I M.Sc., BOTANY

PLANT DIVERSITY II

UNIT: I, II &V

Unit :I General topics in pteridophytes

Introduction of pteridophytes

Pteridophytes (ferns and lycophytes) are free-sporing vascular plants that have a life cycle with alternating, free-living gametophyte and sporophyte phases that are independent at maturity. The body of the sporophyte is well differentiated into roots, stem and leaves. The root system is always adventitious. The stem is either underground or aerial. The leaves may be microphylls or megaphylls. Their other common characteristics include vascular plant apomorphies (e.g., vascular tissue) and land plant plesiomorphies (e.g., spore dispersal and the absence of seeds.

General characters of pteridophytes:

Pteridophyta (gr, pteron = feather, phyton = plant), the name was originally given to those groups of plants which have well developed pinnate or frond like leaves. Pteridophytes are cryptogams (gr. Kruptos = hidden, and gamos = wedded) which have well developed vascular tissue.

Therefore, these plants are also known as vascular cryptogams or snakes of plant kingdom. They are represented by about 400 living and fossil genera and some 10,500 species. Palaeobotanical studies reveal

that these plants were dominant on the earth during the devonian period and they were originated about 400 million years ago in the silurian period of the palaeozoic era.

(i) Majority of the living pteridophytes are terrestrial and prefer to grow in cool, moist and shady places e.g., ferns. Some members are aquatic (e.g., marsileci, azolla), xerophytic (e.g., selaginella rupestris, equisetum) or epiphytic (e.g., lycopodium squarrosum) (fig. 1).

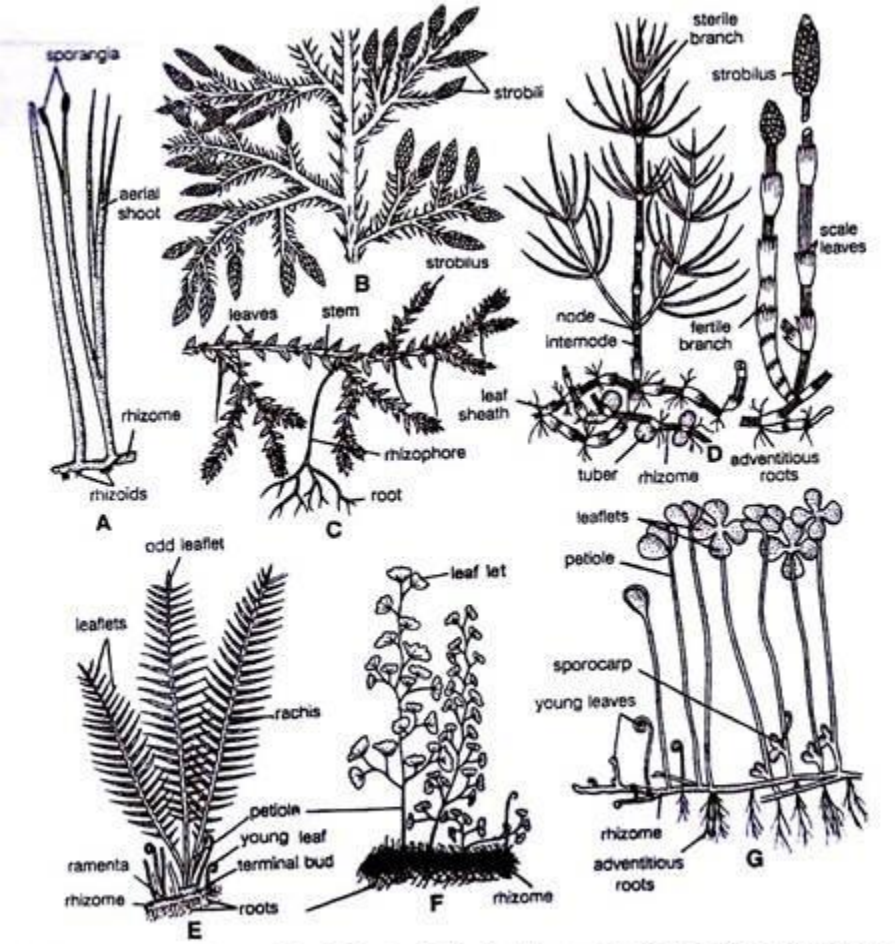


Fig 1 (A–G). Different forms of Pteridophytes A. *Rhynia*, B. *Lycopodium*,C. *Selaginella*, D. *Equisetum* E. *Pteris*, F. *Adiantum*, G. *Marsilea*

(ii) Majority of the pteridophytes are herbaceous but a few are perennial and tree like (e.g., angiopteris). Smallest pteridophyte is azolla (an aquatic fern) and largest is cyathea (tree fern).

(iii) Plant body is sporophytic and can be differentiated into root, stem and leaves.

(iv) Roots are adventitious in nature with monopodial or dichotomous branching. Internally usually they are diarch.

(v) Stem is usually branched. Branching is monopodial or dichotomous. Branches do not arise in the axil of the leaves. In many pteridophytes stem is represented by rhizome.

(vi) Leaves may be small, thin, scaly (microphyllous e.g., equisetum), simple and sessile (e.g., selaginella) or large and pinnately compound (megaphyllous e.g., dryopteris, adiantum).

(vii) Vascular tissue is present in stem and root. It consists of xylem and phloem. Xylem consists of tracheids only and phloem has only sieve tubes.

(viii) The steel is protostele (e.g., rhynia, lycopodium), siphonostele (e.g., equisetum), dictyostele adiantum) or polycyclic (e.g., angiopteris).

(ix) Cambium is absent; hence, they do not show secondary growth.

3. Reproduction in pteridophytes:

(i) Reproduction takes place by means of spores which are produced inside sporangia.

(ii) The development of the sporangium may be leptosporangiate (sporangium originates from a single cell) or eusporangiate (sporangium develops from a group of cells).

(iii) Sporangia may be borne either on stem or leaves. On the stem they may be terminal (e.g., rhynia) or lateral (e.g., lycopodium). On the leaves (sporophylls) they may be ventral, marginal (pteris, adiantum) or

dorsal (e.g., polypodiceae). In equisetum the sporangia are borne on special structures called sporangiophores which constitute a cone. In marsilea, azolla, salvinia sporangia are produced in sporocarps.

(iv) Spores on germination give rise to multicellular gametophytic bodies called prothalli (sing. Prothallus).

(v) In homosporous pteridophytes prothalli are monoecious (antheridia and archegonia develop on the same prothallus). In heterosporous species prothalli are always dioecious. Microspores on germination give rise to male prothalli and megaspores to the female prothalli.

(vi) Antheridia and archegonia are developed on prothalli.

(vii) Antheridium is surrounded by a single layered sterile jacket.

(viii) Archegonium consists of four vertical rows of neck cells, 1-2 neck canal cells, ventral canal cell and egg.

(ix) Antherozoids are unicellular, biflagellate (e.g., selaginella) or multiflagellate (e.g., equisetum and ferns) and motile.

(x) Antherozoids are attracted towards the neck of the archegonium chemotactically by certain substances like malic acid) present in the mucilaginous substance formed by the degeneration of neck canal cells and venter canal cell.

(xi) Water is essential for fertilization (zooidogamous). Therefore, pteridophytes are also known as amphibians of the plant kingdom.

(xii) Fertilization results in the formation of zygote or oospore, which ultimately develops into well-developed sporophyte.

(xiii) The fertilized egg divides transversely or vertically. Another cross wall forms a quadrant stage producing stem, leaf, foot and root.

(xiv) Plants show heteromorphic alternation of generation. The main plant body is sporophytic and forms a dominant phase in the life cycle.

Classification of pteridophytes (parihar 1996): the modern classification of pteridophytes have been suggested by many scientist according to the **Sporne(1975**) pteridophytes have been classified into six classes. They are psilopsida, psilotopsida, lycopsida, sphenopsida, pteropsida and progymnospermopsida. This classification is a modification is a modification **of Reimer's (1954**) system. According to the modern system of classification by **Parihar in 1996**; pteridophytes have been divided into seven divisions. They are rhyniophyta, trimerophytophyta, zosterophyllophyta, psilotophyta, lycopodiophyta, equisetophyta and polypodiophyta. **Bold (1973**) differentiated psilophytes into living and fossil groups. The living psilophytes were placed under the division psilotophyta and extinct psilophytes were divided into three division. They are rhyniophyta, trimerophytophyta and zosterophyllophyta

Types of stele in pteridophytes:

Stelar system of plant: definition and types (with diagrams)

Definition of stelar system:

According to the older botanists, the vascular bundle is the fundamental unit in the vascular system of pteridophytes and higher plants. Van tieghem and douliot (1886) interpreted the plant body of vascular plant in the different way.

According to them, the fundamental parts of a shoot are the cortex and a central cylinder, is known as stele. Thus the stele is defined as a central vascular cylinder, with or without pith and delimited the cortex by endodermis.

The term stele has been derived from a Greek word meaning pillar. Van Tieghem and Douliot (1886) recognized only three types of steles. They also thought that the monostelic shoot were rare in comparison of polystelic shoots.

It is an established fact that all shoots are monostelic and polystelic condition rarely occurs. The stele of the stem remains connected with that of leaf by a vascular connection known as the leaf supply.

Types of steles:

1. Protostele:

Jeffrey (1898), for the first time pointed out the stelar theory from the point of view of the phylogeny. According to him, the primitive type of stele is protostele. In protostele, the vascular tissue is a solid mass and the central core of the xylem is completely surrounded by the strand of phloem. This is the most primitive and simplest type of stele.

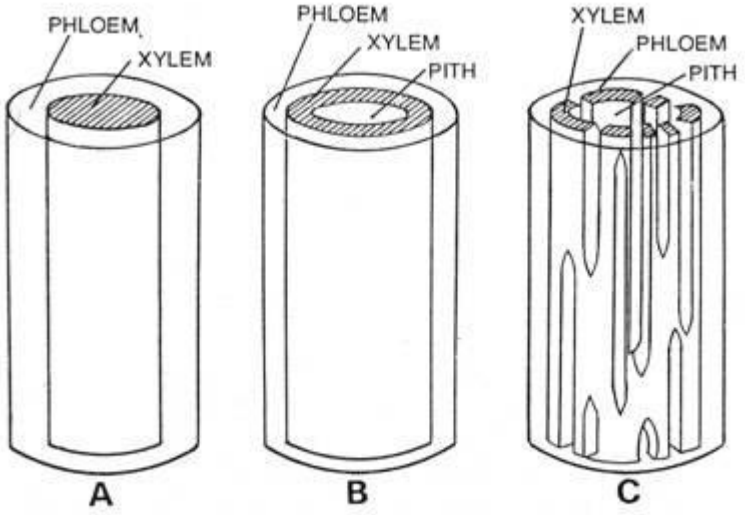


Fig. 37.42. Types of arrangements of vascular tissues in steles. A, protostele; B, siphonostele; C, dictyostele.

There are several forms of protostele:

(a) Haplostele:

This is the most primitive type of protostele. Here the central solid smooth core of xylem remains surrounded by phloem (e.g., in selaginella spp.).

(b) Actinostele:
This is the modification of the haplostele and somewhat more advanced in having the central xylem core with radiating ribs (e.g., in psilotum spp.).

(c) Plectostele:
This is the most advanced type of protostele. Here the central core of xylem is divided into number of plates arranged parallel to each other. The phloem alternates the xylem (e.g., in lycopodium).

(d) Mixed-pith stele:
Here the xylem elements (i.e., tracheids) are mixed with the parenchymatous cells of the pith. This type is found in primitive fossils and living ferns. They are treated to be the transitional types in between true protosteles on the one hand and siphonosteles on the other (e.g., in gleichenia spp. And osmunda spp.).

2. Siphonostele:
This is the modification of protostele. A stele in which the protostele is medullated is known as siphonostele. Such stele contains a tubular vascular region and a parenchymatous central region. Jeffrey (1898) interpreted that the vascular portion of siphonostele possesses a parenchymatous area known as a gap immediately above the branch traces only or immediately above leaf and branch traces.

On the basis of these branch and leaf gaps Jeffrey (1910), distinguished two types of siphonosteles. In one type, however, the leaf gaps are not found and they are known as cladosiphonic siphonosteles. In the other type both leaf and branch gaps are present and they are known as phyllosiphonic siphonosteles.

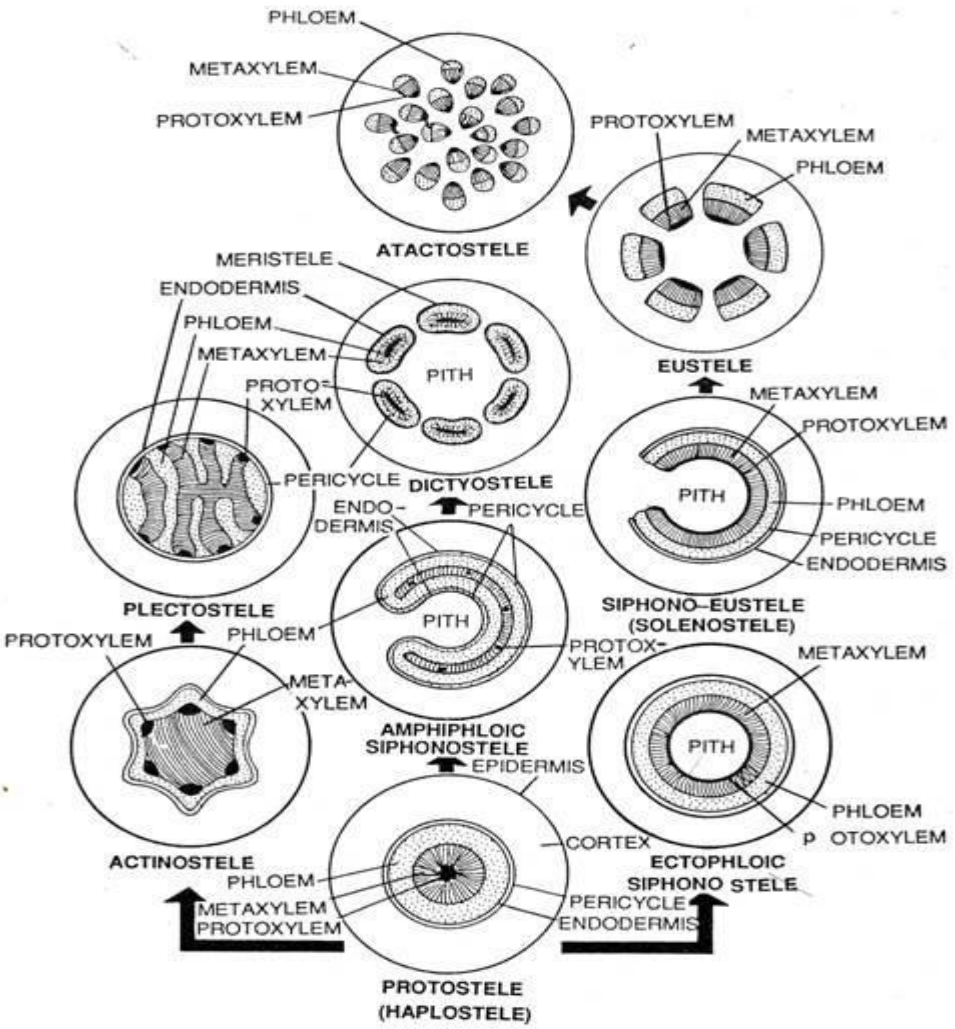


Fig. 37.43. The stelar system. Different types of steles arranged in evoluntionary sequence.

Jeffrey (1902, 1910, and 1917) interpreted the evolution of the siphonostele from the protostele as follows. He supported that the parenchyma found internal to the phloem and xylem has been originated from the cortex.

The supporters of this theory believe that the inner endodermis found to the inner face of the vascular tissue and the parenchyma encircled by this endodermis have been originated from the cortex. According to Jeffrey and other supporters of this theory the siphonosteles with internal endodermis are more primitive than those without an internal endodermis.

The siphonosteles which do not possess the inner endodermis are believed to have been originated by disintegration of inner endodermis during evolution.

According to the theory proposed by Boodle (1901), and Gwynne Vaughan, the siphonostele has been evolved from the protostele by a transformation of the inner vascular tissue into parenchyma.

A siphonostele may be of the following types:

(a) Ectophloic:

In this type of siphonostele, the pith is surrounded by concentric xylem cylinder and next to xylem the concentric phloem cylinder.

(b) Amphiphloic:

In this type of siphonostele the pith is surrounded by the vascular tissue. The concentric inner phloem cylinaer surrounds the central pith. Next to the inner phloem is the concentric xylem cylinder which is immediately surrounded by outer phloem cylinder (e.g., in marsilea).

3. Solenostele:

The vascular plants have been divided into two groups on the basis of the presence or absence of the leaf gaps. These groups are—pteropsida and lycopsida. The ferns, gymnosperms and angtosperms are included in pteropsida, whereas the lycopods, horse-tails, etc., are included in lycopsida.

The simplest form of siphonostele has no gaps, such as some species of selaginella. However, among the simplest siphonostelic pteropsida and siphonostelic lycopsida, the successive leaf gaps in the stele do not overlap each other and are considerably apart from each other.

According to Brebner (1902), Gwynne-Vaughan (1901) such siphonosteles which lack overlapping of gaps are known as solenosteles. They may be ectophloic or amphiphloic. Some authors (Bower, 1947;

wardlaw, 1952; Esau, 1953) however, interpret the solenostele as an amphiphloic siphonostele.

4. Dictyostele:

In the more advanced siphonosteles of pteropsida, the successive gaps may overlap each other. Brebner (1902) called the siphonosteles with overlapping gaps as dictyosteles. In such cases the intervening portion of the vascular tissue between lateral to such leaf gaps is known as meristele. Each meristele is of protostelic type. The dictyostele with many meristeles looks like a cylindrical meshwork.

5. Polycylic stele:

This type of stelar organization is the most complex one amongst all vascular cryptogams (pteridophytes). Such type of steles are siphonostelic in structure. Each such stele possesses an internal vascular system connected with an outer siphonostele. Such connections are always found at the node.

A typical polycyclic stele possesses two or more concentric rings of vascular tissue. This may be a solenostele or a dictyostele. Two concentric rings of vascular tissue are found in pteridium aquilinum and three in matonia pectinata.

6. Eustele:

According to Brebner (1902), there is one more modification of the siphonostele known as eustele. Here the vascular system consists of a ring of collateral or bicollateral vascular bundles situated on the periphery of the pith. In such steles, the inter-fascicular areas and the leaf gaps are not distinguished from each other very clearly. The example of this type is equisetum.

Leaf trace and leaf gap:

The **leaf gap** is a break in the vascular tissue of a stem above the point of attachment of a **leaf trace**. It exists in the nodal region of the stem as a "**gap** in the continuity of the primary vascular cylinder above the level where a **leaf trace** diverges toward a **leaf**. This **gap** is filled with parenchyma tissue".

Telome theory:

It is now widely accepted (on the basis of overwhelming amount of evidence) that the land- dwelling plants evolved from aquatic ancestors. Ail organisms known in the precambrian, cambrian and ordovician periods of paleozoic era lived in aquatic environment.

The evolutionary conquest of land probably occurred sometimes between the late cambrian and early silurian. The concrete evidence of early vascular land plants came from the silurian in the form of fossil plant cooksonia of rhynia group of plants.

A number of theories on land-plant evolution exists of which the telome theory of Walter Zimmermann (1930, 1952) is the most comprehensive. This theory is based on fossil record and synthesises the major steps in the evolution of vascular plants.

According to this theory, all vascular plants evolved — either directly or indirectly — from a simple leafless rhynia type ancestral form made up of sterile and fertile axes (the telomes). Evolutionary modification of its parts produce more advanced vascular plants with roots, stems, leaves, more complex vascular systems and protected sporangia.

Meaning of telome theory:

A telome is defined as “the single-nerved ultimate terminal portion (at base or apex) of a dichotomising axis” i.e., it is the point of the most distal dichotomy to the tip of a branch. The connecting axes

between dichotomies are called mesomes (fig. 7.134). Functionally, telomes are of two types viz., fertile telome and sterile telome.

If the ultimate branch is terminated by a sporangium then it is a fertile telome (fig. 7.134), whereas those terminal branches without sporangia are called sterile (vegetative) telomes (fig. 7.134). Several telomes, either fertile or sterile, becomes grouped together by connecting mesomes to form a more complex structure, called syntelome or telome truss (fig. 7.134).

A syntelome is designated as phylloid truss if composed of only sterile or vegetative telomes, or as fertile truss when composed of only fertile telomes, or a mixed telome truss when composed of both sterile and fertile telomes.

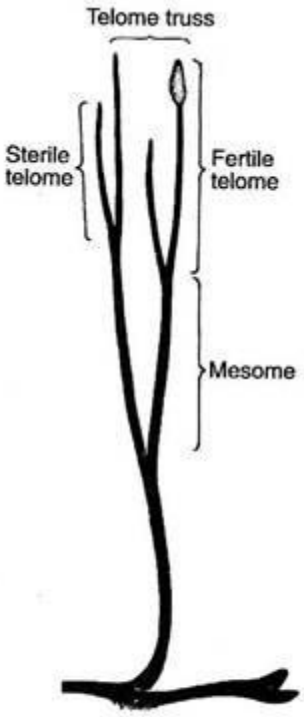


Fig. 7.134 : A primitive *Rhynia* plant showing telome and mesome

Telome and the evolution of the independent sporophyte among pteridophytes:

Processes of telome theory:

According to Zimmermann, these telomes or telome trusses of primitive rhynia type of vascular plants have been subjected to certain evolutionary processes in varying degrees among the various taxonomic groups.

These evolutionary processes are:
(i) Overtopping

(ii) Reduction,

(iii) Plantation,

(iv) Syngenesis or webbing, and

(v) Curvation.

(a) Overtopping:

In this process, one of the two dichotomising branches of the primitive axis produced by the apical meristem outgrows or overgrows the other. The larger axis thus produced becomes the stem, while the shorter or overtopped branches represent the beginnings of lateral branches or leaves (fig. 7.135a-c). Now the earlier dichotomy will be transformed to pseudomonopodial branch.

(b) Reduction:

In this process, the activity of terminal meristem of each telome of the truss becomes suppressed resulting into much shorter branches by decreasing the length of telomes and mesomes (fig. 7.135b, c). This process is responsible for the formation of microphyllous leaves of the lycopsida and sphenopsida as well as the needle-like leaves of conifers.

