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## THE SEARCH FOR A PRIMITIVE FERN\*

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SEARCH for the origin of any group of plants today is beset with difficulties as it is not easy to define exactly what is primitive. It is possible to recognize what is advanced, but not the primitive, as what could be primitive might as well be reduced; and hence a retrospective search for the origin of any group may not always be successful. Generally, what one considers primitive is only a reflex of what one thinks of the opposite; and that may be wrong as all parts do not evolve similarly, and as all the facts of Evolution are not reproducible, its processes often being irreversible. The strange thing about Evolution is the survival of the simple or the primitive with the advanced together at the same time. In such an ensemble search for the origin of any group is a search in a dark labyrinth, *e.g.*, search for the origin of angiosperms, origin of life, etc. Having engaged myself in studies on ferns for the past 35 years, I thought I might venture to do so, as some new light on the problem has been thrown during this period from the recent work on their cytology, culture of sporophytic tissues, especially the stelar tissues, gametophytes, in addition to morphology, past and present distribution. At the same time much new material of early vascular plants has come out, and their origin is now firmly established in the Silurian period and not in the Devonian as we used to think (Lang and Cookson, 1935; Leclercq, 1954, 1956; Danze-Corsin, 1956; Andrews, 1959; Chaloner, 1960, 1967; Stewart, 1960; Baxter, 1961; Obrhel, 1962; Banks, 1964; Richardson, 1964, 1965; Eggert and Delevoryas, 1967; Streel, 1967). Still it is yet not easy to point out a particular genus or a larger taxon as the ancestor of ferns. The difficulty here arises from the fact that whereas our knowledge of their morphology, life-history, cytology, anatomy is complete, it cannot be gainfully applied to fossil ferns—whose structure we well understand. But alas! they are all extinct. The chronologically most primitive ferns have disappeared by the end of the Carboniferous period; only the later members like the Schizaeaceae, Gleicheniaceae, Matoniaceae, Osmundaceae

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continued further. The great bulk of the present-day ferns, the Polypodiaceae, begins to appear still later from the Jurassic onwards. The vast assemblage of the Devonian and Carboniferous ferns, Pre-ferns, Protopterids, Pteridosperms, Psilophytes suffered terrible destruction in the cold climate of the Permian. Most of them have not left even a single representative unlike the other great groups of Pteridophytes, the Lepidodendrales and Articulates. We are, therefore, forced to take a recourse to the study of living ferns and compare them with their pre-Triassic predecessors. This creates a highly unbalanced situation, as in one's eagerness to trace their origin, one is led to compare the most primitive among the living with the most primitive among the ancients, without knowing what that primitive was in the most ancient period. The time gap between the two is approximately of the order of 350 million years; and hence such a comparison loses much of its value. Even then the search has to be on, and that is the chief purpose of this paper.

The question naturally arises, how to compare a very primitive ancient group with another primitive group among the living. Some criteria have to be used such as follows:—

1. *Morphology*—form venation, sporangia.
2. *Anatomy*—Stele and leaf trace.
3. *Cytology*—Chromosomes.
4. *Palynology*—Spores, their kinds and sporoderm.
5. *Behavioural pattern*—in genetics, physiology and experimental studies on the culturing of gametophytic and sporophytic tissues in the laboratory.

They are the same as have been adopted for other groups by Linnaeus (1737), Bentham and Hooker (1862–83), Engler and Prantl (1902), Hallier (1905), Bower (1923, 1926), Copeland (1947), Holttum (1949, 1954), Takhtajan (1954) and others. Biosystematics is useful in narrow circles of affinities as shown by Manton (1950), Ninan (1956), Verma (1956), Mehra (1960), Panigrahi (1960), Abraham, Ninan and Mathew (1962). Weittstein (1935), Wetzel (1938) and others have used biochemical characters. Stokey (1951), Allsopp (1955), Mahabale (1962 a), Nair and Surjit Kaur (1968) have used gametophytic features, and Wetmore (1951), Wardlaw (1952, 1955) and others, the cultural behaviour of tissues and meristems. Still the origin of angiosperms or ferns is problematic. In angiosperms homoxyle and tracheidal nature of xylem provide useful criteria for checking primitiveness, but that is of no significance here. The fact is during the long conquest of land by vascular and non-vascular plants, too many changes have taken place too many a time, at too many places on similar lines, resulting in a number of generalised patterns and structures. Thus the primitive and the advanced coexist and it is impossible to derive

