies (Pryer *et al.*, 1995; Hasebe *et al.*, 1995; Pryer and Smith, 1997; Cranfill, 2001 per. comm.) also show that the Polypodiaceae and Davalliaceae are sister groups and share a recent common ancestor with some members of the Dryopteridaceae. The phylogenetic tree based on molecular data mostly correlates well with overall morphological similarities reported here. Thus, molecular data are consistent and support conclusions based on traditional comparative morphology.

There is currently a need for detailed study of the vascular organization in the various groups of homosporous ferns and it is reasonable to expect that such studies will bring to light more evidences with which the evolution and relationships of Filicopsida could be better assessed.

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