PTERIDOPHYTES

INTRODUCTION:

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.

GENERAL CHARACTERS OF PTERIDOPHYTES:

SPOROPHYTIC GENERATION

(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., *Marsilea, Azolla*), xerophytic (e.g., *Selaginella rupestris, Equisetum*) or epiphytic (e.g., *Lycopodium squarrosum*) (Fig. 1).

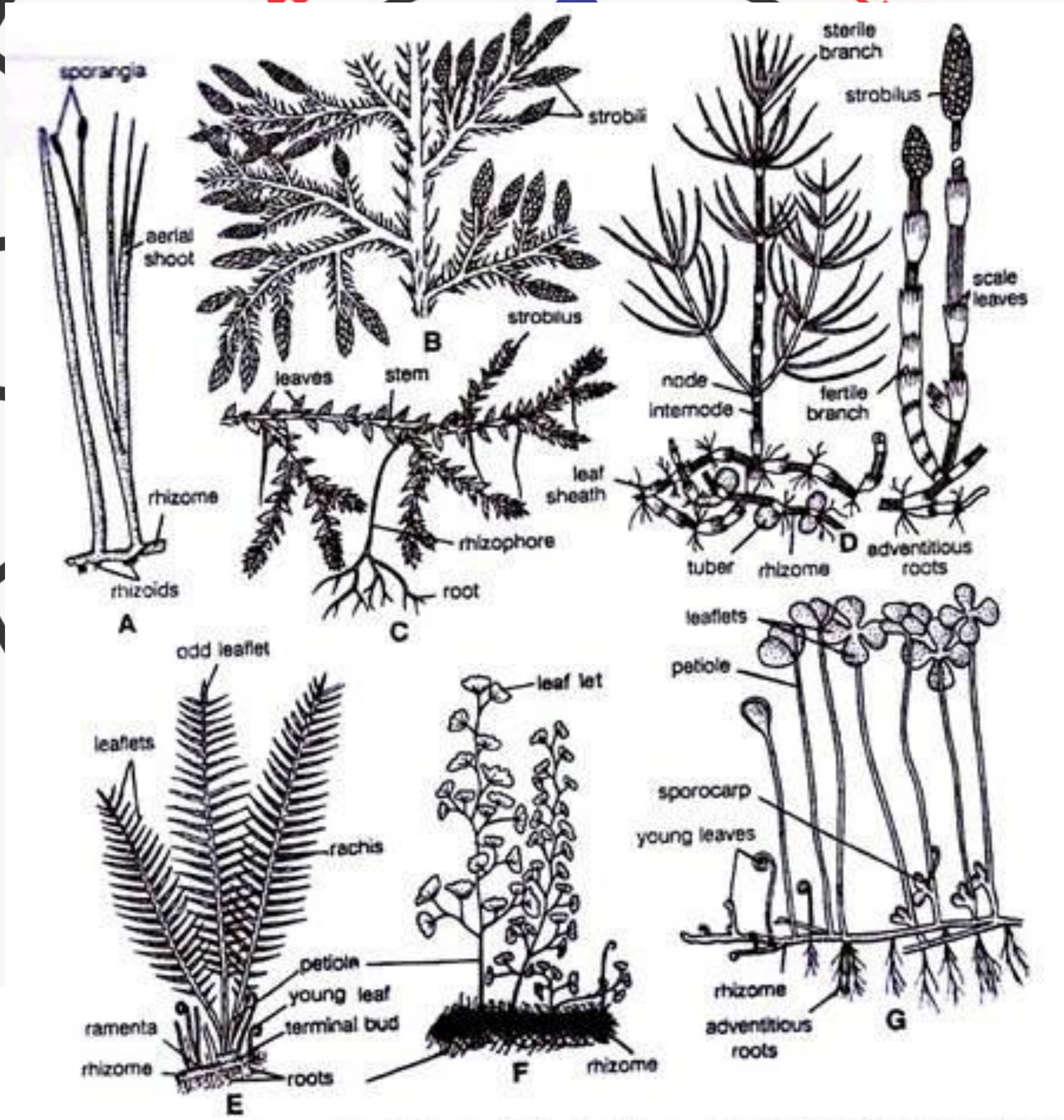


Fig 1 (A–G). Different forms of Pteridophytes A. *Rhynia*, B. *Lycopodium*, C. *Selaginella*, D. *Equisetum* E. *Pteris*, F. *Adiantum*, G. *Marsilea*

(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 stele is protostele (e.g., *Rhynia*, *Lycopodium*), siphonostele (e.g., *Equisetum*), dictyostele (e.g., *Adiantum*) or polycyclic (e.g., *Angiopteris*).
(ix) Cambium is absent; hence, they do not show secondary growth.

3. Reproduction in Pteridophytes:

The sporophyte of Pteridophytes generally reproduces by two methods i.e., Vegetative propagation and spore production.

(A) Vegetative reproduction:

- It is rare and may take place by **fragmentation** (Ex: *S. rupestris*). The prostrate branches develop roots and break into small fragments each developing into a new plant. Certain species of *Selaginella* propagate by **bulbils or by smaller tuber** (Ex: **surface tubers** in *S. chrysocaulos* and **underground tubers** in *S. chrysorrhizos*). In *Dryopteris* **adventitious buds** arise in the axil of leaves and are detached from the plant and form new plants.
- In some ferns the rachis produces a **vegetative bud or gemmae**, these ferns are called proliferous. When this bud falls on the ground a new plant develops, as in Tectaria gemmifera. Sometimes the new plant will already start to grow while still being attached to the rachis. Through the weight of this small plant, the frond will bend towards the ground. When it makes contact with the soil, the small new fern can start to root. (Ex: *Pneumatopteris unita*, *Asplenium sandersonii*).

(B) Asexual Reproduction: takes place by means of spores. Sporophyte produces meiospores inside a little capsule called 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.

GAMETOPHYTIC GENERATION

Sexual Reproduction

(iv) Spores on germination give rise to multicellular gametophytic bodies called prothalli (sing. prothallus) which are small and inconspicuous. The gametophytes in some pteridophytes are subterranean and in others they are retained within the resistant wall of the spore.
(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.

Vegetative propagation of gametophyte is uncommon and it takes place by the formation of gemmae or brood bodies (Ex: *Lycopodium*)

Life Cycle Patterns in Pteridophytes:

- Pteridophytes show heteromorphic alternation of generation. The main plant body is sporophytic and forms a dominant phase in the life cycle. Sporophytic plant body develops sporangia in which sporogenous tissue is formed. Sporogenous tissue divides meiotically to form haploid spores.
- Majority of the Pteridophytes are homosporous e.g., Lycopodium, Pteris etc. Spores on germination produce monoecious gametophyte. Some Pteridophytes are heterosporous and produce two types of spores: microspores and megaspores.
- Microspores on germination produce male gametophyte (prothallus) while megaspores on germination produce female gametophyte (prothallus). So, the prothalli are dioecious.
- Antheridia and archegonia develop on the same prothallus (monoecious)

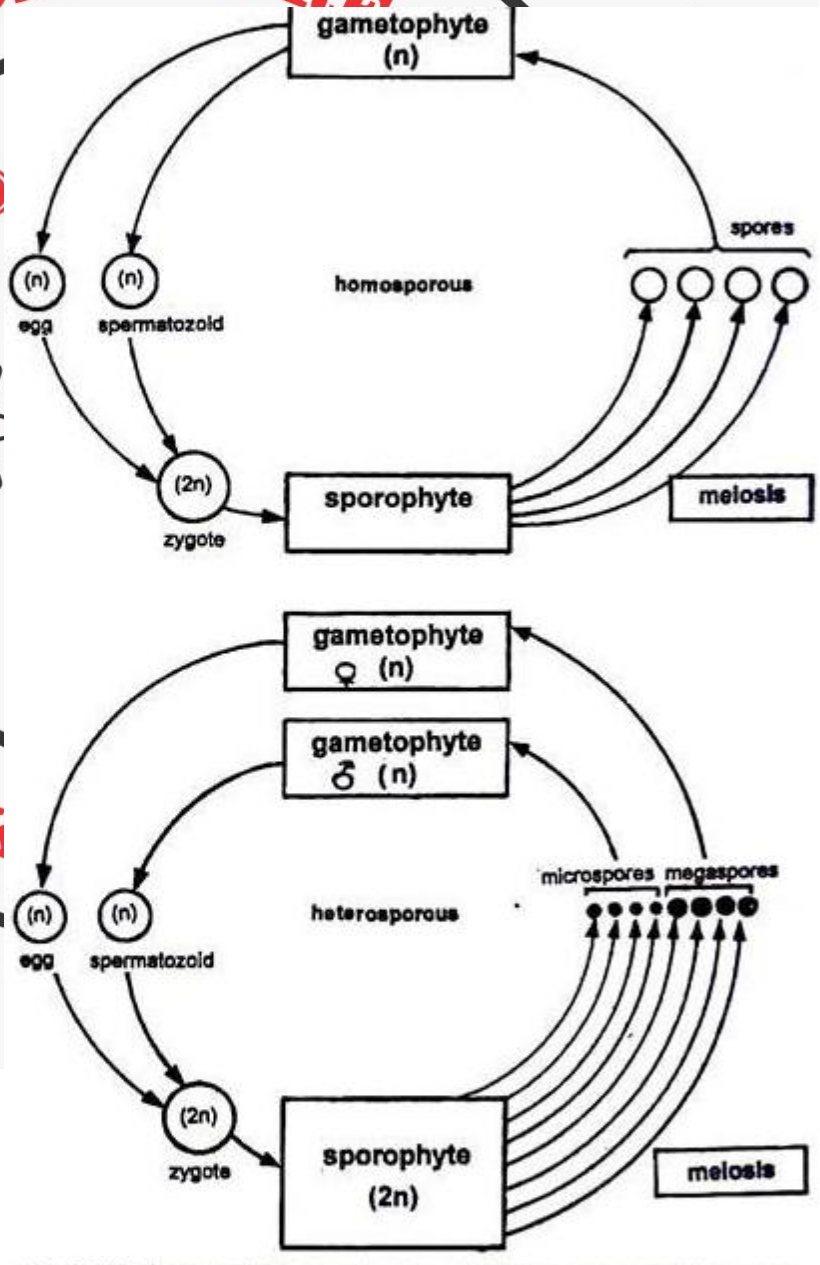


Fig. 4. Life Cycles of Homosporous and Heterosporous Pteridophytes

or on different prothalli (dioecious). The male and female gametes fuse to form zygote which develops into sporophyte. Thus, the life cycle of a Pteridophyte consists of an alternate succession of sporophytic and gametophytic generations.

CLASSIFICATION OF PTERIDOPHYTES AS PER K R SPORNE

- The term Pteridophyta was first coined by Haeckel. Eichler (1883) divided the plant kingdom into Cryptogamia and Phanerogamia. The Cryptogamia was further divided into Thallophyta. Bryophyta and Pteridophyta. Engler (1909) included the Bryophyta and Pteridophyta under Embryophyta.
- Due to discovery of the fossil plants, the classification of Pteridophytes has undergone vast changes in the recent past. Older taxonomists divided the vascular plants in two divisions—Pteridophyta (primitive vascular plants with absence of seeds) and spermatophyta (presence of seeds).
- However, this distinction became invalid due to the discovery of seed bearing fossil plants (Cycadofilicales). Sinnott (1935), therefore, introduced a new term Tracheophyta for a division which possess sporophyte with a well-developed vascular tissue.
- **Arthur J. Eames (1936) classified Tracheophyta into following four groups on the basis of nature and relation of leaf and stem vascular anatomy and position of sporangia:**
- Tippo (1942) called the 'groups' of Eames as sub-phylum. Wardlaw (1955) gave them the rank of sub-division.
- According to recommendations of I.C.B.N. (1952), the name of the division should end in the suffix-phyta, of a sub-division in-phytina and a class in -opsida.
- Sporne (1975) suggested a system of classification in which he has divided Pteridophytes into five classes. Sporne's system of classification is actually a modification of the Reimer's (1954) system.

CLASS- A. PSILOPHYTOPSIDA*
Order- Psilophytales* - *Rhynia*
CLASS- B. PSILOTOPSIDA
Order- Psilotales - *Psilotum*
CLASS- C. LYCOPSIDA
Orders- 1 Protolepidodendrales* - *Protolepidodendron*
2 Lycopodiales - *Lycopodium*
3 Lepidodendrales* - *Lepidodendron*
4 Isoetales - *Isoetes*
5 Selaginellales - *Selaginella*
CLASS- D. SPHENOPSIDA
Orders- 1 Hyeniales* - *Hyenia*
2 Sphenophyllales* - *Sphenophyllum*
3 Calamitales* - *Calamites*
4 Equisetales - *Equisetum*
CLASS- E. PTEROPSIDA
SUB CLASS- a Primofilices*
Orders- 1 Cladoxylales* - *Cladoxylopsid*
2 Coenopteridales* - *Botrypteris*
SUB CLASS- b Eusporangiatae
Orders- 1 Marattiales - *Angiopteris*
2 Ophioglossales - *Ophioglossum*
SUB CLASS- c Osmundidae
Order- Osmundales - *Osmunda*
SUB CLASS- d Leptosporangiatae
Orders- 1 Filicales - *Pteris*
2 Marsileales - *Marsilea*
3 Salviniales - *Salvinia*

SYSTEMATIC POSITION:
Division: Psilophyta
Class : Psilotopsida
Order : Psilotales
Family : Psilotaceae
Genus : *Psilotum*

Distribution of *Psilotum*:

- There are two well defined species, viz., P. nudum (*P. triquertum*) and *P.flaccidum* (*P. complanatum*).
- *Psilotum* is distributed both in the tropics and the subtropics. *P. nudum* is widely distributed being found in all the warmer regions of the world, including India.
- In India it is found in Bengal, Assam and the hilly districts of Madhya Pradesh, Himachal Pradesh and Karnataka. *P. nudum* is also cultivated as a curiosity in botanical gardens. *P. flaccidum* is somewhat uncommon and is reported from tropical islands like Jamaica, Java, Malayan peninsula, Mexico etc.,
- In their habitat they are either terrestrial or epiphytic. While *P. nudum* is predominantly terrestrial, *P. flaccidum* is mainly epiphytic growing in the humus packets of trees.

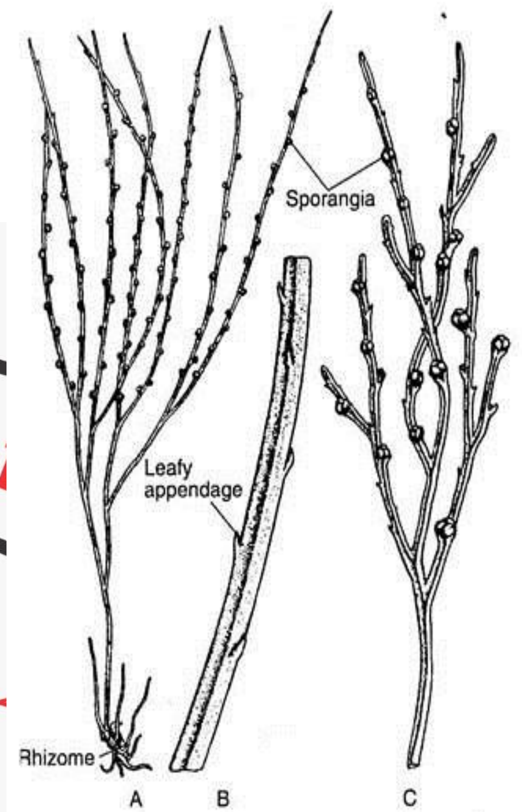


Fig. 7.11 : *Psilotum nudum* : A. A sporophyte plant, B. An enlarged part of stem showing scaly appendage, C. A fertile twig

Sporophyte of *Psilotum*:

Morphology:

- The plant body of Psilotum is differentiated into two parts viz., a horizontal underground rhizome and an erect aerial shoot. The rhizome is brownish in colour and dichotomously branched. The rhizome is studded with a number of long, fine, thread like rhizoids.
- Some of the branches of the rhizome grow up and constitute the erect (*P. nudum*) or pendulous (*P. flaccidum*) shoot system. The aerial shoots are 20-75 cm long and are usually ribbed and multi-angular. The ultimate branches however are triquertous.
- In *P. flaccidum* the base of the aerial shoot is triquertous while the tips are flattened. Unlike the rhizome, the aerial shoots are regularly dichotomously branched and are deep green in colour indicating their photosynthetic activity.
- Here and there on the aerial shoot are found a number of scales or appendages which are often called leaves. These are of two types viz., sterile and fertile.
- The sterile ones are found all along the length of the aerial shoot while the fertile ones are generally restricted to the upper portions and bear in their axils a trilobed spore bearing structure which is often called a Synangium. The leaves whether fertile or sterile are devoid of any vasculature and could be regarded as only emergences.

