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# STUDIES IN PTERIDOPHYTES VIII. AN APPRAISAL OF THE NATURE OF THE RHIZOMORPH IN ISOETES[1]

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## ABSTRACT

The paper mentions the salient features of the gross anatomy of the axis of *Isoetes* based on the author's study of ten species of the genus and presents a review of the morphology of the rhizomorph. *Isoetes* possesses three types of meristems: (1) apical, (2) lateral (cambium) and (3) basal. The presence of a basal meristem is a unique feature of *Isoetes*. It is embedded, self perpetuating and is responsible for the formation of the rhizomorph as well as is the seat of origin of roots. Anatomically the rhizomorphic region of the axis of *Isoetes* is similar to that of the stem region.

A critique on the subject has also been made and the nature of the rhizomorph has been considered under five categories viz. (i) product of cambium activity, (ii) fusion product of roots, (iii) a main root, (iv) an organ 'sui-generis' and (v) a shoot. Though nothing is strikingly different from what has already been described by Lang (1910, 1915a, b), Eames (1936) and Stewart (1947). It has nevertheless become clear from a comparison of the rhizomorphic and the stem region that it is axis like in its nature and finds its best ally in *Stigmaria*.

In earlier communications the author has described the shoot apex organization, nature of secondary growth, development and structure of leaf, ligule, velum and sporangium, arrangement and organization of roots in some species of *Isoetes* and its affinities (Bhambie, 1957, 1962 a, b, 1963 a, b, 1965, 1969 ; Bhambie and Puri, 1963). It has also been

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mentioned earlier that there exists a controversy regarding the nature of the rhizomorph in *Isoetes* the lower portion of the axis which is made up of 2 to 4 lobes. In the present paper, an attempt has been made to see whether anatomical studies on the axis of different species of *Isoetes* throw any light on the nature of the rhizomorph of this plant.

The anatomy of ten species of *Isoetes* (*I. coromandelina* L., *I. sahyadrii* Mahabale, *I. sampathkumarani* Rao, *I. panchananii* Pant and Sriv., *I. engelmannii* A. Br., *I. echinospora* Duv., *I. lacustris* L., *I. malinverniana* Cesat et De not., *I. asiatica* Makino and *I. japonica* A. Br.), has been studied in detail (Bhambie, 1962 a ; Bhambie and Sharma, 1965). In general the axis has the appearance of a 'corm' and is a continuous structure with a somewhat proximal portion bearing leaves and sporophylls and a distal portion made up of 2 or 3 lobes separated by furrows and bears roots. It is this distal region of the axis which is designated as the rhizomorph. In other species e.g., *I. coromandelina*, *I. lacustris* etc., also it is made up of *four* or five lobes (Bhambie, 1965).

The external appearance of the axis in *Isoetes* is quite simple in comparison to the complicated internal structure (Bhambie, 1962a). The stele is roughly anchor shaped and has two well demarcated regions : (1) the upper cylindrical stem stele which sends off leaf traces and (2) bi—, tri—, or tetra-radiate rhizomorphic stele which gives off root traces. The distal region of the stem stele is connected with the centre of the rhizomorphic stele. The stelar lobes of the rhizomorph have upturned free ends and are centrally fused and alternate with the cortical ridges of the axis.

Three types of meristems found in *Isoetes* are apical, basal and lateral (Fig 1). The origin and activity of the latter two are peculiar. The apical meristem is normal in its activity and forms the stem stele (Bhambie, 1957). The basal meristem, which is a unique feature of *Isoetes*, can be compared with the detached meristem, of *Selaginella* rhizophore as in developing axis there is a continuous meristematic zone from apex up to the base. It occupies a position all along the ridges of the rhizomorphic stele. It adds new tissue to the rhizomorphic stele (Bhambie, 1962). Further, it is self-perpetuating and is the