one from the other. So we have to use all the available data collectively. In this particular problem, we have a double handicap as the Ophioglossaceae supposed to be very primitive among the living ferns have no fossil record and the Protopterids and Pre-ferns of the Silurian and Devonian period have left no living representatives. Besides, their identity is bogged in the midst of numerous unidentifiable and identifiable Psilophytes. Several of them look like an alga, a fern, a fern-ally or a progymnosperm. *Archaeopteris* is a classical example of this jumble, slowly getting cleared up through the work of Leclercq (1954, 1956), Baxter (1961), Hueber (1964) and Banks (1968 a, b). The early ferns became a distinct group only in the later Carboniferous, and more so after the Permian and Triassic.

However, in this connection it is necessary to remember that ferns despite their checkered past are the first successful conquerors of land which produced numerous representatives from the Devonian to Carboniferous. For example, Banks (1968 a) has cited twenty-three identifiable spores of the Devonian plants, some of which should be of ferns. Even the Devonian spores like *Lophotritetes*, *Leicotritetes* exhibit triradiate mark although they vary in their sporoderm ornamentation. They had various patterns of foliage but not all were ferns. The triradiate mark is a distinctive feature of the spores of early land plants, the Bryophytes and Pteridophytes. Hueber (1961) has already recognised *Hepaticites devonicus* in the Devonian of New York and a search for liverworts elsewhere is bound to be rewarding. But the triradiate mark only suggests a common method of simultaneous spore formation in which tapetum envelops each tetrad till the spores ripen. Ripening in all such cases was above water in wet mud under subaerial conditions. The spores of aquatic algae with a few exceptions like *Tamnogametum indicum* or *T. cylindrospermum*, *Debaria jogensis*, *D. smithii* have no mark. In these green algae there is a straight or sigmoid "*Riss-linie*" which is the precursor of triradiate mark. In the rest of the algae the spores are formed in water and are turgid and round. In subaerially growing fungi such as Ascomycetes varied ornamentation of sporoderm is developed but no colpi or triradiate mark. In the underground Tuberales exosporium is ornamented but no colpi. This character, therefore, though not common suggests a far remote ancestral connection that binds the Bryophytes to Pteridophytes (Mehra, 1968).

However, notwithstanding the common features such as dichotomy of vegetative parts, presence of antheridia, archegonia and embryo, there is a great hiatus between the Bryophyta and Pteridophyta as Bower (1935) pointed out, due to the difference in their life-cycle and the cytological status of the alternating generations. The ferns certainly are not the vascularized sporogonia of liverworts, nor liverworts devascularized ferns having lost the tracheids.

Anatomically, ferns are distinguished by their stelar structures and leaf-trace pattern. This rules out the entire set of non-vascular

plants from the Silurian, Devonian and Carboniferous period, and all the Bryophytes in our search. Even then it is not easy to separate them from Pre-ferns, and plants like *Aldanophyton* or other Psilophytes in which vessels are not yet found. The Psilophytales have dichotomy of aerial parts, swollen bases, monangial or synangial thick-walled terminal sporangia, simple vascular strands but no roots. Long ago I had suggested that root is a secondary organ of absorption of land plants, the primary organ of absorption being foot (Mahabale, 1947). The Lycopsidea despite their other similar characters had endosporic prothalli. The Articulates had relatively small leaves and sporangio-phores. We know nothing of their gametophytes. The claim that *Rhynia minor* is the gametophyte of *Rhynia gwynne-vaughani* as made out by Merker (1958, 1959) and Pant (1960) looks plausible due to the discovery of vascular prothalli in *Psilotum triquetrum* by Holloway (1939). But what about the gametophytes of the stately *Calamites* or *Sphenopsids*? Could the dark dust obtained sometimes from the base of *Calamites* be their decomposed prothalli? One can only conjecture. But the sporophytes of these groups are quite distinct from the ferns morphologically and anatomically and one cannot mistake one for the other.