Internal Structure:

1. Aerial shoot:

- A transverse section of the stem shows three regions, viz., epidermis, cortex and stele (Fig.21). Epidermis is single layered and has closely packed cells. The layer is discontinuous due to the presence of stomata. The stomata are restricted to grooves between the longitudinal ridges and are sunken in nature. Above the epidermis there is a thick cuticle.

- The cortex is divided into three zones. The outer zone is chlorenchymatous and is made up of 2-5 layers of cells. The cells are loosely arranged with intercellular spaces. As the leaves are reduced, this constitutes the chief photosynthetic tissue of the plant.
- The presence of thick cuticle, sunken stomata, photosynthetic stem and reduced leaves indicate the xerophytic nature of *Psilotum*. The middle region of cortex consists of 4-5 layers of sclerenchyma offering mechanical support to the stem. The inner cortex is made up of a few layers of closely packed parenchyma cells.
- The stele occupies the central region of the stem. The outermost layer of the stele is endodermis. Next to the endodermis is an ill-defined pericycle. The nature of the stele varies in the ultimate branches and in the basal portion. In the ultimate branches the stele is an actinostelic protostele with a solid core of stellate xylem mass in the centre. In the basal portion however, the central region of the stele consists of a sclerotic pith (Fig.21). The xylem is exarch with the protoxylem points located at the tips of the rays. The xylem consists of scalariform pitted or annular tracheids. Sometimes spiral tracheids are also found. Surrounding the xylem is the phloem.

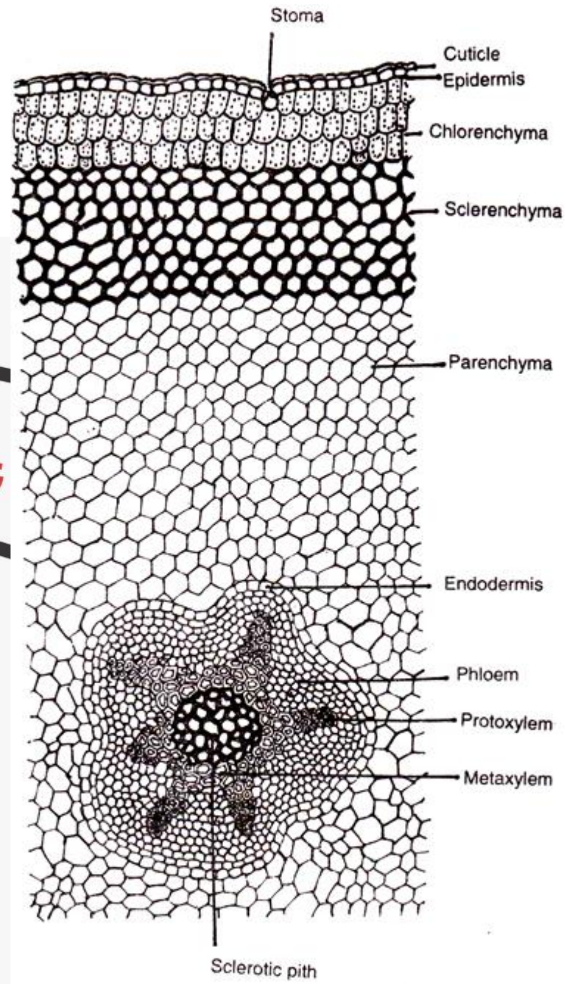


Fig. 21. *Psilotum* : T.S. of Aerial Shoot (a sector enlarged)

2. Rhizome:

- This also shows an epidermis, a cortex and stele. The epidermis is ill defined. The cortex is divided into three zones. The outer cortex is parenchymatous and the cells have mycorrhizal fungus. The middle cortex has parenchyma cells rich in starch grains.
- The innermost region of the cortex also consists of parenchyma that are usually dark brown in colour due to the deposition of a substance called phlobaphene. This is believed to be an oxidation product of tannins.
- The stele is protostelic and is

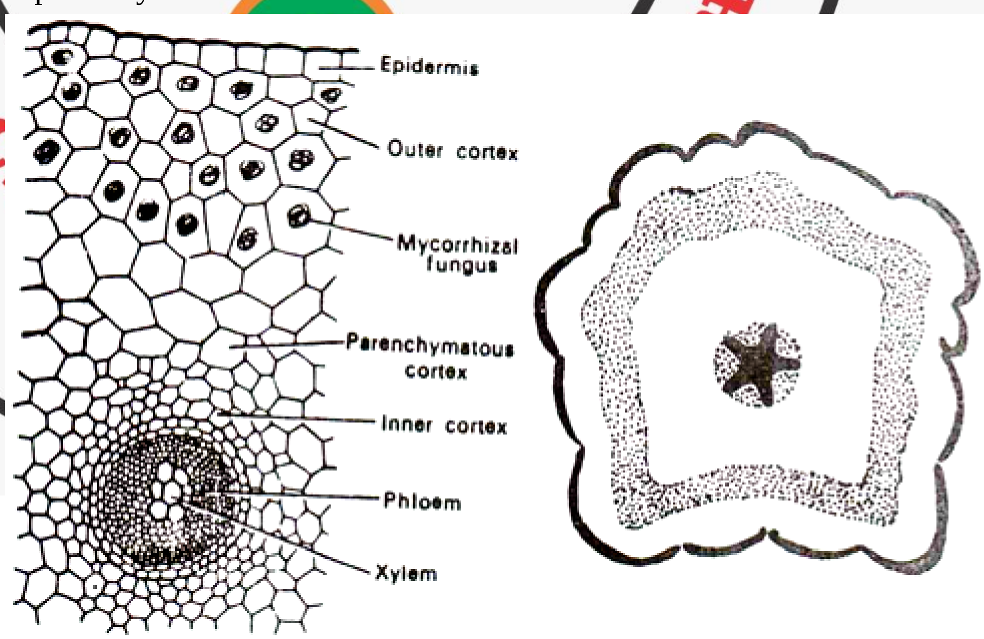


Fig. 20. *Psilotum* : T.S. of Rhizome.
A. Sector Enlarged, B. Ground Plan.

surrounded by a typical endodermis which is followed by a layer of pericycle. The shape of the xylem varies with the diameter of the axis. Usually it is circular in outline. The xylem is exarch and is surrounded by phloem.

3. Leaf:

- Anatomically the leaves show epidermis and the mesophyll. The epidermal cells are cutinised. The mesophyll has chlorophyllous cells which may be loosely or closely packed. The stomata are absent in the epidermis as such the chlorophyllous cells have no means of gaseous exchange. There is no vascular supply to the leaf. But in *P. flaccidum* a leaf trace which starts from the stem terminates at the leaf base. The absence of stomata and the lack of vascular supply make the chlorophyllous cells of the leaf ineffective in photosynthesis.
- Apical growth: A single wedge shaped apical cell contributes to the growth of the stem.

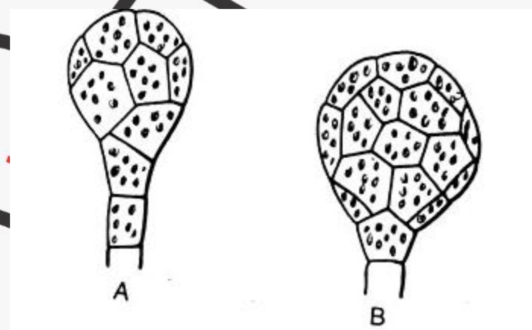


Fig. 25. *Psilotum* : Sporophytic Gemmae (Note the starch grains in cells)

Reproduction:

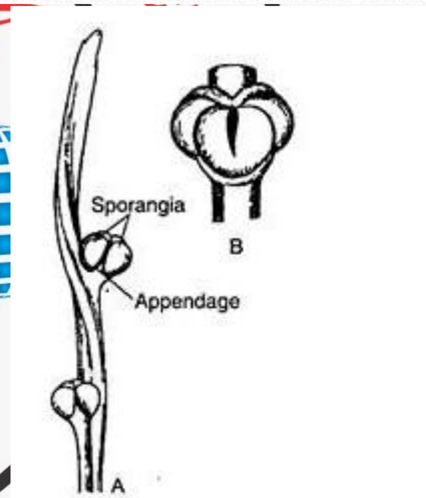
The sporophyte reproduces by vegetative propagation as well as by spore production.

1. Vegetative Propagation:

The sporophyte increases its number by the production of gemmae or brood bodies. These are formed on the rhizome and are usually restricted to the tips or the axils between the branches. Each gemmae is an oval body, one cell in thickness having an apical cell with two cutting faces. The cells are rich in reserve food especially starch. The gemmae detach from the plant body germinate and give rise to a new plant of *Psilotum*.

2. Spore Production:

The sporophyte reproduces asexually by the formation of spores. Spores are produced in special trilobed structures called synangia which are generally restricted to the upper portions of the aerial shoots where they are borne in the axils of minute bifid scales.



Psilotum nudum : A. A part of fertile axis bearing sporangia with bifid appendages, B. A trilocular synangia showing dehiscence

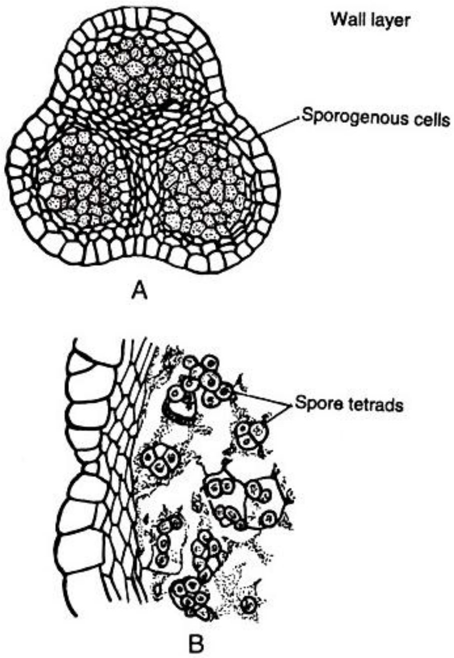


Fig. 23. *Psilotum*
A. T.S. of Young Synangium, B. Sectional View (a portion) of Synangium with Spore Tetrads

Development of the Synangium:

- The development is apparently of the eusporangiate type, even though each sporogenous mass appears to originate from a single cell.
- In many cases the first division of the synangial initial produces an outer jacket initial and an inner archesporial cell (Fig.22). The jacket initial undergoes a number of anticlinal and periclinal divisions to produce the multilayered wall of the synangium.

Meanwhile, the archesporial cell divides in all the planes to form a large number of sporogenous cells (Fig.23). There is no well-defined tapetum. In the sporogenous tissue some cells here and there distinguish themselves by their dense granular cytoplasm from the remainder. These are the spore mother cells. Rest of the sporogenous cells gradually degenerate.

The spore mother cells undergo reduction division to produce tetrads of haploid spores.

Structure of the Mature Synangium:

The wall of the trilobed synangium is made up of 4-5 layers of cells. The outermost layer of the wall is prismatic. Within the synangium there are three chambers of spore cavities containing spores. All the spores are of the same type.

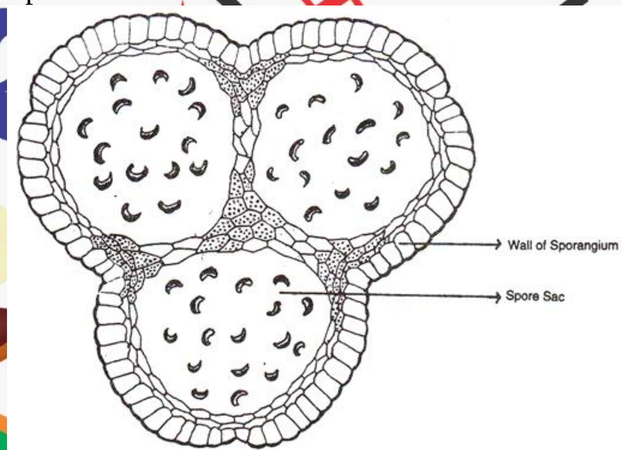


Fig. 24. *Psilotum*, T.S. of Mature Synangium with Spores

Dehiscence of the Synangium:

When the spore mother cells are undergoing reduction division some of the wall cells thicken except in a small vertical row marking the future line of dehiscence. The synangium splits open along this line liberating the spores.

Structure of the spore: Spores vary in shape from bilateral to tetrahedral type.

Gametophyte of Psilotum:

Germination of the Spore and Development of Gametophyte:

Germination starts after four months on placing the spores on a suitable substratum. The first sign of germination is the splitting of the outer spore wall and the projection of a small tubular outgrowth.
Later a cross wall cuts off the outgrowth from the remainder of the spore. In this way two cells are formed.
Of the two cells, the upper by further divisions establishes an apical cell which produces a mass of tissue.
Early in the development, the gametophyte gets infected by the fungus.

Structure of the Mature Gametophyte:

- The gametophyte is partly or totally subterranean. It is usually cylindrical in shape with dichotomous branches or irregular branching. In size, the gametophyte ranges from 0.5 to 2 mm. The colour of the gametophyte is usually dark brown. This is due to the presence of endophytic fungus.
- The gametophyte is wholly parenchymatous with strongly cutinised cell walls. The outermost layer of the cells gives rise to a number of rhizoids. In the hypodermal region the cells have the endophytic

fungus.

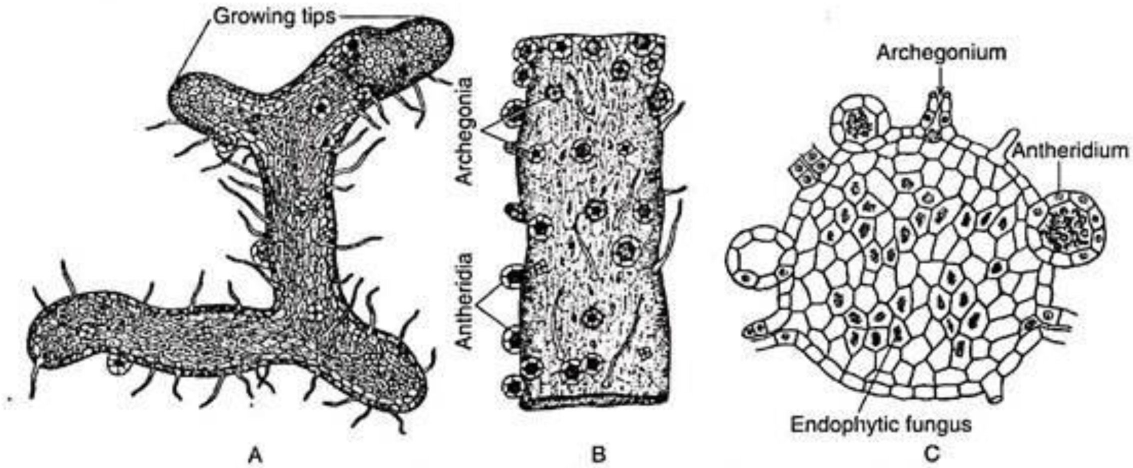


Fig. 7.18 : *Psilotum nudum* : A. A gametophyte, B. An enlarged portion of the gametophyte showing sex organs and rhizoids, C. T.S. of gametophyte

Internal Structure of the Gametophyte:

- A transverse section of the mature gametophyte shows that it is wholly parenchymatous. Some of the superficial cells give rise to rhizoids. The outer walls, radial walls and even the inner corner of the walls of the peripheral cells are highly cutinised. Mycorrhizal association is found in some of the cells. The central region of the gametophyte also consists of parenchyma with no trace of any vasculature.
- The interesting feature in these gametophytes was the presence of a central vascular strand.
- The vascular strand consisted of a few annular and scalariform or scalariform reticulate tracheids. The tracheids were surrounded by phloem. There was even a clearly recognizable endodermis. In these prothalli there was a cortex of parenchyma cells between the vascular strand and the superficial layer.

