As per New Revised Syllabus for Bangalore University

COLLEGE BOTANY

VOLUME - III

(Pteridophytes, Paleobotany, Environmental Biology and Ecosystem Management)

S. Sundara Rajan

Himalaya Publishing House
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PREFACE

College Botany Vol. III has been revised thoroughly keeping in mind the recent changes introduced in the syllabus. Many chapters have been rewritten and many additions have been made the text. A new chapter ‘Watershed Management’ has been added in the division ‘Ecosystem Management’. Examples are chosen from the Indian context so that students can easily relate to them.

I am thankful to Dr. Venugopal of SJRC College Bengaluru for his suggestions. I am also thankful to all my students (direct and indirect) who have been using my books. They are the target for the books and the source of my inspiration. Suggestions are welcome from readers for the improvement of the book.

My thanks are also due to M/s Himalaya Publishing House Pvt. Ltd., specially to Mr. Niraj Pandey and Vijay Pandey for their abiding patitence and encouragement.

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SYLLABUS

III SEMESTER

PAPER - III: PTERIDOPHYTES, PALEOBOTANY, ENVIRONMENTAL BIOLOGY AND ECOSYSTEM MANAGEMENT

52 hrs

UNIT I : PTERIDOPHYTES 13 hrs

Introduction and general character with classification (As per Sporne). Study of diversity in morphology, anatomy and reproduction of the following groups in representative forms.

1. Psilotopsida – E.g.: *Psilotum.*
2. Lycopsida – E.g.: *Lycopodium, Selaginella.*
3. Filicopsida – E.g.: *Marsilea.*

(Developmental stages not required)

Brief account of Stelar evolution, heterospory and seed habit.

UNIT II : PALEOBOTANY 13 hrs

Contribution of Paleobotanist-Birbal Sahni.

Outline of geological time scale with emphasis on Paleozoic and Mesozoic Era. Process of fossilization – Compression, Impression and Petrifaction.

Type Study: *Rhynia, Cycadeoidea* and *Pentaxylon.*

UNIT III : ENVIRONMENTAL BIOLOGY 13 hrs

Introduction and Scope of Environmental Biology

Ecological Factors: Climate – Light, Temperature, Rainfall, Wind and Atmospheric humidity.

Edaphic Factors: Soil Formation, Soil Profile, Soil Air, Soil Microorganisms

Soil Erosion: Water and Wind.

Soil Conservation:

Biological – Contour farming, Mulching, Strip cropping, Terracing and Crop rotation.

Mechanical – Basin Listing, Construction of dams

Soil reclamations

Biotic Factors – Positive and negative interactions.

Ecosystem – Concept, Components, Study of marine, Grass land and Crop land Ecosystems.

Ecological Succession – Hydrosere and Xerosere.

Ecological Adaptations – Hydrophytes, Xerophytes, Halophytes, Epiphytes and Parasites.

UNIT IV : ECOSYSTEM MANAGEMENT 13 hrs

Watershed Management.

Conservation of natural resources:

- Over Exploitation of Natural resources – e.g.: Forest
- Afforestation, Social Forestry and Agroforestry.

Conservation of plant diversity:

In-situ and *Ex-situ* Conservation – National park, Sancturies and Bioreserves. Role of Seed Bank and Gene Bank.

PHYTOGEOGRAPHY

Phytogeographical regions of India, Vegetational types of Karnataka.

CONTENTS

UNIT – I

PTERIDOPHYTES

1

Introduction and General Characters

Pteridophytes constitute a significant and important group in the plant kingdom. As the first true land plants, they offer a very favourable material for the study of various adaptations that have made the colonization of land possible for the plants.

Pteridophytes have a long geological history on our planet. They are known from as far back as 380 million years. Fossils of pteridophytes have been obtained from rock strata belonging to Silurian and Devonian periods of Palaeozoic era.

The life cycle of a typical member comprises a regular heteromorphic alternation of generations in which both the gametophyte and the sporophyte exist as independent individuals. Nevertheless, the sporophyte is the predominant generation. In terms of duration in the life cycle, the gametophyte is insignificant. In this respect, pteridophytes are totally different from bryophytes. The reasons for the predominance of the sporophyte in the life cycle are not far to seek. Being a more robust body, a sporophyte can effectively meet the challenges of the terrestrial environment better than the gametophyte.

As a group, the pteridophytes lies between bryophytes and spermatophytes. They share the characters of both these groups in addition to their own unique features.

The following are some of the resemblances and differences between pteridophytes and other groups.

Pteridophytes and Bryophytes

Similarities

1. Life history always encompasses heteromorphic alternation of generations.
2. Gametophyte generally lacks vascular tissue and is predominantly parenchymatous.
3. Sporophyte reproduces by spore formation and spores are always haploid.
4. Sex organs are multicellular and male sex organ is antheridium and female is archegonium.
5. Sexual reproduction is oogamous.
6. Male gametes are motile and female non-motile.
7. Reduction division takes place in the sporophyte before spore formation whereas mitiotic division produces the gametes.
8. There is no separate asexual reproduction by spores as noticed in Algae and Fungi.
9. Organs of anchorage are rhizoids in all bryophytes and in some pteridophytes (psilotopsida).
10. Spores are of one kind in all bryophytes and in a good number of pteridophytes.
11. Fertilization is internal but the presence of moisture is essential as there is no siphonogamy.
12. Sperms are attracted chemotactically towards the archegonia in both groups.