Ferns as a class are essentially macrophyllous plants having a solid core of xylem in rare instances like *Thamnopteris*. But in others the large leaf imposes alteration in stem stele which becomes phyllosiphonic—amphiphloic or dictyostelic as Jeffrey (1917) pointed out. The leaf trace also with a few exceptions becomes fluted. It is rarely a single solid strand, e.g., in *Thamnopteris schlechtendalii*, but in most of them it is abstricted by opening out of the stem stele at one end as in *Gleichenia*, but more often by abstricting alternately two strands marginally from the two ends of a broken semilunar stele. In others it is made up of many leaf-trace bundles as in *Polypodium* or *Angiopteris*. In fossil ferns also it is so, but in *Clepsydropsids* it was extruded as a pariphal bud or included in a patch of thick or thin-walled parenchyma in the cortical tissues as in *Reimannia* or curved as in *Tubicaulis* or nearly free from the cortex as in *Iridiopteris*. Phyllosiphonic stem stele and marginally abstricted leaf trace are distinct characters of ferns, whether living or ancient. Their other morphological characters such as dichotomised aerial axes, flattened or cylindrical, leafless or with leaf enations, accompanied usually by tracheidal strands, tetrad spores, give half-hearted support to them as ferns, because many of the Psilophytes like *Aneurophyton*, *Hedeia*, *Swalbardia*, *Hyaenia*, *Taeniochrada* had branch-like leaves and leaves looking like branches. They provide excellent examples of telomic structures but not only of ancient ferns. The thick-walled sporangia single or in bunch are clear in *Taeniochrada* or *Dowsonites*. They were radially arranged around the parent axis in *Botryopteris* symmetrically, and possibly spirally in Zygoteridinae. From their varied fructifications, eusporangiate sori producing homo- or heterospores, sac-like or panicle-like sporangiferous parts on leaf, or distinctly separate on lateral or terminal stalks as in different species of *Botrychiunt*-subtended

by a bract or without it, we get no assurance that they were all ferns. Some of them might as well represent Psilopsids or Zygopsids. And, therefore, barring *Rhacopteris*, *Protopteridium*, *Reimannia*, *Aracnoxylon* in which the majority of characters coincide with those in ferns, the rest of them cannot be taken as true ferns.

The same thing is true of their venation. Luerssen (1819), Bower (1923), Zimmermann (1930) have emphasized the relation between the expansion of an axis into a lamina terminally or subterminally, in the same plane as that of the parent axis as in the Protopteridineae, or in varied planes as in the Zygopteridineae. Venation is uncertain in Silurian and Devonian genera and deceptive in Carboniferous, as it gets mixed up with that in the members of the Pteridosperms. We are, therefore, left with very few genera as ferns like *Rhacopteris*, *Protopteridium* as true ferns. Furcate venation believed to be a fern character is rather confusing in the early pteridophytes and pro-gymnosperms, just as stele is in the Asteroxylales and *Reimannia*. Thick-walled sporangia or homospority also have proved unreliable as in an early fern such as *Stauropteris burntislandica* Surange (1952), Chaloner (1958) and Richardson (1964, 1965) found heterospority.

Some botanists like Banks (1968 a), Arnold (1947) and Andrews (1961) are inclined to take Cladoxylales as the ancestors of ferns or what Andrews (1961) designates "pre-ferns". But it is necessary to add here that they had secondary growth and polystelic structure. Both these are advanced characters, so rare in modern ferns. Thus we are on the horns of a dilemma. The early Lower Devonian or Silurian plants are too simple to be called ferns, and the mid-Devonian and Carboniferous ones are too advanced to be considered as the progenitors of ferns. But this has always been so in Evolution. The ferns or Filicophyta were struggling throughout Devonian to shape themselves distinctly as ferns apart from the several other different members already differentiated or advanced as the Psilophytes. They seem to have succeeded in doing so only after the mid-Devonian. Like early Psilophytes, they also seem to be different from each other and might have taken their origin from pre-fern stock derived from several green algae. But unlike Lepidodentrales they did not survive. Possibly, their prothalli were not endosporic or protected, but were exposed for years together to Permian frost, like those of modern *Equisetum ramosissimum* exposed to frost or snow in winter, and die. Their expanded lamina was not followed up by commensurate internal tissues, the ratio of vascular tissues to cortical pith in them being adverse (Bower, 1923). This disparity was removed later by the reduction of cortical pith and augmentation of the woody and stelar tissues, and by the development of subdermal sclerenchyma in stem and rachises. That made the emergence of Gleicheniaceae *Oligocarpia*, *Schizaeaeaeous Senftenbergia*, *Klukia* or later of *Psaronius*, *Osmunda* or *Marattiopsis* possible. Several members of these families have survived till today except the genus *Psaronius*. The general impression, therefore, that all Psilophytes, Protopterids or Coenopterids are simple