Reproduction:

The gametophyte reproduces by two methods

(1) Vegetative propagation and (2) Sexual reproduction.

(1) Vegetative Propagation:

- Holloway (1939) and Bierhorst (1953) have described the production of gemmae on the surface of the gametophyte. The gemmae arise as proliferations from a rhizoid like structure and are similar to those produced on the rhizome.

- A mature gemmae has 8-12 cells, usually spheroidal or occasionally flattened and on germination gives rise to a new gametophyte. Holloway (1939) has also described the formation of special vegetative buds on the gametophyte.

(2) Sexual Reproduction:

This is brought by the formation of antheridia (male) and archegonia (female). The gametophytes are monoecious.

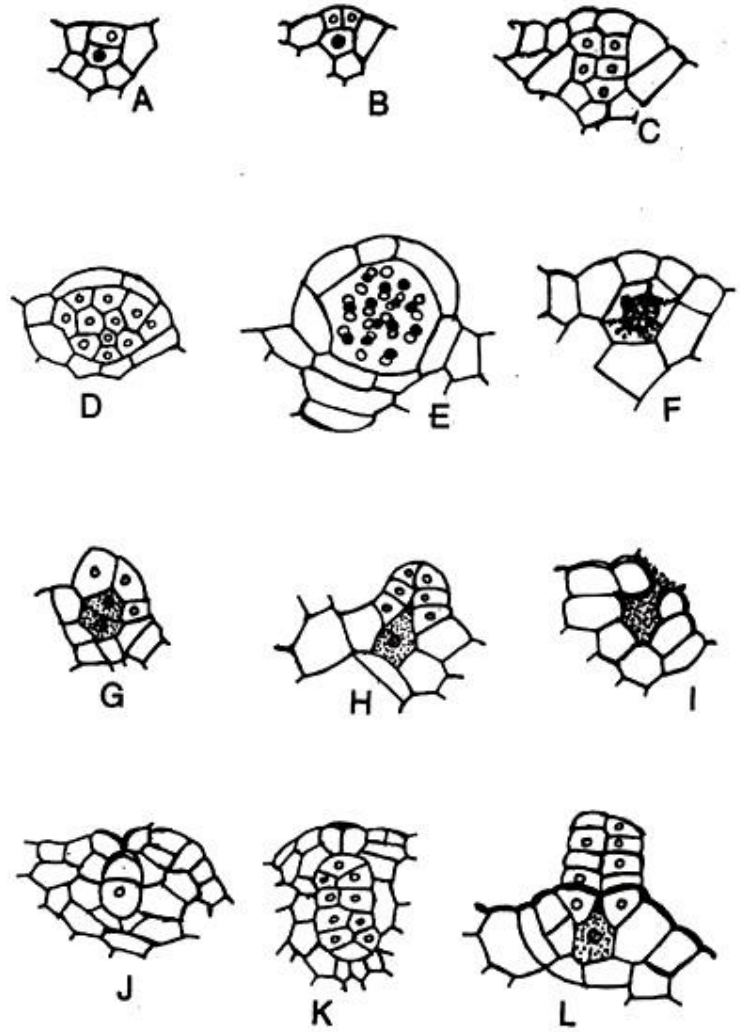


Fig. 28. ***Psilotum*** **: Development of Sex Organs in the Gametophyte of *P.nudum*; A-E. Antheridium, F-J Archegonium, K-l. Archegonium and embryo respectively**

Structure of the Antheridium:

- A mature antheridium is somewhat spherical in shape and projects out of the gametophyte as a hemispherical protruberance. The jacket is made up of about 12 cells and has a special cell called the opercular cell which degenerates at maturity allowing for the liberation of the antherozoids. Approximately about 250 antherozoids are found inside the antheridium.

Structure of the Archegonium:

- The archegonia are also produced from the superficial cells of the gametophyte. A superficial cell which is destined to form an archegonium is called an archegonial initial.
- Archegonia has 4-7 neck cells, two neck canal cells, an upper short-lived venter canal cell and a lower egg cell with a prominent nucleus.
- As the archegonium is reaching maturity, the neck canal cells degenerate. In some cases they degenerate as soon as they are formed. In a mature archegonium; some of the terminal tiers of the neck slough off (Fig.28j) leaving only the basal one or two tiers. At this stage except for egg all other cells in the archegonium disintegrate.

Fertilization:

- The antherozoids come out of the antheridium through the passage formed by disintegration of the opercular cells. They swim in a thin film of moisture, approach the archegonium, enter into it and fertilize the egg.

Embryogeny:

- Soon after fertilization, the zygote enlarges in the cavity of the venter. First division of the zygote is transverse and it results in forming an upper epibasal cell (cell nearer to the archegonial neck) and a lower hypo basal cell (cell away from the archegonial neck) (Fig.28k). The hypo basal cell gives rise to the foot and the epibasal cell gives rise to shoot.
- This type of embryogeny, where the shoot apex is pointed towards the archegonial neck is called exoscopic. The hypo basal cell divides in all the planes to form a bulbous foot which gives rise to haustorial outgrowths into the gametophyte.
- Meanwhile, the divisions in the epibasal cell result in the formation of a three sided apical cell. By the activity of this apical cell the shoot apex projects out of the gametophyte. At this stage it gets infected with the mycorrhizal fungus. This assures independent nutrition to the young sporophyte.
- When the young sporophyte is about 8-10 mm long, it detaches from the gametophyte and leads an independent life. In the beginning it is subterranean, later some of the branches grow Apo geotropically and form the aerial shoots.

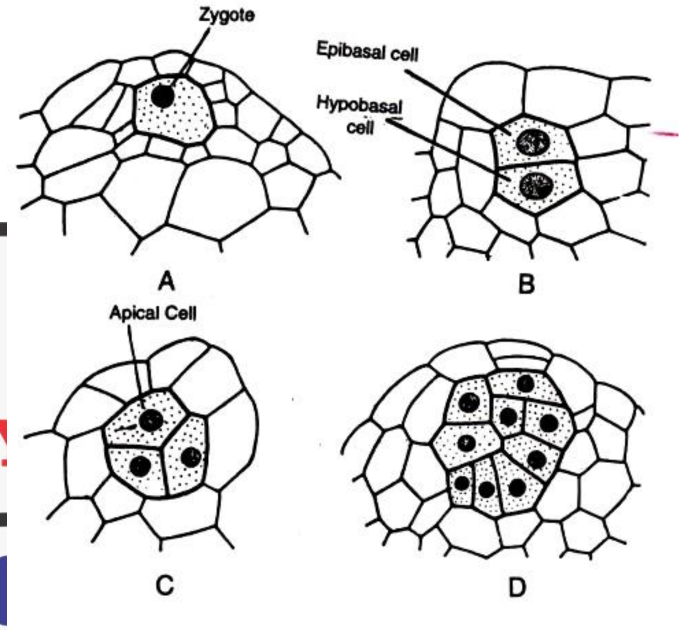


Fig. 29. *Psilotum* : Stages in early Embryogeny of *P. nudum*

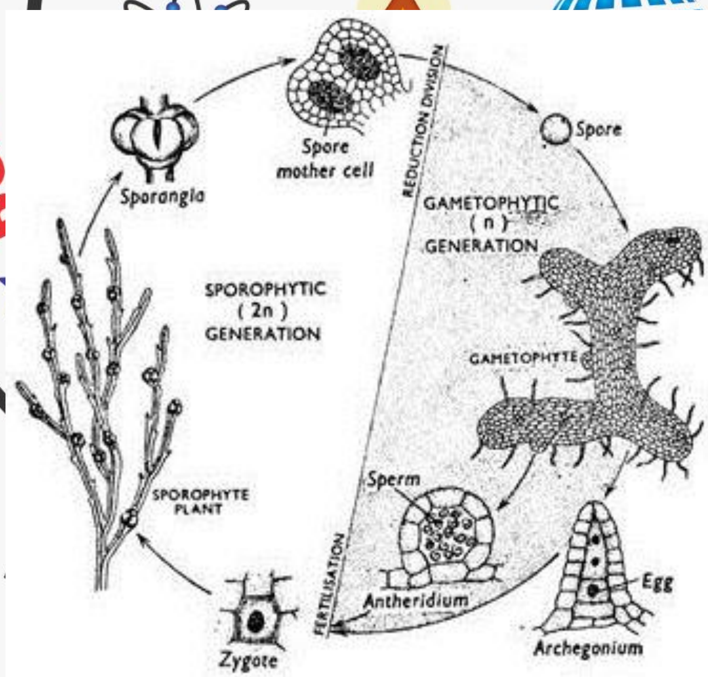


Fig. 7.22 : Life cycle of *Psilotum*

Lycopodium

SYSTEMATIC POSITION:
Division: Lycophyta
Class : Eligulopsida
Order : Lycopodiales
Family : Lycopodiaceae
Genus : *Lycopodium*

Fig. 1 (A–C). *Lycopodium*. Sporophyte with strobili : A. *L. cernuum* (terrestrial), B. *L. clavatum* (terrestrial), C. *L. phlegmaria* (epiphytic)

Habit and Habitat of Lycopodium:

- *Lycopodium* is commonly known as 'club moss' due to their moss like appearance and club shaped strobili. It has about 400 species, which are cosmopolitan in distribution. They are found in colder arctic region as well as in temperate, tropical and sub-tropical regions but they are abundantly found in tropical zones.
- 33 species of *Lycopodium* have been reported from India. Mostly it is found growing in moist and shady places which are rich in humus and other organic matters. Some of the common species are *L. clavatum, L. phlegmaria, L. cernuum,* etc.

It has got 2 sub-genuses:

- *Urostachya*—branching dichotomous and roots originate from the base of the stem.
- *Rhopalostachya*—stem prostrate with erect branching and roots arise adventitiously from all along the stem.
- Mostly the tropical species are epiphytic (e.g., *L. phlegmaria*) and grow hanging from the tree trunks. The temperate species may be erect and shrubby (e.g., *L. reflexum*), creeping (e.g., *L clavatum*) or erect form (e.g., *L. cernuum*) etc.

External Morphology of *Lycopodium*:

- The herbaceous plant body is sporophytic. Usually they may have either prostrate stem with erect leafy branches or weak pendent stem (epiphytes).

The plant body is distinctly differentiated into (i) Stem, (ii) Roots, and (iii) Leaves. (Fig. 1 A-C):

(i) Stem:

- In *Urostachya* stem is erect (terrestrial) or pendent (epiphytic) and may be branched (dichotomously) or unbranched. In *Rhopalostachya* the stem is prostrate with erect branches. First the branching is dichotomous and later on becomes monopodial.

(ii) Root:

- Usually small, adventitious roots are present. In *Urostachya* roots originate only from the base of the stem (not arising from the whole length of the stem). In some species e.g., *L. selago* etc. the roots arise endogenously from pericycle of the stem, do not penetrate the cortex of the stem but turn downward through the cortex and finally emerge only at the base of the stem.
- Due to this reason a T. S. of stem usually shows roots within the cortex and are known as cortical roots (inner roots). In *Rhopalostachya* also roots are adventitious and arise all along the underside of the prostrate portion of the stem.

(iii) Leaves:

- Leaves are simple, sessile, small in size, eligulate and possess a single unbranched midrib and are known as microphylls. Usually the leaves are spirally arranged (e.g., *L. clavatum*) but may be arranged in whorls (e.g., *L. cernuum*) or pairs (e.g., *L. alpinum*).
- In all the cases they condensely cover the surface of the stem. Leaves are usually homophyllous (isophyllous) i.e., of same size and shape but in some cases e.g., in *L. complanatum* the leaves are heterophyllous (anisophyllous) i.e., of different size.
- Usually the leaves near the apical portion of the branches bear sporangia and are called sporophylls. Depending upon the species the sporophylls may or may not be differentiated from the ordinary leaves.
- These sporophylls usually form a condense structure at the apex of the branches which are known as strobili. The numbers of strobili at the tip of branches differ in different species.

Internal Structure of *Lycopodium*:

(a) Stem:

A transverse section (T.S.) of the stem of *Lycopodium* is somewhat circular in outline and can be differentiated into following three regions:

1. Epidermis:

- It is the outermost covering layer comprising of single cell in thickness. The epidermis is cutinised on the outer side and interrupted at places by the presence of stomata.

2. Cortex:

- Inner to the epidermis is present a wide zone of cortex which shows a great variation in its structure in different species.

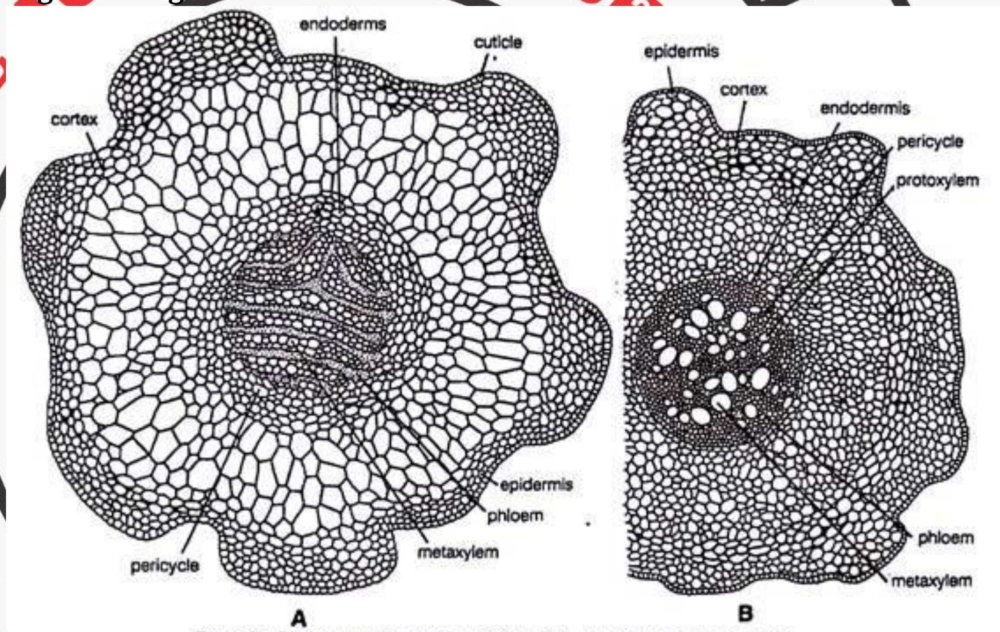


Fig. 2 (A–B). *Lycopodium* : T. S. of Stem A. *L. clavatum*, B. *L. cernuum*

Usually four types of cortex are recognized:

- The whole of the cortex is made up of parenchymatous cells with small or large intercellular spaces (e.g., *L. selago*). Such cortex is called homogeneous.
- The whole of the cortex is made up of sclerenchymatous cells, without intercellular spaces.
- The cortex is differentiated into outer and inner sclerenchymatous cells and middle parenchymatous cells (e.g., *L. clavatum*, Fig. 2 A).