Differences

1. The predominant plant body is sporophyte in pteridophytes, while it is a gametophyte in bryophytes.
2. The sporophyte is relatively undifferentiated and does not go beyond foot, seta and capsule, while in pteridophytes, it is distinguished into root, stem, leaves, etc.
3. The sporophyte is dependent on the gametophyte in bryophytes, while in pteridophytes both are independent.
4. The gametophyte in bryophytes may be thalloid or leafy, but in pteridophytes, it is always thalloid.
5. Rhizoids are of two types in bryophytes, whereas they are of only one kind in pteridophytes.
6. Archegonia and antheridia of pteridophytes are highly reduced when compared to those of bryophytes.
7. There is no vasculature is bryophytes, but the sporophytes of pteridophytes have a well developed vasculature.
8. There are no roots in bryophytes, but pteridophytes have roots.
9. All bryophytes are homosporous, while pteridophytes may be homosporous or heterosporous.
10. Gametophytes of pteridophytes may be autotrophic, saprophytic or extremely reduced microscopic structures, whereas in bryophytes, they are always autotrophic and macroscopic.
11. ‘Leaves’ are produced in the gametophytes of some bryophytes, while only the sporophytes are leafy in pteridophytes.

Pteridophytes and Gymnosperms

Similarities

1. There is a regular heteromorphic alteration of generations.
2. Sporophyte is the predominant plant body and is differentiated into root, stem and leaves.
3. Some pteridophytes and some gymnosperms exhibit air cinate vernation in young leaves.
4. There are no vessels anatomically in both pteridophytes (except *Selaginella, Marsilea*) and gymnosperms (except *Gnetales*).
5. Phloem does not have companion cells.
6. Spores are always haploid as they are always a product of meiosis.
7. Some pteridophytes and all gymnosperms are heterosporous.
8. Gametophyte is comparatively a reduced structure in both.
9. In heterosporous pteridophytes and all gymnosperms, megaspore is always retained within the megasporangium.
10. Sex organs of the gametophytes are always antheridia and archegonia.
11. Root hairs are absent in both.

Differences

1. The sporophytic plant body is, by and large, arborescent in gymnosperms while it is not so in pteridophytes.

2. Roots are adventitious in pteridophytes while they arise from the radicle (tap root) in gymnosperms.
3. Pteridophytes may be homosporous or heterosporous, while all gymnosperms are heterosporous.
4. Most of the pteridophytes have a preference for cool, moist areas, while gymnosperms generally exhibit xeric characters.
5. Branching of the stem is dichotomous in pteridophytes while it is lateral in gymnosperms.
6. Heterospory has never resulted in dioeciousness in the sporophyte in pteridophytes, while it is so in many gymnosperms.
7. Generally, secondary growth is absent in pteridophytes, while it is present in gymnosperms.
8. In pteridophytes, both microspores and megaspores are released from their respective sporangia, whereas in gymnosperms, megaspore is permanently retained.
9. There is pollination in gymnosperms, while it is absent in pteridophytes.
10. Siphonogamous fertilization (pollen tube development) is seen in only gymnosperms.
11. Male gametes are ciliate in pteridophytes, while they are not in gymnosperms (except for few like Cycas).
12. Gymnosperms are seed plants (spermatophytes), while there is no seed in pteridophytes.

SPOROPHYTIC GENERATION

As has already been pointed out, it is the sporophytic generation which constitutes the main plant body in pteridophytes. In any description whenever we refer to the plant body of pteridophytes, we mean the sporophyte.

There is a great variety in the nature and organisation of the sporophytic plant body in pteridophytes. The simplest sporophyte in an extant member is to be found in *Psilotum*. The plant body here is a naked, branched axis with no evidence of roots. The axis is distinguishable into an underground prostrate system and an erect aerial system. Rhizoids help in anchoring the plant to the substratum. There are no leaves. The stem itself takes up the function of photosynthesis.

From such a simple plant body, further evolution (mainly necessitated by the environment) resulted in the complex and diverse types of sporophytes that we see today. The first step is the differentiation of photosynthetic laterals (leaves) and roots.

The leaves of pteridophytes are basically of two types, *viz*., microphylls and megaphylls (macrophylls).

Microphylls have a single unbranched mid vein. Further, when a leaf trace departs from the main vascular cylinder to provide the leaf, no gap is left.

In megaphylls, there is a branched venation. The branching may be dichotomous or reticulate. Further, there will invariably be a leaf gap in the main vascular cylinder above the leaf trace.

Microphylls are seen in members like *Lycopodium. Selaginella, etc.* Megaphylls are found in members like *Adiantum, Pteris, etc.*

Stomata: These are found in the leaves and stems of all members.

Mehra and Soni (1983) have studied the stomatal structure and ontogemy in a number of pteridophytes. They have classified the pteridophyte stomata into the following four types.

(i) Psilophytaceous,
(ii) Equisietaceous,
(iii) Marattiaceous, and
(iv) Filicinean.

Mehra and Soni (1983) believe that the psilophytaceous stoma is the basic type and the others are derived.

Origin of Leaves

According to general opinion, the fundamental nature of the sporophyte was mainly axial. The leaves and branches arose later as a modification of the axis.

Bower (1908) first suggested that originally the plant was wholly axial in nature and that the leaves arose later in the course of evolution. Lignier (1908) proposed that primitive pteridophytic shoot was basically a leafless dichotomously branched structure and some of the branches got themselves modified into leaves.

Mainly, there are two theories to account for the origin of leaves. These are the *telome theory* and the *enation theory*. While telome theory accounts for the origin of both microphylls and megaphylls, enation theory explains only the origin of microphylls.

Origin of Megaphyll

According to telome theory first proposed by Zimmermann (1930, 1938), primitive pteridophytic shoot was naked and dichotomously branched. The plant body resembled the fossil member *Rhynia*. The ultimate dichotomies are called telomes and the internodes below the telomes are known as the mesomes. The telomes and mesomes together constitute a telome truss.

According to telome theory, a megaphyllous leaf originates as per the following steps:

1. *Overtopping*: In this, the original dichotomous branching system changes to unequal dichotomy resulting in the formation of short and long branches. This leads to sympodium and ultimately to a monopodium with a main stem and lateral branches.