or primitive is unwarranted as Leclercq (1954) pointed out long ago. Only a few of them may be primitive. They all seem to represent the end products of early pre-ferns, ferns, Psilophytes which were quite advanced in their own time. They could hardly, therefore, be considered as ancestors of the existing ferns, primitive or advanced. At best they indicate a few flimsy bonds with them. The great heterogeneity among the ancient "*Sporae dispersae*", their exine patterns, or venation of leaf suggest polyphyletic origin for ferns, modern or ancient. This is a conclusion that needs close scrutiny of the so-called primitive ferns living today.

In our search for the ancestors of ferns in fossils we have been landed in the midst of living ferns which may have survived over ages, because we believe that the survivors of any group today contain some unchanged, some fully changed and some half-changed members. The Devonian and Carboniferous ferns seem to contain advanced members representing a high level of differentiation and adaptation. But since most of them are extinct Palaeobotany does not help much to locate the ancestors of Protopterids. We have, therefore, to scrutinize the claims of primitive members in the living ferns on their own merits, using the same criteria as we used for the fossil ferns making an allowance for the possible progress they might have made through millions of years through which they have been evolving. The most advanced amongst ferns are the Hydropteridineae, as they have heterospores protected in capsules, endosporic prothalli, provision for the nutrition of the embryo, and effective means of dispersal. With all these they have not discarded the zoidogonial mode of fertilization which was advantageous in the climate of the Carboniferous, but a distinct disadvantage in the arid or semi-arid climate of the Triassic and later periods of the progressively desiccating terrain. They were, therefore, slowly pushed into the background by members more suitable for the subaerial life such as pteridosperms, gymnosperms and angiosperms. This was a big setback to them in the conquest of land and they started growing on wet lacustrine, riparian or estuarine soils or in ledges of wet rocks.

Naturally, they sought asylum in isolated corners in high hills, moisture-laden valleys, crevices of rocks fed by underground sources of water. They are the largest group of land plants (10,000 species and 305 genera) next only to angiosperms (1,95,000 species and 10,000 genera). Still they do not seem to be co-dominant all over except at high altitudes and in secluded valleys. They practically cease to spread beyond 30° N. and 40° S. of equator, being absent in deserts. According to Manton (1954) there is high concentration of their genera and species in the tropics, but less species in the temperate regions, though the members of an individual species may be numerically superior there. One, therefore, meets ferns again and again in the hills like perigrine creatures. You simply cannot avoid them there. In dry deciduous forests they abound in monsoons on trees, wet rock river-banks, gravel, alluvium, grassy plains or mossy slopes. It is no