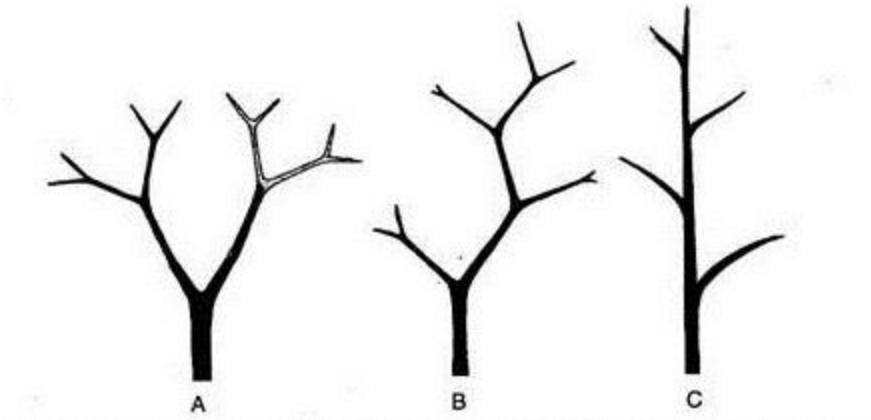


Fig. 7.135 : Telome concept : A–C. Evolutionary process of overtopping and reduction

(c) Planation:

The process of planation caused the telomes and mesomes of the truss to shift from a three-dimensional pattern (cruciate dichotomy) to a single plane (fan-shaped dichotomy) (fig. 7.136a, b).

The process of infilling with photosynthetic and other tissues between the planated branches is called webbing which have led to the evolution of flattened leaf-like structure with a dichotomously veined lamina.

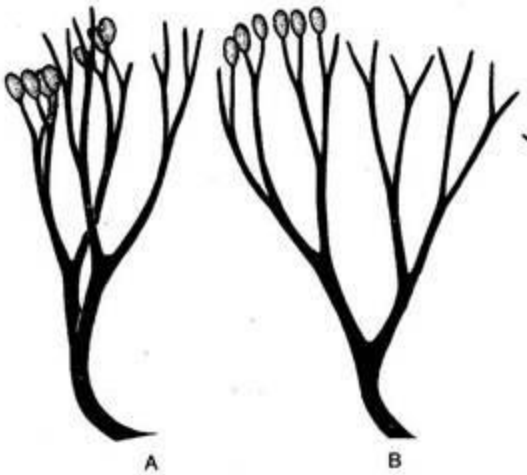


Fig. 7.136 : Telome concept : A–B. Evolutionary process of planation

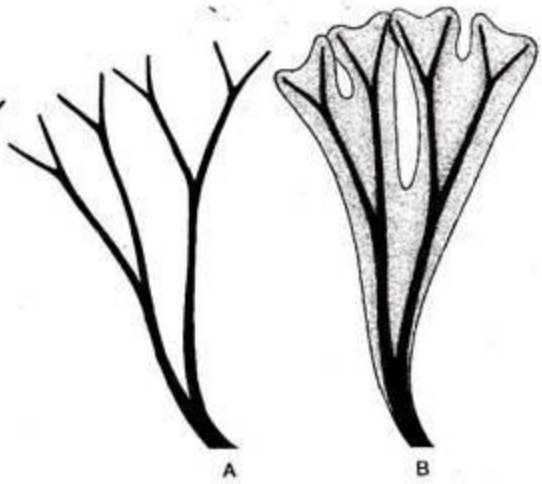


Fig. 7.137 : Telome concept : A–B. Evolutionary process of webbing

(d) Syngenesis:

This is an evolutionary process where tangential fusion of mesomes and telomes takes place (fig. 7.137a, b). The lateral fusion of

sterile vegetative telomes and mesomes resulted into complex anastomosing vascular systems in stem (e.g., polystelic condition in selaginella).

The fusion of fertile trusses with their terminal sporangia resulted in the formation of synangia of psilotum. The closed or reticulate venation pattern of some ferns, gymnosperm and many flowering plants are the result of syngenesis of the dichotomising veins of the primitive leaf.

(e) Curvation:

This evolutionary process is caused due to the unequal growth of the tissues on two opposite flanks of the telome.

It has two sub-processes:

(i) Recurvation:

In this sub-process the telome bends inward toward an axis (fig. 7.138a, b). The inward-projecting sporangia on a sporangiophore of equisetum (sphenopsida) is the result of this sub-process.

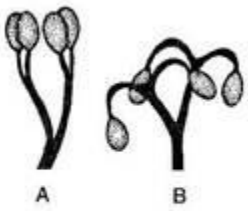


Fig. 7.138 : Telome concept : A–B. Evolutionary process of recurvation

(ii) Incurvation:

In this sub-process, the fertile telome bends downward resulting in the downward shifting of the sporangia from terminal to the ventral surface of the leaf. This sub-process is responsible for the formation of ventral position of the sporangia in fern (pteropsida) leaf.

Origin of pteridophytes

Bryophytic origin:

Even among the proponents of bryophytic ancestry there is no unanimity as to the precise group which constituted the ancestral stock or the mode of origin. There are four theories.

Anthocerotean theory:

Campbell (1895) and Smith (1938) are the chief supporters of this theory. They believe that the sporophyte of anthoceros has all the attributes of becoming the ancestor of land plants. Of all the members in bryophytes, according to Campbell (1895), anthoceros is the most advanced, in having a mechanism for indefinite growth, limited tissue for spore production etc.

Campbell (1895), has reported that in one of the californian species; (a. Fusiformis), the sporophyte almost reached the stage of an independent plant body. Campbell (1939) compares the sporophyte of anthoceros to the plant body of rhynia and points out many similarities between the two.

The green naked plant body, possession of a meristem assuring indefinite growth, presence of a columella remotely resembling the vasculature of land plants are some of the characters in the sporophyte of anthoceros which support its claim of being the ancestral stock of land plants.

Campbell (1939) states, considering the extraordinary close resemblance between the structure of these ancient pteridophytes (rhynia etc.) And the sporophyte of the anthocerotaceae, it is a fair assumption that the rhyniaceae were derived either directly from some anthocerotaceae or from forms very much like them.

Smith (1938) has further elaborated the anthocerotean hypothesis. He traces the origin of rhynia, from an anthocerotean type

stock, with some modifications (fig.203). He suggests if an anthocerotean type of sporophyte had a shifting of the meristematic region from the base to apex, this would make possible an initiation of dichotomous (fig.203c) branching by the meristem and the restriction of spore formation to branch apices.

He believes that if the columella in the sporophyte of anthoceros were to evolve into a vasculature in the course of evolution, a land plant of the type of rhynia could be visualised. Smith (1938) extended his observations to the sex organs and opined that the sex organs of pteridophytic gametophytes have much in common with those of anthoceroies.

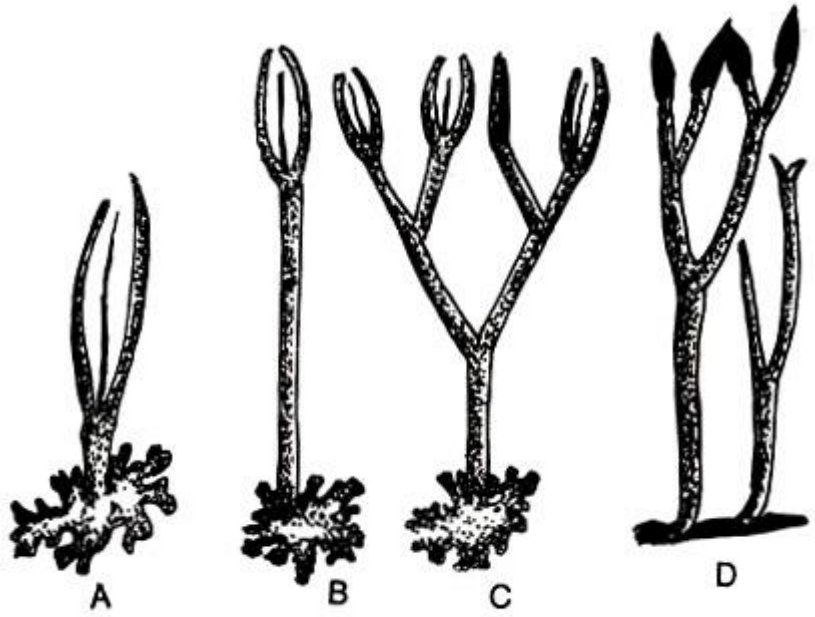


Fig. 203. *Origin of Pteridophytes* : Stages illustrating the origin of Pteridophytic Plant Body from an Anthocerotean type of Sporophyte

The points of resemblance in the sex organs are as follows:
Antheridia (fig.204):

These are embedded in both anthoceros and pteridophytes. The primitive type of antheridium seen in eusporangiate forms like lycopodium, equisetum, etc., consists of a large number of fertile cells embedded in the gametophytic tissue and surrounded by a single layer of jacket.

Smith (1538) compares the fertile cells of this eusporangiate type antheridium to the entire antheridium of anthoceros and observes that the jacket of the antheridium is comparable to the roof of the antheridial chamber in anthoceros.

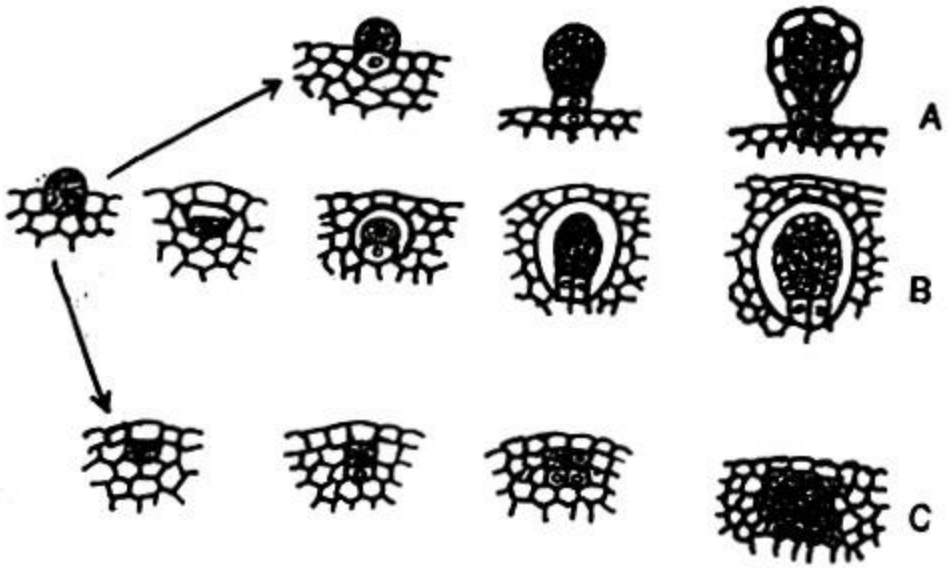


Fig. 204. *Origin of Pteridophytes* : Homologies in the development of Antheridia A. Marchantiales, B. Anthocerotae, C. Eusporangiate type

Archegonia:

The archegonium of anthocerotes is more reduced than in hepaticae; (fig.205b). Evolution of the pteridophytic archegonium is the result of further reduction in antogeny. Since the archegonial initial in pteridophytes (fig ,205c) directly forms the axial cell, the entire archegonium is comparable to the axial row and cover cells of the anthocerotean archegonium.

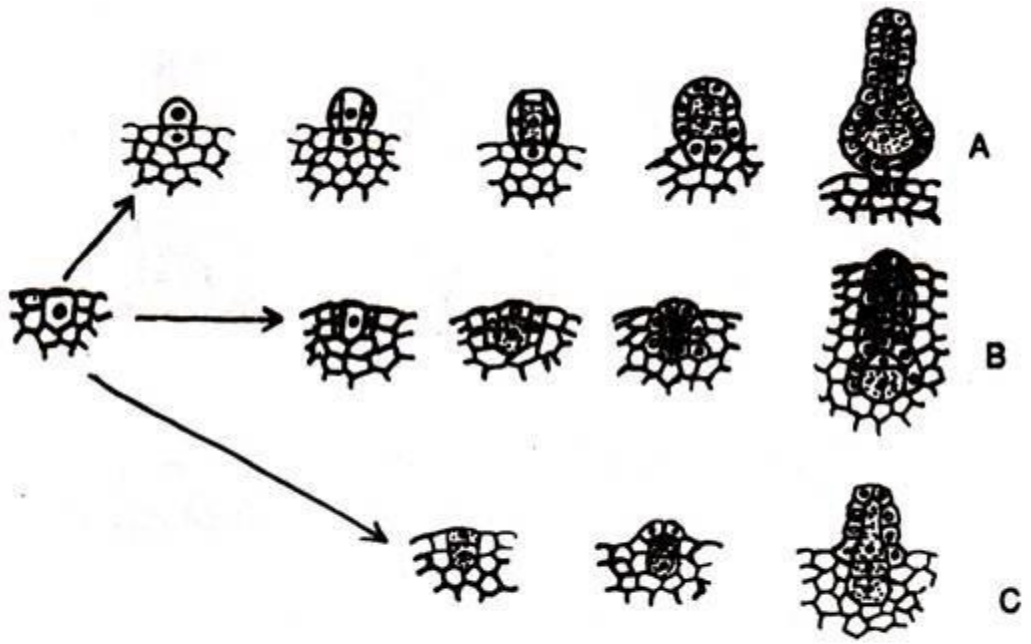


Fig. 205. *Origin of Pteridophytes* : Homologies in the Development of Archegonia
A. Hepaticae, B. Anthocerotae, C. Pteridophytes

Most of the botanists however do not favour an anthocerotean origin for land plants.

Strobilar theory:

This theory has been advocated by, Bower (1894) favouring a bryophytic origin for a sporophyte, from the zygote with a great amount of elaboration.

According to him in a life cycle without alternation of generations, the zygote immediately undergoes reduction division producing haploid cells (spores, zoospores, etc.) Which develops into a new plant body. Hence the entire zygote is fertile i.e., it produce fertile cells. Bower postulated the origin of a sporophyte (antithetic origin) from such a zygote by the postponement of reduction division to a later stage.

Meanwhile the zygote divides mitotically to produce a diploid tissue which forms the sporophyte. Hence originally in a sporophyte all the tissues are devoted to spore production i.e., fertile. Subsequently by

the progressive sterilization of the potentially sporogenetic tissue, a well differentiated sporophyte arose.

Such sterilization is necessary, because for a free living sporophyte reproduction is not the only function. It has to sustain itself first and only then comes the perpetuation of the race. Bower (1894) gave a series of examples from both liverworts and early pteridophytes to prove his point.

While Bower's theory seems to be quite appealing and logical it has also been discarded as the broyophytic origin itself is in dispute. Further, some of the fossils of early pteridophytes were quite complex and not simple strobiloid plants as bower liked them to be.

Phyton theory:

According to this theory the sporophyte was originally leafy i.e., the fundamental part of the plant body was a leaf and not the axis (stem). The axis arose later due to the fusion of leaf bases.

The phyton theory proposed by Celekovsky (1901) is related to the strobilar theory in that at the stage where the sporophyte is like a strobilus (a cluster of leaves – sporophylls, attached to a central core) the plant is a cluster of leaves and there is no axis as such. Subsequently the leaf bases fuse resulting in the formation of an axis. The pericaulome and leaf-skin theories are related to the phyton theory in that both these theories assume that a considerable portion of the axis is built up by the leaf bases.

According to Eames (1964), in the face of overwhelming evidence in support of the axial nature of the sporophyte, the phyton theory seems to be irrelevant. He states that the cauloid theory, an old theory which assumes the derivation of the modern sporophyte from a primeval cauloid, (an axis) seems best to fit the facts of history.

Protocorm theory:

This theory was put forward by Treub (1890) who regarded that basically a primitive pteridophytic sporophyte was an undifferentiated mass very much like a gametophyte. He cites the example of the protocorm in some species of lycopodium as an evidence to the protocormous origin of the sporophyte.

He regards the protocorm to be a vestige of an archaic sporophyte and a transitional stage recalling an earlier step in the evolution of the sporophyte.

Another evidence cited by Treub (1890), is the similarity between the protocorm and the adult plant body of phylloglossum, which according to him is a permanent protocorm. But it has to be conceded that the so called protocorm is present not in the primitive species, but in the more advanced species of lycopodium.

Many morphologists opine that protocorm is nothing but an opportunistic growth, evidently being an adaptation to certain special environmental conditions when it is not possible to organise a definite sporophyte. Detailed investigations conducted on phylloglossum have revealed that its simplicity is not due to primitiveness but due to reduction.

Algal origin:

The current trend seems to favour a direct algal origin for vascular plants. But even here, there is no consensus as to which group among algae could be regarded as the ancestral stock. Below is given a few hypotheses of some prominent botanists.

Church's hypothesis:

Church (1919), has enunciated his theory of the origin of land plants in his famous essay entitled thallasiophyta and the sub-aerial transmigration. He believed in a polyphyletic origin. According to him a hypothetical group of marine algae called thallassiophyta (brown algae) formed the ancestral stock for all land plants.

The main points of his theory are as follows:

1. The surface of the earth in the remote past was completely enveloped by a common ocean.

2. There were many kinds of marine plants which were mostly planktonic (free floating).

3. Due to geological changes there was upheaval of the ocean bottom.

4. Due to the emergence of the land, planktonic forms changed to benthic (fixed) forms.

5. The new environment (terrestrial) gradually introduced all the adaptations like roots, leaves, vasculature etc.

The observed geological phenomena in the earth's history do not envisage an all pervading ocean. There was in fact the land first and only later oceans came into existence. Another demerit of this theory is the non-homology of marine algae and early land plants in their pigmentation.

If land plants indeed arose from brown algae they should have at-least had some traces of the brown pigments. Scott (1924), supports Church (1919) and states the discovery of rhynie plants goes to show that they evolved from a fairly highly evolved group of algae.

Greguss's hypothesis:

Based mainly on the branching similarities, Greguss (1955) derived bryophytes and pteridophytes from three groups of algae viz., chlorophyceae, phaeophyceae, and rhodophyceae.

He derived mosses from chlorophyceae and liverworts from the phaeophyceae. Similarly rhynia and horneophyton were derived from chlorophyceae while psilotum and temesepteris were derived from phaeophyceae. All these based only on the branching pattern without any regard to the phylogenetic relationships.

Andrew's hypothesis:

Andrews (1956, 1959) also is a believer of polyphyletic origin for vascular plants. His observations are based on the discovery of fossils of certain marine algae (nemotothallus, crocelophyton and protosalvinia) which had several adaptations for a terrestrial life.

Occurrence of such plants made andrews to believe that several algal groups independently attempted the invasion of the land. These groups gave rise to different groups of vascular plants. He believes that the morphological diversity exhibited by psilophyta, lycophyta etc., is due to their independent origin.

Leclercq's hypothesis:

Based on the paleopalynological studies, Leclercq (1954, 1956) proposed a polyphyletic origin for vascular plants. According to her, land plants must have had their origin somewhere during the precambrian era. This assumption is supported by the discovery of fossil spores probably of land plants in the rock strata belonging to ordovician and cambrian periods.

She considers the simple psilophytes like rhynia as the descendants of complex race that existed prior to the devonian period. Axelrod (1959) supported the polyphyletic origin of leclercq and elaborated it by his own palaeopalynological discoveries.

Sporangial development in pteridophytes:

Development of sporangia in pteridophytes:

On the basis of development, the sporangia in pteridophytes are divided into two types:

(i) Eusporangiate type

(ii) Leptosporangiate type

(i) Eusporangiate type:

Sporangium develops from group of superficial cells. These cells divide periclinally into primary wall layers and inner primary sporogenous cells (fig. 2a, b). The outer wall layers form the wall of the sporangium while inner sporogenous cells divide meiotically and form spores (fig. 2 a-f).

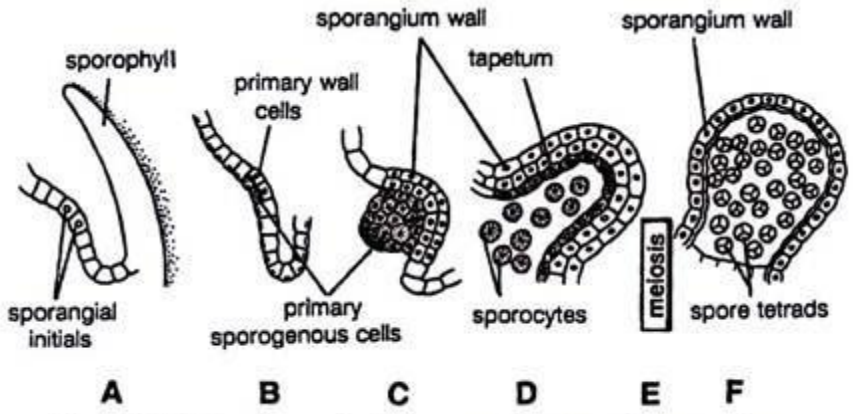


Fig. 2. (A-F) Development of Eusporangiate type of Sporangium

(ii) leptosporangiate type:

This type of sporangium arises from a single superficial cell. It divides transversely to form an outer and an inner cell (fig. 3a, b). While the inner cell forms the stalk, the entire sporangium develops from the outer cell. The outer cell divides by three successive periclinal divisions and in this way a tetrahedral apical cell is formed (fig. 3c).

It divides by periclinal division to form the outer jacket cell and inner primary sporogenous cell (fig. 3d). Jacket cell forms the single layered sporangial wall while primary sporogenous cell divides into tapetal initial and sporogenous tissue (fig. 3e). Sporogenous tissue divides meiotically to give rise to haploid spores while tapetal initial forms two layered tapetum (fig. 3 f, g).