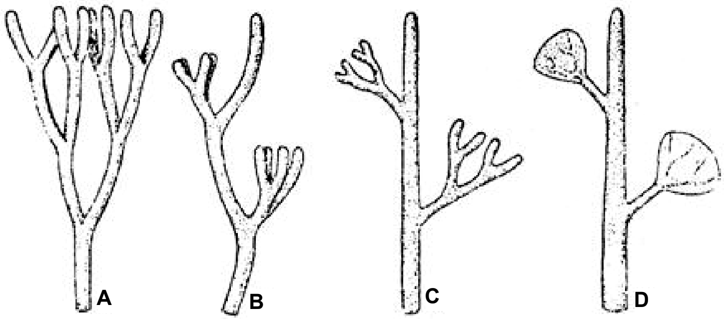

Fig. 1.1: Origin of Megaphyll (Various Stages)

2. *Planation:* The branching of the telome trusses which were originally in all directions orient themselves in a single plane and come closer.
3. *Syngenesis or webbing:* The telomes which have come closer, laterally fuse by the development of parenchymatous tissues between them. This results in a leaf blade possessing a number of free ending veins.

Evidence for this theory is obtained from many fossil ferns where the leaves have an open venation. A further evidence is in the ontogeny of the fern leaves, where the adult leaves have a closed venation, while the first formed ones have open veins.

Origin of Microphyll

The origin of a single veined leaf is explained by both the telome theory and the enation theory.

Followers of the telome theory argue that the leaf arose from a surviving telome. After overtopping and planation, only one of the telomes survived (reduction), the remaining degenerated. The surviving telome developed parenchymatous pads which formed the lamina.

There are, however, some objections to the telome theory accounting for the origin of the microphyll. These are:

1. If indeed a telome has transformed itself into the central vein of the microphyll, then in all instances, the microphylls should possess a complete vein running to the tip. But there are any number of examples of microphylls having no veins or incompletely developed veins. This is indeed difficult to comprehend as per the telome theory.
2. It is one of the morphological principles that an organ develops first and only later the vasculature travels into it. If we accept the telome theory for the origin of microphyll, we will be arguing for the emergence of vasculature first and then to justify the vasculature, the development of the leaf.

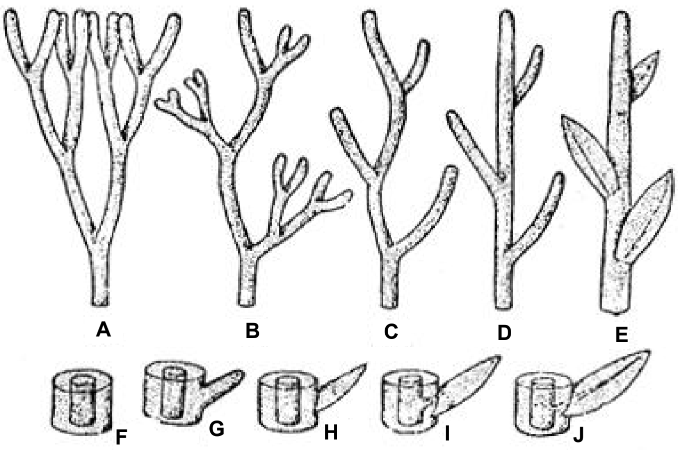

Fig. 1.2: Origin of Microphyll (Various Stages)
(A-E: According to Telome Theory, F-J: According to Enation Theory)

According to Enation theory proposed by Bower (1908), the leaves are not the modifications of telomes (branches), but new developments or outgrowths from the shoot. According to Bower, the outgrowths which he called enations were first spine-like, later became flattened and leaf-like. In the beginning, these were only emergences and lacked a vasculature. Subsequently, the main vasculature of the stem gave out a branch which ran up to the base of the leaf only. From this stage by further evolution, a vascular strand grew up to the leaf-tip. Indeed, there are quite a good number of fossil evidences depicting these stages.

In the evolution of the vasculature, *Psilophyton* (a fossil member of the order psilophytales) is quoted as the first step (no vasculature), *Asteroxylon*, the second step (vasculature only up to the base of the leaf), and *Arthrostigma*, the third step (vasculature traversing half way up the leaf apex). In the present day, *Lycopodium* and *Selaginella*, the vasculature runs up to the leaf apex.

Regarding the origin of the microphyllous leaves, enation theory seems to be more convincing than the telome theory.

Origin or Equisetaceous Leaf

It is difficult to account for the origin of the equisetaceous leaves because of their whorled condition. Neither telome theory nor enation theory can explain convincingly the origin of whorled leaves. Members like *Sphenophyllum* (a fossil member of sphenopsida) had sessile wedge shaped leaves with dichotomous venation. Such leaves may be modifications of a telome. The single veined leaves found in *Equisetum* and others, may be a reductional form.

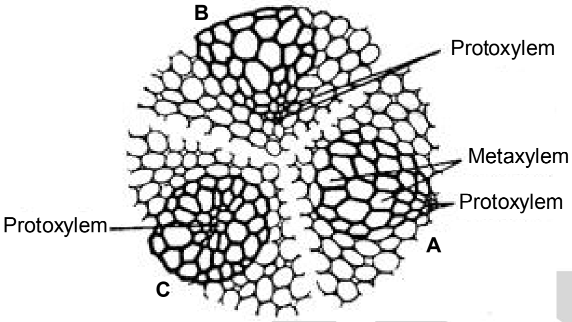

Fig. 1.3: Direction of maturation of xylem elements
A. Exarch, B. Endarch, C. Mesarch

Origin of Roots

According to Zimmermann (1930), some of the branches of the fundamental axis grew downwards thus forming the root system. In some primitive members, in the type of branching, and mode of growth, the root and the aerial shoot are similar indicating that they are modifications of the same axis. Zimmermann (1930) believes that the roots differentiated before the origin of leaves.