small task to locate the most primitive among them in such a bountiful multitude ranging from trees as in *Cyathea*, *Alsophila*, *Cibotium* reaching a height of 20-25 m to minute *Gymnogramme leptophylla* hardly 3-4 cm. or *Ophioglossum simplex* or *O. gramineum* seldom more than 1-3 cm. Using the simple or hairy character of the stipules, erect nature of rhizome, simple or divided lamina, furcate venation, aphanogonia, thick-walled sporangia, green cordate prothalli resembling liverworts, bilaterally or radially distributed embedded reproductive organs, numerous spermatozoids, alike spores, pteridologists have thought that the "Eusporangiatae" and in them the Ophioglossaceae seem to represent the most primitive stock of ferns. But the difficulty here is, whereas the Marattiaceae types begin to appear from the Upper Carboniferous onwards, there is no record of any fossils belonging to the Ophioglossaceae. What happened to them in the earlier or later period is a matter of conjecture. Pre-Ophioglossums, Protopterids and Coenopterids disappeared by the end of the Carboniferous. From Jurassic period onwards the Marattiaceae begin to be conspicuous. Very probably the Permian cold followed by Triassic dryness seems to have conspired to kill all Protopterids and Coenopterids. The only thing which possibly helped the Ophioglossaceae to survive these trying times must have been the geophilous habit with limited growth in time and space, and aestivation of the plants again and again. One does not expect woody or hard tissues in tuberous plants, but only fleshy ones. However, sclerenchyma, hard woody parts, and even cambium were not uncommon in the early pteridophytes. The Eusporangiatae on the other hand have soft tissues, large leaves, bulky fleshy stem and large rachises as in many monocots. Arber (1925) has shown that the large leaf in monocotyledons is due to the condensation of phyllopodium and suppression of laminar expansion. So, it is in the Ophioglossaceae. In *Ophioglossum* pinnae or lobes get condensed to form a fleshy leaf. There is no fibrous tissue in the leaf as in *Drynaria*, *Acrostichum* or *Pipal* (*Ficus religiosa*). The geophilous habit of their gametophytes also encouraged tuberization of stem and prothalli and their survival. The prothalli of pteridosperms were helped to survive by their endosporic nature, but the prothalli of Coenopterids were possibly exposed to air like those of *Equisetum* and died under the stress of extreme cold of Permian followed by severe dryness of Triassic. On the other hand, *Anthoceros*-like prothalli of the Schizaeaceae, Gleicheniaceae, Osmundaceae survived due to their perennial habit. In the warm climate of Jurassic the Marattiaceae is abundant but no Ophioglossaceae. In India one species of *Marattia*, *M. macrocarpa* and five of *Daneopsis* are abundant in the Raj Mahal Hills. Here it looks as if the Marattiaceae is more ancient than the Ophioglossaceae. Both the families have fleshy leaves, large stumpy non-soboliferous rhizome with a loose dictyostele, two or many leaf-trace bundles arranged in a circle, long cordate prothalli, occasionally underground in *Angiopteris*, embedded reproductive organs and thick-walled sporangia. Their roots, however, differ much in anatomy. The sporangia in the Marattiaceae lie superficially on sporophylls. In the Ophioglossaceae they form a highly controversial organ—the spike.

The morphological nature of it has been settled as foliar by Chrysler (1910) who found that the two leaf traces enter the base of the leaf as well as spike exactly the way they do in the spore-bearing parts of *Aneimia* or *Marsilea*. The spike has a central midrib on the two sides of which sporangia lie. It has stomata. Numerous variations of the spike in relation to leaf and in its branching occur as I showed in 1937 (Mahabale, 1937 a, b). The branching of spike in abnormal specimens, or of the sterile pinnae may be in different planes in *Zygopteris* (Mahabale, 1937 b). In *Helminthostachys* the spikelets of sori bear terminally leafy appendages as in *Corynepteris*. A green, flat or pointed nail-like tip is present in the spike of *Ophioglossum* in several species. In *Botrychium* spikes are distinctly stalked as in *Helminthostachys*, but they are much more branched. They all are thick-walled as in Protopterids or Coenopterids, but in *Ophioglossum* they get embedded in the tissues of the spike. There is no similarity between the marginally embedded sporangia of *Ophioglossum* and those of any fossil fern. From its middle vitta veins enter alternately at the base of the sporangia. A tendency to condense, therefore, is very clear in the spike of *Ophioglossum* and in its leaves. In *Helminthostachys* the pinnae are pedately divided and have distinct midrib, and furcate venation. In *Botrychium* the leaf may be simple as in *B. lunaria* or *B. simplex*, or ternate as in *E. ternatum*, *B. daucifolium* or *B. virginianum*. The venation is fan-shaped as in *Sphenopterids*. In *Ophioglossum* the leaf has no true midrib. The so-called midrib of *O. aitchisoni*, *O. reticulatum* or *O. vulgatum* contains only elongated cells. The leaf trace is double in *Eu-ophioglossum*, and multiple in *Cheiroglossa* as in *Angiopteris* (Mahabale, 1962 b). The leaf in *Ophioderma* (*O. pendulum*) is simple and strap-shaped, often dichotomously divided once or twice. In epiphytic *O. palmatum* it has many lobes. Each lobe bears a spike at the point of dichotomous division of pinna into lobes. It is supplied by two strands from the peripheral veins of the palmatifid lamina, exactly the same way as in the spike of the small-leaved species of *Eu-ophioglossum* like *O. nudicaule*, etc. In *O. simplex* the sporangia are fused with the flat spike at the margin. It thus seems that there is a strong tendency to fuse and condense on the part of pinnae and lobes in *O. vulgatum*, *O. aitchisoni* or *O. simplex*. The venation as a result becomes reticulate in all species of *Ophioglossum*, small or large. In *O. aitchisoni* it forms even secondary areoles and recurrent veins. The condensation of pinnae and of sporangia thus seems to be an important factor in shaping the fleshy reticulate leaf and fertile spike in *Ophioglossum*, like that in the fleshy, reticulately veined leaves of epiphytic *Platycterium* or *Pleopeltis*. It is this reticulate character of its veins that really is the stumbling block in considering *Ophioglossum* as the most primitive genus in the family *vis-a-vis* ferns. Campbell (1911) and Bower (1926) think that *Botrychium* is the most primitive, and I think it to be *Helminthostachys* on account of its furcate veins and two-rowed spike like that in *Ophioglossum* but studded with sporangia having terminal appendages as in some members of the Coenopteridinae. The stele in *Botrychium* is protostele and in *Helminthostachys* amphiphloic siphonostele. In