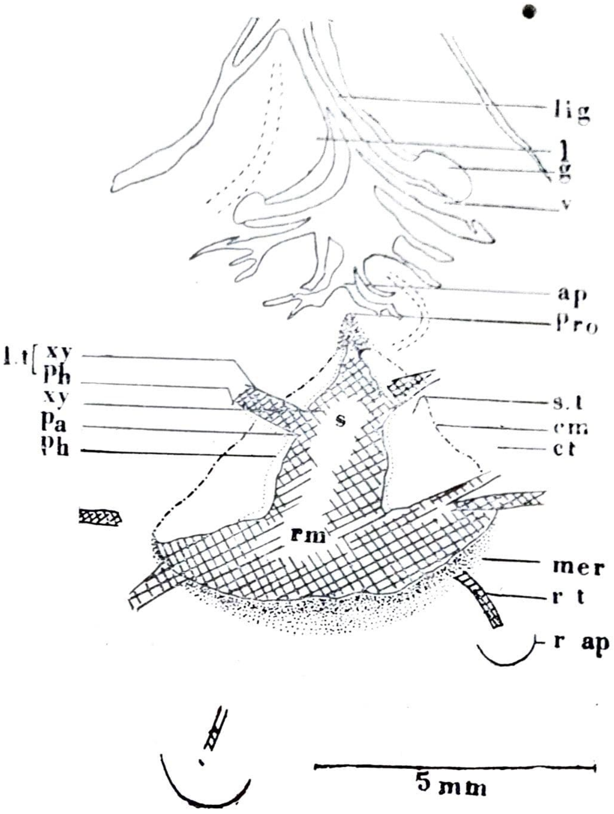

Fig. 1. A part of the median longitudinal section cut in the plane of the furrows of the axis of *Isoetes Panchananii* showing apical, basal and lateral meristems.

*ap*, shoot apex (apical meristem) ; *cm*, cambium (lateral meristem) ; *ct*, cortex ; *g*, glossopodium ; *l*, developing leaf ; *lig*, ligule ; *l.t*, leaf trace ; *mer*, rhizomorphic meristem (basal meristem) ; *pro*, procambium ; *ph*, phloem ; *r. ap*, root apex ; *rm*, rhizomorphic stele ; *r. t*, root trace ; *s*, stem stele ; *sp*, sporangium ; *s. t*, secondary tissue ; *v*, velum ; *xy*, xylem.

seat of origin of roots. The peculiarity of the lateral meristem lies in its origin just adjacent to the primary phloem of the stele. It surrounds the stem stele completely just beneath the procambium, but in the rhizomorphic region it is present in the form of strips bridging the gaps between the two to four ridges of the stele where the basal meristem surrounds the terminal face of the ridges.

The centre of the stem and rhizomorphic stele is occupied by xylem which consists of loosely arranged spiral and helical tracheids and parenchyma without any differentiation of proto and meta-xylem. A few layers of parenchyma surround the xylem cylinder. It is followed by a few layers of irregularly arranged smaller primary phloem sieve elements. A cambium originates outside the primary phloem and cuts off usually secondary phloem and parenchyma centripetally and secondary cortex centrifugally (Fig. 1).

The tracheids of the rhizomorphic stele are slightly smaller than those of the stem stele. Their differentiation from the basal meristem has also been observed. However, on the lateral side of the rhizomorphic stele there is no meristem. A cambium develops on the lateral sides in between the furrows of the rhizomorphic stele. It acts just like the cambium of the stem stele.

A comparison of the stem region of the axis with that of the rhizomorph reveals: (1) that anatomically the stem region of the axis is similar to that of the rhizomorph part (2) that both of them have their own meristem. They, however, differ in some minor structural features i. e., small size of tracheids in the rhizomorph, and cambium not encircling the rhizomorphic stele as the basal meristem of the rhizomorph goes up to the upturned edges of it.

## DISCUSSION AND CONCLUSION

As has been alluded to earlier, the morphological nature of the rhizomorph has remained a subject of controversy for a long time since it is an organ peculiar to *Isoetes* and *Stylites* only. The various interpretations of the rhizomorph can be considered under the following categories: (i) it is a secondary product of cambium activity, (ii) it is partly or wholly formed by the fusion of the basal portions of roots, (iii) it is a root, (iv) it is an organ '*sui-generis*' and (v) it is shoot like in nature.

(i) *Secondary product of cambium.*—Hofmeister (1862) recognized the rhizomorph as a downwardly growing region bearing roots and explained its formation as due to "......an apparent irregularity depending upon the usually vigorous development of the bark and its yearly renovation from within outwards". Obviously he did not consider it as a fundamental part of the plant body. Schoute (1938) also believed that the rhizomorphic lobes are only humps of tissue formed by cambium activity (secondary activity) of the plant. As has been mentioned earlier the portion of the cambium in the lower region is abnormal since it occurs only in the furrows. Yet its behaviour is exactly similar to that in the leaf-bearing region of the axis and it is thus difficult to visualize as to how it can give rise to a new structure. In a recent communication Paolillo (1963) has considered the lateral meristem of *Isoetes* as a part of the basal or root-producing meristem. There is no doubt that the lateral meristem or cambium in the rhizomorphic region, is partly formed by the basal meristem, but functionally it is quite similar to the cambium of the stem. It appears, therefore, that these workers probably overlooked the activity of the basal meristem or considered it functionally similar to cambium.