Development of Root and Shoot Apex

The stem and roots usually develop with the help of a single two or three sided apical cell. Bhambie and Puri (1963) have worked on the shoot apex organisation in lycopodiales, while Bhambie and Rao (1973) have worked on the root apical organisation in ferns. According to them, the single apical cell found in the roots of leptosporangiate ferns are simpler than the group of initials found in the root apex of eusporangiate ferns.

Vasculature in Pteridophytes

All the pteridophytes possess a vasculature in the center of the axis traversing from one end to the other and branching with all the branches.

The two main vascular elements are the xylem and phloem. The xylem consists of mostly, tracheids and rarely, vessels (*Selaginella, Pteris,* etc.) The tracheids have different types of thickenings like scalariform, pitted, annular, etc. The tracheids or vessels are of two types, *viz*., protoxylem and metaxylem. The former matures early and has a narrow lumen while the latter matures later and has a wide lumen.

The relative distribution of protoxylem and metaxylem elements forms the basis for the classification of xylem group into three types, *viz*., *exarch* (centripetal-protoxylem pointing towards the periphery), *endarch* (centrifugal-protoxylem pointing towards the center), and *mesarch* (protoxylem having metaxylem on either side).

The phloem is composed of sieve tubes and phloem parenchyma. A sieve tube consists of a series of long, living cells with sieve plates. Sometimes distinction could be made between protophloem and metaphloem. But there is no pronounced morphological difference between the two.

Types of Vasculature (Stele)

A transverse section of the stem or root of the plant body shows an outer epidermis, middle cortex and central stele. The cortex is either parenchymatous or may have sclerenchyma also.

The central region consists of the concentration of the vasculature known as the stele. A stele may be defined as a vasculature surrounded by pericycle and endodermis.

Originally, plant anatomists thought that only the vascular bundles (xylem and phloem) formed the fundamental unit of the vasculature. Stele as the fundamental unit of the vasculature was first proposed by Van Tieghem and Douloit (1886). According to them, the cortex and the stele are separated by the endodermis (the Endodermis consists of barrel shaped cells and possesses thickenings known as casparian thickenings on the radial and tangential walls).

There are mainly three types of steles in pteridophytes. These are:

1. Protostele,
2. Siphonostele, and
3. Dictylostele.

A protostele has the vasculature (xylem) occupying the central region of the stele. There is no pith. In a siphonostele, the vasculature is like a tube or siphon. Here, the central region consists of non-vasculated cells (parenchyma) forming the pith. In a dictylostele, the siphon breaks up into a number of individual bits called meristeles.

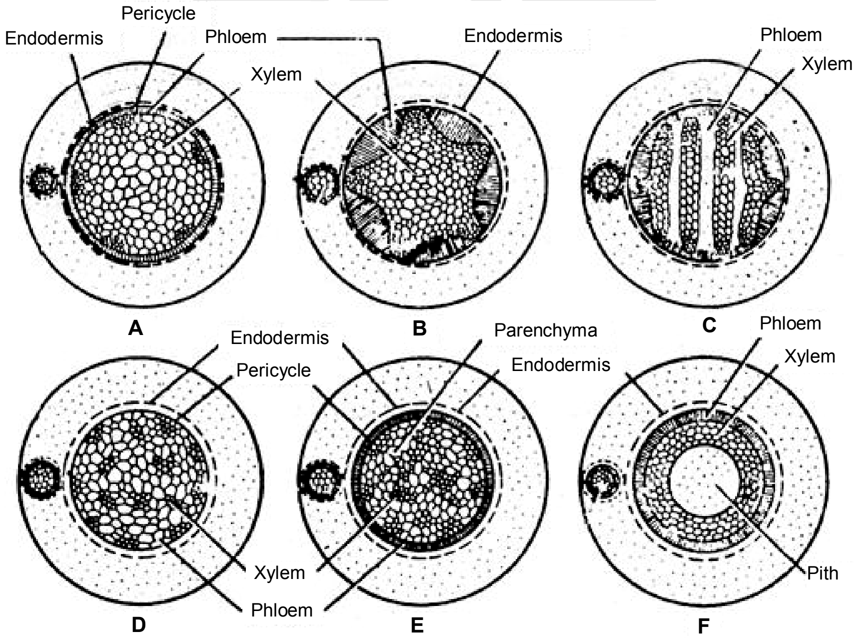

Fig. 1.4: Types of Vasculature in Pteridophytes
A. Haplostele, B. Actinostele, C. Plectostele, D. Mixed Protostele, E. Mixed Protostele (with pith), F. Ectopholic Siphonostele.

Protosteles

Basically, all protosteles are alike in not having a pith. They may be classified into the following types based mainly on the configuration of the xylem.

Haplostele: This is the simplest type of stele that could be visualized for a vascular plant. The central region of the stele consists of a smooth core of xylem surrounded by phloem. This type of stele is seen in *Rhynia*.

Actinostele: The xylem is star-shaped and the phloem completely surrounds the xylem. The contour of the stele is smooth (Fig. 1.4 B), e.g., *Psilotum, Lycopodium phlegmaria,* etc.

Plectostele: The xylem breaks up into a number of bands or plates arranged parallely. The phloem not only surrounds the xylem but is distributed between the xylem plates (Fig. 1.4 C), e.g., *Lycopodium wightianum*.

Mixed Protostele: In this type, the xylem breaks up into a number of small masses. The phloem is intermixed with the xylem (Fig. 1.4 E), e.g., *Lycopodium cernuum*.

Polystele: Generally, the stem is traversed by a single stele. But in some cases, as in some species of *Selaginella*, several independent steles run parallely in the stem. Each stele has its own *endodermis*. The individual steles are haplostelic (Fig. 1.4 F).