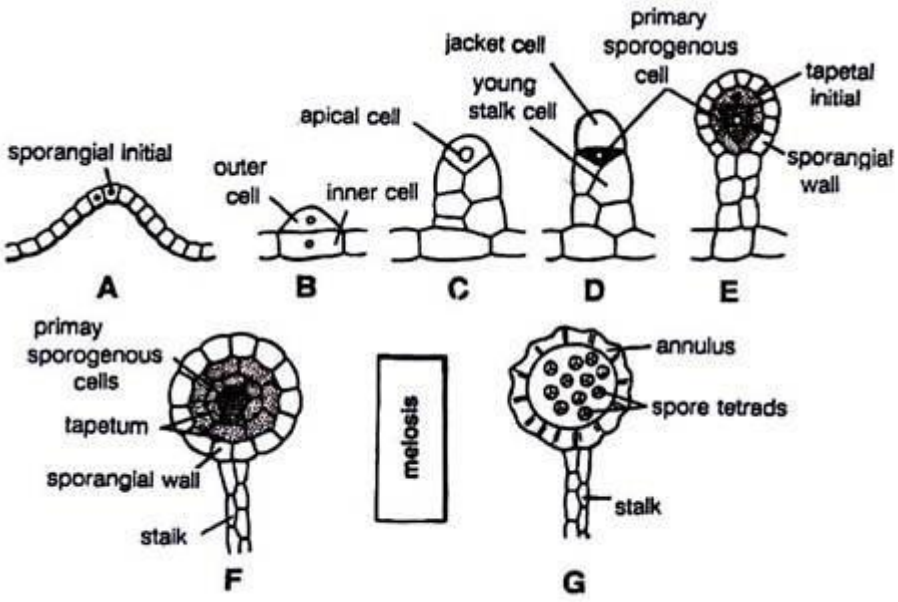


Fig. 3. (A-G) Development of Leptosporangiate type of Sporangium

Differences Between Eusporangiate and Leptosporangiate Type of Sporangium

S. No.	Eusporangiate Type	Leptosporangiate Type
1.	Sporangium is massive	Sporangium is small
2.	Sporangium is formed from many initials	Sporangium is formed from single initial
3.	Sporogenous tissue is derived from the inner daughter cell	Sporogenous tissue is derived from the outer daughter cell.
4.	Wall is several cells thick	Wall is only one cell thick.
5.	Examples : *Lycopodium, Selaginella, Equisetum*	Examples : *Pteris, Polypodium, Marsilea.*

Unit II Morphology and reproduction of pteridophytes:

Heterospory in pteridophytes:

Most of the pteridophytes produce one kind of similar spore. Such peridophytes are known as homosporous and this phenomenon is known as homospory. However, there are some pteridophytes which produce two different types of spores (differing in size, structure and function).

Such pteridophytes are known as heterosporous and the phenomenon is known as heterospory. The two types of spores are microspores and megaspores. Microspores are smaller in size and develop into the male gametophyte while the megaspores are large and develop into female gametophyte.

Origin of heterospory:

The origin of heterospory can be better discussed on the basis of evidences from paleobotany, developmental and experimental studies.

1. Palaeobotanical evidences:

It has been suggested that heterospory arose due to degeneration of some spores in a few sporangia. As more nutrition becomes available to less number of spores, the surviving spore grow better, hence increase in their size.

Palaeobotanical evidences show that the earlier vascular plants wert all homosporous and the heterosporous condition appeared subsequently in the lowermost upper devonian. Anumber of heterosporous genera belonging to the lycopsida, sphenopsida and

pteropsia were known in the late devonian and early carboniferous periods.

During this period important heterosporous genera were lepidocarpon, lepidostrobus, mazocarpon, plaeuromeia, sigillariostrobiis (members of lycopsid) calamocarpon, calamostachys, palaeostachys (members of sphenosida). Some of these forms even arrived at the seed stage.

According to williamson and scot (1894) two species of calamostachys form the initial stage that might lead to the heterospory. These species were c. Binneyana and c. Casheana. In c. Binneyana most of the sporangia were with large number of small spores in tetrads but in some sporangia spores were large.

However, in c. Casheana two different types of spores-microspores and megaspores were present in different sporangia. Similar type of abortion of spores was also observed in stauropteris (Chaloner, 1958l epidocarpon and calamocarpon).

2. Evidences from developmental studies:

In heterosporous pteridophytes the development of micro and megasporangia follow the same pattern. They have identical organization but for their size. While in megasporangia most of the spore mother cells degenerate but in microsporangia only a few mother cells are disorganize.

The phenomenon of heterospory becomes distinct either before or after meiosis. In selaginella isoetes it is distinct before meiosis. In the microsporangium all the sporocytes undergo meiosis and form a large number of microspores. However, in megasporangium, a part of the sporogenous tissue degenerates they provide nutrition to growing sporocytes (megaspores).

In isoetes there are only 50-300 megaspores in megasporangium. In selaginella erythropus megasporangium contains only one megaspore which is functional.

In marsilea, salvinia and azolla the phenomenon of heterospory becomes distinct after meiosis. In marsilea 64 microspores and 64 megaspores are formed after meiosis in microsporangium and megasporangium respectively. In microsporangium all the microspores are functional while in magasporangium one megaspore is functional and rest degenerate.

3. Evidences from experimental studies:

Experimental studies on selaginella (Goebel, 1905) and marsilea (Shattuck, 1910) suggest that nutritional factors mainly govern the heterospory. Under conditions of low light intensity, the photosynthetic activity of selaginella was retarted and it produced microsporangia. By sudden lowering of the temperature, the size of the microspores in the sporocarp of marsilea increases by six times.

Seed habit in pteridophytes:

The adoption of heterospory and the retention and germination of a single megaspore within megasporangium to form a female gametophyte, led to the phenomenon of "seed habit", a characteristic feature of the spermatophytes. A seed is that ovule which contains an embryo developed as a result of fertilization.

The origin of seed habit is associated with the following:

(i) Production of two types of spores (heterospory).

(ii) Reduction in the number of megaspores finally to one per megasporangium.

(iii) Retention and germination of the megaspores and fertilization of the egg.

(iv) Continued development of the fertilized egg into the embryo while still in situ.

From the above observations it is concluded that the life history of selaginella approaches towards seed habit because of the following features:

1. The occurrence of the phenomenon of heterospory.

2. Germination of megaspore inside megasporangium.

3. Retention of megaspore inside megasporangium either till the formation of female gametophyte or even after fertilization.

4. Development of only one megaspore per megasporangium for example, in selaginella monospora, s. Rupestris, s. Erythropus etc.

Though selaginella as well as lower spermatophytes shows homologies in their structure as follows:
Selaginella:

1. Megasporangium.

2. Megaspore.

3. Female gamestophyte.

4. Archegonium.

5. Egg.

Lower spermatophytes (gymnosperms):

1. Nucellus of ovule.

2. Megaspore (embryosac).

3. Endosperm.

4. Archegonium.

5. Egg.

Even then the seeds are not formed in selaginella because:

1. Megasporangium is not surrounded by integument.

2. The retention of megaspore permanently inside the megasporangium has not been well established.

3. The embryo immediately gives rise to the sporophyte without undergoing a resting period.

Economic importance of pteridophytes:

(1) Food:

Like other plants, pteridophytes constitute a good source of food to animals. Sporocarps of marsilea, a water fern, yield starch that is cooked and eaten by certain tribal.

(2) Soil binding:

By their growth pteridophytes bind the soil even along hill slopes. The soil is protected from erosion.

(3) Scouring:

Equisetum stems have been used in scouring (cleaning of utensils) and polishing of metals. Equisetum species are, therefore, also called scouring rushes.

(4) Nitrogen fixation:

Azolla (a water fern) has a symbiotic association with nitrogen fixing cyanobacterium anabaena azollae. It is inoculated to paddy fields to function as biofertilizer.

(5) Medicines:

An anthelmintic drug is obtained from rhizomes of dryopteris (male shield fern).

(6) Ornamentals:

Ferns are grown as ornamental plants

Psilopsida

Occurrence

Psilotum is distributed in tropical and subtropical regions. It may grow as an epiphyte on the bark of trees. It also grows on soil where humus is abundantly available.

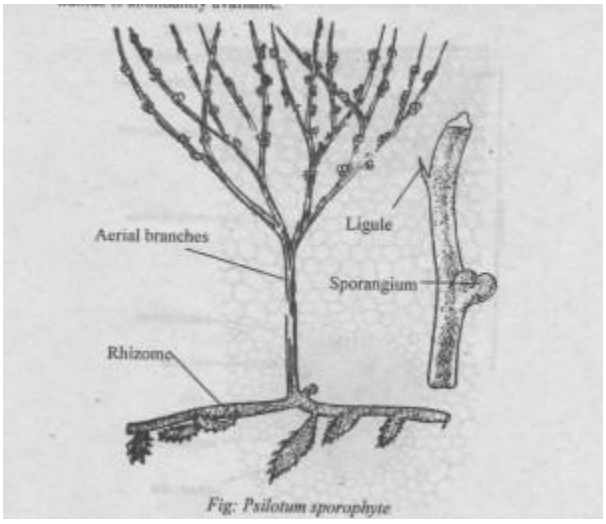


Fig: Psilotum sporophyte

General structure

The plant body is sporophyte. The plant is a small shrub. The plant body is differentiated into rhizome and aerial branches.

1. Rhizome: Rhizome is underground part of stem. Leaves and roots are absent on rhizome. Rhizome develops rhizoids for absorption of water.

2. Aerial branches: Aerial branches arise from the rhizome. Aerial branches are green and cylindrical at the base. These branches are dichotomously branched repeatedly. Leaves are present on aerial branches. The leaves are small and scale-like. They are irregularly scattered over these branches.

3. Sporangia: The sporangia are borne in triads. They have very short stalks. They are borne in the axils of small bifid leaves on the aerial branches. This triad of sporangia is called a **synangium.** The two lobes of the leaf are closely united with the synangium.

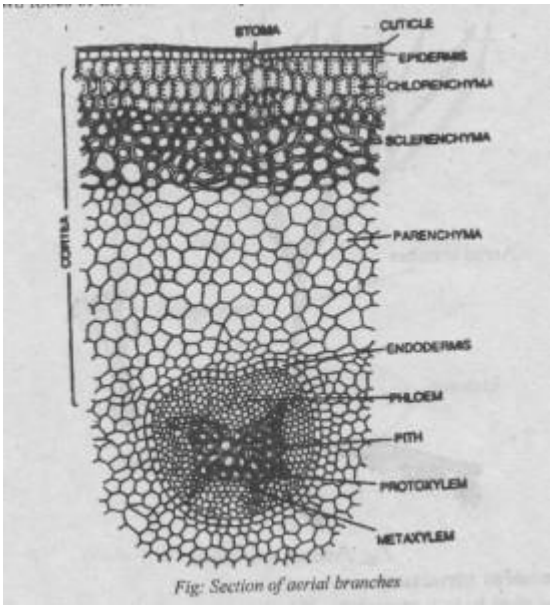


Fig: Section of aerial branches

Internal structure

Aerial branches:

In transverse section, the aerial branches have central stele and outer cortex.

1. Cortex: The cortex is covered by a single layered epidermis. Stomata are present in the epidermis. The inner part of the cortex is formed of parenchymatous cells. Outer to this parenchyma are few layers of sclerenchymatous cells. The cells in outer most part of the cortex are rich in chloroplasts. Cambium is absent in the stem.

2. Stele: There is a well developed endodermis between the stele and the cortex. The xylem is actinostelic. It has six rays. A core of thick walled sclerenchymatous fibers (pith) is present in the centre of the xylem. Phloem is present between the endodermis and xylem.
Rhizome: The structure of the rhizome is similar to that of aerial branches. But pith or sclerenchymatous tissues are not present in the centre of the xylem core. The phloem is poorly developed. The cortex is composed of thin walled parenchyma. A mycorrhizal fungus lives in it. The cells of lower epidermis contain rhizoids.
Leaves: The leaves have simple structure. The epidermis is formed of cutinized cells and is without any stomata. The internal tissue is formed of photosynthetic tissue. The leaves are without a vein.

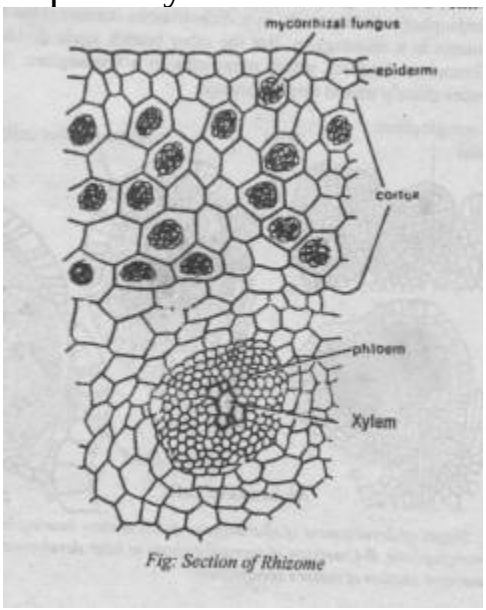


Fig: Section of Rhizome

Reproduction

Vegetative reproduction:

Vegetative reproduction takes place by the death of the older parts of the rhizome. The younger parts of rhizome separate from the dead rhizome. They grow as long as independent plants. Sometimes, the upper cell of the rhizoids divides and produces a small gemma. The gemma develops into a new rhizome after detachment.

Sporangium:

Psilotum is homosporous. Sporangia form groups of three on short stalks. This stalk is present in the axils of small bifid leaf. The group of three fused sporangia is called a **synangium.** It is believed that synangium is sporangiophore. It has bifid bract at its base. The sporangia develop independently from each other. The sporangiophore divides early in a dichotomous manner. One branch terminates in a sporangium. But the other branch again divides into two branches. Each of which terminates in a sporangium. Thus it produces closely united three sporangia.

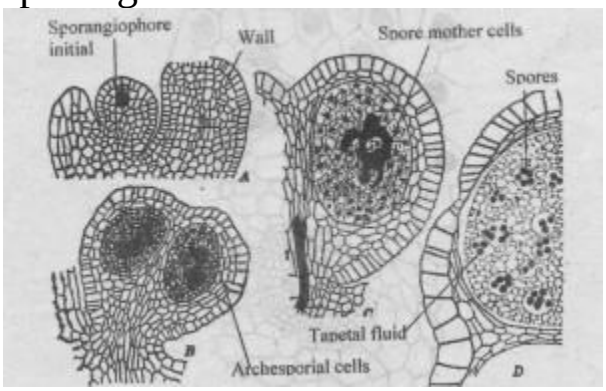


Fig: *stages of development of sporangium, a- vs of stem bearing leaf and sporangiophore. B-c-section of sporangiophore at later development, d-transverse section of mature sporangium.*

Development of sporangia

1. Each sporangium develops from a superficial cell of the sporangiophore. This cell divides transversely into an outer **jacket initial** and an inner **archesporial initial.**

'2. The jacket initial divides to produce **wall.** This wall is four to five cells thick. The archesporial initial divides to produce a mass of **archesporial cells.** Tapetum is not produced in psilotum.

3. In the mature sporangium some of the archesporial cells become elongated. They are filled with dense cytoplasmic contents. These cells act as **spore mother cells.** Each spore mother cell undergoes meiosis and produces four spores. The rest of the archesporial cells disintegrate to form protoplasmic mass or **tapetal fluid.** It nourishes the developing spores.

The epidermal cells of the sporangial wall become thick walled. But a single vertical line from the base of the sporangium to the apex remains thin walled. The mature sporangium dehisces along this line and the spores are liberated.

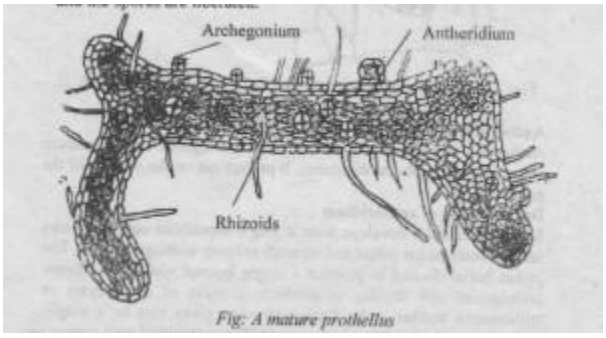


Fig: A mature prothellus

Gametophyte:

Each spore germinates to produces a small thallose gametophyte or prothallus. The gametophyte is colourless and subterranean (underground). It has one two or more short dichotomous branches. Gametophyte is infested with mycorrhizal fungi. There are no vascular strands in the gametophyte. It bears numerous unicellular rhizoids. The gametophyte does not have much internal differentiation of tissues. It is monoecious. The sex organs are produced near the growing apex.

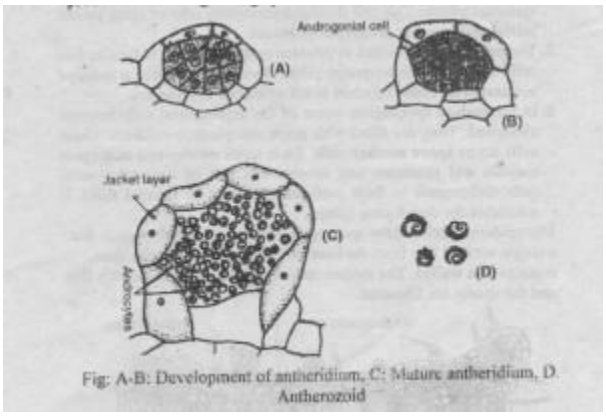


Fig: A-B: Development of antheridium, C: Mature antheridium, D. Antherozoid

Antheridia:

Antheridia are produced earlier than archegonia. The mature antheridium is globular structures. It project out on the surface of the gametophyte.

Development of antheridium:

Each antheridium develops from a single superficial cell. It divides into an outer jacket initial and an inner primary androgonial cell. The jacket initial divides to produce a single layered wall. The primary androgonial cell divides to produces a mass of **androcytes** or antherozoid mother cells. Each androcyte gives rise to a single, coiled and multiflagellate antherozoid. The antheridial wall ruptures to release the antherozoid.

Archegonium:

The mature archegonium consists of a neck and basal part. The neck contains one or two neck canal cells. The basal part is embedded in the gametophytic tissue. It is without any well defined venter. It contains a single large oosphere.

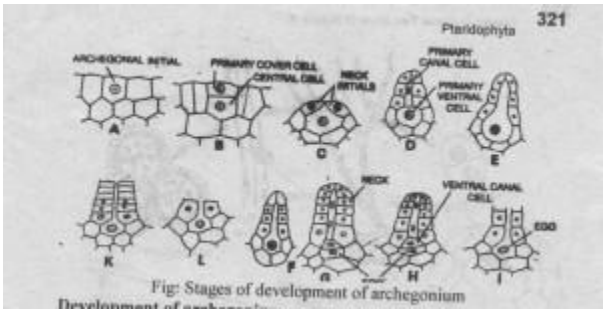


Fig: Stages of development of archegonium

Development of archegonium

Each archegonium develops from a single superficial cell. It divides transversely into an upper **primary cover cell** and a **lower central cell.** The primary cover cell divides to produce a group of four neck initials. These neck initial divides to produce neck. The central cell divides transversely into a primary neck canal cell and a primary ventral cell. Primary ventral cell functions as an egg directly.

Fertilization:

The neck canal cells of mature archegonium disintegrate. It produces a pore through which antherozoids enter the archegonium. Only one antherozoid fuses with the oosphere to produce oospore.

Development of sporophyte:

I. The oospore divides transversely into an upper and a lower cell.

2. The lower cell by further divisions produces a foot. Foot buried into the tissue of the prothallus. It absorbs nourishment for the developing embryo.

3. The upper cell divides to produce a mass of cells. Its one or two peripheral cells act as apical cells. The apical cell divides and increases the size of embryo. The gametophytic tissue completely surrounds the young embryo like calyptra in early stages. But later, it comes out of the calyptra. Some of its surface cells produce rhizoids. Other cells are infested with the mycorrhizal fungi and the embryo becomes independent. The embryo by further growth becomes the rhizome. Rhizome develops aerial dichotomous branches.

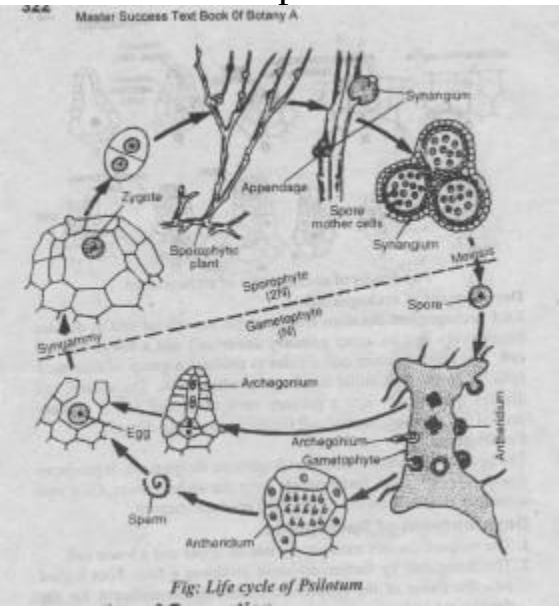


Fig: Life cycle of Psilotum

Alternation of generation

Psilotum shows regular alternation generations. The vegetative plant is sporophyte. It produces haploid spores by meiosis. Spores germinate to give rise to the prothallus or gametophyte. The prothallus produces antheridia and archegonia. Fertilization produces diploid oospore. Oospore gives rise to the sporophyte. Thus sporophyte and gametophyte alternates with each other.

Lycopsida:

Occurrence

Selaginella is a tropical plant. It has world wide distribution. It grows in damp forests. Some species occur in temperate regions. They grow in moist shady places.

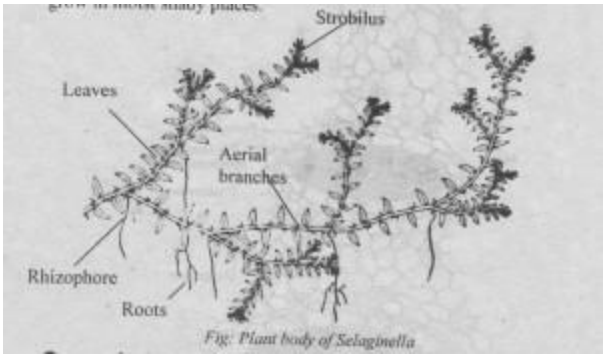


Fig: Plant body of Selaginella

General structure

The plant body is sporophyte. The body is divided into root, stern and leaves.

Stem: the main stein is prostrate. Some erect braches arise form the main stem.

Rhizophore:

Main stem develops leafless structures called rhizophore. Rhizophore grows downward. It develops adventitious roots at its tip. The rhizophore are intermediate in structure between the root and the stem. It is without nodes and intemodes.

Leaves: The main stem and the branches are covered by green leaves. Each leave has a ligule**.** The leaves are of two sizes, large and small. The leaves are arranged in four vertical rows. Leaves present in pairs. The larger leaf of each pair is attached toward, die ventral side of the stem and the smaller leaf towards the dorsal side. The leaves bearing sporangia in their axils are called sporophylls. Many sporophylls form cones or strobili.