- The cortex is differentiated into outer and inner parenchymatous cells and middle sclerenchymatous cells (e.g., *L. cernuum* Fig. 2. B).

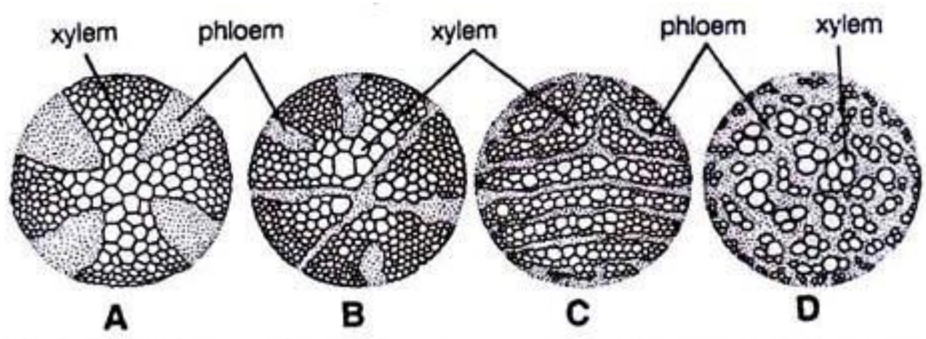


Fig. 3 (A–D). ***Lycopodium*** **: Various types of steles in stem : A. Actinostele, B. Stellate shaped, C. Plectostele, D. Mixed protostele**

- Next to the cortex is present a single layer of well-defined cells known as endodermis with conspicuous casparian strips but at maturity the endodermis may or may not be a distinct structure. Endodermis is followed by pericycle which is composed of one or more layers of compactly arranged parenchymatous cells.

3. Stele:

- It is made up of only primary xylem and primary phloem. It is a protostele i.e., pith is absent and the stele is situated in the centre. The arrangement of xylem and phloem tissues is different in different species and the stele is also named differently.
- In case of *L. serratum, L. phlegmaria* etc. the xylem is star shaped with a protoxylem situated at the periphery (protoxylem exarch Fig. 3 A). In *L. annotinum* in actinostele the furrows in the xylem are much more and show stellate arrangement (Fig. 3B). The phloem lays in the space between the xylem rays. This type of stele is known as actinostele. In case of *L. clavatum. L. volubile* etc. xylem appears to be in the form of separate plates arranged somewhat parallel, with phloem in between them. This type of stele is known as plectostele (Fig. 2 A, 3 C). In case of *L. cernuum*, *L. drummondii* etc. xylem and phloem are uniformly distributed i.e. it appears as if strands of xylem are embedded in the phloem. This type of stele is known as mixed protostele (Fig. 2 B, 3 D).
- The protoxylem is usually exarch in all the cases. Xylem is usually composed of tracheids and phloem of sieve tubes and phloem parenchyma.

(b) Root:

The roots are adventitious.

- A transverse section (T.S.) of the aerial root of *Lycopodium* is somewhat circular in outline and shows the following internal structure:

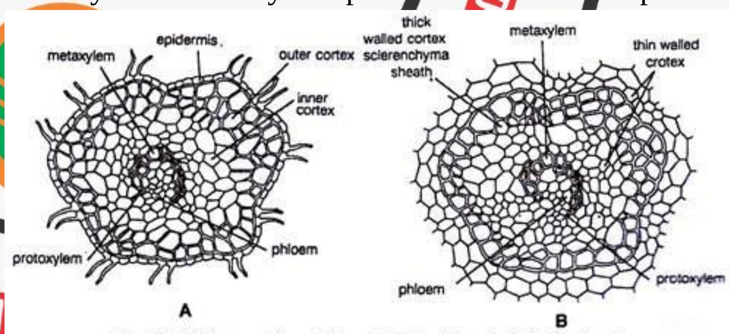


Fig. 4 (A–B). ***Lycopodium*** **. T. S. root : A. Aerial root, B. Cortical root**

(i) Epidermis:

- It is the outermost covering layer and is only one cell thick. The cells are thin walled. Epidermis is provided with numerous root hairs present in pairs (characteristic of *Lycopodium*).

(ii) Cortex:

- Just below the epidermis is present a wide zone of cortex. It is differentiated into outer sclerenchyma and inner parenchyma. The outer one gives the mechanical strength to the root.

(iii) Stele:

- It may be di-, tetra-, or polyarch. In prostrate species it is polyarch i.e., having 6-10 plates of xylem arranged radially (star shaped). The xylem is exarch. The phloem is present between the radiating arms of xylem. In erect or pendent species stele is diarch or tetrarch. In *L. selago*, *L. serratum* it is diarch and xylem is C, U or crescent shaped. The phloem is present between the 2 ends of xylem, only in one group.

- The cortical roots are exactly similar in their internal structure to that of aerial roots, except that the epidermis and root hairs are absent.
- The xylem is composed of tracheid and phloem of sieve tubes and phloem parenchyma. The endodermis and pericycle are indistinct structure at maturity.

(c) Leaf:

T. S. of the leaf shows epidermis, mesophyll tissue and a single median vascular bundle:

1. Epidermis:

- It is the outermost surrounding layer and is only one cell in thickness. The cells of epidermis are parenchymatous and cutinised on their outer side. The epidermis is also interrupted by the presence of stomata. In homophyllous (isophyllous) species the stomata are present on outer as well as inner epidermis (amphistomatic) but in heterophyllous (anisophyllous) species the stomata are mostly restricted on the lower epidermis (hypostomatic).

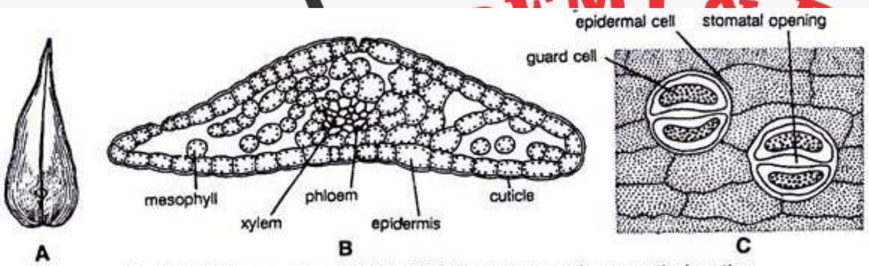


Fig. 5. (A–C). Lycopodium : (A) A leaf, (B) Transverse section or vertical section (T.S. or V.S.) of leaf, (C) stomata on leaf surface.

2. Mesophyll:

- It occupies a wide zone between the epidermis and the vascular bundle. It is usually made up of thin walled chlorenchymatous cells which may be with or without intercellular spaces.

3. Vascular bundle:

- In the centre of the leaf is situated only a single concentric vascular bundle made up of only xylem and phloem. The vascular bundle is surrounded on all sides by a sclerenchymatous sheath.

Reproduction in *Lycopodium*:

- *Lycopodium* reproduces by two methods vegetatively and by spores.

Fig. 6 (A–C) *Lycopodium* : Vegetative reproduction : (A) Stem bearing gemma, (B) A gemma, (C) A germinating gemma.

1. Vegetative reproduction takes place by the following methods:

(i) Gemmae or bulbils:

- In a few species like *L. selago*, *L. lucidulum* etc. certain buds like structures known as gemmae or bulbils are usually produced in large number on new stem tips annually. The morphological nature of gemmae is still not fully known. The gemmae when fall on ground, develop root primodia and soon form the root.

(ii) Death and decay:

- Species with creeping stem reproduces vegetatively by the death and decay of older parts of the stem up to the point of branching. This separates the branches which later on grow independently.

(iii) Resting buds:

- In *L. inundatum* the whole of the plant body except the growing tip of rhizome is dead during winter. This tip portion of the rhizome acts as resting bud which in the coming spring resumes growth and develops into a new plant.

(iv) Fragmentation:

- In several epiphytic species fragments of the plant body are capable of giving rise to new plants.

2. Sexual Reproduction:

Spore Producing Organs:

- *Lycopodium* is a sporophytic plant and reproduces sexually. The plants are homosporous i.e., produces only one type of spores (without differentiation of mega- and microspores). These spores are produced in sporangia which, in turn, are produced on fertile leaves known as sporophylls. Usually the sporophylls are grouped together to form a compact structure known as strobili (Sing. strobilus) which are terminal structures (Fig. 1 A).

Strobilus (Reproductive organ):

- In the primitive species of *Urostachya* every leaf on the plant is a sporophyll or at least potentially so and the fertile and sterile zones alternate. The sporophylls are loosely arranged. In species of *Rhopalostachya* and in some species of *Urostachya* the leaves of the apical portion of the branches only bear sporangia and are called sporophylls. The rest behave as vegetative leaves.
- The sporophylls may be of the same size or of different size from the foliage leaves in different species. The arrangement of sporophylls is same on the central axis as that of the vegetative leaves on the stem i.e., spiral, whorled or decussate etc.
- The position of the sporangium is also different in different species. The sporangia may be axillary and protected with the help of sporophylls (e.g., *L. inundatum* Fig. 7 A) or foliar and protected (e.g., *L. cernuum* Fig. 7 B) or subfoliar and exposed (e.g., *L. squarrosum*, Fig. 7 C) or axillary and exposed (e.g., *L. lucidulum*, Fig. 7 D).

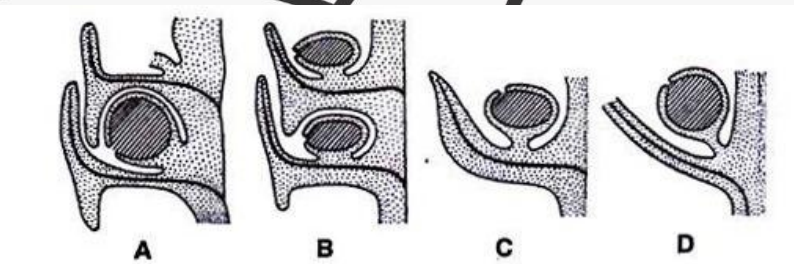


Fig. 7 (A–D) ***Lycopodium*** **: A strobilus showing position of sporangia in various species; A. *L. inundatum*, B. *L. cernuum*, C. *L. squarrosum*, D. *L. lucidulum***

- Longitudinal section (L.S.) of strobilus shows the presence of a strobilus axis in the centre. On both sides of the strobilus axis are present sporophylls (Fig. 8 A). Each sporophyll bears only one sporangium (Fig. 8 B). All the sporangia are similar in structure and are arranged acropetally in a strobilus i.e., the youngest are at the top (Fig. 8 C).

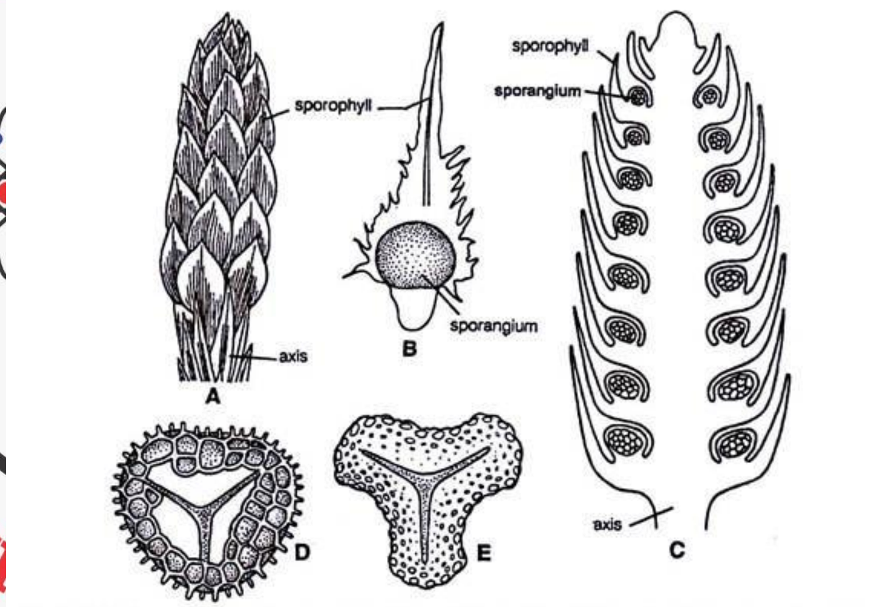


Fig. 8. (A–E). *Lycopodium* : Structure of strobilus; (A) A strobilus, (B) Longitudinal section of strobilus, (C) A sporophyll showing sporangia on the adaxial surface, (D, E). Spores.

Structure of Sporangium:

- Sporangia are sac-like structures but usually kidney shaped in appearance (Fig. 8 B). Sometimes they are sub-spherical in appearance. Their colour varies from orange to yellow. Each sporangium consists of a basal short massive stalk i.e., sub-sessile, with an upper globular unilocular body containing numerous spores.
- The body of the sporangium consists of 3 or more layers of wall surrounding a cavity. The inner most layer of the wall of sporangium is called as tapetum (Fig. 9 F) which is nutritive in nature and persists till maturity.
- In the young sporangium inside the wall is present a mass of sporogenous cells which in due course of development form spore mother cells which by meiotic divisions, produce haploid tetrad of spores. The spores at maturity separate from each other.
- The wall of the sporangium is provided with a transverse strip of cells known as stomium from where the sporangium at maturity splits into 2 valves and the spores are dispersed away in the air.

- The spores produced by a sporangium are all alike (homosporous). They are small, rounded or even spherical structures. The surface of the spores is usually rough due to the presence of reticulate ridges or knob like protrusions. Each spore is provided with a triradiate ridge (Fig. 8, D, E) and is somewhat yellow in colour. A small amount of chlorophyll may or may not be present in spores. Reserve food is in the form of oil in the spores.

Development of sporangium and formation of spores: The sporangium develops from a small group of superficial cells arranged in a transverse row on the adaxial side of the sporophyll near the base.

- Its development is of eusporangiate type. These superficial cells are called sporangial initials (Fig. 9A, B). These cells divide by periclinal divisions forming an outer and inner layer of cells. The outer cells divide periclinally and anticlinally forming three celled thick wall of the sporangium (Fig. 9A-F).

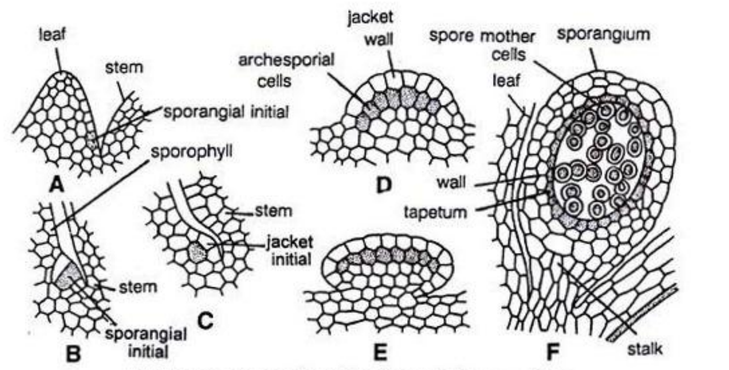


Fig. 9 (A–F). *Lycopodium* : Development of sporangium

The inner layer or archesporial cells divide in all directions forming a group of cells known as sporogenous tissue which finally give rise to spore mother cells. During these developments the inner-most layer of wall is differentiated as a nutritive layer and is known as tapetum. It is a persistent structure and rich in reserve food material. Each spore mother cell undergoes a process of meiosis thus producing a tetrad of spores (haploid) with tetrahedral arrangement. These spores later on separate from the tetrad, as a result of which, a large number of spores are produced inside each mature sporangium.

- **Dehiscence of sporangium and liberation of spores.** As the sporangium approaches towards maturity, a transverse row of cells is differentiated near the apical portion from the wall of a sporangium known as stomium.
- The walls of the cell of stomium thicken and differ from the walls of other cells of the sporangium. As the sporangium loses water, it creates a pressure on the wall which leads to the appearance of slit in the stomium as a result of which the wall splits opens into two halves and the spores are disseminated by air current.