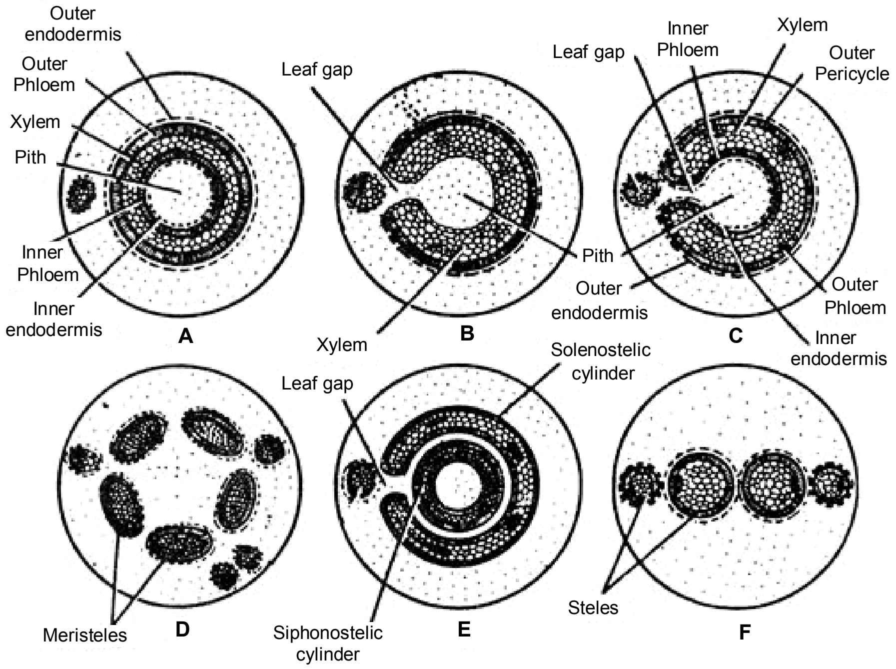

Fig. 1.5: Types of Vasculature in Pteridophytes (Contd...)
A. Amphipholic Siphonostele, B. Ectopholic Solenostele (with leaf gap),
C. Amphipholic Solenostele (with leaf gap), D. Dictyostele. E. Polycyclic Solenostele, F. Polystele.

Siphonosteles

The steles having a pith in the centre are referred to as siphonosteles. These are further classified into two types, viz., simple siphonostele and solenostele.

Simple Siphonostele: Here, the central region of the stele consists of a parenchymatous or sclerotic pith. Leaf traces that depart from the main vascular cylinder do not leave any leaf gaps (a parenchymatous cavity found immediately above the leaf trace in the vascular cylinder). This type of siphonostele is also called *medullated protostele* or *'cladosiphonic'* stele. For example, *Psilotum* sp.

Solenostele: Siphonosteles with leaf gaps are called solenosteles. In solenosteles, the leaf gaps are successive so that there is only one break in the vascular cylinder at anyone given point. Solenosteles are also known as *phyllosiphonic steles.* Depending on the pattern of distribution of phloem, solenosteles may be classified into two – *Amphiphloic solenostele* in which the phloem lines the xylem both on its inner and outer face, e.g., *Adiantum, Marsilea* and *Ectophloic solenostele* in which phloem lines the xylem only on its outer face, e.g., *Osmunda*.

There is also a third category of solenostele called polycyclic solenostele in which there will be more than one concentric ring of vasculature (Fig. 1.5 E).

Dictyosteles: Basically, dictyosteles are similar to solenosteles in having a pith and leaf gap. In dictyosteles, however, the leaf gaps overlap (many occur at a point). As a result, the vascular ring breaks up into many arcs. Each are is known as a 'meristele'. All the meristeles are surrounded by a common endodermis.

Based on the number of vascular rings dictyosteles may be classified into simple dictyosteles in which there is only one ring and polycyclic dictyosteles in which there will be at least two concentric rings of vasculature.

Origin of the Vasculature

The origin of the vascular tissue is one of the unsolved problems of plant morphology. It is closely linked with the problem of origin of land plants, which also is eluding a solution. If the legal ancestry for a land plant is proposed, then there are no steps indicating the origin of vasculature. If one believes in the bryophytic ancestry of land plants, the columella in the sporophyte of *Anthoceros* seems to be a good starting point of the origin of vasculature. Indeed in its ideal location and to some extent in its function (through not in structure), the columella of the sporophyte of *Anthoceros* tempts any one to consider it as precursor of the vasculature.

Evolution of the Vasculature

Among the different types of steles, it is generally believed that a solid core of vasculature is more primitive than a cylinder of vasculature. From this standpoint, protosteles are admittedly primitive in not having a pith.

Among the different types of protosteles, haplostele is regarded as the most primitive and the mixed protostele as the most advanced. The tendency seems to be towards the breaking up of single xylem group into several bits.

If we regard that siphonostele is more advanced than a protostele and that the former evolved from latter, we have to account for the origin of the pith. The method by which pith originated is debatable. There are mainly two theories, *viz*., *medullation theory* and *cortical intrusion theory*.

According to medullation theory, the pith originated *in situ*, i.e., by metamorphosis of the vascular elements into parenchyma (Boddle, 1901; Gwynne Vaughan, 1903). The presence of 'mixed pith' (tracheids intermixed with parenchyma in the pith) is used as an evidence to show the medullation of the central vasculature. Steles with mixed piths are regarded as transitional stages between protosteles and siphonosteles.

According to the cortical intrusion theory, the cortical parenchyma cells intruded into the stele and produced the parenchymatous pith (Jeffrey, 1902). Similarity of tissues (parenchyma) in the pith and cortex is an evidence of cortical intrusion. An additional evidence for cortical intrusion is the presence of an inner endodermis. Jeffrey (1902) regards endodermis to be a part of cortex. In such a case, presence of an inner endodermis lining the pith proves the cortical origin. Supporters of this theory believe that steles with inner endodermis are more primitive than those with outer endomermis. It is held that steles of the latter type arose during the course of evolution by obliteration of inner endodermis. This theory is mainly based on the cortical origin of the endodermis. But the origin of the endodermis, whether cortical or stelear is an open question.