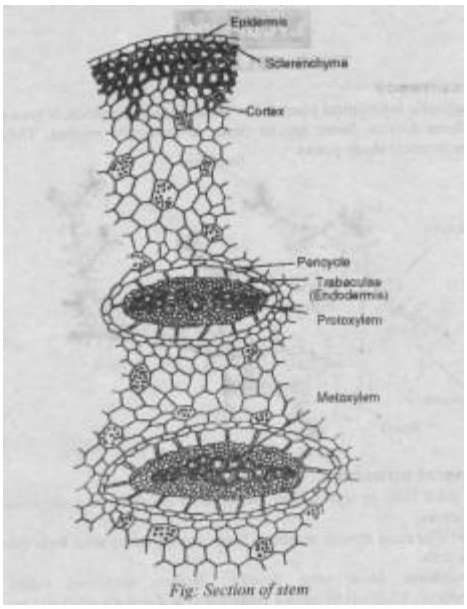


Fig: Section of stem

Internal structure of the stem

In cross section, the stem is composed of epidermis, cortex and central stele.

1. **Epidermis:** It is outermost layer. It is without stomata.
2. **Cortex:** Cortex is present inner to the epidermis. It has many layered. It composed of parenchymatous cells. The cortex surrounds central stele. Cell of peripheral region of cortex contain chloroplasts. In mature regions of stem, the cortex form sclerenchymatous hypodermis.

3. Stele: Their stele is from monostelic to polystelic condition. Each stele is protostelic in nature. The metaxylem forms the solid central core. The protoxylem groups on the periphery. The xylem core is surrounded by the phloem. Outside the phloem is the pericycle. It is composed of single layer of parenchymatous cells. The stele is separated from the cortex by a wide,air space. These spaces have long radiating cells called **trabeculea.** Trabeculea connect the stele with the cortex.

Internal structure of the root:

The root has a single layered epidermis. Inner to the epidermis is a many layered cortex. A well developed single layered endodermis separates the cortex from the stele. There is no air space surrounding the stele. The stele is protostelic and monarch. There is a single layered pericycle

between the phloem and the endodermis. The internal structure of the rhizophore is similar to that of the root

Internal structure of the leaf:

The leaf is covered by a single layered epidermis. The cells of epidermis contain chloroplasts. Stomata are present on the upper, or on the lower, or on both sides of the leaf. The mesophyll is formed of parenchymatous cells. These cells are loosely arranged and they have numerous intercellular spaces. Each cell contains one or more chloroplasts. Each chloroplast contains several pyrenoid-like bodies. The mesophyll is traversed by a single vein.

Sporangia

Selaginella is **heterosporous.** The larger spores are **megaspores** and the smaller spores are **microspores.** Megaspores are produced in megasporangia and microspores are produced in microsporangia. Both sporangia are borne in the axils of leaves called microsporophyll and megasporophylls. This condition is called **stachyosporous.** The sporophylls form definite **cones or strobili.** Both kinds of sporangia are found in the same strobilus. Megasporangia are present in the basal portion and the microsporangia are present in the upper part of the cone.

Each microsporangium contains several microspores. But them are only four megaspores in each sporangium. The mature spores are pyramidal in shape. The sporangial wall consists of three layers. The inner most layer is **tapetum.** They provide nourishment to the developing spores. A slit is produced in mature sporangia.the spores come out of this slit. The spores germinate to develop gametophytes. Microspore give rise to male gametophytes and the megaspores produces female gametophytes. Both male and female gametophytes remain within the walls of the spores. The young embryo develops in the megaspore. This is an approach towards the seed habit.

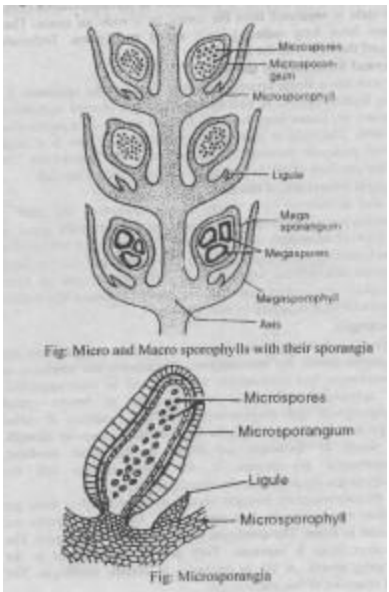


Fig: Micro and Macro sporophylls with their sporangia

Fig: Microsporangia

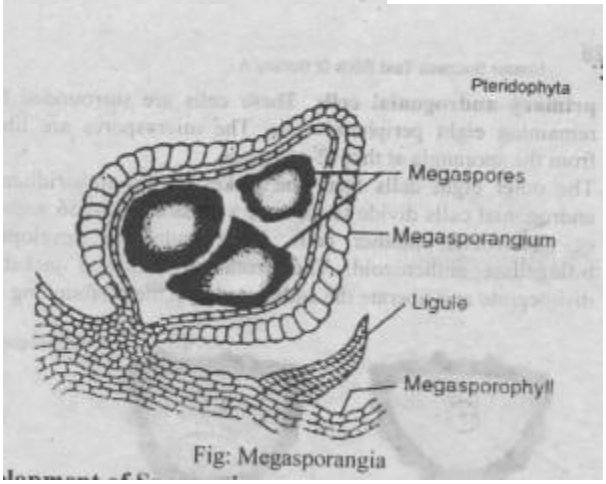


Fig: Megasporangia

Development of sporangia

The development of micro and megasporangia is similar upto the formation of spore mother cells.

1. The sporangia initials are present in the axil of the leaf. The sporangial initials divide to form outer cells called the **jacket initials,** and an inner group of cells called **archesporial initials.**

2. The archesporial initials divides to form mass of **sporogenous tissue.** The outer most layer of the sporogenous tissue forms **tapetum.** The jacket **initials by** further divisions give rise to a jacket.

3. All the sporogenous cells in the **microsporangia** become spore mother cells. The spore mother cells separate from each other. They undergo meiosis to form microspores. Several spore mother cells are produced in the **megasporangium.** But only one spore mother cell is functional. All others disintegrate. The spore mother cells divide meiotically to produce four megaspores. The development of the megaspores started before their shedding from the sporangia.

Gametophytes

Development of the male gametophyte:

I. The development of the male gametophyte started within the microsporangia. Microspore divides into two unequal cells. The smaller cell is called **prothalial cell.** The larger cell is called the **antheridial cell.**
2. The prothalial cell does not divide further. Antheridial cell divides to produce 12 cells. Four cells occupy the centre. They become **primary androgonial cells.** These cells are surrounded by the remaining eight peripheral cells. The microspores are liberated from the sporangia at this 12-cell stage.

3. The outer eight cells form the jacket of the antheridium. The androgonial cells divide to produce a mass of 128-256 androcytes or antherozoid mother cells. Each androcyte develops into biflagellate antherozoid. The prothalial cell and jacket cells disintegrate and liberate the antherozoids in the surrounding water.

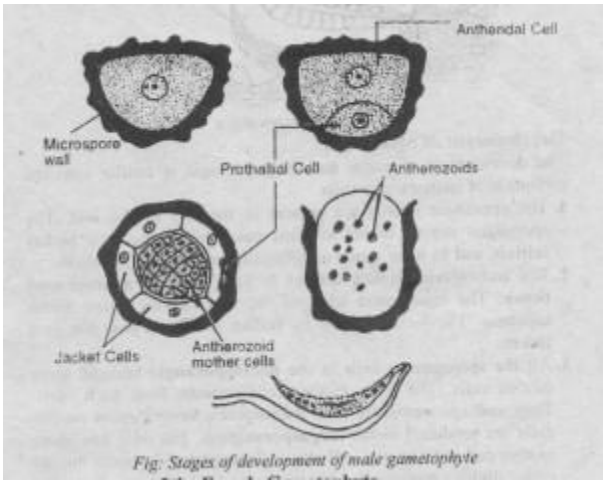


Fig: Stages of development of male gametophyte

Development of the female gametophyte:

The germination of the megaspores started in the megasporangium. Spore increases in size. Nucleus of the spore undergoes several divisions. It makes the spore multinucleate. A large central vacuole develops in the spore. It pushes the whole of cytoplasm towards the pointed end of the spore. The vacuole gradually disappears. Two or three layers of cells are formed towards the pointed end of the spore. A clear membrane **diaphragm** separates the cellular layers from the rest of the cytoplasm. The spore wall ruptures at the pointed end exposes the cellular layers. The exposed cells develop chloroplasts. Some cells produce rhizoids.

1. Several superficial cells of exposed tissues become **archegonial initials.** The archegonial initial divides into an upper **primary cover cell** and a lower **central cell.**

2. The primary cover cell divides to form the neck of the archegonium. The central cell divides to produce an upper **primary canal cell** and a lower **primary ventral cell.** The primary canal cell functions as single **neck canal cell:**

3. The primary ventral cell divides **to** produces a lower egg or **oospbere** and an upper ventral canal cell. The surrounding vegetative tissue forms the wall of the venter. The ventral canal cell and the neck canal cells of mature archegonia disintegrate. They form a passage for the entry of antherozoids.

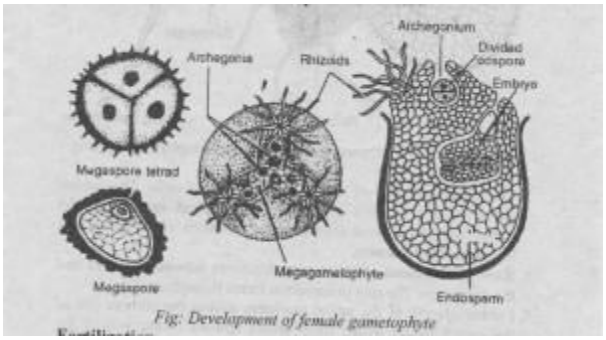


Fig: Development of female gametophyte

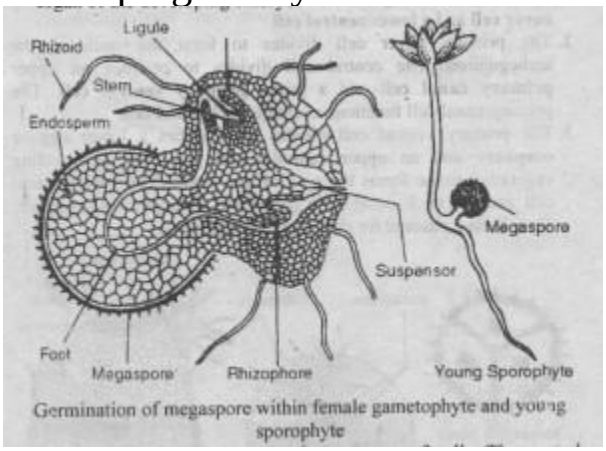
Fertilization

Fertilization always takes place in moisture. Antherozoids swim in water. One antherozoid enters into archegonium. It fuses with oosphere to produce oospore.

Development of the embryo:

1. The oospore divides into two cells. The upper cell enlarges. It is cilled **suspensor.** The lower cell is called the **embryonal cell.** It develops into the embryo. The suspensor pushes the developing embryo into the tissue of the gametophyte.

2. The embryonal cell divides to form eight cells or **octants.** Two cells of the octants divide more rapidly. They produce an outgrowth called **foot** on one side. Foot is the chief food absorbing organ of the developing embryo.



Germination of megaspore within female gametophyte and young sporophyte

3. The remaining cells of octant form a mass of cells. The central group of cells in this miss forms the **apical meristem.** The remaining cells of these mass produce rudiments of the first leaves or **cotyledonary leaves.**

4. Root primordium arises as a protuberance between the foot and the suspensor. The root primordium forms rhizophore.

5. Further growth of the apical meristem pushes the embryo out of the gametophytic tissue. Stem grows upward taking with it the cotyledonary leaves. The rhizophore grows downward and produces adventitious roots.

Alternation of generation

Selaginella shows a regular alternation of sporophytic and gametophytic generations. The vegetative plant is diploid sperophyte. It produces haploid micro and mega spores by meiosis. These spores give rise to male and female gametophytes. Gantetophytes produce male and female gametes. The gametes fuse to form diploid oospore. This oospore develops into the sporophyte.

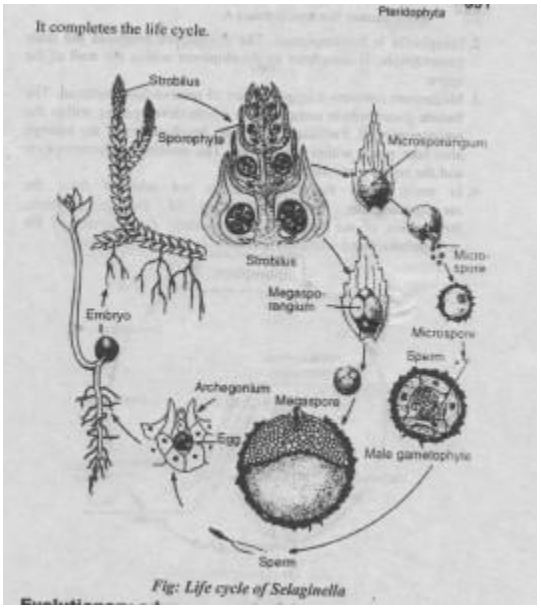


Fig: Life cycle of Selaginella

Evolutionary advancement of selaginella:

Approach to seed habit:

Selaginella shows an evolutionary advancement over the other pteridophyta. It has an approach towards seed habit due to following advanced characteristics.

1. The production of gametes, fertilization and the development of the embryo, take place on the sporophyte. Megaspore is never released from the sporophyte.
2. Selaginella is heterosporous. The microspore produces the male gametophyte: it completes its development within the wall of the spore.
3. Megaspore contains a large amount of reserve food material. The female gametophyte completes its whole development within the megaspore wall. Fertilization and the development of the embryo also take place within spore wall. The developing gametophyte arid the embryo use the reserve food.
4. In many cases the megaspore is not released from the megasporangium. The development of the gametophyte, fertilization of the oosphere and the early development of the embryo take place while the spore is still in the sporangium.

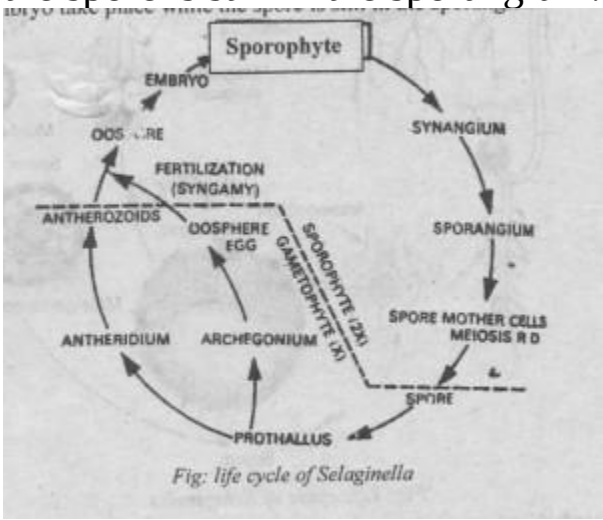


Fig: life cycle of Selaginella

Spenopsida:

Habit and habitat of equisetum:

The plant body of equisetum has an aerial part and an underground rhizome part (fig. 7.83). The rhizome is perennial, horizontal, branched and creeping in nature. The aerial part is

herbaceous and usually annual. Majority of the species are small with a size range in between 15 and 60 cm in height and 2.0 cm in diameter.

However some species grow up in higher heights [e.g., e. Giganteum (13 m), e. Telmateia (2 m); e. Ramosissimum (4 m), though their stem are relatively thin (0.5-2.0 cm in diam.)] Showing vine-like habit and climb over adjacent forest trees.

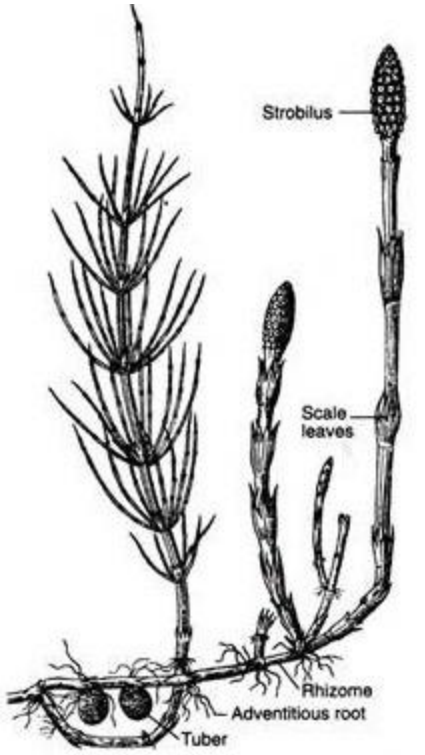


Fig. 7.83 : *Equisetum arvense* sporophyte

Equisetums generally grow in wet or damp habitats and are particularly common along the banks of streams or irrigation canals (e. Debile, e. Palustre). However, some species are adapted to xeric condition (e.g., equisetum arvense). Some common indian species are : e. Arvense, e. Debile, e. Diffusum, e. Ramosissimum.

Some species of equisetum are indicators of the mineral content of the soil in which they grow. Some species accumulate gold (about 4.5 ounce per ton of dry wt.), thus they are considered as ‘gold indicator plants.

Hence these plants help in prospection/exploration for new ore deposits. In equisetum, silica is deposited on the outer wall of the epidermal cells giving the characteristic rough feeling, thus it provides a protective covering against predators and pathogens.

Structure of equisetum:

The sporophyte:

The sporophytic plant body of equisetum is differentiated into stem, roots and leaves (fig. 7.83).

Stem:

The stem of equisetum has two parts: perennial, underground, much-branched rhizome and an erect, usually annual aerial shoot. The branching is monopodial, shoots are differentiated into nodes and internodes.

In majority of the species, all the shoots are alike and chlorophyllous and some of them bear strobili at their apices (e.g., e. Ramosissimum, e. Debile). Sometimes shoot shows dimorphism (two types of shoots i.e., vegetative and fertile) e.g., e. Arvense.

Some shoots are profusely branched, green (chlorophyllous) and purely vegetative. The others are fertile, unbranched, brownish in colour (achlorophyllous) and have terminal strobili.

The underground rhizome and the aerial axis appear to be articulated or jointed due to the presence of distinct nodes and internodes. Externally, the internodes have longitudinal ridges and furrows and, internally, they are hollow, tube-like structures. The ridges of the successive internodes alternate with each other and the leaves are normally of the same number as the ridges on the stem.

Internal features of stem:

In T.S., the stem of equisetum appears wavy in outline with ridges and furrows (fig. 7.84). The epidermal cell walls are thick, cuticularised and have a deposition of siliceous material.

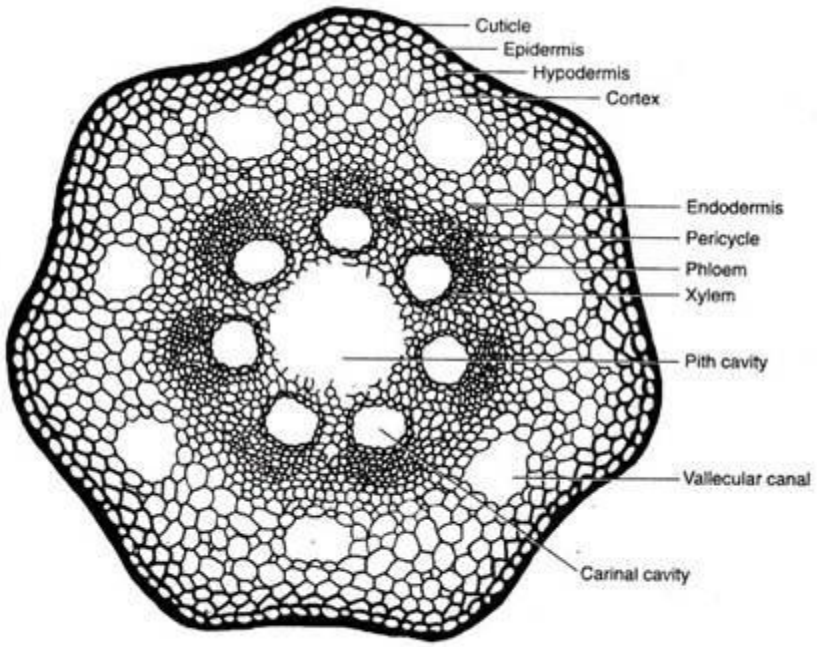


Fig. 7.84 : *Equisetum* T.S. of stem (rhizome)

Stomata are distributed only in the furrows between the ridges. A hypodermal sclerenchymatous zone is present below each ridge which may extend up to stele in e. Giganteum. The cortex is differentiated into outer and inner regions.

The outer cortex is chlorenchymatous, while the inner cortex is made up of thin-walled parenchymatous cells. There is a large air cavity in the inner cortex corresponding to each furrow and alternating with the ridges, known as vallecular canal. These are schizolysigenous canals extending the entire length of internodes and form a distinct aerating system.

New leaves and branches of equisetum are produced by the apical meristem, however, most of the length of the stem are due to the activity of intercalary meristem located just above each node. The activity of intercalary meristem causes rapid elongation of the inter- nodal region.

The stele is ectophloic siphonestele which is surrounded by an outer endodermal layer. An inner endodermis is also present in some

species of equisetum (e.g., e. Sylvaticum). The endodermis is followed by a single-layered pericycle.

The vascular bundles are arranged in a ring which lies opposite to the ridges in position and alternate with the vallecular canals of the cortex. Vascular bundles are conjoint, collateral and closed. In the mature vascular bundle, protoxylum is disorganised to form a carinal cavity which lies opposite to the ridges.

The metaxylem tracheids (scalariform or reticulate) are present on both sides of the phloem. In some species vessels with reticulate perforations are reported. The central part of the internode of aerial shoot is occupied by a large pith cavity which is formed due to rapid elongation of the internodal region.

The vascular bundles remain unbranched until they reach the level of node. At the nodal region, each vascular bandle trifurcates (divided into three parts).

The middle branch of the trifurcation enters the leaf. Each lateral branch of the trifurcate bundle joins a lateral strand of an adjacent trifurcate bundle to form a vascuiar bundle of internode (fig. 7.85). Thus the vascular bundles of internode alternate with those of internodes above and below.

In the nodal region, the xylem is extensively developed as a conspicuous circular ring. There are no vallecular or carinal canals at this level. In addition, a plate of pith tissue occurs at the node which separates one internode from another.

The internal structures of the shoot of equisetum is peculiar because it shows xerophytic as well as hydrophytic features.

The xerophytic features are:

(i) Ridges and furrows in the stem,

(ii) Deposition of silica in the epidermal cells,

(iii) Sunken stomata,

(iv) Sclerenchymatous hypodermis,

(v) Reduced and scaly leaves, and

(vi) Photosynthetic tissue in the stem.