Gametophytic Generation:

The development of the gametophyte (prothallus) takes place from the haploid spores which are the unit of gametophytic generation. Each spore is unicellular, uninucleate haploid structure, 0.03 mm in diameter and surrounded by 2 layers, with a triradiate ridge at the surface (Fig. 8 D, E).

Chlorophyll may or may not be present in different species. In few species spores may germinate within a few days after liberation but in some species the spores germinate when they are 3-8 years old and the development of gametophyte upto formation of mature sex organs may take a time of 8 months to 6 or even 15 years.

The rate of the formation of photosynthetic tissue is usually proportional to the rate of growth of gametophyte. Both the male and female reproductive organs are produced on the same gametophyte. The male sex organs are produced earlier than female sex organs.

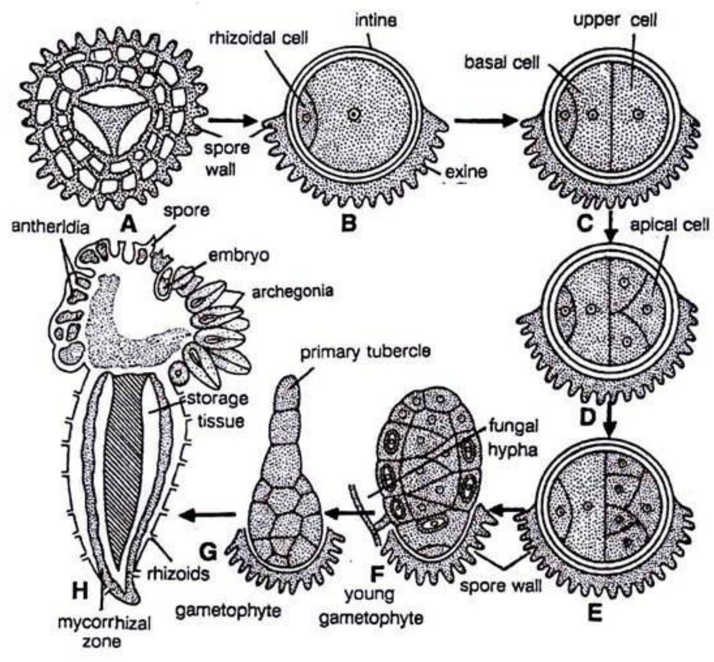


Fig. 10 (A–H). *Lycopodium* : Successive stages in the development of prothallus

- Usually at the time of germination of spore, it swells up to absorb water. First the spore divides into two unequal cells by a lenticular division, forming a very small lens shaped cell known as rhizoidal cell and a bigger cell (Fig. 10 A, B).
- This rhizoidal cell takes no part in further development of gametophyte and is a colourless structure. At this two celled stage the spore will rupture at the triradiate ridge. Second division divides the bigger cell into two equal halves, the cell near the rhizoidal cell is known as basal cell and the other one is known as upper cell (Fig. 10 C).
- The upper cell further divides by two successive divisions in such a way as to form an apical cell with two cutting faces (Fig. 10 D). At this stage the gametophyte is 5 celled structures and the symbiotic phycomycetous fungus (mycorrhizal fungus) attacks it.
- If this fungus fails to attack at this stage, further development of gametophyte stops. This infection takes place through the basal cell. During further course of development of gametophyte the apical cell further divides to form six or more cells which later on develop into meristematic cells. These cells, by further divisions form a multicellular structure, the gametophyte (prothallus) (Fig 10 E-H).

Structure of the Mature Gametophytes:

The form and structure of the gametophytes varies greatly in different species.

In general they have been grouped under three categories:

Type I or Cernuum type:

- Gametophyte is partially aerial and partly in soil. The prothalli are usually 2 to 3 millimetre in height and 1-2 millimetre in diameter. The gametophytes (prothalli) grow at the surface of the ground and consist of a colourless basal portion buried in soil and a conspicuous upright, fleshy, green aerial portion having lobes (Fig. 11 A).
- The sex organs develop between the green expanding lobes. The prothallus itself is a nourishing body. The underground part contains endophytic fungus e.g., *L. cernuum*, *L. inundatum* etc.

Type II or Clavatum Type:

- The gametophyte is wholly subterranean and totally saprophytic i.e., non- green structure. It is tuberous and without lobes. It may be one to two centimentre long or wide and is top shaped, conical or discoid in shape (Fig. 11 B, C). The endophytic fungus is present. Sex organs are formed on the upper surface e.g. *L. annotinum*, *L. complanatum*, *L. clavatum* etc.

Type III or Phlegmaria type:

- The gametophyte is subterranean, saprophytic and colourless. This type of prothallus is seen in L. phlegmaria and other epiphytic species. The prothallus is about 2 millimeter in diameter and monopodially branched (Fig. 11 D). Sex organs are borne on upper surface of large branches and are interspersed with slender filaments known as paraphyses.

- Besides these three forms some intermediate forms of prothalli are also observed. In *L. selago* the prothalli may be subterranean or epiterranean (aerial). If the spores are buried under the soil after liberation, they form subterranean prothalli and if the spores are not buried under soil after their liberation, they form epiterranean prothalli.
- The internal structure of the prothallus is very simple. The outermost layer is epidermis, followed by cortical mycorrhizal region, palisade region and central storage region. It is attached with the substratum by unicellular rhizoids. The prothalli of all species are monoecious i.e., antheridia and archegonia develop on the same prothallus.

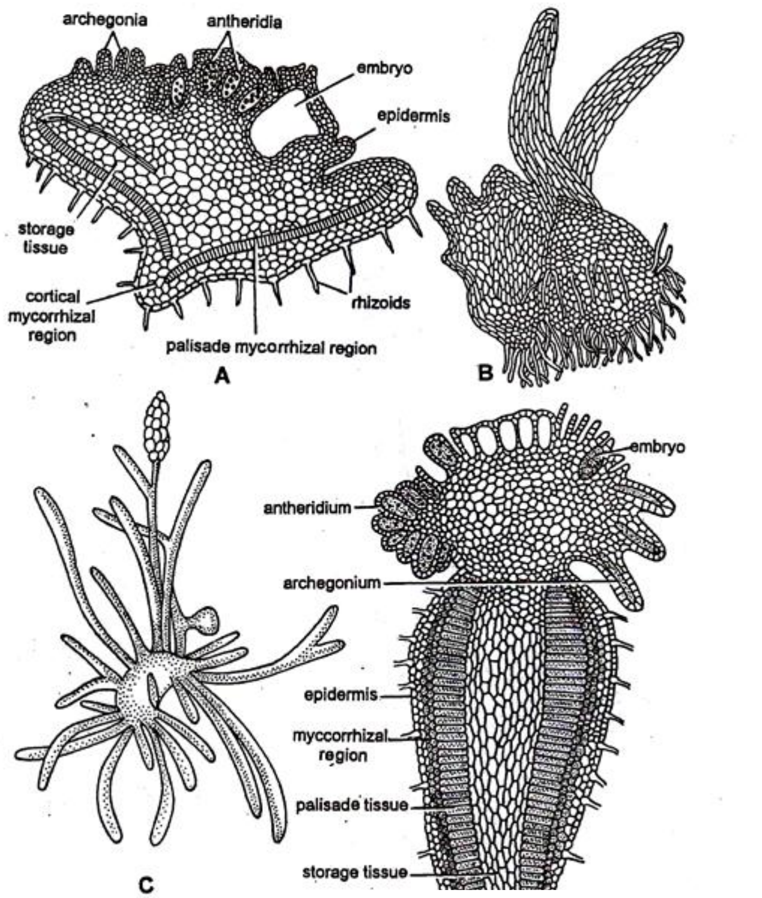


Fig. 11 (A–D). *Lycopodiun*

Development of sex organs:

- Both the sex organs i.e., antheridia (male) and archegonia (female) develop on the same prothallus, usually in distinct patches on the upper surface. The gametophytes are protandrous i.e., antheridia develop before archegonia. Sex organs develop just on the back of the apical meristem.

Development of antheridium:

- A single superficial cell situated just away from the meristematic cells gives rise to an antheridium. This superficial cell is known as antheridial initial (Fig. 12 A). This cell divides periclinally to form an outer cell known as jacket initial (primary wall cell) and an inner cell known as primary androgonial initial or cell (Fig. 12 B).
- The jacket initial divides only anticlinally by several divisions resulting in the formation of single layered covering known as jacket layer. In the middle of the jacket layer a triangular cell is differentiated, which is known as opercular cell.

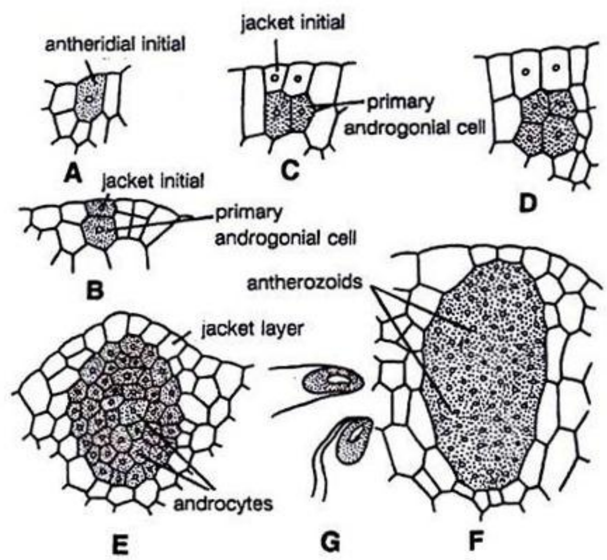


Fig. 12 (A–F). *Lycopodium* : Development of antheridium

- Simultaneously, the primary androgonial divides by various divisions, forming a mass of cells embedded in the prothallus, known as androgonial cells which finally give rise to androcytes (antherozoid mother cells, Fig. 12 C-F). The number of androcytes per antheridium varies in different species.

- Each androcyte later on metamorphosis into a biflagellated antherozoid. Each antherozoid is a haploid, uninucleate, fusiform structure with broad rounded posterior end and an upper pointed biflagellated anterior end (Fig- 12 G).
- The triangular opercular cell becomes mucilaginous as a result of which an opening is formed at the apex of antheridium through which water enters into it. The antherozoids absorb water and swell up as a result of which a pressure is created on the wall of antheridium which finally ruptures and the antherozoids are liberated.

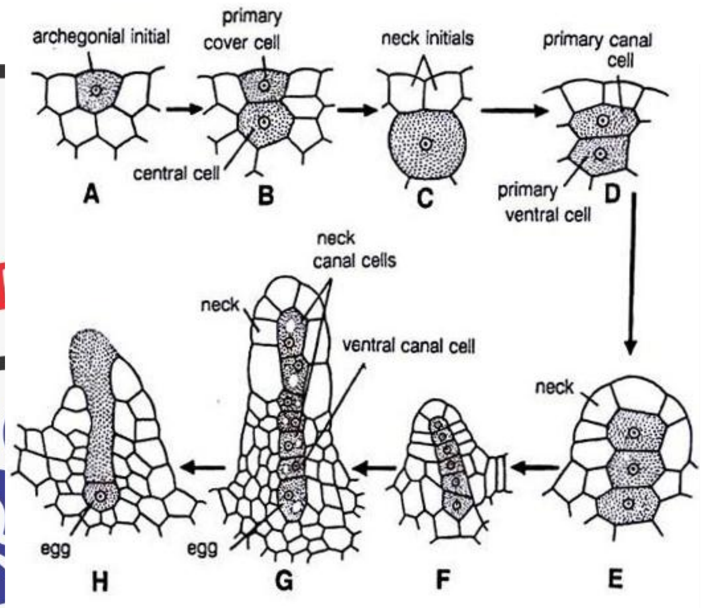


Fig. 13 (A–H). *Lycopodium* : Development of archegonium

Development of archegonium:

- Just like antheridium, the archegonium also arises from a single superficial cell called archegonial initial, situated just away from the meristematic cells at the apex (Fig. 13 A). The archegonial initial divides by periclinal division into an upper primary cover cell and lower basal central cell (Fig. 13 B).
- The primary cover cell later on divides vertically by two successive divisions at right angle to each other forming four neck initials which later on by transverse divisions form a 3-4 cells high neck. Each tier of the neck consists of 4 cells.
- The central cell divides transversely forming an, upper primary canal cell and a lower primary ventral cell (Fig. 13 D). The primary canal cell by successive transverse divisions produces a variable number of neck canal cells (usually one in *L. cernuum*, seven in, *L. selago* and 14-16 in *L. complanatum*).
- The primary ventral cell may directly behave as an egg or may divide transversely to form an upper ventral canal cell and a lower egg (Fig. 13 E-G). The egg is somewhat broader then the rest part of archegonium. The archegonial jacket is absent. The archegonium is a sunken flask shaped structure with neck projecting out of the prothallus.

Fertilization:

- At the time of fertilization the neck canal cells and the ventral canal cell disorganise and the cells of the upper-most tier of neck slightly separate apart forming a passage upto the egg (Fig. 13 H). Fertilization is brought about in the presence of water.
- The biflagellate antherozoids reach the archegonium by swimming in water on the surface of prothallus. The antherozoids are perhaps attracted towards the neck of archegonium by a chemotactic movement. They enter the archegonium through neck and reach the egg.

- Only the nucleus of one antherozoid fuses with the egg nucleus thus forming a diploid structure-known as oospore (2x). The act of fertilization ends the gametophytic generation and the initial stage of sporophytic generation is formed.

Embryo Development (Young Sporophyte):

- The rate of development of the embryo is extremely slow. In *Lycopodium* embryo develops downward into the gametophytic tissue instead of developing upward i.e., towards the neck of archegonium. The first division of the oospore is always transverse, forming an upper cell (epibasal) and a lower cell (hypobasal) known as embryonic cell.

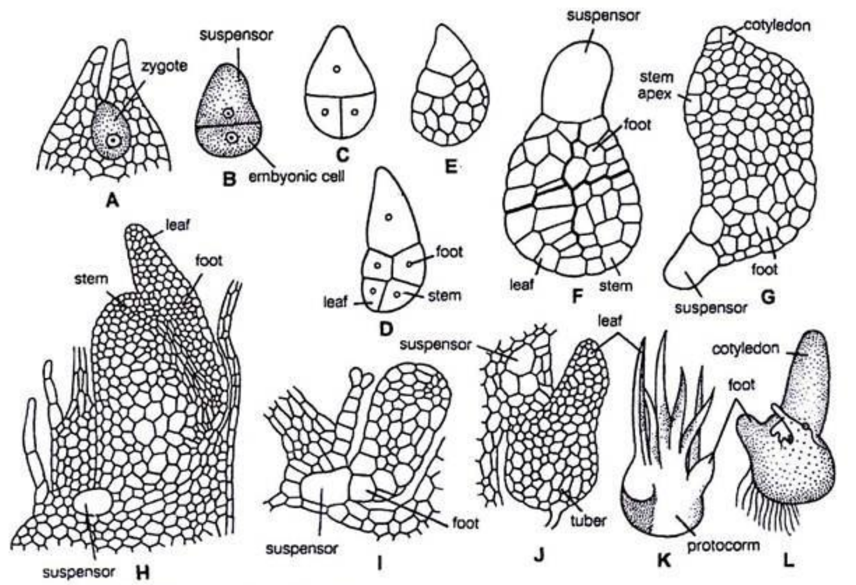


Fig. 14 (A–L). *Lycopodium* :(A–J). Stages in the development of embryo, (K, L). Portocorm

- The upper cell does not divide further and behaves as suspensor. The lower cell (embryonic cell) divides by two vertical divisions at right angle to each other, followed by a transverse division, forming 8 cells (octant, Fig. 14 A-D). The 4 cells of the octant, situated near the suspensor by further division, form a multicellular foot which acts as a haustorium and helps in the absorption of food material from the gametophytic tissue.
- Out of the 4 remaining cells of the octant, the 2 cells towards the meristematic region give rise to stem and the other 2 cells give rise to primary leaf and primary root (Fig. 14 D-J). The primary stem is short lived and is replaced by adventitious outgrowth which gives rise to horizontal stem. More roots develop from the stem.
- The primary roots of the sporophyte are exogenous in origin while those arising later on are endogenous in origin. The embryo obtains its nourishment for a long time from the gametophyte.
- In some species e.g., *L. cernuum* etc. the gametophyte is generally green. The oospore normally divides transversely forming suspensor and embryonic cell. The embryonic cell forms an octant. The tier which gives rise to stem, leaf and primary roots, develops into a massive spherical structure of parenchymatous cells, known as protocorm (Fig. 14 K, L).