Whatever may be the course pith took in its origin, siphonosteles are no doubt more complex and more evolved than the protesteles. The overlapping of the leaf gaps in the siphonosteles seems to have given rise to a dictyostele. A dictyostelic condition may also result due to lacunae in the vascular cylinder which are not associated with the leaf. Such lacunae are called ‘perforations’.

Polycyclic dictyostele is the most complex type of vascular organisation seen in pteridophytes.

Reproduction

The sporophyte of pteridophytes generally reproduces by two methods, *viz*., vegetative propagation and spore production.

Vegetative propagation takes place by a variety of methods such as fragmentation, bulbil formation, resting bud formation, persistent apices, etc. (The details of these are given with the life histories of individual forms).

Spore Production

The characteristic method of reproduction is by the formation of spores. Spores are haploid and are produced in sporangia. The sporangia are generally borne on the adaxial surface of a leafy appendage called the sporophyll. There are mainly three lines of evolution seen in sporophylls.

Evolution of Sporophylls of Lycopsida: The sporophylls of lycopsids always have a single sporangium borne on their adaxial surface (surface close to the axis). According to telome theory, the sporophylls originated by the modification of telomes in a telome truss. Followers of the telome theory believe that in a telome truss, of the two telomes, the upper was fertile and the lower sterile. The sterile gradually flattened while the fertile telome had a gradual reduction of the basal sterile portion, with the result, the sporangium came to lie on the leafy appendage below (Fig. 1.6 A-C).

According to enation theory, the lycopodian sporophylls were evolved on a naked shoot bearing a number of sporangia. Below each sporangium, an emergence evolved which ultimately grew into the sporophyll. Thus, according to this theory, the sporophyll and sporangia are fundamentally different (Bower, 1935).

Evolution of Sporangiophores in Sphenopsida: The fertile appendages of sphenopsida are strikingly different from the usual sporophylls of other pteridophytes. Hence, they are referred to as sporangiophores (Scout 1900). According to telome theory, after overtopping and planation, the fertile telomes bearing sporangia at their tips recurved and the bent arms fused resulting in a sporangiophore with sporangia on the lower surface. The recurved appendages of *Calamophyton, Hyenia,* etc. give credence to this view.

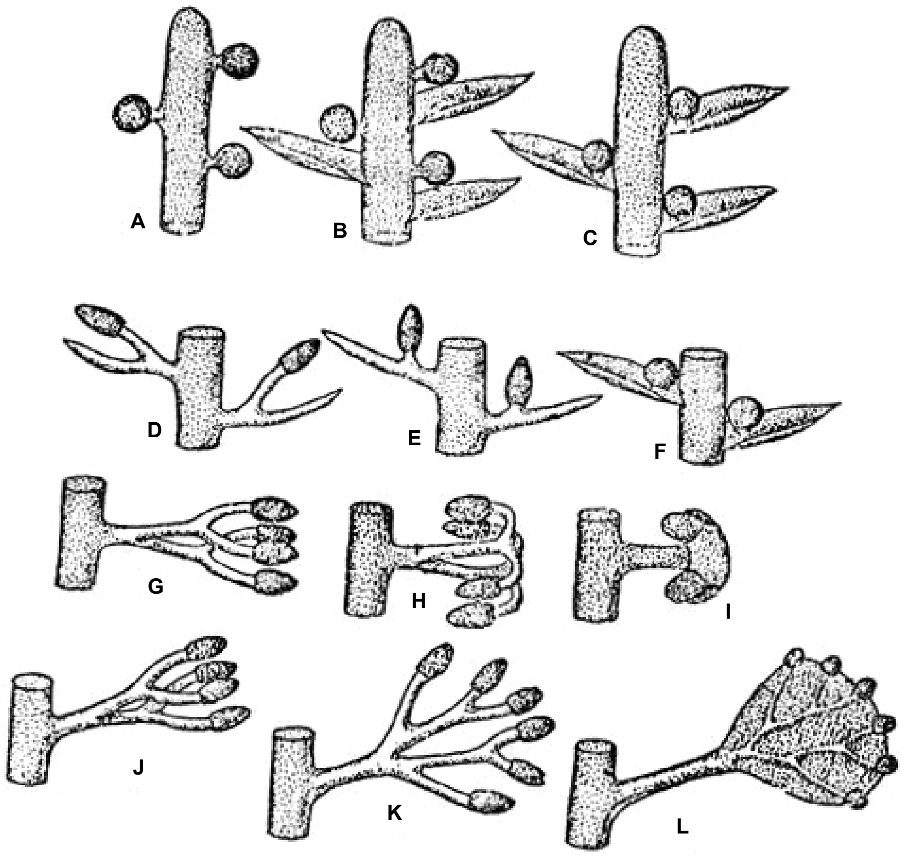

Fig. 1.6: Evolution of Sporophylls in Pteridophyta

A-C. Evolution of fertile leaves of Lycopods, D-F. Evolution of Lycopsid Sporophyll, G-I. Evolution of sphenopsid sporangiophore, J-L. Evolution of fertile leaves of ferns, (A-C according to Enation Theory, D-L according to Telome theory)

Evolution of Sporophylls in Pteropsida: According to telome theory, in a fertile telome truss, the usual processes of overtopping, planation and syngenesis resulted in the formation of a web like sporophyll with the sporangia borne at the tips of veins in the margin of the lamina (Fig. 1.6 J-L).

In Lycopsida, as also in Sphenopsida, there is a tendency for the sporophylls or the sporangiophores to aggregate at the apices of branches to form a compact strobilus or cone.

The organisation of strobilus or cone takes place after the sporophylls are clearly differentiated from the sterile foliage leaves.

In ferns of the present day, generally there is no difference between sporophylls and foliage leaves. A foliage leaf besides helping in photosynthesis also bears the sporangia. While in lycopods and sphenopsids, the tendency is for the accumulation of sporophylls to form strobili, in ferns, the tendency seems to be towards the aggregation of sporangia into a sorus. A special case is that of *Marsilea* where the spore bearing organs form a compact bean-shaped structure called the *Sporocarp*.