(ii) *Fusion product of roots.*—Sachs (1882) and De Bary (1884) were of the opinion that the basal disc in *Isoetes* is formed by the fusion of the basal portions of the roots. This view was later modified by Scott and Hill (1900), who believed that the rhizomorph is partly formed by the fusion of the basal portion of the roots and partly by the activity of the cambium. It appears to me that the supporters of this viewpoint were probably influenced by the foliar hypothesis of the shoot and attempted to explain the nature of the rhizomorph in such terms. From the present anatomical study the rhizomorph appears to be a solid structure having its own entity, in which there is no indication of fusion of root traces. Moreover, the root primordia arise just below the rhizomorph and later their steles become connected with the stele of the rhizomorph (Bhambie, 1963b).

(iii) *Root-like nature.*—Stokey (1909), dealing with the histology of the secondary tissue, suggested "that the tuberous body is not wholly stem but a contracted stem and main root" (Stokey, 1909, p. 314). Her remark appears to be a cursory one as she did not describe any characters in favour of the root nature of this organ. The anatomical structure of the rhizomorph also does not support such a contention. The rhizomorph is not only anatomically similar to the stem but is formed by the activity of a basal embedded, self-perpetuating meristem. A root in *Isoetes* has got its own entity and cannot be compared with the rhizomorph at all.

(iv) *Organ 'Sui-generis'.*—According to West and Takeda (1915), the plant body of *Isoetes* possesses two parts: a stem bearing leaves, and a basal rhizomorph (or rhizophore), bearing roots. They regard the basal region as an organ 'sui-generis'. Further, while discussing the affinities of *Isoetes*, they point out that the resemblance between the axis of *Isoetes* and other fossil lycopods is only superficial as the stelar lobes of the rhizomorph do not coincide with the cortical lobes found in a 'stigmarian base'. Lang (1915a) considers these cortical lobes as storage organs having very little morphological value. He further argues that if the *Isoetes* axis is allowed to undergo sufficient longitudinal growth, then the steles of the shoot and the rhizomorph would be clothed with their respective cortex and there may be no cortical lobes. Bower (1935) considers it as an organ of indeterminate character, strictly speaking, neither stem nor root. Sporne (1963) also feels that the root-producing structures in lycopods and *Isoetes* belong to a category of plant organization that is quite unique. He further points out that one is forced to the conclusion that the categories root, stem and leaf have no clear distinction at the lower level of evolution. This difficulty has also been realized by Wardlaw (1965) who recognizes seven fundamental categories instead of three or four pointed out by Sachs (1882).

It is always easy to interpret an organ as 'sui-generis', but it is always worthwhile to try to understand a new organ in terms of other common organs. A clear understanding of the axis of *Isoetes* clearly indicates that the rhizomorph has its own entity and it is similar to the stem.

(v) *Shoot-like nature.*—Von Mohl

(1840) regarded the rhizomorph as 'caudex descendens', that is a descending organ of the axis upon which roots arise. Lang's work on the subject (1910, 1915a, 1915b) is exhaustive. In his first paper he restated the view of Von Mohl and he compared the rhizomorph with the 'stigmarian base'. Later on after a detailed study of *I. lacustris* he came to the conclusion that the rhizomorph was a downwardly growing rhizophore. The primary apex of the rhizophore, according to him, behaves like the stem apex. Eames (1936) while recognizing the difficulty of interpreting the nature of the rhizomorph, considers it as comparable to the rhizophore of *Selaginella* to some extent, which he believes to be of shoot nature although in position and function he thinks it suggestive of a root.

Smith (1955) following Seward (1910), points out that the plant body of *Isoetes* can be compared with that of *Pleuromeia*, the only difference being that in *Isoetes* the axis is so condensed that the stem and basal rhizomorphic regions are not externally distinguishable. On the basis of a comparative study of 'stigmarian appendages' and roots of *Isoetes*, Stewart (1947) suggests that the stem of *Isoetes* may be divided into two regions, the upper bearing the leaves and the lower the roots. Andrews (1961) is of the opinion that in *Isoetes* the entire root and stem system is reduced to a point where there is very little of either of them left.

On the basis of the anatomical comparison and also on account of the peculiar arrangement of the roots, I agree with Lang (1915a, b), Stewart (1947) etc., in regarding the rhizomorph as having the morphological value of an axis (Bhambie, 1962a, b, 1965). The leafless character of the rhizomorph is not against this idea as several cases are known where axes in certain regions have lost the power of forming leaves e.g., the rhizomes of *Psilotum*, *Tmesipteris*, *Asteroxylon* and the lower subterranean stems of *Lycopodium obscurum* etc. Besides, with the changed concept of the plant body, axis being the only fundamental part, the controversy whether it is a root, fusion product of roots etc., no longer has any significance.