- It grows through the gametophyte, becomes green and develops rhizoids on its lower surface. The upper surface of the protocorm gives rise to a few to many erect outgrowths which are leaf like and are known as protophylls.
- The protophylls are provided with stomata. At this stage the protocorm separates from the gametophyte. Now at the upper side of protocorm a region is differentiated which develops into stem. Protocorm is regarded as the intermediate phase in between normal embryo and definite leafy shoot.

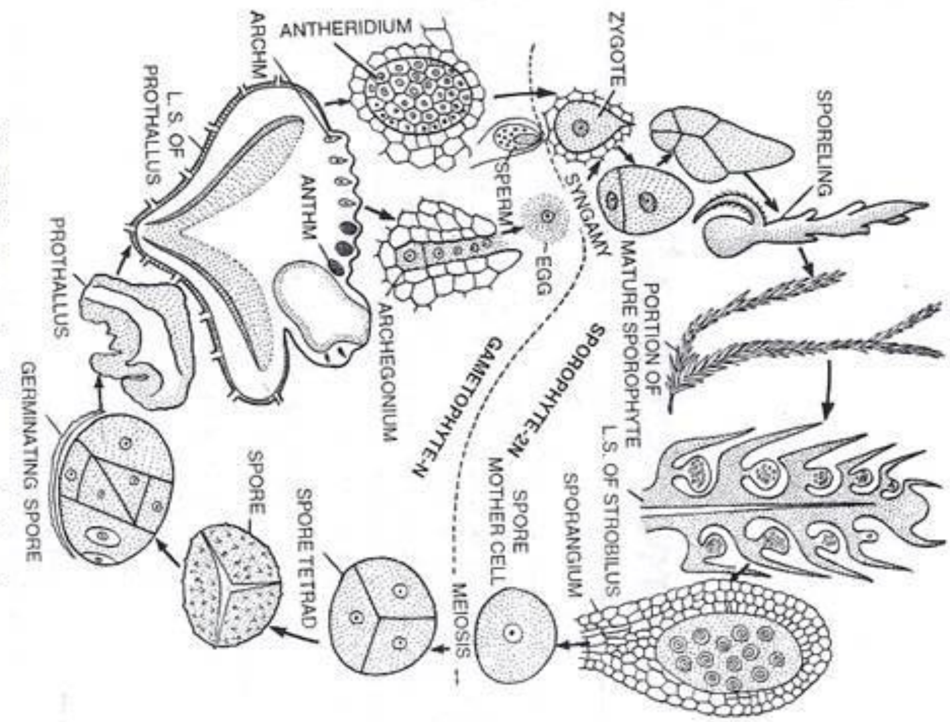


Fig. 27.26. *Lycopodium*. Diagrammatic life-cycle.

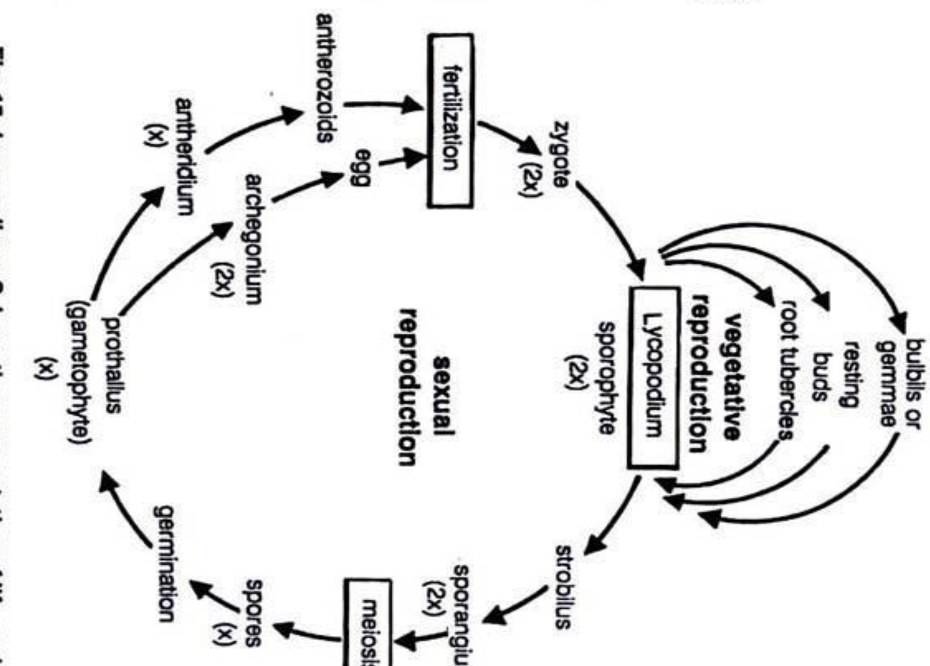


Fig. 15. *Lycopodium* : Schematic representation of life cycle

Selaginella

SYSTEMATIC POSITION:

Division : Lycophyta
Class : Ligulopsida
Order : Selaginellales
Family : Selaginellaceae
Genus : *Selaginella*

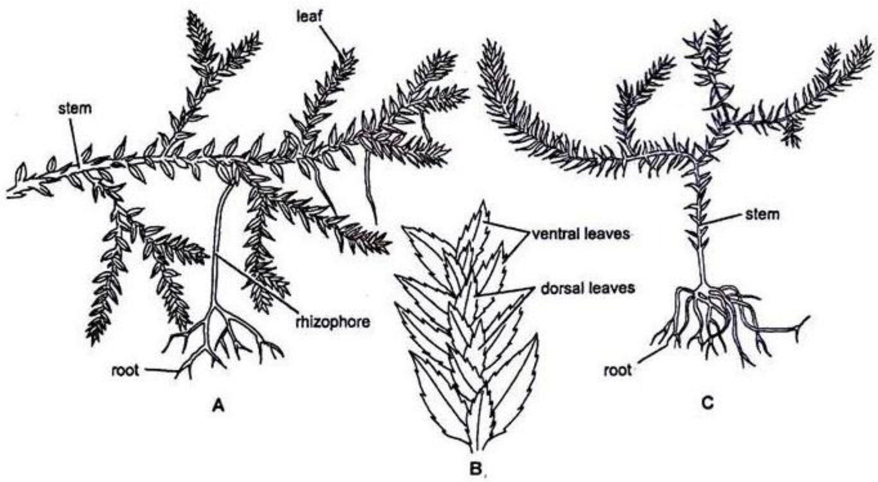


Fig. 1 (A–C). *Selaginella*. External features : A. *S. kraussiana*, B. Leaf arrangement in a branch of *S. kraussiana*, C. *S. spinulosa*

Habit and Habitat of *Selaginella*:

- *Selaginella* is commonly known as 'spike moss' or 'small club moss'. It is a large genus comprising of about 700 species distributed all over the world. Abundantly it is found growing in tropical rain forests.
- Mostly the species prefer moist and shady places to grow but a few species are also found growing in xerophytic conditions i.e., on dry sandy soil or rocks e.g., *S. lepidophylla*, *S. rupestris* etc. A very few species are epiphytes e.g., *S. oregena*. It is found growing on tree trunks.
- A few xerophytic species of Selaginella e.g., *S. lepidophylla* and *S. pilifera* show cestipose habit and are sold as curiosities under the name of resurrection plants. They curl and become ball like when dry and again become green and fresh when moisture is available. About 70 species have been reported from India.
- They are mainly found growing in eastern as well as Western Himalayas and the hills of South India. Some of the common Indian species are *S. repanda*, *S. biformis*, *S. denticulata*, *S. monospora*, *S. semicordata*, *S. adunca* etc. *S. kraussiana* is cultivated in green house.

External Morphology of Selaginella:

- The sporophyte is an evergreen, delicate herb. Its size varies greatly from species to species i.e., from a few cm. to 20 meters. Plants may be erect or prostrate depending upon the sub-genus. In the sub-genus *homoeophyllum* the plants are erect e.g., *S. rupestris*, *S. spinulosa* etc. and in the sub-genus *heterophyllum* the plants are prostrate e.g., *S. kraussiana*, *S. lepidophylla* etc.

The plant body is distinctly differentiated into following structures (Fig. 1 A, C):

(i) Stem (ii) Leaves (iii) Ligules (iv) Rhizophore (v) Roots

(i) Stem:

- It is usually profusely branched, delicate and evergreen. The branching is of monopodial type. The growing apex of the stem consists of either meristematic tissue or a single apical cell. In *homoeophyllum* the stem is erect and somewhat cylindrical and in *heterophyllum* it is prostrate with stout erect branches and is somewhat dorsiventral.

(ii) Leaves:

- They are usually small, simple and lanceolate with a pointed apex. Each leaf is provided with a single unbranched midrib. In *homoeophyllum* all the leaves are of same size and are spirally arranged forming a dense covering.
- In *heterophyllum* the leaves are dimorphic i.e., of two size (small and big) and are arranged in pairs. Small leaves are present on the dorsal side of the stem and bigger ones on the ventral side of the stem (Fig. 1 B). The bigger leaves alternate with bigger ones and smaller leaves alternate with smaller ones.
- Usually the leaves near the apical portion of the branch, bear sporangia (micro-or mega) and are called as sporophylls (micro-or mega) respectively. The sporophylls are usually aggregated into a condense structure which is known as strobilus.

(iii) Ligules:

- On the adaxial side of the leaf, near the base is present a small membranous out-growth known as ligule. It is embedded at the base of a leaf in a pit like structure known as ligule pit.
- It may be tongue shaped (e.g., *S. vogelii*), fan shaped (e.g., *S. martensii*), fringed (e.g., *S. cuspidata*), or lobed (e.g., *S. caulescens*). It is more than one cell in thickness except at the apex. The structure of the ligule can be differentiated into two parts, glossopodium and the body of the ligule (Fig. 2 A, B).

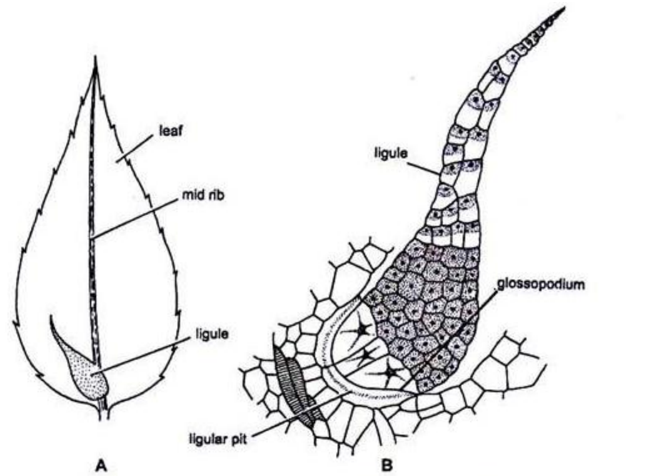


Fig. 2 (A, B). *Selaginella*. Structure of ligule : A. Leaf with ligule, B. Longitudinal section of ligule

Glossopodium:

- It is the basal hemispherical part made up of large thin walled cells. It is surrounded by a glossopodial sheath.

Body of the ligule:

- Above the glossopodium is the body of ligule. It is made up of many large and small cells. The function of the ligule is not well known. It may be a water secreting or water absorbing or protective organ. According to Earner (1936) the ligule is perhaps a vestigial organ.

(iv) Rhizophore:

- This structure arises from the prostrate axis at the point of dichotomy and elongates downward. It is a colourless, leafless, unbranched and cylindrical structure.
- As soon as the free end of rhizophore touches the soil it develops a tuft of adventitious roots at its free end. In few species the rhizophore is present e.g., *S. kraussiana* while in others it is absent e.g., *S. cuspidata*. It differs from root in having no root cap and from stem in having no leaves.

(v) Roots:

- They originate either from the tips of rhizophores or directly from the stem or from the swollen base of hypocotyl (Fig. 1 A, B). Their origin is endogenous. They are usually dichotomously branched structures. The roots are provided with root caps and root hairs.

Internal Structure of Selaginella:

1. Stem:

A Tranverse section (T.S.) of the stem of Selaginella is somewhat circular in outline and shows the following structures:

(i) Epidermis:

- It is the outer most covering layer comprising of a single cell in thickness. The cells of the epidermis are without stomata. The epidermis is surrounded on all sides by a thick coating of cuticle.

(ii) Cortex:

- Inner to the epidermis is present a well-defined zone of cortex. The cortex may or may not be differentiated into inner and outer cortex. In case of *S. selaginoides*, the whole of the cortex is made up of parenchymatous cells while in *S. kraussiana*, it is differentiated into sclerenchymatous outer cortex and parenchymatous inner cortex.
- The parenchymatous cortex is usually made up of angular cells i.e., without intercellular spaces but in some cases the cells are rounded and provided with a few inter-cellular spaces.

(iii) Stele:

- The central portion of the stem is occupied by a well-developed stele. The stele is of protostelic type i.e., xylem is present in the centre and surrounded by phloem on all sides. Phloem, in turn, is surrounded by a single layered pericycle. Pith is absent.

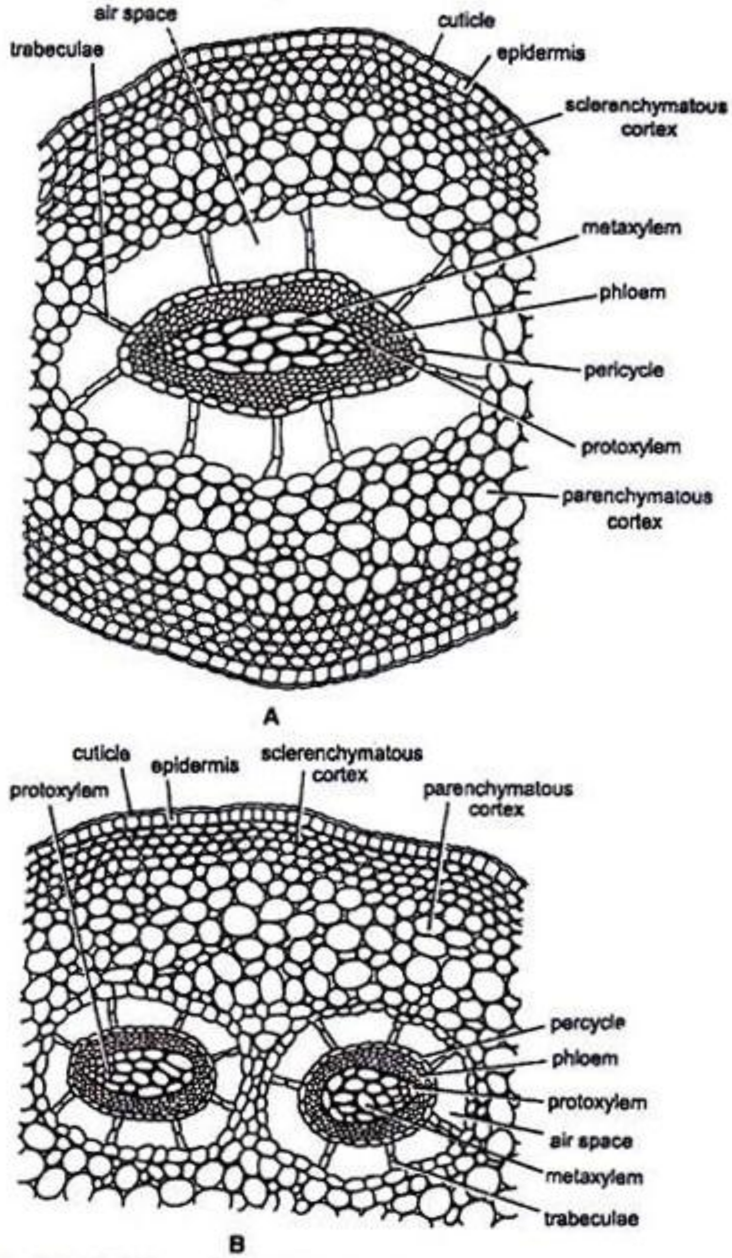


Fig. 3 (A–B). *Selaginella*. T. S. Stem. (A) T. S. monostelic stem, (B) T. S. distelic stem (a part cellular),

- The stele remains suspended in the centre by radially elongated tubular, unicellular structures known as trabeculae. These are formed by the radial elongation of the endodermal cells. Trabeculae are provided with conspicuous casparian strips. In between the trabeculae are present large spaces known as air spaces.
- The number of stele is variable in different species of Selaginella. It is 1 (monostelic e.g., *S. spinulosa*), 2 (distelic e.g., *S. kraussiana*) or 12-16 (polystelic e.g., *S. laevigata*). The organization of the stele is also variable in different species. It may be protostele (e.g., *S. spinulosa*) to siphonostele (e.g., *S. laevigata*, var. *lyalli*).