*Ophioglossum* it is a diffused dictyostele without endodermis. There is clear mesarchy in *Helminthostachys* and cambium in *Botrychium*. The latter also has vessels with pits. Thus form, spike and venation in *Botrychium* suggests primitiveness but not its anatomy. The venation of leaf and spike suggest *Helminthostachys* as the most primitive genus, but not its dorsiventral rhizome. The double or multiple leaf trace in *Ophioglossum*, slight periderm formation in the rhizome of *O. fibrosum* and *O. lusitanicum*, highly reticulate and areolated venation in species like *O. lusitanicum*, in *O. aitchisoni*-developing secondary meshes, preclude it from being considered as a highly primitive member among themselves. Morphology suggests *Botrychium* and *Helminthostachys*, but not their anatomy. The spike and leaf form suggest *Ophioglossum* but not its venation. The condensation of its sporangia rather suggests its advanced nature in the family. It is very difficult to say thus which really is the most primitive on account of the conflicting suggestions emerging from their heterogeneous characters.

The heterogeneity in them is evident in their chromosomes also. In *Helminthostachys* there are  $n = 90$  chromosomes, in *Botrychium* 45. In *Ophioglossum* they vary enormously from  $n = 120$  in *O. nudicaule* and *O. gramineum* to  $2n = 1,260$  and odd in *O. reticulatum* (Abraham and Ninan, 1954; Mehra, 1960; Verma, 1956; Miss John, 1966). In our investigations we found polyploid races in *O. nudicaule*, *O. reticulatum*, *O. gramineum* and *O. pedunculosum*. Ninan (1956) and Verma (1956) had seen them in *O. vulgatum*, *O. reticulatum* and *O. nudicaule*. Very high chromosome numbers are a special feature of the living pteridophytes like *Psilotum* which is the lonely survivor of the Psilophytaceae ( $n = 52-54$ ), *Equisetum* ( $n = 108$ ), *Lycopodium* ( $n = 34, 78$ ), *Phylloglossum* ( $n = 255$ ). But the highest chromosome number in the plant kingdom so far known is in *O. reticulatum* ( $n = 631 \pm 10$ ). How this has come about is a deep mystery. Stebbins (1964) has suggested duplication and endomeiosis as the cause of such high numbers as in some Gramineae. Manton (1950, 1954) believes it to be the result of repeated polyploidy in quick succession in short time, at least in some species. But these provide only a partial answer. What caused such a quick succession at least 4-5 times from  $n = 120$  in *O. nudicaule*, or *O. vulgatum* to 1,260 in *O. reticulatum* is unknown. Some botanists think that it may be still many more times as they take 15 as the basic number. It is extremely unlikely that such high polyploidation would not have produced adverse, unbalanced or even lethal effects extirpating those clones that had lower numbers in struggle for survival. But possibly the saving factor was geophilous habit which helped them in reducing the stresses imposed by repeated polyploidy and survival of some individuals with balanced lethals. It also must have killed others when required to face repeated glaciation and desiccation from Protopterid times. Cytology, therefore, only suggests, that they are the isolated left-overs of a long historical sequence, unfolding a variety of environments which they must have been required to face. In this struggle *Ophioglossum* developed 30 species all over the world growing today in all climates and altitudes,