The rhizormorph of *Isoetes* offers striking similarities to the root-bearing region of *Pleuromeia*, *Nathorstiana* and lepidodendroid type of stem and Walton (1940) considers *Pleuromeia* and *Nathorstiana* as forming a connecting link between *Isoetes* on the one hand and *Lepidodendron* on the other. Andrews (1961) also believes that *Pleuromeia—Nathorstiana—Stylites-Isoetes* present an unbroken sequence of a line of evolution in which the *axis* got reduced progressively and its culmination can be seen in *Isoetes*. The condition in *Isoetes* could have been brought about by an up-turning of the basal lobes met with in *Pleuromeia* while that in lepidodendroid (*Stigmaria*) could have resulted through continued horizontal growth of these lobes (Bhambie, 1965).

A comparison of the rhizomorph of *Isoetes* with the 'stigmarian base' was first attempted by Williamson (1887) and subsequently supported by Lang (1910, 1915a) Leclercq (1930), Weiss (1931–32), Eames (1936), Andrews (1961) and Phillips and Gilbert (1966). In spite of the differences in size of these two organs they show several striking similarities such as the position of 'stigmarian bases', the formation of four radiating arms, activity of the cambium, the yearly renovation of the cortex, etc. But the fact that these 'stigmarian bases' are mostly endarch offers some difficulty. However, in some, 'stigmarian bases' e. g., in *Stigmaria bacupensis* (Leclercq, 1930) the central region is occupied by spiral elements and parenchyma without any differentiation into proto-and meta-xylem. This is essentially similar to what is observed in the rhizomorph. Besides, centripetal wood is recorded in some other species of *Stigmaria* also by Weiss (1908) and Leclercq (1930) which according to Weiss (1931–32) is a character of the shoot. Another point which requires attention is the occurrence of two cambia in 'stigmarian bases' instead of one of *Isoetes*. Stewart (1947) suggested the possibility of deriving the bifacial cambium of *Isoetes* by the elimination of the middle cortex in *Stigmaria* resulting in proximity of phellogen and vascular cambium. I agree with such a contention as a detailed account of *Paurodendron*—a rhizomorphic fossil (Phillips and Gilbert, 1966), clearly shows a similarity between it and *Isoetes*. Both of them not only possess bifacial cambium but are similar in the origin of roots, activity of cambium and other aspects. The roots of *Isoetes*, as well as the 'stigmarian appendages have eccentrically placed monarch and exarch vascular bundles, with similar arangement of xylem and phloem. The middle cortex in the rootlets of both degenerates and results in the formation of a 'C' shaped cavity.

Schoute (1938), however, did not attach much value to these similarities. He believed that the appendages of *Stigmaria* are modified leaves and thus the *Stigmaria* corresponds to a rhizome (leaf-bearing stem) and not a rhizophore (root-bearing stem) as is found in *Isoetes*. But the leaf-nature of 'Stigmarian appendages' has not been accepted by Weiss (1931–32), who believes that the appendages are probably endogenous in origin.

In this connection the rhizophore of *Selaginella* too should be considered. Among the living forms this is the only organ with which the *Isoetes* rhizomorph finds some similarity (cf. Eames, 1936). The rhizophore is an exogenous, leafless, negatively geotropic organ which produces lateral endogenous roots. It is quite similar to the rhizomorph of *Isoetes* but its anatomy and origin from the region of forking of a leafy shoot creates some difficulty. According to Bruchmann (1905, quoted from Worsdell, 1910), the definite place of origin of the rhizophore in a plane at right angles to the stem-fork is suggestive of shoot. Worsdell (1910), Eames (1936) and Schoute (1938) also regard the rhizophore as having a shoot nature while Cusick (1954) working on the ontogeny of rhizophore regards its meristem as basically an embryo shoot. In *Selaginella selaginoides*, roots arise in regular sequence from a swollen knot of tissue with a secondary meristem. This knot appears to simulate with the rhizomorph of *Isoetes* and *Paurodendron* (Phillips and Gilbert, 1966).

Thus on a careful analysis of all the details worked out so far and the other available from the investigations of previous workers (Von Mohl, 1940: Lang, 1915 a, b; Stewart, 1947; Bhambie, 1962b; Phillips and Gilbert, 1966, etc.,) it appears that the rhizomorph is of axial nature and finds its closest comparison in the 'stigmarian axes' or basal tuberous portions of the Paleozoic and Mesozoic lycopods. The development of rootlets in the Mesozoic lycopods is, however, unknown.

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