The hydrophytic characteristics on the other hand are (i) we 11-developed aerating system like carinal canal, vallecular canal and central pith cavity, and (ii) reduced vascular elements.

Root:

The primary root is ephemeral. The slender adventitious roots arise endogenously at the nodes of the stems. In T.S., the root shows epidermis, cortex and stele from periphery to the centre. The epidermis consists of elongated cells, with or without root hairs.

The cortex is extensive; cells of the outer cortex often have thick walls (sclerenchymatous) and those of the inner cortex are thinner parenchymatous. The stele is protostelic where the xylem is triarch or tetrarch, or, in smaller roots, may be diarch.

A large metaxylem element is present in the centre of the stele and the protoxylem strands lie around it. The space between the protoxylem groups is filled with phloem. There is no pith.

Leaves:

The leaves of equisetum are small, simple, scale-like and isophyllous; they are attached at each node, united at least for a part of the length and thus form a sheath around the stem. The sheath has free and pointed teeth-like tips.

The number of leaves per node varies according to the species. The species with narrow stems have few leaves (e.g., 2-3 leaves in e. Scirpoides) and those with thick stem have many leaves (e.g., up to 40 leaves in e. Schaffneri).

The number of leaves at a node corresponds to the number of ridges on the internode below. The leaves do not perform any photosynthetic function and their main function is to provide protection to young buds at the node.

Reproduction in equisetum:
Equisetum reproduces vegetatively and by means of spores.

I. Vegetative reproduction:

The subterranean rhizomes of some species (e.g., e. Telmateia, e. Arvense) form tubers (fig. 7.83) which, on separation from the parent plant, germinate to produce new sporophytic plants. The tubers develop due to irregular growth of some buds at the nodes of the rhizomes.

Ii. Reproduction by spores:

Spores are produced within the sporangia. The sporangia are borne on the sporangiophores which are aggregated into a compact structure termed strobilus or cone or sporangiferous spike.

Strobilus:

The strobilus are terminal in position and generally are borne terminally on the chlorophyllous vegetative shoot (fig. 7.86a). However, they may be borne terminally on a strictly non- chlorophyllous axis (e.g., e. Arvense).

The strobilus is composed of an axis with whorls of sporangiophores (fig. 7.86b, c). Each sporangiophore is a stalked structure bearing a hexagonal peltate disc at its distal end (fig. 7.86d). On the under surface of the sporangiophore disc 5-10 elongate, cylindrical hanging sporangia are borne near the periphery in a ring.

The flattened tips of the sporangiophores fit closely together which provide protection to the developing sporangia. The axis bears a ring-like outgrowth, the so-called annulus immediately below the whorls of sporangiophores which provide additional protection during early development.

The annulus has been interpreted as a rudimentary leaf sheath by some botanists, whereas others consider it to be sporangiophoric in nature as occasionally it bears small sporangia.

Development of sporangium:

The mode of development of sporangium is eusporangiate, as it is not entirely formed from a single initial. Superficial cells adjacent to the original initial may also take part in the development of sporangium.

Sporangia are initiated in single superficial cell around the rim of the young sporangiophore. The periclvnal division of the sporangium initial forms an inner and an outer cell. The inner cell, by further divisions in various planes, gives rise to sporogenous tissue.

The outer cell, by periclinal and anticlinal divisions, gives rise to irregular tiers of cells, the inner tiers of which may transform into sporogenous tissue and the outer tiers become the future sporangial wall cells.

The innermost layer of the sporangial wall differentiates as the tapetum. The sporogenous cells separate from each other, round off and eventually transform into spore mother cell. All but the two outermost wall layers disorganise to form periplasmodial fluid.

However, not all of the sporogenous cells function as spore mother cells. Many of them degenerates to form a multinucleate nourishing substance for the spore mother cells. Each spore mother cell undergoes meiotic division (reductional division) and produces spore

tetrad. All spores in a sporangium are of same size and shape i.e., homosporous.

Structure of mature sporangium:

The mature sporangium is an elongated saclike structure, attached to the inner side of the peltate disc of the sporangiophore (fig. 7.86d). It is surrounded by a jacket layer which is composed of two layers of cells. The inner layer is generally compressed and the cells of the outer layer have helical thickenings which are involved in sporangial dehiscence.

Dehiscence of sporangium:

At maturity, the strobilar axis elongates, as a result the sporangiophores become separated and exposed. Then the sporangium splits open by a longitudinal line due to the differential hygroscopic response of the wall cells.

Spores:

The spores are spherical and filled with densely packed chloroplasts. The spore wall is laminated and shows four concentrate layers. The innermost is the delicate intine, followed by thick exine, the middle cuticular layer and the outermost epispore or perispore. The intine (endospore) and exine (exospore) are the true walls of the spore.

The outer two layers i.e., cuticular layer and epispore are derived due to the disintegration of the nonfunctional spore mother cells and tapetal cells. At maturity, the epispore (the outermost layer) splits to produce four ribbon like bands or strips with flat spoon-like tips.

These bands are free from the spore wall except for a common point of attachment and remain tightly coiled around the spore wall until the sporangium is fully matured.

These are called elaters (fig. 7.87a). The elaters are hygroscopic in nature. The spores remain moist at early stages of

development, thus the elaters are spirally coiled round the spore. The spores dry out at maturity and consequently the elaters become uncoiled.

These uncoiled elaters become entangled with the elaters of other spores. Through these actions the elaters help in the dehiscence process and also the dispersal of spores in large groups from the sporangium.

The elaters of equisetum are different from those of the bryophytes (table 7.6).

Gametophyte generation:

Equisetum is a homosporous pteridophyte. The haploid spores germinate to form gametophyte. The germination takes place immediately if the spores land on a suitable substratum. If the spores do not germinate immediately, their viability decrease significantly.

The spores swell up by absorbing water and shed their exine (fig. 7.87b). The first division of the spore results in two unequal cells: a small and a large cell (fig. 7.87c). The smaller cell elongates and forms the first rhizoid. The larger cell divides irregularly to produce the prothallus. The prevailing environmental conditions determine the size and shape of the prothallus.

If a large number of spores are developed together within a limited space, then the prothalli formed are of thin filamentous type. But a relatively thick and cushion-shaped prothalli are formed from sparsely germinating spores. Mature gametophytic plants may range in size from a few millimeters up to 3 centimeters e.g., e. Debile) in diameter.

They are dorsiventral and consist of a basal non-chlorophyllous cushion-like portion from which a number of erect chlorophyllous muticellular lobes develop upwards. Unicellular rhizoids are formed from the basal cells of cushion (fig. 7.87d).

The prothallus bears sex organs and reproduces by means of sexual method.

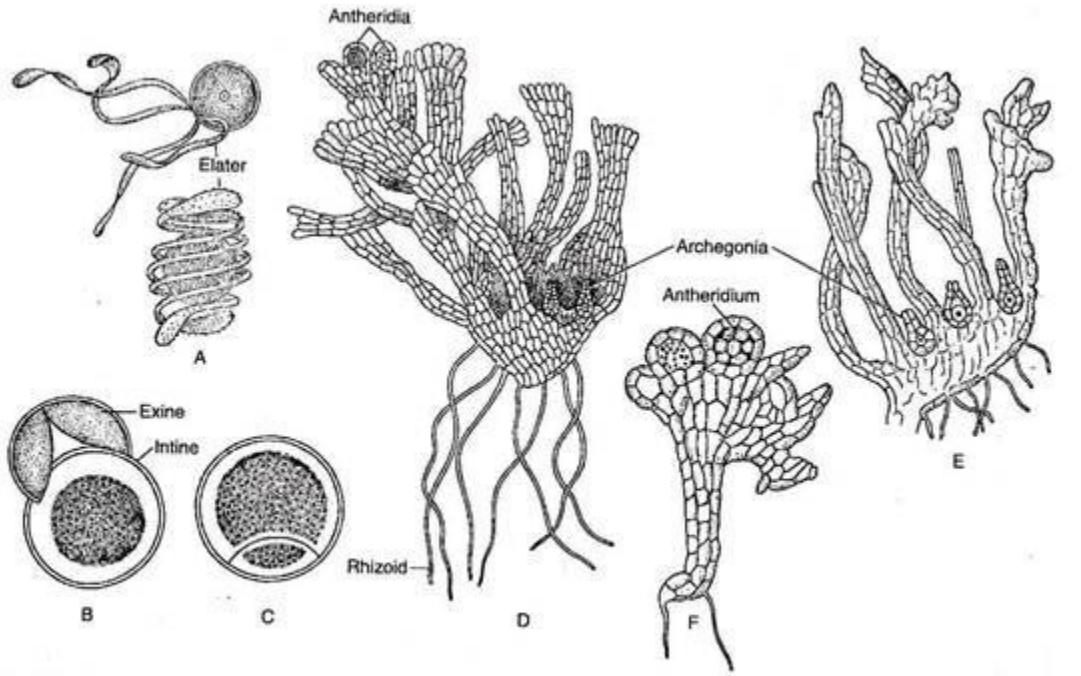


Fig. 7.87 : *Equisetum* : A. Spores with elaters, B–C. The stages of germination of spore, D. Monoecious gametophyte, E. Female gametophyte, F. Male gametophyte

Sexuality in equisetum:

The gametophytic plant body bears sex organs i.e., antheridium (male) and archegonium (female). The gametophyte are basically bisexual (homothallic) i.e., they bear both male and female sex organs (fig. 7.87d). Although, some unisexual (dioecious) members are also reported (fig. 7.87e, f). Some are initially unisexual and then become bisexual.

This early sex determination appears to be related to the environmental conditions viz., temperature, light, humidity and the supply of nutrients as well. Ducket (1977), in order to explore the sexuality in equisetum, observed that some of the fragments of male gametophyte remained male throughout the successive subcultures under laboratory conditions.

Some other fragments produced archegonia, which subsequently bore antheridia in increasing numbers. This phenomenon supports the contention that equisetum gametophytes are potentially bisexual. However, Hanke (1969) observed that gametophyte of equisetum bogotense were unisexual (bearing antheridia) and never change to bisexual type.

Schratz (1928) observed that 50% spores germinate to produce male gametophytes, while the remaining 50% spores produce female gametophytes though they do not loose their male potentiality (i.e., antheridia develop later if fertilisation fails). He termed this as 'incipient heterospory'.

A study of sexuality based on enzymatic analysis revealed the intragametophytic self- fertilisation in e. Arvense.

Equisetum is homosporous and, therefore, definite sex-determining mechanism is absent. But, the sexuality demonstrated by some of the members appears to be related to environmental factors. Therefore, it is termed as environmental sex determination.

Sex organs of equisetum:

I. Antheridium:

In monoecious species, antheridia develop later than archegonia. They are of two types — projecting type and embedded type. Antheridia first appear on the lobes of the gametophyte (fig. 7.87d). The periclinal division of the superficial antheridial initial gives rise to jacket initial and an androgonial cell (fig. 7.88a, b).

The jacket initial divides anticlinally to form a single-layered jacket. The repeated divisions of androgonial cells form numerous cells which, on metamorphosis, produce spermatids/antherozoids (fig. 7.88c-e). The antherozoids escape through a pore created by the separation of the apical jacket cell.

The apical part of the antherozoid is spirally coiled, whereas the lower part is, to some extent, expanded (fig. 7.88f). Each antherozoid has about 120 flagella attached to the anterior end.

Ii. Archegonium:

Any superficial cell in the marginal meristem acts as an archegonial initial which undergoes periclinal division to form a primary cover cell and an inner central cell (fig. 7.89a, b). The cover cell, by two vertical divisions at right angle to each other, forms a neck (fig. 7.89c). The central cell divides transversely to form a primary neck canal cell and a venter cell (fig. 7.89d).

Two neck canal cells are produced from the primary neck canal cell. While, the venter cell, by a transverse division, forms the ventral canal cell and an egg (fig. 7.89e).

At maturity, an archegonium has a projecting neck comprising of three to four tiers of neck cells arranged in four rows, two neck canal cells of unequal size, a ventral canal cell, and an egg at the base of the embedded venter (fig. 7.89f-g). The archegonia are confined to cushion region in- between the aerial lobes (fig. 7.87d).

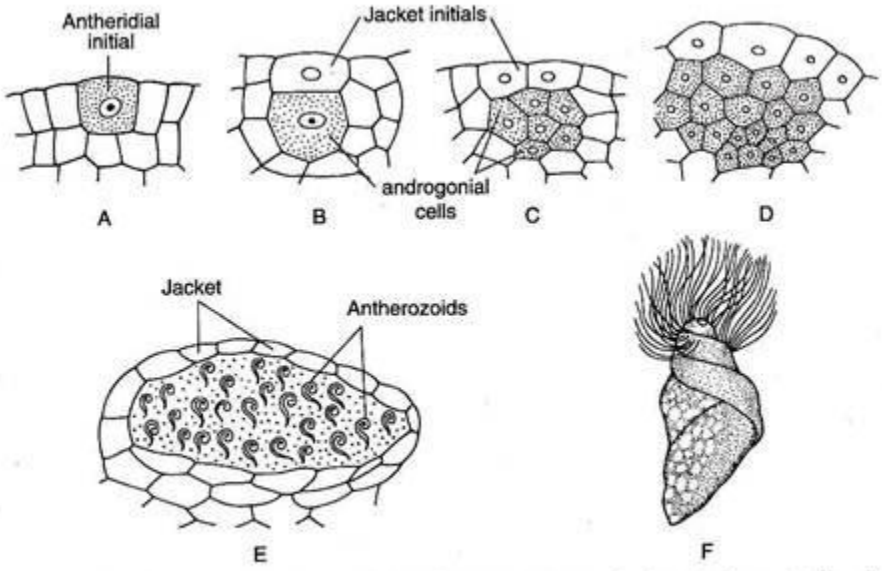


Fig. 7.88 : *Equisetum* : Development of antheridium. A–D. Successive stages in the development of antheridium, E. A mature antheridium, F. An antherozoid

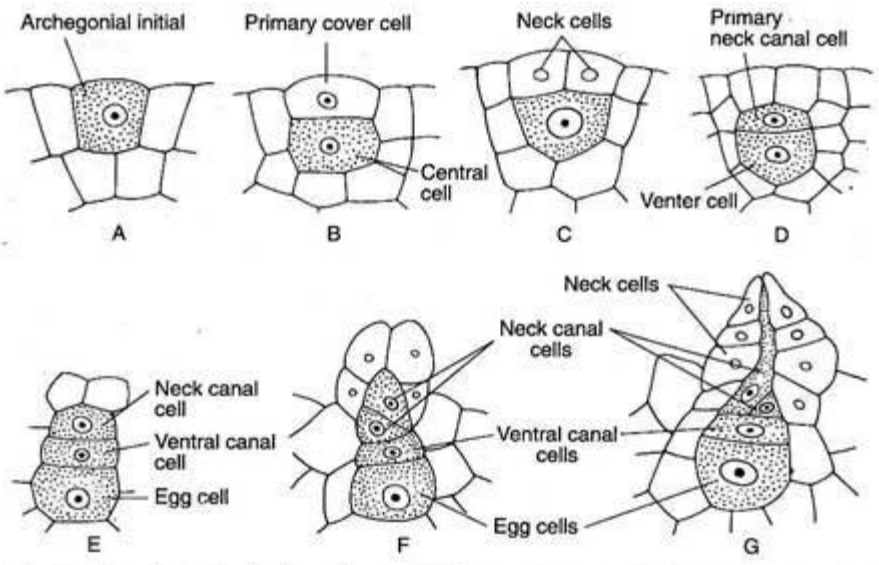


Fig. 7.89 : *Equisetum*. Development of archegonium : A–E. Successive stages in the development of archegonium, G. A mature archegonium

Fertilisation:

Water is essential for fertilisation. The gametophyte must be covered with a thin layer of water in which the motile antherozoides swim to the archegonia. The neck canal cells and ventral canal cell of the archegonia disintegrate to form a passage for the entry of antherozoids.

Many antherozoids pass through the canal of the archegonium but only one of them fuses with the egg. Thus diploid zygote is formed. Generally more than one archegonia are fertilised in a prothallus.

Embryo (the new sporophyte):

The embryo is the mother cell of the next sporophytic generation. Unlike most pteridophytes, several sporophytes develop on the same prothallus. The first division of the zygote is transverse. This results in an upper epibasal cell and lower hypobasal cell. The embryo is therefore exoscopic (where the apical cell is duacted outward i.e., towards the neck of the archegonium) in polarity.

No suspensor is formed in equisetum. The epibasal and hypobasal cells then divide at right angles to the oogonial wall, and as a

result a tour-celled quadrant stage is established (fig. 7.90a). All the four cells of the quadrant are of different size and shape.

The four-celled embryo undergoes subsequent divisions and the future shoot apex originate from the largest cell and leaf initials from the remaining cells of one quadrant of the epibasal hemisphere.

One cell of the epibasal quadrant and a portion of the adjacent quadrant of the hypobasal region contribute to the development of root. The first root develops from one of the epibasal quadrants and a portion of the adjacent hypobasal quadrant. The shoot grows rapidly.

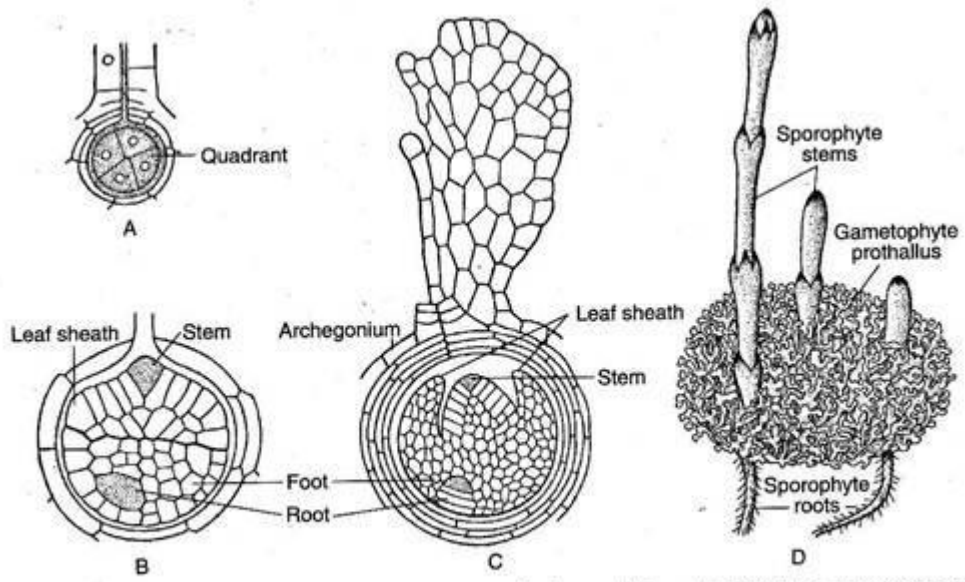


Fig. 7.90 : *Equisetum* : A–C. The stages in the development of embryo within venter, D. Young sporophytes developing from a gametophyte

Later the root grows directly downward and penetrate the gametophytic tissue to reach the soil or substratum (fig. 7.90b, c). A number of such sporophytes may develop from a large mature gametophyte if more than one egg is fertilised (fig. 7.90d).

Life cycle of equisetum:

Fig. 7.91 depicts the life cycle of equisetum.

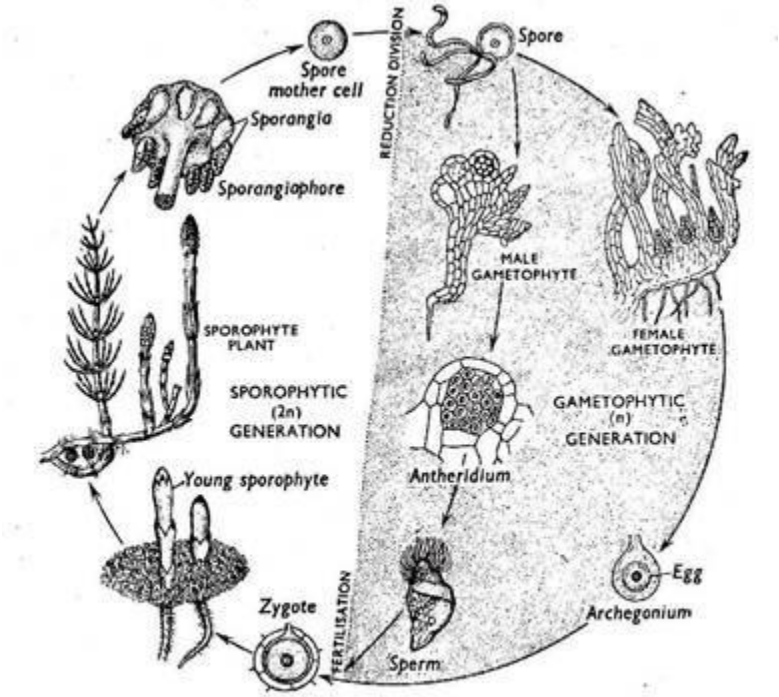


Fig. 7.91 : Life cycle of *Equisetum arvense* (dioecious)

Pteropsida:

Introduction to pteropsida (ferns):

Pteropsida represent the most highly evolved group among the lower vascular plants. In this group are included some of the most beautiful, and most familiar plants called ferns which are the joy and pride of a gardener.

The delicate, varied and highly attractive foliage of ferns have made them a must in any garden. Of all the pteridophytes, ferns are the most widely distributed. The living ferns are represented by 305 genera and nearly 10,000 species.

Geologically ferns have been known since the carboniferous period. It is believed, however, that the group must have had its ancestors during the Devonian period itself. A unique feature of ferns is that their persistent basic characters are still sufficiently plastic to be receptive to the environmental fluctuations.

Pteropsida are distinct from lycopsida and sphenopsida in several characters. Among the vegetative characters, the megaphyllous leaves with the attendant leaf gaps are most notable. Among the reproductive features, (though some primitive members show some sort of a semblance to the strobilar organisation seen in the previous groups), the aggregation of sporangia on the abaxial or adaxial surface of the leaf into sori is the most significant.

Plant body of pteropsida (ferns):

Stem:

The sporophyte has an underground rhizomatous stem which may be elongated or tuberous. The branching of the rhizome may or may not be dichotomous. In some cases the rhizome is covered by hairs called ‘ramenta’.

Leaves:

The leaves are compound and once or twice pinnate. They are megaphyllous, having a dichotomous or reticulate type of venation. The size of the leaves varies from few centimeters to several metres (angiopleris). Usually only the leaves are aerial while the rest of the plant body is

Which is generally over looked in fern description is an organ which is of potential systematic value.