and *Botrychium* about 12 at high altitudes only. *Helminthostachys* became monotypic endemic in the Old World tropics and is often found near the seashore in India and Ceylon, e.g., Trivandrum. But it may also be found at higher altitudes such as Gokakhpur on the Tarai Plains or at still higher altitude at Santaveri in the Jager Valley of the Baba Budhan Hills in Mysore. The presence of relatively more species, varied stipules, scaly or hairy, and details of venation suggest the highly pliable nature of the genus *Ophioglossum*, whereas the scaly stipules in *Botrychium* and *Helminthostachys* and their leaf venation conservative nature. Of the two, *Helminthostachys* is more isolated and restricted in its distribution. *Ophioglossum* has the widest spread-out being cosmopolitan. It is also capable of growing under a variety of soils and climatic conditions (Mahabale, 1938).

The thick-walled sporangia of the Protopteridineae or Coenopteridineae and Ophioglossaceae are undoubtedly similar but they differ much in details. Anatomically Ophioglossaceae indicates a lower level of organization than Gleicheniaceae and Pteridospermae. The three members of the Ophioglossaceae, therefore, are quite distinct and isolated from each other. *Helminthostachys* is closer to Zygopteridineae and Pteridospermae, *Botrychium* to Botryopteridineae and *Psilotum*. *Ophioglossum* seems to be the lonely survivor of an extremely ancient group which owes its survival to geophilous habit and mycorrhiza. It is well known that mycorrhiza occurs in ancient and modern Psilophytales in their underground parts and helps them in the perennation of the rhizome and prothalli. The roots and prothalli of *O. aitchisoni* harbour a non-pathogenic strain of *Fusarium oxysporum* endophytically. Those of *O. pedunculosum*, *O. nudicaule* other strains of *Fusaria*. In 1933, I collected prothalli in 4-5 species of *Ophioglossum* (Mahabale, 1933, 1937 c, d, e). In *O. aitchisoni* and *O. pedunculosum* they were branched dichotomously 3-5 times, their dichotomised tips reaching the surface of soil and becoming green. In *O. fibrosum* they were carrot-like and only underground. Bruchmann (1904) and Campbell (1911) had also found a great variety of them in the species they studied. But the prothalli in *Botrychium virginianum* and *B. lanuginosum* were only white button-like or peg-like underground bodies highly infected by mycorrhiza (Campbell, 1911; Rao, 1939). Prothalli of *Helminthostachys* described by Campbell (1911) and Nozu (1961) were non-green or green at the apex only. The tuberisation of the prothallus and endophytic association seem to be secondary characters, but they seem to have saved them. I found that in the sporophyte of *O. nudicaule* and *O. pedunculosum* some roots could be without fungi and that the young plants in them could grow without fungus for some time, but they do not survive. The nutritional chain dependent on fungi seems obligatory in the later stages. It is also so in the prothalli of *Angiopteris evecta* growing under precarious conditions on the vertical walls which bury them occasionally at Castle Rock. It is normally cordate but in such situation tuberous. I observed the same thing in the semituberous prothalli of *Scolopendrium vulgare* growing in Caucasus mountains in Georgia, U.S.S.R.

Embryogeny of the Ophioglossaceae is also peculiar. Suspensor is present in *Botrychium* and *Helminthostachys* but not in *Ophioglossum*. But the embryonic root in all of them comes out first leaving the gametophyte. At some stage it looks as if the whole embryo of *Ophioglossum* is all root, just as it looks foot in *Psilotum* (Mahabale, 1947). The adult plant arises as a secondary bud on the primary root in *Ophioglossum* as in *Equisetum debile* and other species (Mahabale, 1945) or as that in *Chara*. This happens when the root has wintered over, and conditions for the sprouting of root-bud are favourable; otherwise both embryonic root protruding out of the gametophyte and the gametophyte and primary root aestivate again or die. To the best of my knowledge this is rather unique mode of perennation and survival, and I presume it has no parallel in the plant kingdom except in *Equisetum* embryos. What about the ancient *Calamites* and other Articulates? Did they have the same habit? We do not know.