Pteridophytes are homosphorous (isosporous) or heterosporous. Homosporous members produce only one type of a spore in the sporangium which develops into a gametophyte bearing both antheridia and archegonia. Heterosporous members produce two types of spores, i.e., microspores and megaspores (macrospores). The micropsores are smaller in size and are produced in microsporangia which are borne on microsporophylls. Microspores develop into the male gametophyte (Microgametophyte). Megaspores are bigger in size and are produced in megasporangia borne on megasporophylls. On germination, megaspores develops into the female gametophyte (mega or macrogametophyte).

Structure and Development of Sporangium: A sporangium usually has a stalk which bears the globular capsule region in which are produced the spores. The wall of the sporangium is one to many layered. Within the wall are found the spore mother cells which undergo reduction division to give rise to haploid spores.

There are mainly two types of sporangial development, i.e, *Eusporangiate* type and *Leptosporangiate* type.

In Eusporangiate type, the sporangium is derived from a *group of cells.* Further after the initial periclinal division, the sporogenous tissue is derived from the inner daughter cell. In *Leptosporangiate* type, the sporangium is derived from a single initial cell. Further, the sporogenous tissue is derived from the outer daughter cell of the sporangial initial (The details of the development of Eusporangiate or Leptosporangiate sporangia are discussed with the individual forms).

A mature sporangium dehisces either vertically or transversely. Special types of cells may or may not be present in the wall to help in the dehiscence. Usually, in ferns, the sporangia have a thick-walled annulus and a thin-walled stomium. The annulus may be vertical, shield-shaped or cap-shaped. By the differential hygroscopic response of these cells, the sporangium breaks liberating the spores.

GAMETOPHYTIC GENERATION

The haploid spore is the starting point in the development of the gametophyte. In heterosporous forms, two types of spores are formed (mega and microspores). Hence, there will be two types of gametophytes (male and female). In homosporous forms, there will be only one type of a gametophyte.

The spores rarely exceed a few mm in size. Their shape varies from triradiate to spherical. They have a two layered wall. The outer sculptured layer is known as exine (exospore) and the thin inner layer is known as intine (endospore). Sometimes, there will be an outermost epispore and a middle mesospore in addition to exine and intine.

The germination and development of the gametophyte is different in homosporous and heterosporous forms.

Rashid (1976) recognises two stages in the germination of spores of pteridophytes. These are: (i) a spore distension process and (ii) a spore extension process. During the first phase, the spore absorbs moisture and becomes swollen, while during the latter, germ tube is formed.

Nayar and Kaur (1968) have classified spore germination in homosporous pteridophytes into three categories. These are:

(i) Bipolar, e.g., *Equisetum, Lycopodium, Osmunda,* etc.
(ii) Tripolar, e.g., *Trichomanes, Hymenophyllum,* etc.
(iii) Amorphous, e.g., *Angiopteris.*

In heterosporous forms, the gametophytes are extremely reduced and their size is limited to the confines of the spore. The development of the gametophyte here is called endosporic.

In homosporous forms, the gametophytes are comparatively bigger and they break open the spore to grow independently on the soil. This type of development is said to be exosporic. Homosporous gametophytes are filamentous, cordate or tuberous in shape. Some of them exhibit dorsiventral symmetry. The gametophytes are composed mainly of parenchyma. The nutrition is either autotrophic (when chlorophyll is present) or saprophytic (when mycorrhiza is present).

Reproduction

Gametophytes also reproduce by two methods, *viz.*, vegetative propagation and sexual reproduction. Vegetative propagation is uncommon and it takes place by the formation of gemmae or brood bodies (See *Lycopodium*).

Sexual reproduction takes place by the formation of antheridia (male) and archegonia (female). Both the sex organs are extremely reduced in comparison with their counterparts in bryophytes.

Antheridium is a globose structure partially or completely embedded in the gametophytic tissue. It has a single layered jacket enclosing the androgonial cells. The atherozoids are spirally coiled and may be bicilliate or multiciliate.

An archegonium is a flask shaped structure having a basal venter and a short neck. Within the archegonium are found one or two neck canal cells, one venter canal cell and egg cell (Details of the development of sex organs are given with the individual forms).

Fertilization

Even in pteridophytes, fertilization is dependent upon external moisture. The antherozoids that come out of the antheridium are attracted chemotactically by the mucilagenous mass produced by the disintegrating cells (neck canal and venter canal cells) of the archegonium. Many antherozoids enter the archegonium. Ultimately, one succeeds in fusing with the egg resulting in the formation of a zygote.

Embryogeny

The zygote represents the first cell of the sporophytic generation. The first division of the zygote is either transverse or vertical. When the division is transverse, two superposed cells are formed, of which the one nearer to the archegonial neck is the epibasal cell and the one away from the archegonial neck is the hypobasal cell. The embryo proper may be derived from either epibasal cell (exoscopic) or the hypobasal cell (endoscopic). In the latter case, the epibasal cell forms a tubular structure known as the suspensor. The function of the suspensor is to push the developing embryo deep into the gametophytic tissue so that it can easily absorb nutrition.

Further divisions in the embryonal cell are variable. After the first few divisions, the characteristic parts of the embryo like foot, root, cotyledons and stem apex are differentiated. Until the root establishes itself on the soil, the foot, behaving like a haustorium absorbs food from the gametophyte. After the root grows into the soil, the sporeling separates itself from the gametophyte and grows independently.

Aberrations in the Life Cycle

In the normal type of life cycle showing alternation of generations, the sporophyte gives rise to a gametophyte and *vice versa*. Syngamy and reduction division occur at specific points in the life cycle so that the gametophyte is always haploid and sporophyte is always diploid.