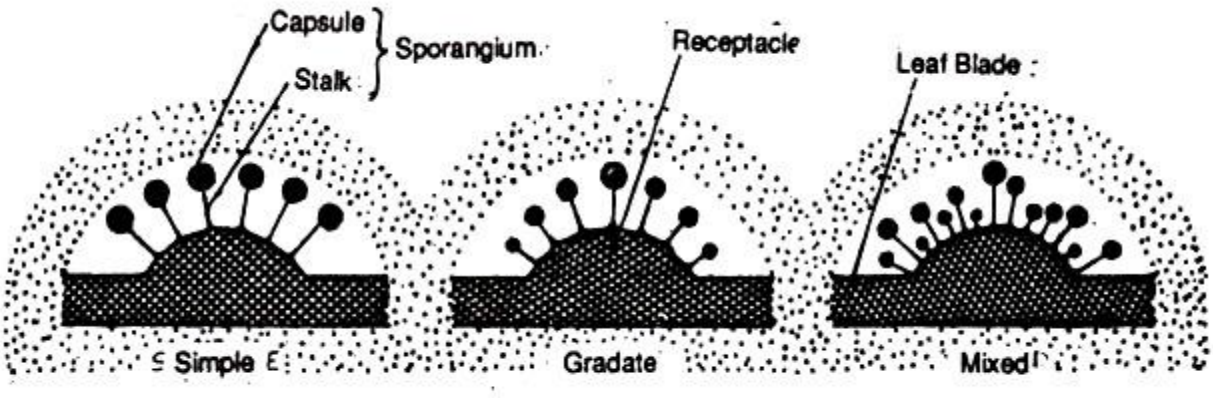


Fig. 112. Types of Soral Development in Ferns

Internal structure:

Rhizome:

Stelar organisation varies from protostele, solenostele to polycyclic, dictyostels (pteris). Cortex may be wholly parenchymatous (ophioglossm) or may be distinguished into outer sclerenchymatous zone and inner parenchymatous zone. Some times muclilage ducts are found in the cortex as in angiopteris. Xylem has mostly tracheids, but vessels are also reported in pteris, marsilea etc. Secondary growth is absent except in botrychium.

Root:

The stele is usually protostelic with variations in xylem groupings. The xylem is exarch and may be mono-di tri or even tetrarch. Root cortex may be homogenous of heterogenous.

Petiole:

The leaves maybe provided with single leaf trace or the trace may be dissected into several meristeles.

Lamina:

The upper and lower epidermal layers enclose the mesophyll which may or may not be differentiated. Distinction of

palisade and spongy parenchyma in the mesophyll is seen in cheilanthes, pyrrosia etc. Lamina may be hypostomatic or amphistomatic.

Reproduction:

Vegetative propagation:

This is brought about by a variety of methods such as fragmentation, adventitious buds, embryonic leaf apices, stem tubers, root tubers etc.

Spore production:

Pterospsida are both homosporous and heterosporous (marsilea). Spore producing organs are varied. They may be fertile spikes (ophioglossum), tassels (osmunda), sori (adiantum, pteris etc.) Or sporocorps (marsilea). Spore producing organs are usually borne on the leaves except in some species of marsilea.

Whatever may be the name given to the spore producing organs they always represent aggregations of sporangia. The sporangia within a sorus are numerous arising from a fertile tissue called receptacle. The sporangia may or may not be surrounded by a flap or tissue (arising from the receptacle) called inducium.

Sometimes a sorus is protected by a false inducium which represents the incurving of the leaf margin. The maturity of sporangia within a sorus is varied. Based on this, the son are classified into three types viz., (i) simple, (ii) gradate arid (iii) mixed. In a simple sorus all sporangia develop simultaneously (eg. Osmunda).

In a gradate sorus sporangia develop in basipetalous succession (e.g. Hymenophyllum) and in a mixed sorus sporangia develop in an irregular sequence (eg. Pteris). It has been widely held that a simple sorus is primitive, a mixed sorus is advanced while a gradate sorus is of the intermediate type.

Sporangia may or may not have a stalk (ophioglossum). Their development is either of the eusporangiate type or of the leptosporangiate type. The capsule region of the sporangium encloses the spores. Except in primitive members such as ophioglossum and angiopteris, the sporangium has a definite dehiscence mechanism brought about by cells of different thickness and differential hygroscopic reaction.

The thick walled cells are called annulus and the thin walled cells are called the stomiuim. The annulus may be shield shaped (osmunda), cap like (lygodium) or obliquely vertical incompletely overarching the sporangium (pteris, adiantum etc.). Spores are wind dessiminated and have a sculptured outer wall (exine) enclosing a thin inner wall (intine).

Gametophyte of pteropsida (ferns):

In homosporous forms the gametophytes are exosporic and in heterosporous forms they are endosporic. Endosporic gametophytes are extremely reduced.

Bower (1923, 1935) has recognised three types of prothalli in homosporous ferns. These are:

(a) Cordate type,

(b) Filamentous type and

(c) Saprophytic type or the mycorhyzic type.

Cordate or heart shaped prothalli are autotrophic and are seen in adiantum, osmunda, pteris etc. The filamentous type is seen in hymenophyllum. The nutrition here also is autotrophic.

Mycorrhizic prothalli are common in members like ophioglossum. These prothalli are tuberous or cylindrical and have a radial symmetry as opposed to the bilateral symmetry of the cordate and the filamentous types. Nutrition is saprophytic.

Reproduction:

Gametophytes reproduce vegetatively as well as sexually. The former type of reproduction is very rare. Sexual reproduction is brought about by antheridia and archegonia which have undergone maximum possible simplification.

Embryogeny may be exoscopic (ophioglossum) or endoscropic with (helminthostachys) or without (angiopteris) a suspensor. In leptosporangiate ferns embroyogeny is said to be lateral because the first division is vertical and does not produce epibasal and hypo basal cells.

Classification of pteropsida (ferns):

The types of classification proposed for ferns are as varied as ferns themselves. Below is given a few systems of classification.

Hirmer (1927) classified fillicophyta into four classes viz.:

(a) Primoftlicopsida,

(b) Eusporangiatae,

(c) Protoleptosporangiatae and

(d) Leptosporangiatae.

Hirmer created protoleptosporangiatae specially to include osmundaceae which exhibits intermediate characters between eusporangiatae and leptosporangiatae.

Pichi-Sermolli (1959) has sub divided filicopsida (pteropsida) into seven sub-classes, viz., primofilicidae, ophiglossidae, marattidae, osmundiade, filicidae, marsilidae and salvinidae.

In this article the classification proposed by Reimers (1954) is followed.

Primofili copsida:
Coenopteridales:

The order coenoptaridales comprises only fossil members belonging to the late paleozoic ara. The fossil remains of the plants of this order include stems and frond parts which are very well preserved structurally. The members represent the fossil ferns.

The order coenopteridales has many alternative names like palaeopteridales, primofilicales and renaultificales. The last mentioned name is in honour of the great french paleobotanist renault. The order comprises a heterogenous assemblage of various ferns and has been treated differently by different paleobotanists.

However, there seems to be general agreement in classifying the order into three families namely, botryopteridacease, zygopteridaceae and cladoxylaceae. Burtrand divided the order into two subgroups namely inversicatenales and phyllophorales. The group inversicatenales includes the family botryopteridaceae while phyllophorales has two families namely, zygopteridaceae and cladoxylaceae.

In this article botryopteris (botryopteridaceae) and zygopteris (zygopteridaceae) are discussed:

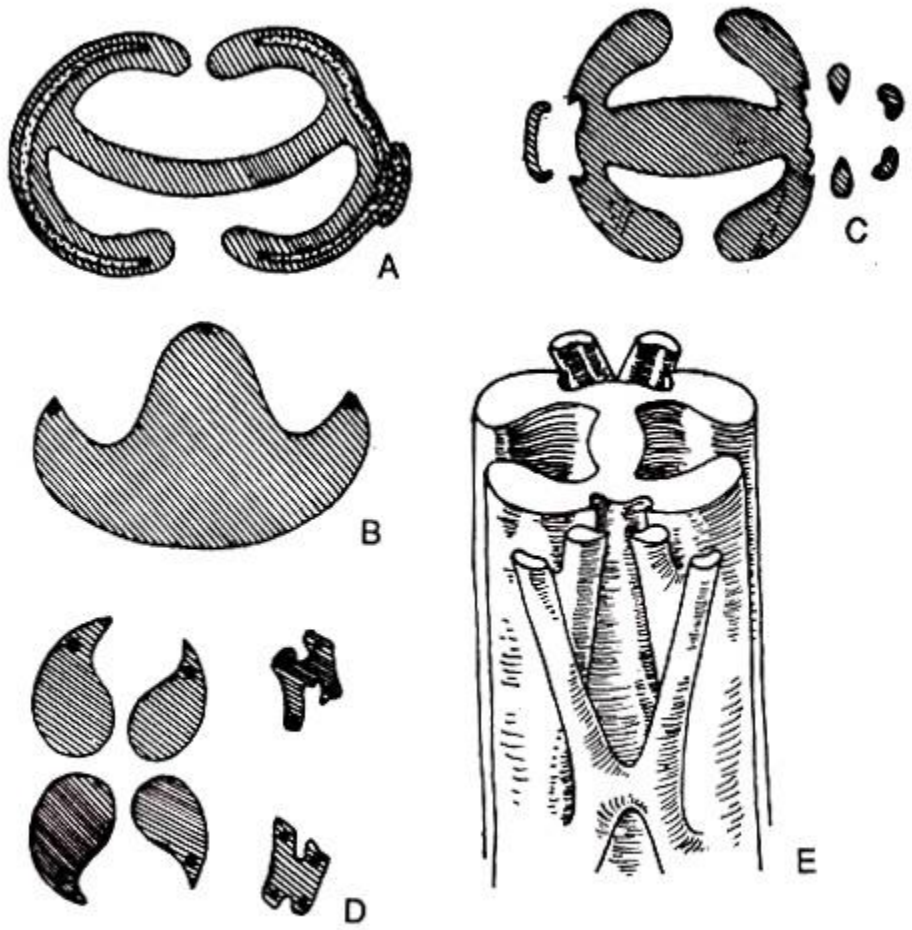


Fig. 113. *Coenopteridales* : Stereodiagram of Steles
A. *Ankyropteris*, B. *Botryopteris*, C. *Stauropteris*, D-E. *Etapteris*

Botryopteris:

The genus botryopteris is one of the best known among coenopteridales. It is the type genus of the family and has 5 species ranging from lower carboniferous to the permian. The name botryopteris is given to the fossil specimens of stem.

The stems are slender, cylindrical and few millimeters in diameter. They are branched and bear spirally arranged fronds. Anatomically, the main stem has a small mesarch protostele, which is surrounded by a broad cortex. The cortex has a prominent band of sclerotic cells. (fig. 114).

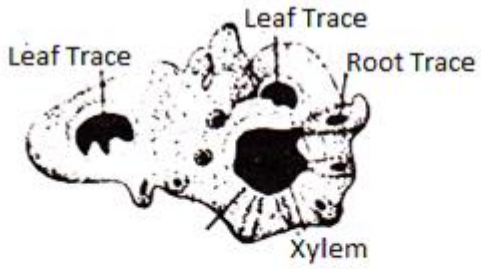


Fig. 114. *Coenopteridales* : Diagrammatic Transverse Section of *Botryopteris ramosa*

In the leaf stalk, the xylem strand is solid and has three prototoxylem points. As in b.forensis the strand is deeply indented looking like a trident. In very few species of botryopteris, sporangia have been found attached to the fronds.

The sporangia are found in clusters which is somewhat rare to ferns. In b. Globosa sporangial cluster has thousands of sporangia. The sporangia themselves are small, oval to pyriform in shape.

They measure 2 mm in length and about 1 mm in diameter. Each sporangium has a short stalk and a capsule which is somewhat oval in outline. The wall of the capsule has a broad annulus represented by thick walled cells. The spores are of the same type.

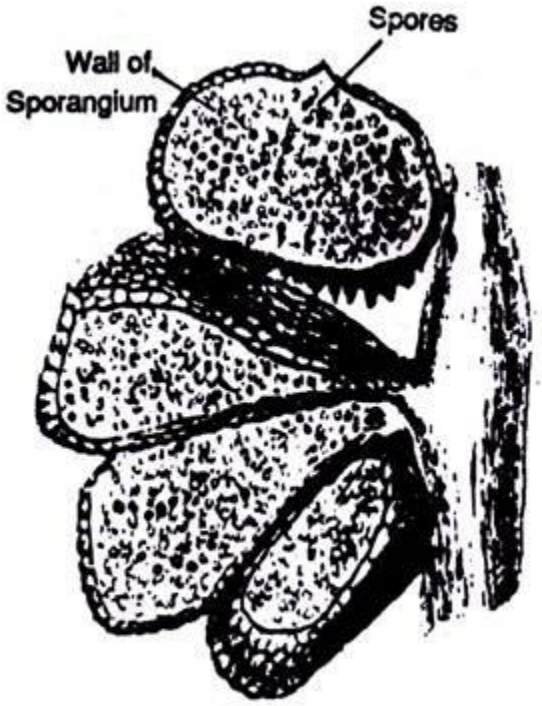


Fig. 115. *Coenopteridales* : Sporangia of *Botrypteris* (sectional view)

Zygopteris:

The ferns belonging to the family zygopteridaceae are more complex and older then botryopteridaceae. The fossil specimens belong to middle devonian and possibly have connection with psilophytales. Zygopteris, the type genus of the family is the best known.

It has several species of which z. Primaria has been studied extensively. The plant body of zygopteris is tree like with a trunk having a diameter of 20 cm. The stem as such, however is only about 1.5 cm in diameter, the rest of the diameter being made up of an armour of leaf stalks and adventitious roots.

The stem of zygopteris bears an elaborately branched frond having a number of leaf stalks. These are usually cylindrical and up to 2 cm in diameter. The leaf stalks have a number of pinnae. Occasionally the leaf stalks are given the name etapteris.

Anatomically the stem of zygopteris has a xylem cylinder consisting of scalariform tracheids. An unusual feature here is the presence of a layer of secondary wood surrounding the primary xylem. This is perhaps one of the rare instances of secondary vascular tissue in a fern extinct or extant.

The leaf stalk internally shows a vascular strand which is h-shaped with a straight median band with some what fixed lateral arms. Two small protoxylem points lie in the shallow depressions at the end of the median band.

Various names have been given to the fructifications of zygopteris. Corynopteris is one such fructification genus. The sporangia in the fructification are large and ovate. They are usually sessile and are grouped into spherical son. The wall of the sporangium has a broad band like annulus. The sporangial cavity is filled with homosporous spores.

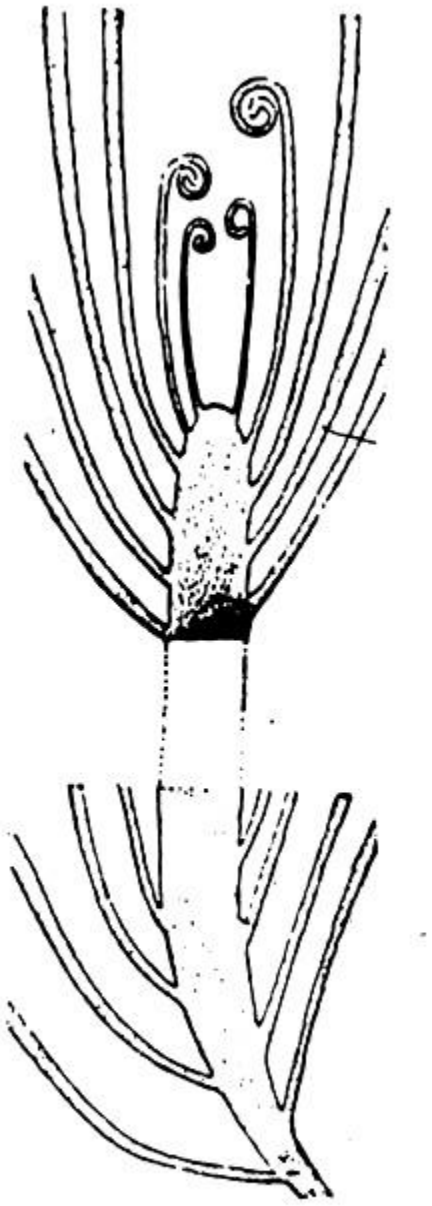


Fig. 116. *Coenopteridales* : Reconstruction of Upper and Lower Portions of Shoots of *Zygopteris primaria* (after Sahni 1933)

Phylogeny of pteropsida (ferns):

The coenopteridales represent the most primitive group among the ferns. They are very ancient having originated perhaps, with psilophytales. One of the prominent features of coenopterids is the lack of distinction between stem and leaves.

According to Delevoryas (1962) this suggests their affinity with psilophytales. The relationship of coenopterids to other ferns is rather obscure. But there is no doubt in the fact that coenopterids may be regarded as ancestral stock from which the modem ferns sprung up.

Eusporantgiatae:

This sub-class includes all eusporangiate ferns. The sporangial wall is more than one layered. Spore output is very high.

There are two orders in this sub-class viz., ophioglossales and marattiales.

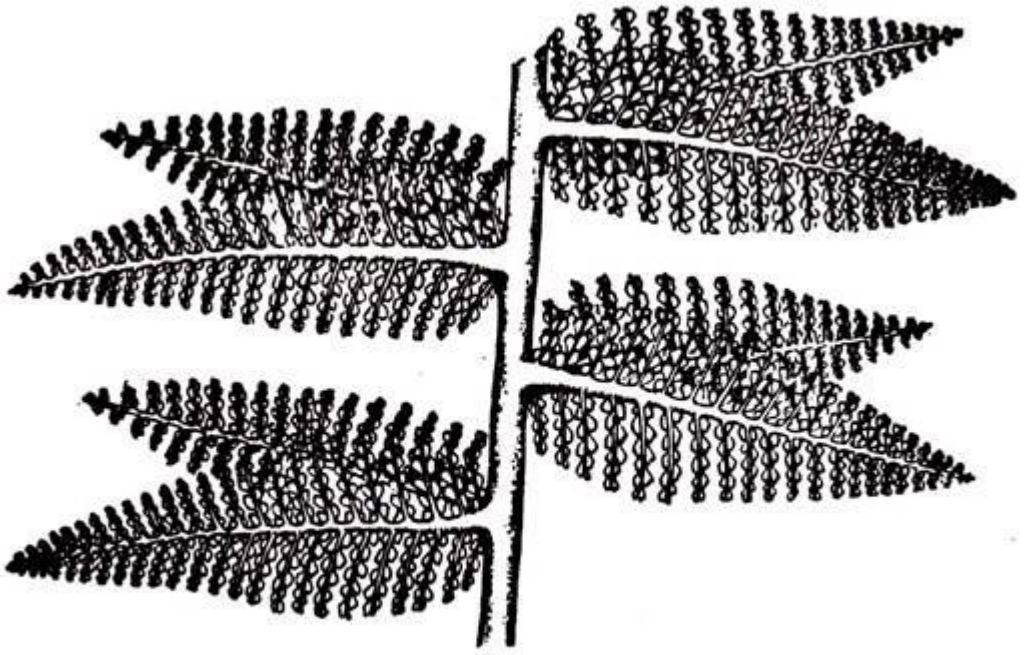


Fig. 117. *Coenopteridales* : Reconstruction of leaves of *Etapteris* (leaves of *Zygopteris*)

Ophioglossales:

The order includes herbaceous, fleshy sporophytes with a short rhizome. Sporangia are borne on a separate outgrowth called ‘fertile spike’. This arises at the junction of the leaf blade and lamina. Sporangia have a multilayered wall with a high spore output.

There is no special dehiscence mechanism. All the members of the order are homosporous. Gametophytes are tuberous and saprophytic. The order has a single family ophioglassoceae, with three genera- ophioglossum, botrychium and llelminlhoslachys.