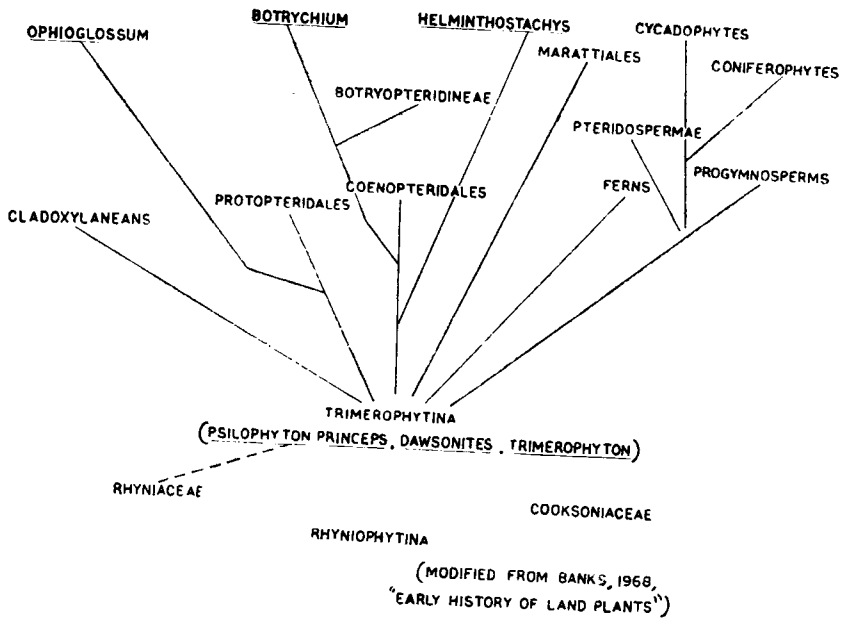
Taking all these characters and peculiarities of the Ophioglossaceae into account we are led to conclude as follows:

That the three living members of the Ophioglossaceae seem to indicate three different tendencies in the early ferns from which three lines might have been evolved. They are persisting in their different patterns of morphology, venation, anatomy, sporangiferous organs and reproduction without undergoing much change.

In two recent papers Banks (1968 *a, b*) has given a new scheme of evolutionary concept of early land plants in which he has created a new group belonging to Coblenzian stage of the mid-Devonian period. In it he has created a new class "Trimerophytina" derived from the family Rhyniaceae named after the genus "*Trimerophyton*". From this hypothetical group, he derives four major lines of Evolution: first the Cladoxyleans, second a bigger stock which gave rise to extinct Coenopterids, Ophioglossales and Marattiales. The third derived from "*Trimerophyton*" gave rise to ferns other than the Eusporangiatae; and the fourth line gave rise to Cycadophytes, Coniferophytes and pro-gymnosperms. I should like to modify this scheme in the light of the above discussion as given below, as I presume that the Ophioglossales are an heterogeneous group in themselves, its three members having been derived from three different sources, related to one other *inter se* and to Coenopterids, Protopterids and also to the hypothetical group of pre-ferns from which *Trimerophyton* may have been derived. *Botrychium*, seems related to the Coenopteridinae. *Ophioglossum* and Protopteridinae though separate are undoubtedly closer to one another, and *Helminthostachys* to *Trimerophyton* and *Rhacophyton*; but they do not seem to have arisen necessarily in a linear sequence. The origin of early ferns has to be searched in the ancestral forms of all these. The ferns as a stock apparently has been polyphyletic.

For the last forty minutes, I have been discussing the origin of ferns which is an important fundamental problem in the study of

early vascular plants. All fundamental problems in any branch of Botany are very enticing. There is great need to build a potential of specialists interested in them in all branches of Botany in our Universities and scientific institutions, as they are of classical importance. Young men and women are prone to take to more easier modern lines of work than these, as they need sustained work spread over several years. If they are unable to do that, they can apply their knowledge of Botany to some problems of practical utility and work on them over a stipulated period, preferably as a group of individuals, interested in solving a particular problem. Isolated individuals working on isolated bits of work would seldom lead to substantial results. Team-work is the essence of research today.



This means we have to reorient our courses, lines of research, techniques, and topics of interest. As the President of the Indian Botanical Society, may I urge you to ponder over these and give new dimensions to botanical studies in our universities and scientific organizations in the country both in fundamental and applied work? I thank you all for patient hearing.

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