In some cases, there are deviations or aberrations in the life cycle disturbing the chromosome constitution of the sporophyte and the gametophyte. The aberrations are of three types, *viz*., apogamy, apospory and parthenogenesis.

Apogamy

This was first discovered by Farlow (1874) in *Pteris cretica*. Winkler (1908) defines apogamy as follows: "It is the formation of sporophyte directly from the vegetative cells of the gametophyte without the act of syngamy or gametic union".

In nature, apogamy has been reported in some twenty genera and fifty species of pteridophytes. Apogamy is of frequent occurrence in ferns. It is seen in *Pteris, Adiantum. Osmunda,* etc.

Apogamy may also be experimentally induced as in *Lycopodium* (Bell, 1959; Freeberg, 1957), *Equisetum,* etc.

Apogamous sporophytes may originate from one or more cells of the gametophyte.

Regarding the causes of apogamy, several explanations have been offered. According to Lang (1902), starving the prothalli of water may induce sporophytic buds. It is generally believed that failure of normal fertilization results in apogamy.

Cytologically, apogamous sporophytes are haploid. But there are many instances of such apogamous sporophytes having 2*x* number of chromosomes. This is possible when both generations have same chromosome numbers. A gametophyte can have diploid chromosomes if there is failure of reduction division during spore formation.

Apospory

The phenomenon of production of a gametophyte directly from the vegetative cells of the sporophyte without reduction division (spore formation) is called apospory. Apospory was first discovered by Druery (1894) in a fern *Athytium fillixfemina var. clarissima*. He observed the development of gametophytes from the sporangia. Subsequently, apospory has been reported in several genera including *Osmunda*. Apospory may also be experimentally induced like apogamy.

In apospory, a filamentous or chordate gametophyte may be formed from one or more vegetative cells of the sporophyte. The aposporous structure may be an antheridium, a rhizoid, or even an antherozoid.

Cytologically, aposporous gametophytes are diploid because they are produced without reduction division.

By experimental induction of apospory, it is possible to produce polyploid gametophytes.

Parthenogenesis

The development of an unfertilized egg into an embryo is called parthenogenesis. This is different from apogamy because here only the egg is capable of developing into an embryo. Parthenogenetic embryos are haploid. But in some cases when the spores are unreduced, the resultant gametophytes are diploid. Consequently, the eggs are also diploid and they develop into an embryo without fertilization. In these instances the parthenogenetic embryos are diploid. This type of regularization of parthenogenesis coupled with failure of reduction division during megaspore formation has been reported in *Marsilea drummondii* (Strassburger 1907).

Chemosystematics of Pteridophytes

Attempts have been made to study pteridophytes from the points of view of chemosystematics.

Czeczuga (1985) has studied the distribution of carotenoids in about 66 representative members of pteridophytes. According to him β carotene, β cryptoxanthin, lutein epoxide and zeaxanthin are seen in Lycopods and horsetails, while ferns are characterized by β cryptoxanthin, lutein epoxide, violaxanthin and rhodoxanthin.

CLASSIFICATION OF PTERIDOPHYTES

Since a long time vascular plants are customarily divided into pteridophyta and Spermatophyta. This classification was based on the assumption that the former lack the seeds while the latter produced them. But the discovery of Pteridosperms (seed bearing ferns) broke down this artificial classification. Sinnott (1935) introduced the term Tracheophyta to include all vascular plants. Tracheophyta are further divided into four main groups *viz*., Psilopsida, Lycopsida, Sphenopsida, and Pteropsida. But it is not certain whether these are divisions or classes. Haupt (1953) considers them as classes in the division Tracheophyta. While Zimmermann (1930) Arnold (1947) Wardlaw (1952) etc., regard them as division.

Reimers (1954) considers pteridophyta as a division and divides it into five classes *viz*., Psilophytopsida, Lycopsida, Psilopsida, Articulatae and Filices.

Smith (1955) Bold (1957) and others divide vascular cryptogams into five divisions *viz*., Psilophyta, Lycophyta, Sphenophyta, Noeggerathiophyta and Pterophyta. Some people have changed the name Lycophyta to Lepidophyta (Smith 1955), Sphenophyta to Arthrophyta or Calamophyta (Smith 1955) and Pterophyta to Filicophyta (Parihar 1965).

In this book, the classification is mainly based on the one proposed by Reimers in the 1954 edition of Engler's Syllabus der pflanzen families.

This classification is simple and easy to follow. Below is given the outline classification.

PTERIDOPHYTES

1. PSILOPHYTOPSIDA	
Psilophytales	e.g., *Rhynia*, Asteroxylon**
2. PSILOTOPSIDA	
Psilotales	e.g., *Psilotum*
3. LYCOPSIDA	
(a) Protolepidodendrales	
(b) Lycopodiales	e.g., *Lycopodium, Phylloglossum*
(c) Lepidodendrales	e.g., *Lepidodendron*, Lepidocarpon**
(d) Isoetales	e.g., *Selaginella*
(e) Isoetales	e.g., *Isoetes*
4. SPHENOPSIDA	
(a) Hyeniales	
(b) Sphenophyllales	e.g., *Sphenophyllum**
(c) Calamitales	e.g., *Calamites*, Calamostachys**
(d) Equisetales	e.g., *Equisetum*

5. PTEROPSIDA

- (A) *Primofilices*
  - (a) Cladoxylales
  - (b) Coenopteridales e.g., *Botryopteris*, Zygopteris**
- (B) *Eusporangiatae*
  - (a) Ophioglossales e.g., *Ophiglossum*
  - (b) Marattiales e.g., *Angiopteris*
  - (c) Osmundidae
- (C) *Osmundales* e.g., *Osmunda*
- (D) *Leptosporangiatae*
  - (a) Filicales e.g., *Hymenophyllum, Adiantum*
  - (b) Marsileales e.g., *Marsilea*
  - (c) Salviniales e.g., *Salvinia, Azolla*

Asterisk (*) mark indicates the fossil members.