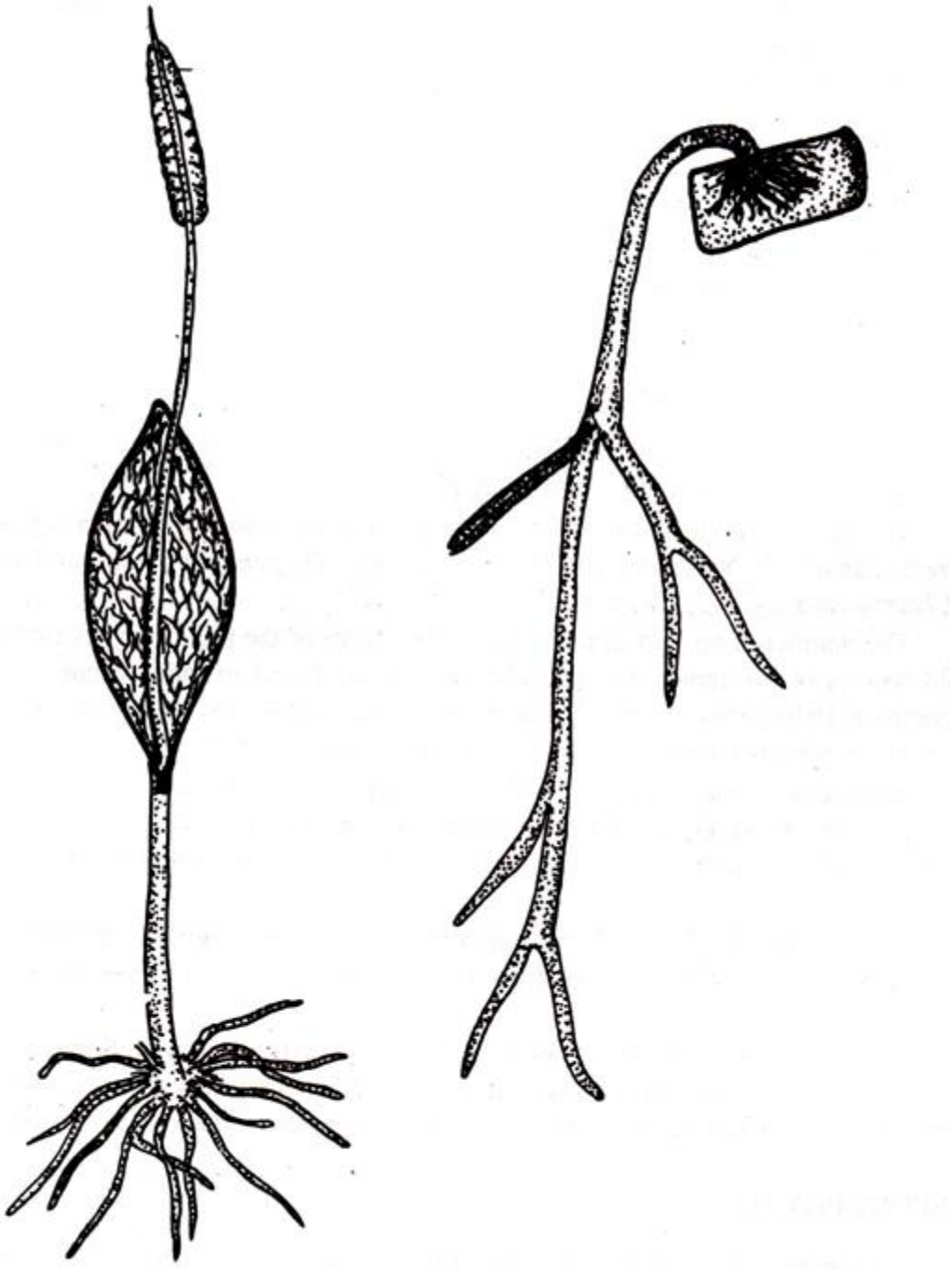


Fig. 118. *Ophioglossum* : Habit of *O. vulgatum* (left) and *O. palmatum* (right)

Unit : V Techniques of paleobotany

A general account on geological time scale:

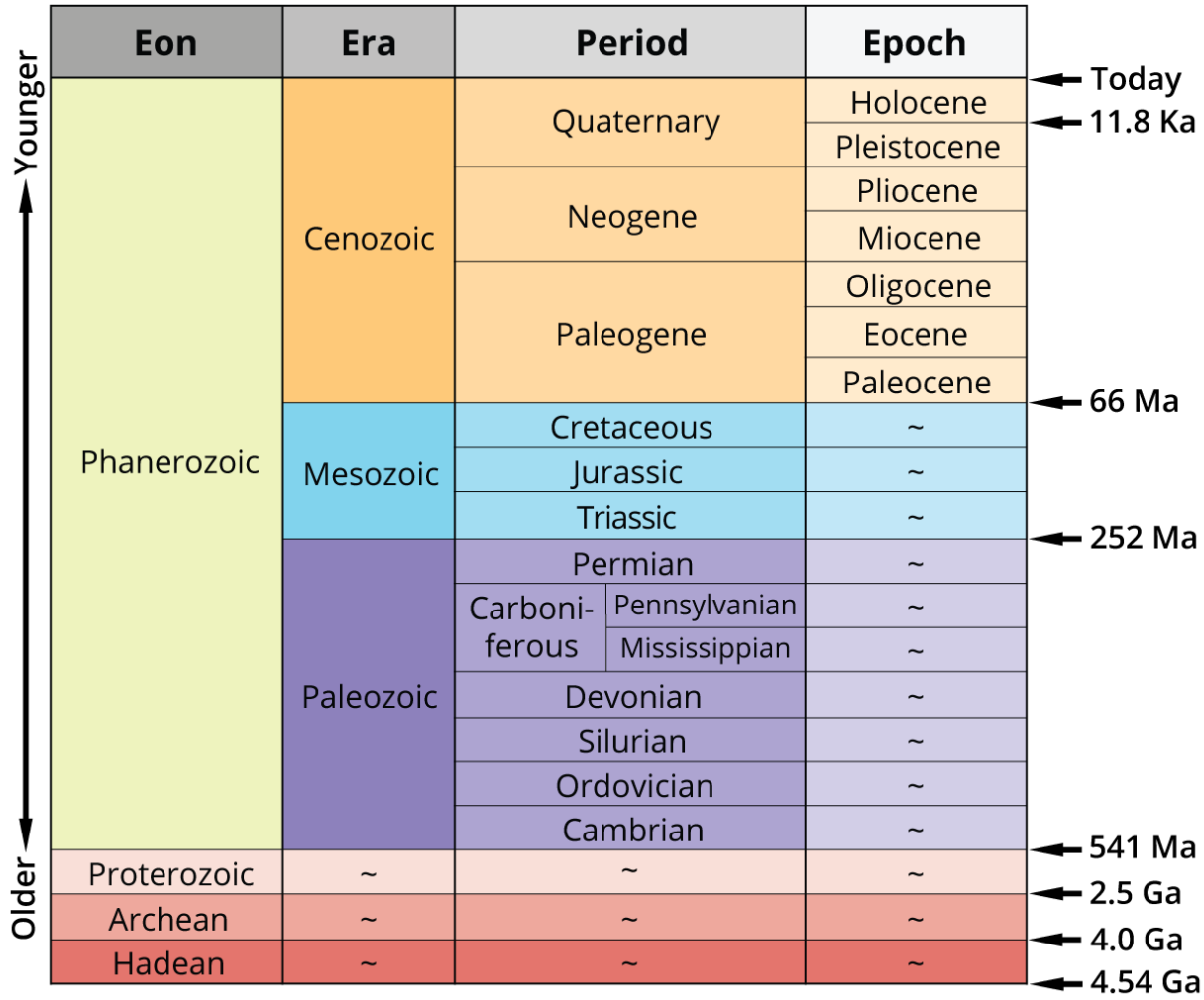
Geological time scale is a record of earth's history based on the organisms that lived at different times.

The geological time scale is a system of chronological measurement that related stratigraphy (the study of rock strata, especially the distribution, deposition and age of sedimentary rocks) to time, and is used by the geologists, paleontologists and other earth scientists to describe the time and relationship between the events that have occurred throughout earth's history.

The first geological time scale was proposed in 1913 by the British geologist Arthur Holmes (1890-1965). This was soon after the discovery of the radioactivity and using it Holmes estimated that the earth was about 4 billion years old (evidence from radioactive dating indicates that earth is about 4.5 million years old). This was much greater than previously believed.

The geological time scale is divided into five main eras: coenozoic, mesozoic, paleozoic, proterozoic and archezoic. Each era is divided into periods and each period is divided into epochs.

It is as follows:



Techniques for paleobotanical study:

Type 1. Petrification:

Petrification is the best but perhaps the rarest type of fossilisation. This literally means transformation of the organic tissues into stone. Although the actual process of petrification is not very well understood, it is clear that no ‘molecule by molecule’ replacement of the organic, molecules by mineral molecules takes place.

The buried plant material absorbs mineral solutions like silicates, carbonates, sulphates, phosphates, etc., and infiltration followed by precipitation takes place so that silica, calcium carbonate, magnesium carbonate, iron sulphide, etc., get impregnated within the tissues. Most of the organic material may get destroyed but at least some original cell wall compounds often remain.

The whole structure becomes stone like so that fine sections may be obtained by stone sectioning methods and exact tissue structures (fig. 504) may be observed under the microscope. Anatomical structures of ancient plants are beautifully obtained from such petrifications.

Petrifications are usually bits of stems, twigs, seeds, sporangia, etc. Silicified bits of wood are often found. Calcified fossils are also known. The best examples are, however, the coal balls. Goal balls (figs. 504 & 505) are irregularly rounded masses ranging in diameter from a few millimetres to a metre.

These occur often in great numbers within chunks of coal. Each ball is a mass of calcium and magnesium carbonate with, sometimes, iron sulphide. These show petrified remains of a great number of plant fragments representing the debris of those days. Even delicate parts remain intact in the coal balls so that the anatomy as well as the morphology is clear.

Type 2. Cast or incrustation:

One of the commonest types of fossils is the cast or incrustation. In the formation of this, the plant part gets covered up by sand or mud. In course of time the plant material inside rots away leaving a hollow. This cavity, a-gain, gets filled up by some rock forming material.

In course of time the inside as well as the outside solidifies into stone from which the external part may be peeled off leaving an exact cast of the plant material showing all its surface features.

The casts are as correct as one may obtain from clay or plaster or paris moulds today. Figure 506 shows a cast fossil of an ancient lycopod stump. Internal casts of pith cavities may also be preserved in the same way (fig. 507). A cast fossil does not actually contain any part of the original plant.

Type 3. Impression:
A leaf or any organic part falling on semi-stiff clay easily leaves an impression on its surface. In course of time this impression becomes permanent when the clay turns into stone. Such impressions are often very clear showing full details of venation, etc. (fig. 508).

The impression is often of a darker colour than the surface of the rock below because it very often retains some of the organic material. Some specimens are extremely beautiful looking like paintings or base-relief of the actual twigs. In some well-preserved material at least the skin or the epidermis remains intact so that structures like stomata are clearly seen in good preparations.

Type 4. Compression:
Compression is only a degree of impression when the organic remain of the plant part actually remains in the fossil but is highly compressed. The great pressure under which fossilisation takes place flattens out all round or solid organs so that what remains in the fossil is usually a carbonaceous film.

But, in good compressions it has been possible to swell out the organ by some chemical treatments so that some details become visible. A good type of compression fossil is the clay nodule. In this the plant material gets encased in a ball of clay, gets compressed and the clay ball turns into stone.

Type 5. Rocks, minerals, etc. Of organic origin:
Any object which might have connection with ancient organisms is considered as a fossil. A stone showing a footprint of an animal or a trail of a worm is a fossil. Gums of ancient resinous, coniferous trees are found in fossilised forms as amber which is of great commercial value. Amber sometimes encloses beautiful fossils of flowers or insects. Coal is nothing but a highly compressed fossil derived from primeval forests.

Diatomaceous earth is formed of skeletons of billions of diatoms depositing on the sea bed. Even petroleum may be considered as a fossil as organisms are responsible for its formation. Graphite used in lead pencils is a fossil in the same sense as this type of carbon is supposed to be of organic origin.

There are different types of algal limestone's (fig. 510) in the formation of which specific algae took part. All such minerals are to be considered as fossils.

On the other hand, it should also be noted that sometimes certain minerals, etc., during their formation or crystallisation resembles some plants (e.g., algae) or animals. There are instances of these being considered wrongly as fossils. Such structures have been termed as pseudofossils.

Contribution of Birbal Sahni:

Sahni worked on living plants species including *nephrolepsis*, *niphobolus*, *taxus*, *psilotum*, *tmesipteris* and *acm opyle* examining evolutionary trends and geographical distributions. His ability to apply theory to observations and make hypotheses based on observations were especially influential on his students. When examining wood remains from harappa, he noted that they were of conifers and inferred that the people there must have had trade links with people in mountains where conifers could grow.[13] He recorded foreign pollen in the ovules of living *ginkgo biloba* and noted in the *new phytologist* (1915), the problem with assuming that fossil pollen in ovules belonged to a single species. Sahni was among the first to suggest a separate order, the taxales, within the conifers to contain the

genera *taxus*, *torreya* and *cephalotaxus*.[14] another major contribution was in the studies on the morphology of the zygopteridaceae.[15] sahni identified *torreyites*, a close relative of *torreya*, which extended the range of the taxales into gondwanaland. He also described glossopteris in detail and identified differences between the flora of india and australia with that of china and sumatra. He also studied the fossil plants of the deccan intertrappean beds. He suggested that the lower narmada area around nagpur and chhindwara was coastal on the basis of fossils that showed a similarity to estuarine palms of the genus *nipa*.[16] Based on the ecology of plants and the altitude of the fossil finds, he also attempted to estimate rates of uplift of the himalayas.

Cordaites:

Tribution of cordaitales:

Cordaitales, an extinct group of palaeozoic tall trees of gymnosperms, formed **"the world's first great forests"**. The name was given to honour an Australian botanist, a.j. Corda. Majority of the cordaitales were tall, large-leaved trees attaining a height of more than 30 metres or so.
The group started declining during permian and became completely extinct by the end of this period. As per records the cordaitales occurred side by side with pteridospermales

Cordaitales fossils have been reported from North and South America, Europe, China, Russia, India, Australia and Africa indicating their world-wide occurrence during Devonian and Permian.

Cordaitales in India are represented in the form of impressions or compressions of leaves, seeds and petrified woods. Representatives of the only family cordaitaceae have been reported from India.

No member of poroxylaceae has been reported. In India, cordaitaceae are represented in lower Gondwana formations. Cordaicarpus,

dodoxylon, noeggerathiopsis and samaropsis are the cordaitalean genera reported from India.

Distinguishing features of cordaitales:

1. This group of fossil plants had tall trees with slender trunks and a crown of several well- developed branches.

2. Plants were present from devonian to permian periods of palaeozoic era

3. The leaves were simple, spirally arranged and strap-shaped, grass-like or paddel-like.

4. The leaves attained a length up to 1 metre or even more, and had parallel venation.

5. A scanty primary wood was present.

6. In mature stems, the secondary wood was mostly pycnoxylic.

7. Compound unisexual cones were present.

8. Each compound cone had a main axis with bracts subtending secondary fertile shoots possessing fertile and sterile appendages.

9. Mega-strobili had sterile appendages below and ovule-bearing fertile appendages above.

10. One to four ovules were present on each female fertile appendage.

11. Micro-strobili had sterile appendages below and pollen-sac containing fertile appendages above.

12. Four to six terminal pollen sacs were present on each male fertile appendage.

13. Sperms have not been reported, but presence of pollen chambers suggests that motile sperms might have been formed.

Classification of cordaitales:

Scott (1923) divided cordaitales into following three families:

1. Cordaiteae, e.g. Cordaites, mesoxylon, etc.

2. Poroxyleae, e.g. Poroxylon.

3. Pityeae, e.g. Pitys, callixylon, dadoxylon.

Chamberlain (1935) named the three families as poroxylaceae, pityaceae and cordaitaceae.

Sporne (1965) classified cordaitales into following two families:

1. Cordaitaceae, e.g., cordaites (leaves), mesoxylon (stems), amyelon (roots), cordaianthus (cones), cordiocarpus (seeds).

2. Poroxylaceae, e.g. Poroxylon (stems), rhabdospermum (seeds).

Chamberlain's classification has been followed in the text.

A brief discussion of cordaitaceae and poroxylaceae is under mentioned:

1. **Cordaitaceae:**

External morphology:

Cordaitaceae grew luxunently and formed large forests of tall trees during upper carboniferous period. Plants attained a height of more than

30 metres. They had terminal and spirally arranged well-spread branches bearing tufts of leaves (fig. 9.1).

The leaves were large, leathery, grass-like or paddle-shaped, and attained a length of about 1 metre and a breadth of about 15 cm (fig. 9.2). They were, however, smaller than that of cycads. Some members also had small needlelike leaves. The leaves had a dichotomous venation.

Fig. 9.1. *Eu-Cordaites* Reconstruction of a plant (after Grand's Eury).

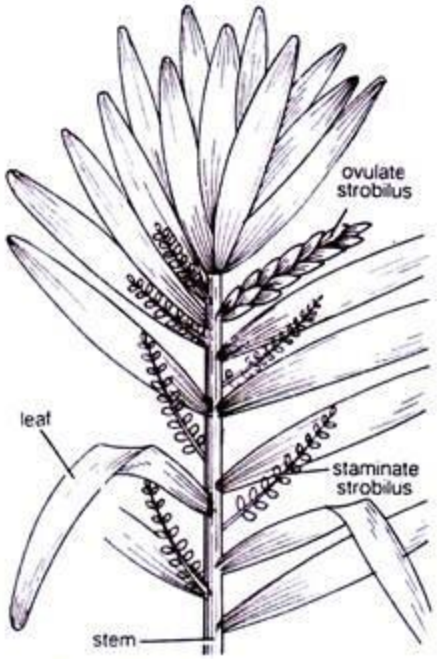


Fig. 9.2. *Eu-Cordaites laevis*. Reconstruction of a branch

The leaves of several members of cordaitaceae were highly variable in shape and were put under a form-genus cordaites. The same name is now given to the stem as well as to the entire plant.

Some other stem-genera of cordaitaceae include mesoxylon, metacordaites, parapitys, caenoxylon, mesopitys, cordaicladus and artisia. Amyelon is a root-genus while cordaianthus is a name give to the cones or inflorescence. Seeds have been described under the form-genera cardiocarpus, mitrospermum and kamaraspermum.

Cridland (1964) studied and reconstructed a cordaitean plant. According to him the plants attained a height of nearly 5 metre with stilt roots similar to mangrove plants. These studies suggest the habitat of cordaites in the swamps along the seashores.

Anatomy of cordaitaceae:

1. Stem:

The stem (fig. 9.3) resembled closely with conifers. Both cordaites and mesoxylon possessed a large central pith and cortex. The wood was scanty in some species while in others it developed a large vascular

cylinder, and in still other cases distinct growth rings were present. The primary wood was endarch but in mesoxylon it was mesarch. The secondary wood consisted of pitted tracheids having multiseriate pittings.

The tracheids were long and slender. Bordered pits were present, and they were confined mainly on the radial walls. In older tracheids, however, the pits were also present on the tangential walls. Medullary rays were one or two cells wide. The bordered tracheids were hexagonal in outline (fig. 9.4) and the large pith was characteristically discoid (fig. 9.5).

Mesoxylon differed from cordaites in the structure of the leaf trace. A network of sclerenchyma, present in the outer cortex of mesoxylon, was absent in cordaites. Since, technically speaking, the genus cordaites refers to the leaves of cordaitaceae, an alternative name cordaioxylon was proposed by Arnold (1967).

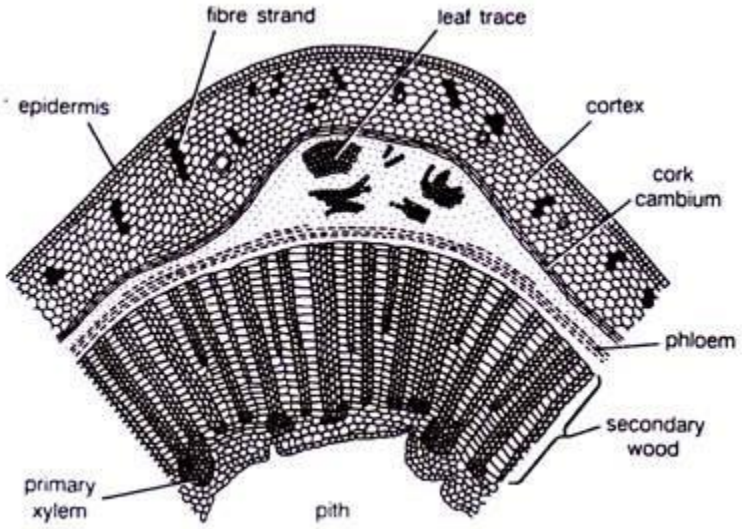


Fig. 9.3. *Cordaites*. Diagrammatic representation of a part of T.S. stem.

Root:

The roots of cordaitales are known as amyelon (fig. 9.6) and resembled very much with the modern conifers. Cridland (1964) studied the root

system of amyelon and found it to be shallow and highly branched forming stilt roots supporting the stem. They were diarch or triarch in structure. Ectotrophic mycorrhizal fungi were present on the roots.

The protoxylem had spiral tracheids while the metaxylem was scalariform in structure. Tracheids had multiseriate bordered pits. The cortex was quite large and divisible into outer and inner cortex. The secondary cortex and cambium were also quite distinct.

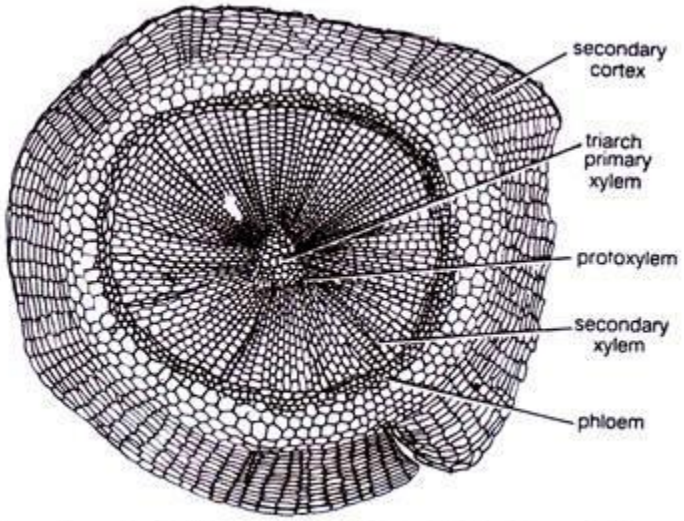


Fig. 9.6. *Amyelon radicans* (probable root of Cordaitales). (after Scott, 1923).

3. Leaf:

The cordaitalean leaf is described under the name cordaites. Several xerophytic internal characters were present in the leaf. The epidermal and hypodermal cells were thick-walled, and the hypodermal cells on both sides were grouped into ribs. Several mesarch vascular bundles were present.

Each vascular bundle was surrounded by a thick-walled strong bundle sheath. The transfusion tissue was present in the form of some elongated cells in between two vascular bundles (fig. 9.7). The mesophyll was clearly differentiated into palisade and spongy parenchyma in species such as cordaites lingulatus (fig. 9.8).

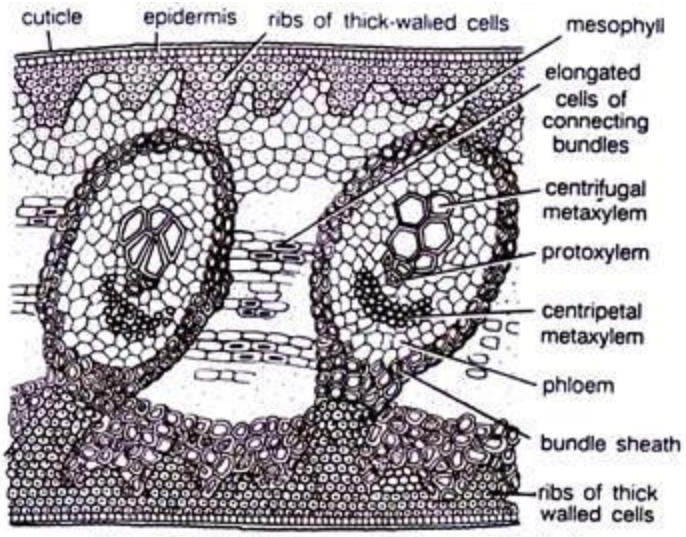


Fig. 9.7. *Cordaites angulostriatus*. T.S. leaf.

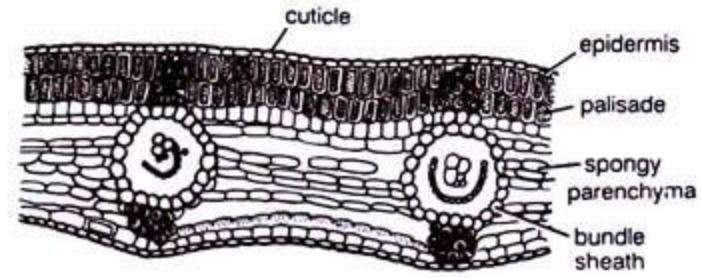


Fig. 9.8. *Cordaites lingulatus*. T.S. leaf.