- The stele is surrounded by a single layered pericycle made of parenchymatous cells. The xylem is usually monarch (e.g., *S. kraussiana*), or diarch (e.g., *S. oregana*) or multiarch (e.g., *S. spinulosa*).
- It is usually exarch but sometimes it may be mesarch (e.g., *S. selaginoides*). Xylem is usually made of tracheids. Vessels are completely absent. Xylem is surrounded on all sides by phloem which consists of sieve cells and phloem parenchyma. Companion cells are absent in phloem.

2. Root:

A T.S. of the root is somewhat circular in outline (Fig. 4) and shows the following internal structures:

(i) Epidermis:

- It is the outermost covering layer and is only one cell in thickness. The cells are large and the unicellular root hairs arise from them.

(ii) Cortex:

- Just below the epidermis is present a wide zone of cortex. The cortex may be either wholly made up of thin walled parenchymatous cells or there may be sclerenchymatous outer cortex (hypodermis), 3 to 5 celled in thickness and parenchymatous inner cortex. In mature roots of *S. densa* the entire cortex may consist of thick walled sclerotic cells. Air spaces have also been reported in the inner cortex (e.g., *S. willedenovii*). It is traversed by trabeculae.

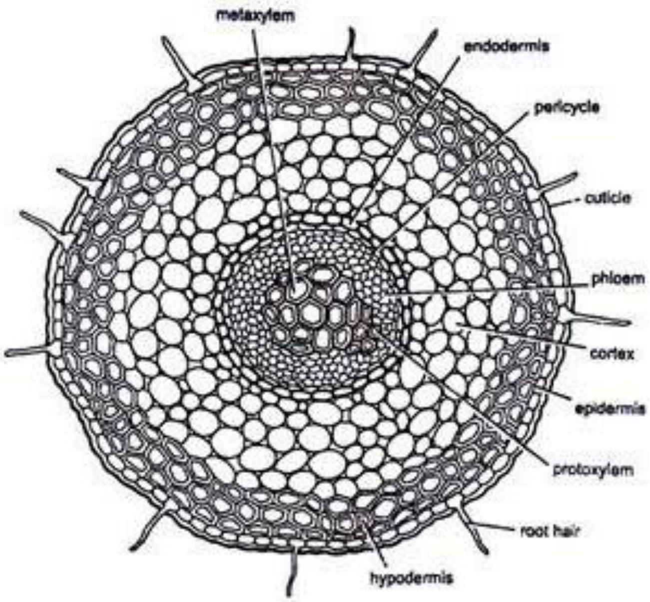


Fig. 4. ***Selaginella*. T. S. of root**

(iii) Endodermis:

- It is usually not well defined but in some species as for example, *S. densa*, it is a distinct structure and only one cell in thickness.

(iv) Pericycle:

- Endodermis is followed by one to three layered pericycle. It is made up of parenchymatous cells.

(v) Stele:

- It is a typical protostele. The xylem is exarch and monarch i.e., there is only one protoxylem group situated at the periphery. Xylem is surrounded by phloem on all sides. The structure of xylem and phloem elements is similar to that of stem.

3. Rhizophore:

- The internal structure of rhizophore is almost similar to that of root. It is also circular in outline.

It shows the following structures (Fig. 5):

(i) Epidermis:

- It is single layered and the outer wall of epidermal cells is covered with a thick cuticle. Root hairs and stomata are absent.

(ii) Cortex:

- Inner to the epidermis is present a wide zone of cortex differentiated into outer sclerenchymatous and inner parenchymatous zones.

(iii) Endodermis:

- It is inner-most layer of the cortex. It is ill defined single layered structure.

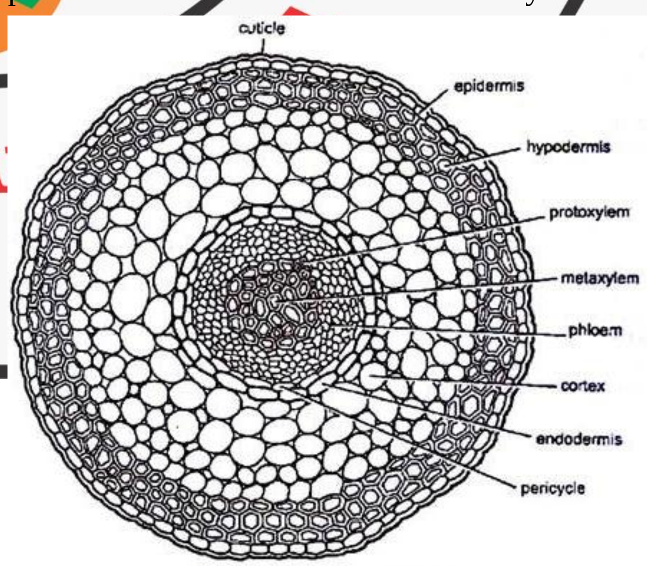


Fig. 5. ***Selaginella*. T. S. rhizophore**

(iv) Pericycle:

- Inside the endodermis is present a single layered parenchymatous pericycle.

(v) Stele:

- It is typically a protostele. The xylem is surrounded by phloem. Xylem shows distinct protoxylem and metaxylem elements. The position of protoxylem is different in different species. In *S. martensii* xylem is exarch and monarch. In *S. atroviridis* the metaxylem is crescentric with a number of protoxylem strands situated on the concave adaxial side. In *S. kraussiana*, *S. poulteri* etc. protoxylem is mesarch (centroxylic).

4. Leaf:

A T.S. of the leaf shows epidermis, mesophyll and a single median vascular bundle which has been discussed below in detail:

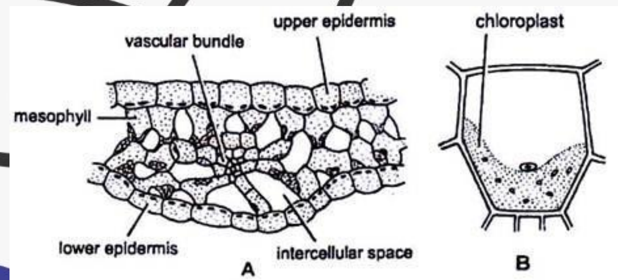


Fig. 6. (A–B). *Selaginella* : Internal Structure of leaf. A. T. S. of a part leaf of *S. kraussiana*, B. A mesophyll cell

(i) Epidermis:

- It is the outermost surrounding layer and is only one cell in thickness. In most of the species the stomata are present only on the lower epidermis near the midrib. The stomata may be present on both the outer and inner epidermis. The cells of the epidermis are provided with chloroplasts.

(ii) Mesophyll:

- It occupies a wide zone between upper and lower epidermis. The mesophyll is usually made up of parenchymatous cells which have conspicuous intercellular spaces. Each mesophyll cell has one (e.g., *S. martensii*), two (e.g., *S. kraussiana*), or eight (e.g., *S. willedenovii*) chloroplasts.
- Each chloroplast has several pyrenoid like bodies. In some species (e.g., *S. concinna*) the mesophyll is distinguished into upper palisade and lower spongy parenchyma.

(iii) Vascular bundle:

- Only one vascular bundle is present in the centre. It is concentric and amphicribal (ectophloic). It is made up of a few xylem tracheids (annular or spiral) surrounded by phloem elements (a few sieve elements). A single layered bundle sheath encircles the phloem on all sides.

Reproduction in Selaginella:

- *Selaginella* reproduces by two methods: Vegetatively and by formation of spores.

1. Vegetative reproduction takes place by following methods:

(i) Fragmentation:

- Under humid conditions in *S. rupestris,* trailing branches of the stem develop adventitious branches. These branches later disjoin from the parent plant and develop into separate individual plants.

(ii) Tubers:

- These appear towards the end of the growing season. The tubers may be aerial, developing at the apical end of aerial branches (e.g., *S. chrysocaulos*) or subterranean (e.g., *S. chrysorrhizos*). Under favourable conditions tubers germinate into a new plant (Fig. 7A).

(iii) Resting buds:

- These are the compact structures which develop at the apical end of some aerial branches. The leaves in this region are closely arranged and overlap the growing points. These resting buds are capable to pass on the unfavourable conditions. Under favourable conditions these buds give off rhizophore that bear roots at their tips (Fig. 7B).

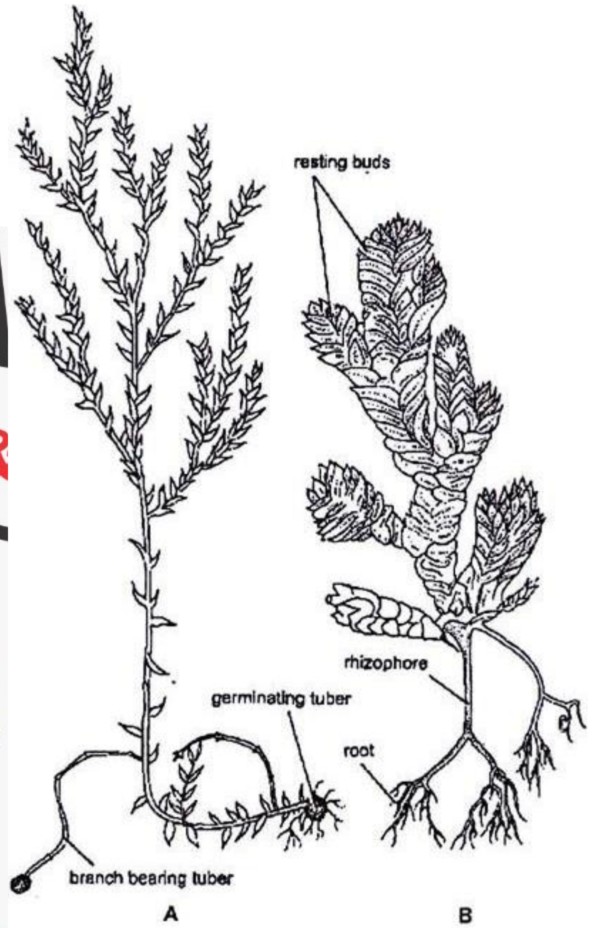


Fig. 7 (A–B). *Selaginella*. Vegetative reproduction, A. Tubers, B. Resting buds

2. Sexual Reproduction:

Spore producing organs:

- *Selaginella* is a sporophytic plant (2x) and reproduces sexually. The plants are heterosporous i.e., produce two different types of spores—megaspores and microspores. These spores are produced in megasporangia and microsporangia, respectively which, in turn, are produced on fertile leaves known as megasporophylls and microsporophylls respectively. Usually both these structures are grouped together to form a compact structure known as strobilus which is usually a terminal structure (Fig. 8 A).

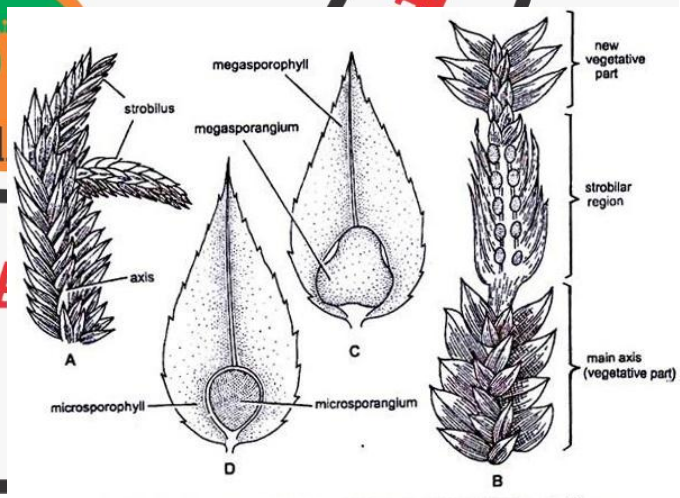


Fig. 8 (A–D). *Selaginella* : Structure of strobilus. A. A branch bearing strobilus, B. A branch after formation of strobilus region again changing into vegetative region, C. A megasporophyll, D. A microsporopyll

Strobilus:

- It is a reproductive structure formed by the aggregation of ligulate sporophylls at the apex of the branches of stem. The length of the strobilus varies from 1/4 inch to 2-3 inches in different species. In some species as for e.g., *S cuspidata*, *S. patula* etc. the growth of the stem continues beyond the strobilus and such condition is called selago condition (fertile part is alternated by vegetative parts, Fig. 8 B).

- The Longitudinal section (L.S.) of strobilus shows that it is a very simple structure. It consists of a central axis covered with spirally and densely arranged ligulate sporophylls. Each sporophyll adaxially bears a single stalked sporangium in its axis (Fig. 8C, D; 9A).
- The positions of the sporangia differ in different species. It may be in axil (axillary) or little upward on in position (cauline). Selaginella produces two types of spores—megaspores and microspores. The dimorphic condition of the spores is known as heterospory.
- In between the sporophyll and sporangium is present a small membranous structure known as ligule i.e., the sporophyll is similar to a vegetative leaf. The microsporangium produces large number of microspores whereas megasporangium produces usually 4 megaspores.