Spore-producing organs:

The strobili were usually monoecious but some cordaitales were also dioecious. They were, however, never bisporangiate. The fructifications were borne on slender branches of about 10 cm length. These branches developed on the stem among the leaves. The slender stalk had many stiff but tapering bracts.

A short bud-like strobilus was present within the axil of each bract. The bracts were probably spirally arranged. Each strobilus attained a length of about 1 cm. Both male and female reproductive organs are known as cordaianthus, but according to Fry (1955) cordaianthus is the new name of the reproductive organs or cones of cordaitaceae.

1. Male strobilus:

It consisted of a thick central axis possessing many spirally arranged bracts and some microsporophyll's. At the tip of each microsporophyll

were present 1-4 microsporangia (fig. 9.9). These sporangia probably dehisced longitudinally. Three well-studied forms of male strobilus include cordaianthus concinnus, c. Penjonii (fig. 9.9) and c. Saportanus.

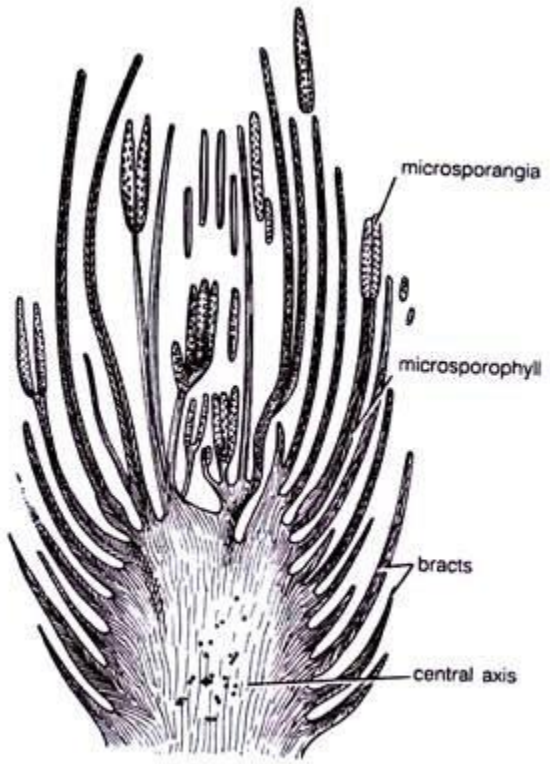


Fig. 9.9. *Cordaianthus penjonii*. L.S. male strobilus.

The microsporangium wall was probably only one-celled thick and enclosed many microspores. Taylor and Taylor (1987) studied the structure of pollen grains of cordaitales. According to them the grains may be alete or range from monolete to trilete.

They are mono-saccate with saccus attached on both distal and proximal poles. Different interpretations of male reproductive organs of cordaites have been given by- Renault (1889), Florin (1951) and Taylor (1973).

2. Female strobilus:

Similar to male strobilus, the female strobilus also had a stout axis bearing a large number of spirally arranged bracts. The bracts were more in number than that of male strobilus. Cordaianthus pseudofluitans possessed a few elongated and dichotomously branched fertile

megasporophylls (fig. 9.10). Two or more ovules were present at the apex of each megasporophyll.

Lepidocarpon:

Lepidocarpon is known only from its strobilus it has been widely held that it could have been borne on a lepidophlois type of stem. The fossils of lepidocarpon have been obtained from the coal strata in England and U.S.A.

The strobili were mososporangiate though the plant was heterosporous. The microsporophyll's were like those of lepidostrobus. Each microsporophyll was peltate and had an elongate microsporangium. The megasporophylls bore elongate microsporangia on their adaxial surface.

The jacket of the mega-sporangium extended at the apex to form a projection. The sporangium was enveloped by the flaps of a tissue which is termed as integument (fig.57). But it is doubtful how far this terminology is appropriate. Because in reality this inegument is nothing but an upturning of the megasporophyll though many people believe it to be a special outgrowth artising from the megasporophyll.

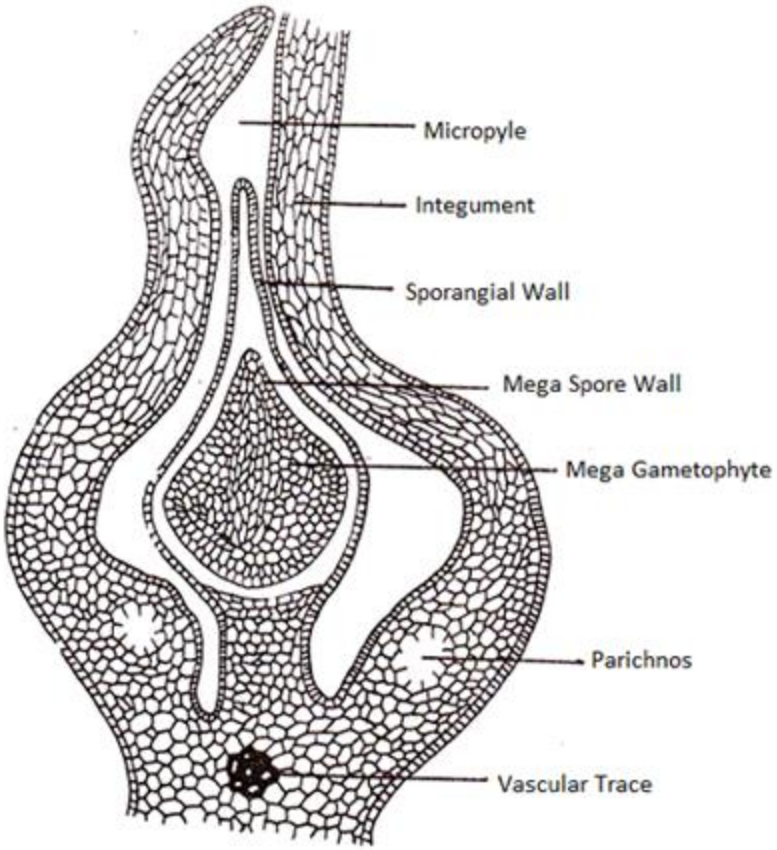


Fig. 57. *Lepidocarpon* : L.S. of Seed (diagrammatic)

There were four spores in a sporangium of which only one developed into the female gametophyte. The size of the gametophyte and the fact as to whether it completely or incompletely filled the sporangium are specific characters. Andrews and Pannel (1941) have reported several fertile mega-gametophytes with archegonia at the apex.

The mega-sporangial cavity also showed many spores of which at least some of them were the microspores of lepidocarpon. This suggests that lepidocarpon had something like an incipient pollination which is also seen in the extant genus selaginella.

The one unique feature of lepidocarpon which is not seen in any lycopods extinct or extant was the permanent retention of the mega-gametophyte within the sporangium thus marking a significant step towards the evolution of seed habit.

The megasporophylls were, ultimately liberated and on falling upon a suitable substratum the embryo developed into the sporophyte. It will be very interesting to analyse whether lepidocarpon could be regarded as having attained a seed habit.

Most of the attributes of lepidocarpon – an integument, a permanent retention of the female gametophyte, development of only one spore in the mega-sporangium, incipient pollination, all point out towards the seed like habit.

But a closer scrutiny reveals that all the seed like features are only superficial, for, the so called integument is a part of the megasporophyll and not of the mega-sporangium. Further there is no formation of pollen tube, no seed coat and in all probability the embryo did not have dormancy characteristic of true spermatophytes.

All these clearly show that though lepidocarpaceae apparently possessed the attributes of a seed-habit (particularly in the permanent retention of the female gametophyte but the additional features to support such a retention were not sufficient) it did not reach the level of a seed habit and hence it could at best be regarded as a pseudo-spermatophyte.

Lyginopteris:

Stematic position of lyginopteris:

Gymnosperms

Class. Cycadopsida

Order. Pteridospermales

Family. Lyginopteridaceae

Genus. Lyginopteris

(calymatotheca)

The genus lyginopteris also known as lyginodendron.

Features of lyginopteris:

1. **Morphological features:**

The stem lyginopteris was slender and covered with large scaly leaves. Near the base of the plant adventitious roots developed. The plant seems to have been a climber.

Lyginopteris oldhamia also known as calymatotheca hoeninghausi was described in detail by Williamson, Scott, Brongniart, Binney, Potonie, and Oliver and Scott. It was found abundantly in the coal ball horizon of lancashire and yorkshire.

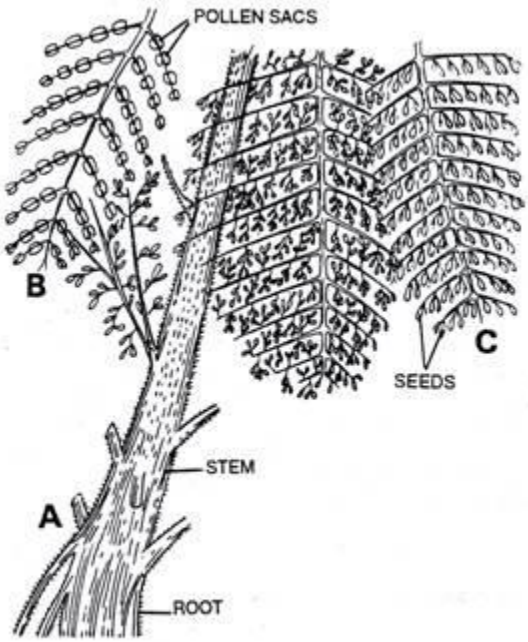


Fig. 2.2. *Lyginopteris oldhamia.* Restoration showing external characters. The frond on the left bears the pollen sacs on peltate leaflets (*Crossotheca*); that on the right bears seeds. Stem and roots also present.

2. **Anatomical features:**

The primary structure was an ectophloic siphonostele with large pith round a number of primary mesarch bundles. Older plants showed

normal secondary growth. In some specimens, however, the xylem portion of primary vascular bundles was in a continuous ring. In some there was an abnormal type of secondary growth.

This abnormality was of two forms, either there was an inner ring of secondary phloem developed or it was that the cambium appeared in strips found separately in vascular bundles giving rise to a polystelic appearance.

Fig. 2.3. *Lyginopteris oldhamia.* A frond.

Reproductive structure of lyginopteris:

Some of these palaeozoic leaves bore microsporangia on them. The fertile pinnules were more or less peltate in form and on their underside they bore usually six sporangia. These sporangia are usually bilocular. Such a type has been described as crossotheca type.

Ut 1/4 but they were highly organized. It was barrel shaped and whole seed enclosed in cupule. This cupule opened out when seed was mature.

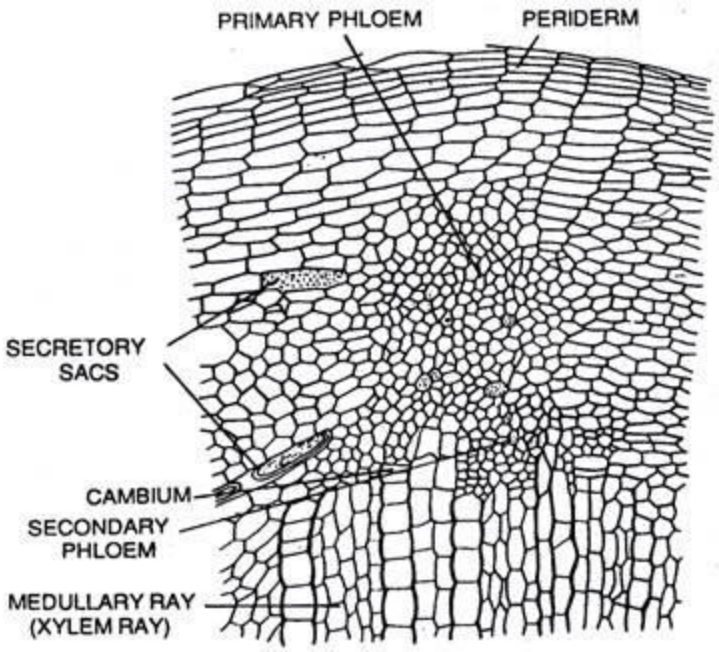


Fig. 2.6. *Lyginopteris oldhamia.* A part of T.S. stem showing the outer portion of the stele.

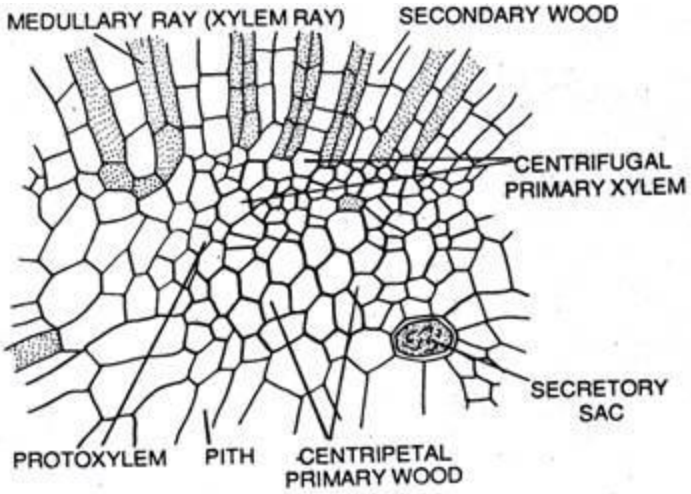


Fig. 2.7. *Lyginopteris oldhamia.* A part of T.S. of stem primary and secondary xylem, medullary rays and pith

Each seed was borne at the tip of stalk. The cupule rose from the base of the seed but not fused with it. The cupule was in three main lobes. These lobes were divided in the upper parts of the seeds. The seed or ovule was orthrotropus and of cycadian type. It was radially symmetrical.

Sphenophyllum:

Sphenophyllales represent a small and compact group of sphenopsida. They have left no surviving representatives. The geological history of sphenophyllales dates back to a time earlier than carboniferous period.

Some of the genera like sphenophyllum appeared during devonian reaching maximum development during carboniferous period. A few of these sphenophyllales survived upto triassic.

The principal genus of the order is sphenophyllum. The compressed fossils of the plant body have been found extensively scattered in coal bearing formations belonging to the carboniferous period. The plant body of sphenophyllum was small and herbaceous. There is a high probability that the plant had a climbing habit. While, some of the morphological features indicate an aquatic habitat, anatomical features however, point out to a terrestrial habitat.

The plant body consisted of a main stem, which was slender and jointed, rarely exceeding 5 mm in diameter. In its externals the stem recalls what is seen in equisetum. The stem was ribbed which did not alternate at nodes.

Leaves which are so typical of sphenophyllum were present in clusters at the nodal regions. At each whorl the number of leaves ranged from 6 to 9. Occasionally the number went upto 18. The leaves were cuneate and the apex variously modified. In s. Emarginatum, the leaf apex had rounded teeth, while they were pointed in s. Cunifolium and s. Majus. The leaves had veins with dichotomous branching, each branch terminating in an apical tooth.

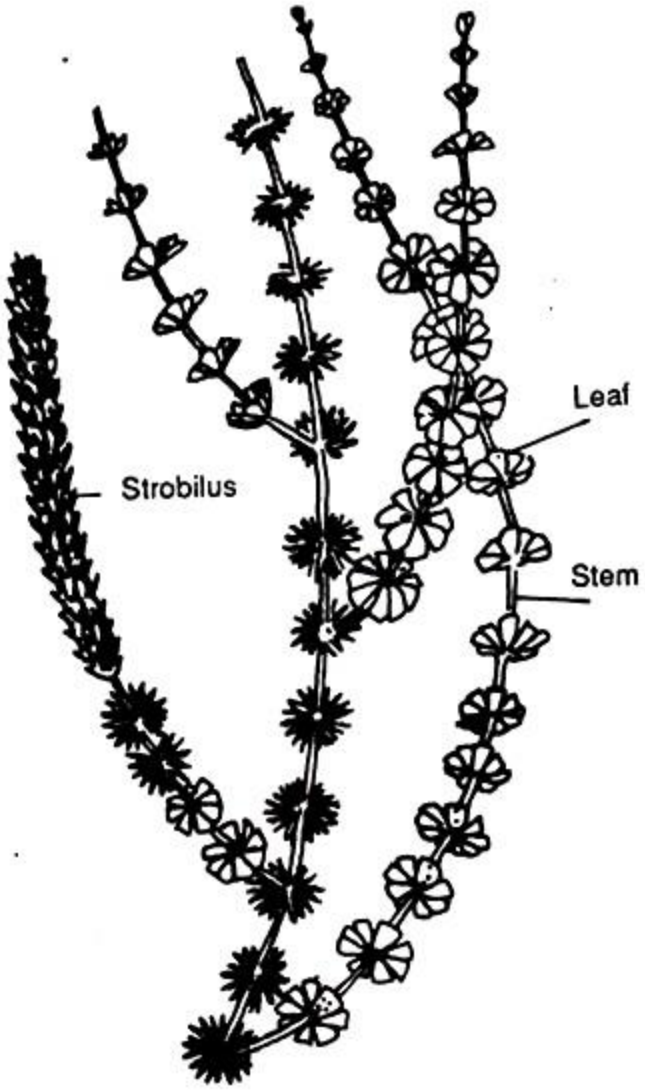


Fig. 91. *Sphenophyllum* : Plant Body of *S. cuneifolium* (Reconstruction)

Anatomy of sphenophylum:

Anatomically the stem showed the occurrence of secondary growth. In some of the details of stem anatomy, sphenophyllum resembled calamites. The central pith was completely absent. Instead, the central region was occupied by a triradiate exarch xylem mass. Secondary xylem formed a thick sheath surrounding the primary xylem. Cortical

region exhibited a corky tissue indicating the activity of phellogen. The phellogen probably arose deep in the primary cortex.

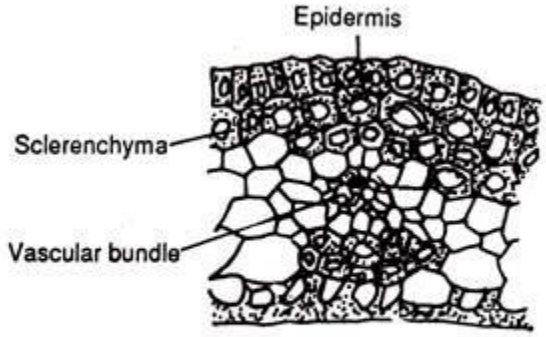


Fig. 92. *Sphenophyllum* : T.S. of Leaf

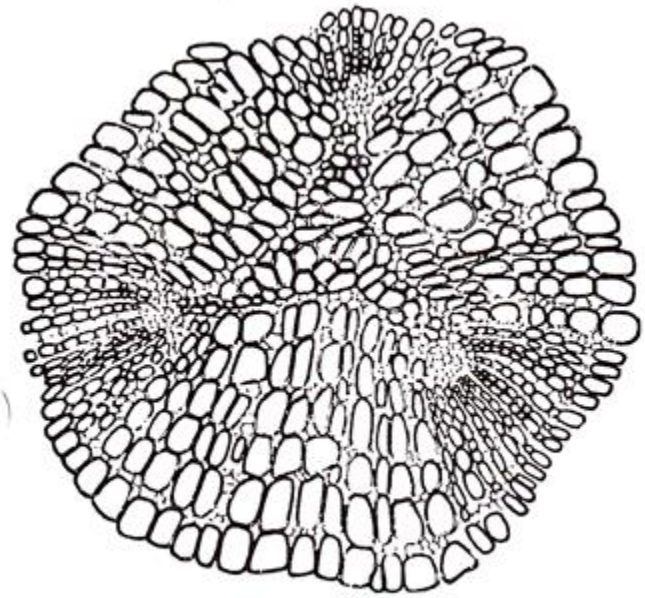


Fig. 93. *Sphenophyllum* : T.S. of Xylem Cylinder of *S. plurifoliatum*

Roots:

The plant body was anchored to the soil with the help of adventitious roots that arose at the nodal regions. Anatomically the roots resembled the stems, except that the former had a two angled xylem. Secondary growth was also seen in roots.

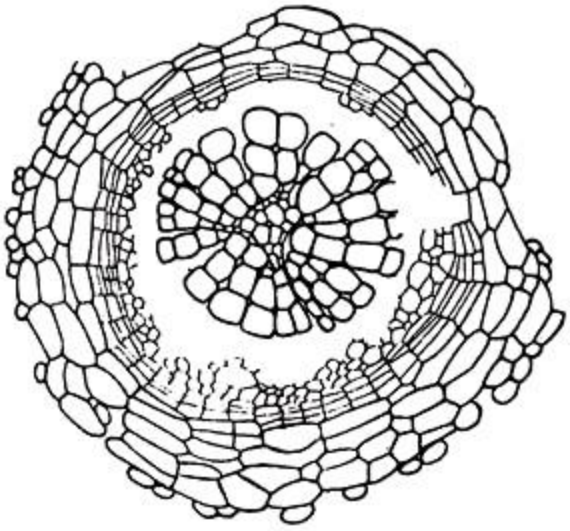


Fig. 94. *Sphenophyllum* : T.S. of Root

Reproduction in sphenophylum:

Sphenophyllum reproduced by means of sporangia borne on sporophylls. The sporophylls aggregated to form long and slender cones terminating the stem apex. The cones which are often given the name bowmanites had a central axis on which were arranged many whorls of sporophylls. The sporophylls of each whorl fused at their base to form a saucer like structure.

The sporophylls had two parts namely an adaxial fertile part and an abaxial sterile part. The sporangia were borne on the fertile part either singly or in pairs. In some cases the fertile lobe had two or three branches each having one to two sporangia.

The number and arrangement of sporangia on the lobe are taxonomic features used in the categorization of the species. The sporangia had a stalk which was highly reduced. Most of the species of sphenophyllum were homosporous. Some species could have been heterosporous.

Calamostachys:

The discovery of specimens of *calamostachys binneyana* in lower pennsylvanan petrifaction material in North America has provided additional information about the structure of this calamitean fructification. The cones consist of regularly spaced alternating whorls of bracts and sporangiophores. Bracts are fused in a disc except at the margin where the individual units become free. Sporangiophores are inserted at right angles to the cone axis and bear four axially directed sporangia. The vascular system of the North American specimens differs from that in other reports of the taxon in the presence of twelve vascular bundles in the cone axis. Each sporangiophore is supplied by a single vascular trace that departs from one axial bundle. There appears to be no constant relationship between the number of vascular bundles and the number of bracts. Spores are spherical, thin-walled, and of the *calamospora* type. Relationships with other structurally preserved members in the genus are discussed in light of the diversity in structure demonstrated by the new specimens.