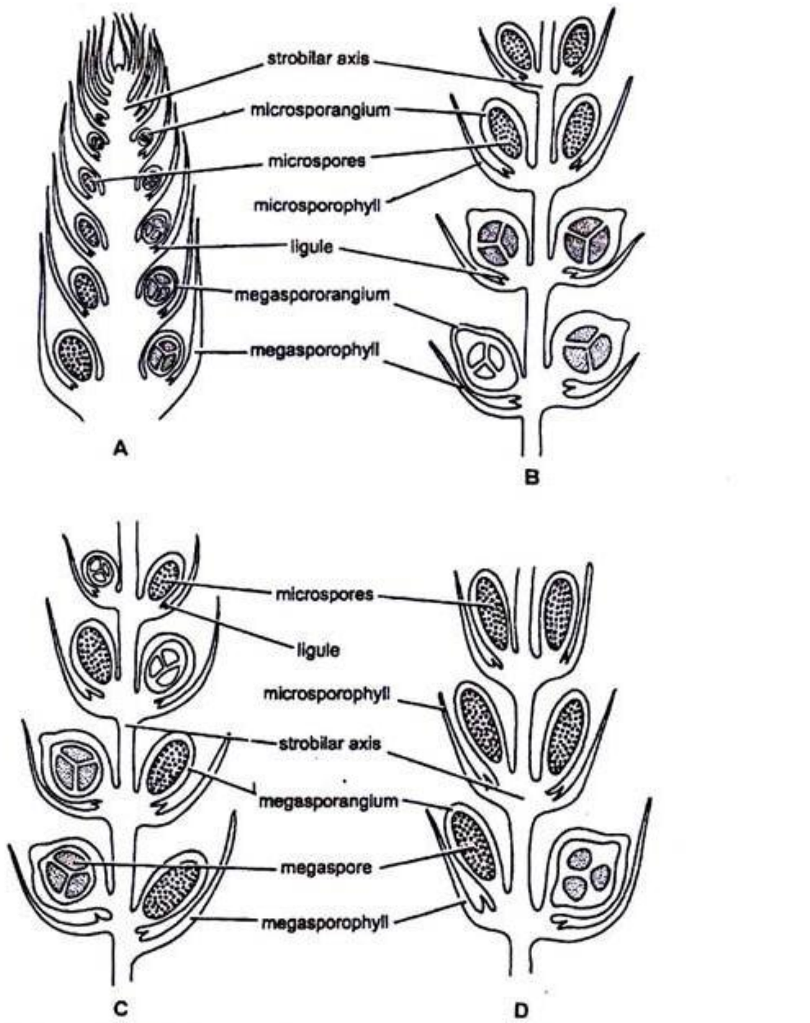


Fig. 9. (A–D). ***Selaginella.*** **Longitudinal sections of strobili of different species showing position of microsporangia and megasporangia A.** ***S. inaequalifolia*****, B.** ***S. rupestris*****, C.** ***S. martensii*****, D.** ***S. kraussiana***

- Strobili are usually bisporangiate but the arrangement of microsporophylls and megasporophylls differ in different species. In *S. inaequalifolia* (Fig. 9 A) the microsporophylls are present on one side and megasporophylls on the other side.
- In *S. rupestris* megasporophylls are present on the lower side and microsporophylls on the upper side of the strobilus (Fig 9 B). In case of *S. martensii* the microsporophylls are mixed irregularly with megasporophylls (Fig. 9 C). In *S. kraussiana* only one megasporophyll is present while all the rest are microsporophylls (Fig. 9 D). In case of *S. gracilis* the strobilus is unisporangiate i.e., either it bears microsporophylls or megasporophylls alone.

Microsporangium:

- Each microsporangium is a stalked, globular or elongated structure (Fig. 8 D). Its colour varies from red, yellow to brown in different species. The wall is 2 layered thick which is followed by a conspicuous tapetum (Fig. 10 F). In the young sporangium inside the wall is present a mass of sporogenous cells which in due course of development separate into microspore mother cells and later on by meiotic divisions produce numerous haploid tetrads of microspores.

- The microspores at maturity separate from each other. At maturity the tapetal cells as well as the inner wall of the microsporangium disorganizes i.e., wall of the sporangium is usually one layered at maturity. Microspores are smaller in size.

Megasporangium:

- Each megasporangium is also a stalked but lobed structure and somewhat bigger than the microsporangium. Its colour varies from whitish yellow to red. Its wall is also 2 layered thick and followed by a single layered tapetum (Fig. 10G). In the young sporangium inside the wall is present a mass of sporogenous cells which in due course of development separate into megaspore mother cells. All the megaspore mother cells accept one degenerate.
- The remaining one later on by meiotic division produces only 4 haploid megaspores. Sometimes less than 4 megaspores are produced inside each megasporangium. As for example, *S. rupestris* produces only one megaspore per megasporangium. At maturity the tapetal cells usually along with inner wall of the sporangium disorganise. Megaspores are larger in size than microspores (Fig. 10 G).
- The sporangia usually dehisce by a vertical slit formed in apical region of the sporangia and the spores are disseminated in the air.

Development of sporangium and formation of spores:

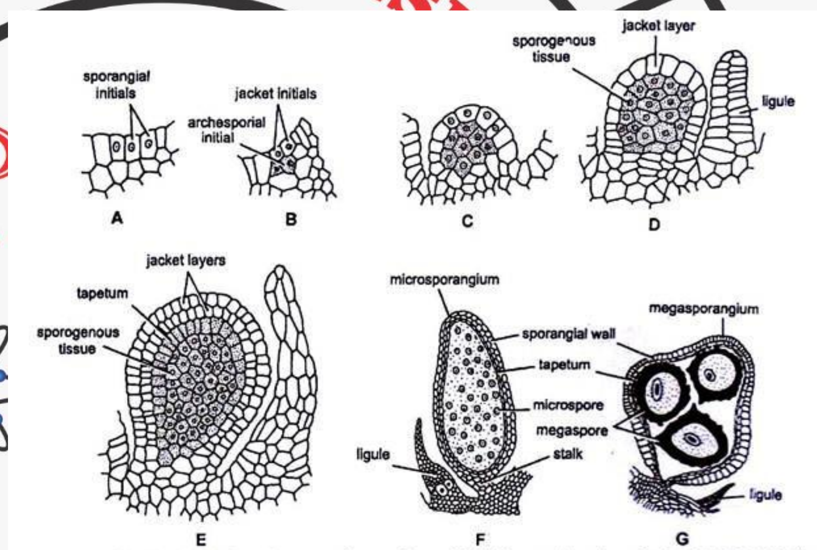


Fig. 10. (A–G). *Selaginella*. Development of sporanigum. (A–E). Successive stages in the development of microsporangium in *S. kraussiana*, F. Mature microsporangium, G. Mature megasporangium

- As the position of sporangium is either cauline or foliar, the initials are either situated on the axis or on the leaf respectively. The development of sporangium and formation of spores (micro-and mega) is similar upto the formation of spore mother cells and is as follows:
- The development is of eusporangiate type i.e., it takes place with the help of a row of initials which are known as sporangial initials e.g., *S. kraussiana* (in some cases from a single sporangial initial cell e.g., *S. spinulosa*). These cells are superficial in position (Fig. 10 A).

Gametophytic Generation:

- The development of male and female gametophytes (prothalli) takes place from the haploid microspores and megaspores respectively i.e., microspores and megaspores are the unit of male and female gemetophytes, respectively.

Spore:

- The microspores are small, 0 015 to 0 05 millimeter in diameter, spherical or round in shape and double layered structures. The outer wall is thick and known as exospore (exine). While inner wall is thin and is called endospore (intine, Fig 11 A-C).

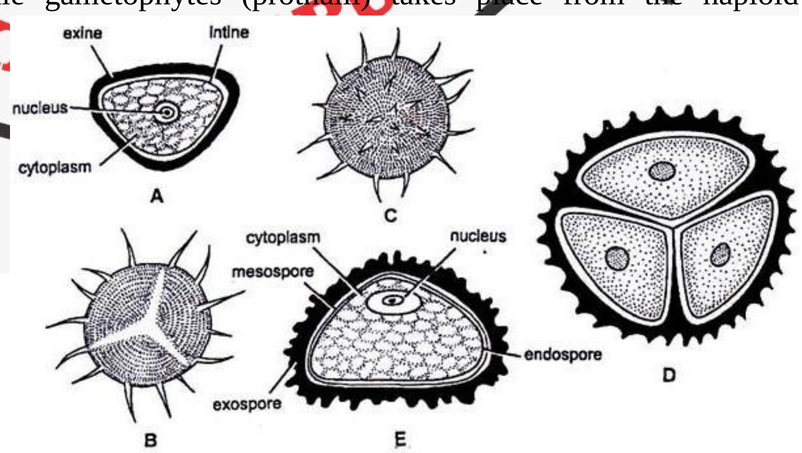


Fig. 11 (A–E). *Selaginella*. Structure of spores : A. A single microspore showing detailed structure, B. Apical view of spore, C. Basal view, D. Megaspore in tetraed, E. A single megaspore.

- The megaspores are much larger than microspores, 1.5 to 5 millimeter in diameter, tetrahedral in shape and show triradiate ridge. The megaspore has three wall layers namely exosporium, mesosporium and endosporium (Fig. 11 D, E). The microspores on germination give rise to male prothalli and megaspores to the female prothalli.

Development of male gametophyte:

- The microspore is the initial stage in the development of male gametophyte. The development of the microgametophyte is in situ or precocious i.e., it starts within the microsporangium.
- Each microspore is a unicellular, uninucleate, rounded or spherical, haploid structure with outer spiny thick exosporium and inner thin endosporium.
- Primary androgonial cells divide and redivide to form 128 or 256 androcytes or antherozoid mother cells.
- Each antherozoid mother cell finally metamorphosis into a single antherozoid (Fig. 13 F, G) which is a spirally coiled, uninucleate and biflagellate structure. The two flagella are unequal in size. The antherozoids are liberated by the rupturing of endosporium and swim in water till they reach the neck of archegonium.

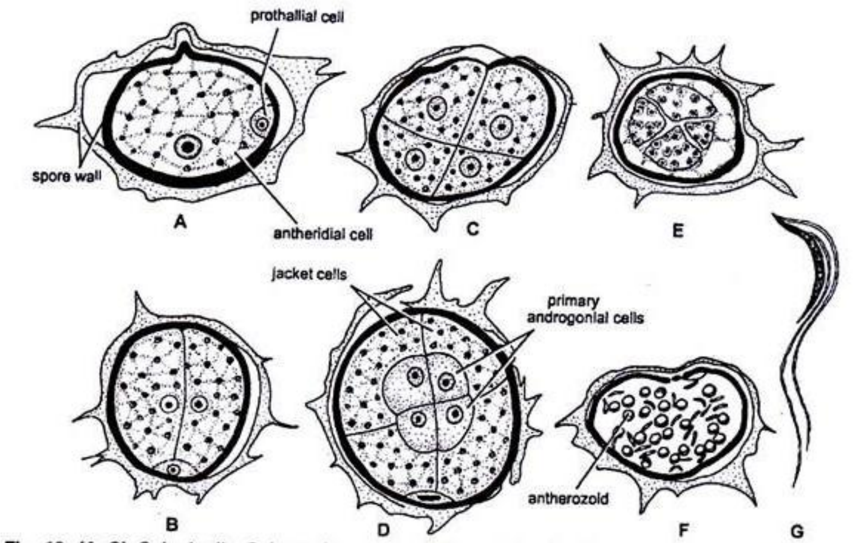


Fig. 13. (A–G) *Selaginella*. Schematic representation of the development of male gametophyte

Development of female gametophyte:

- The megaspore is the initial stage in the development of female gametophyte. The development of female gametophyte starts while the megaspore is still inside megasporangium. The megaspores are liberated from the megasporangium either at the time of first archegonium formation or just after fertilization.
- First of all the exospore or outer wall grows faster than the mesosporium which result in the formation of space between exosporium and mesosporium. The whole structure increases in size as a result of which a big central vacuole appears (Fig. 14 A).

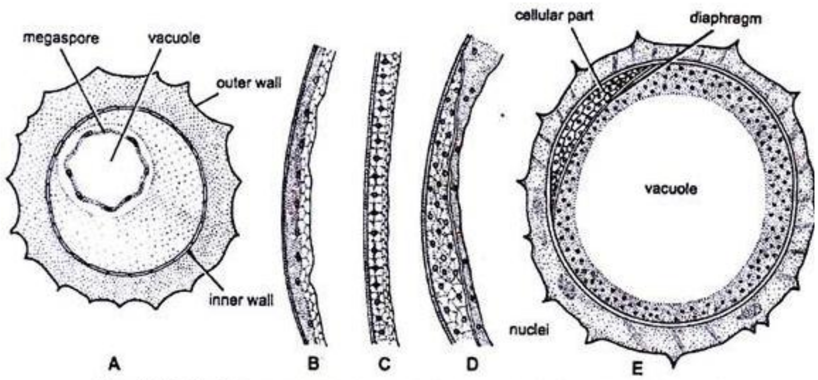


Fig. 14 (A–E). *Selaginella*. Stages in the development of female gametophyte

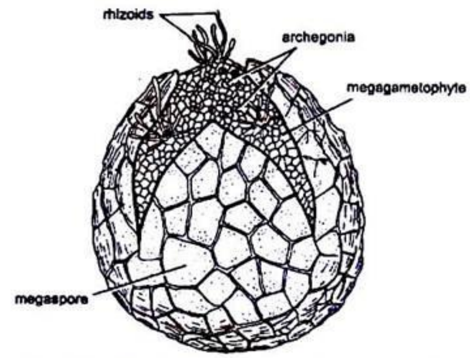


Fig. 15. ***Selaginella*. Female gametophyte. A. Dehiscent megaspore and rhizoids in *S. kraussiana***

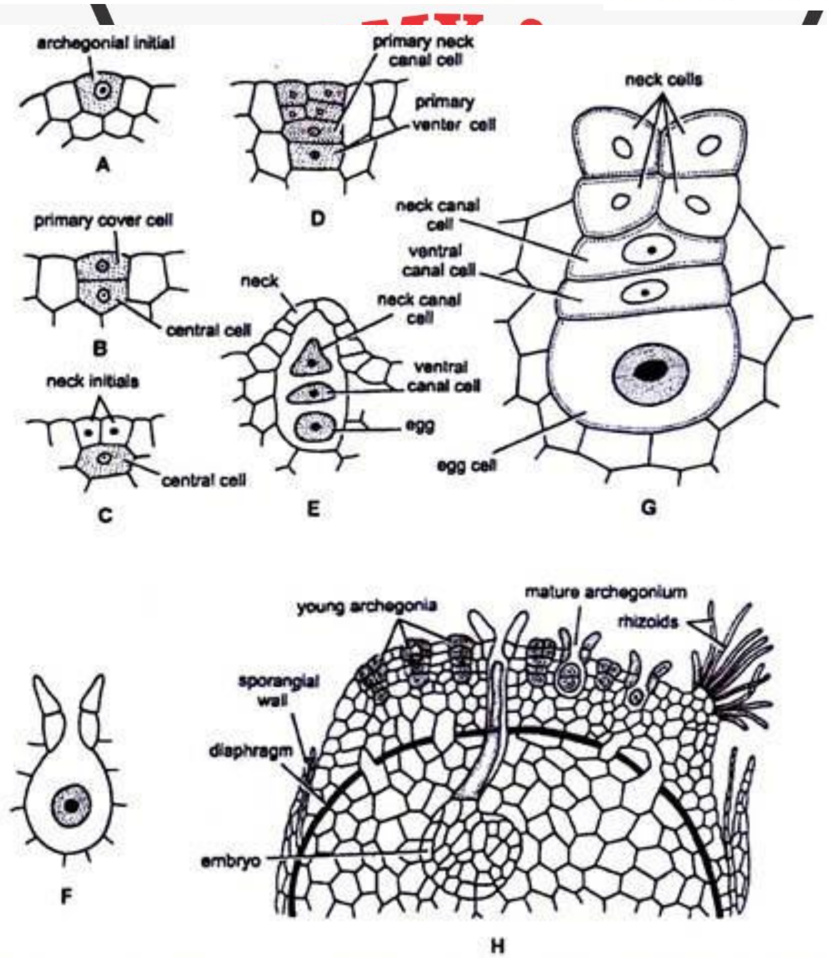


Fig. 16 (A–G). *Selaginella* : Development of archegonium. A–F. Various stages in the development, G. A mature archegonium before fertilization, H. A nearly median section of a mature prothallus showing various stages in the development of archegonium.

Structure of Mature Archegonium:

- The archegonium is a short flask shaped structure embedded in female gametophytic tissue (Fig. 16 H). Only the upper tier of neck cells projects out. Each archegonium consists of a short neck of 2 tiers of 4 cells each and a broad venter. The four cells of the upper tier of neck function as cover cells.
- The neck encloses a single neck canal cell and the venter consists of a ventral canal cell and an egg (Fig. 16 G). There is no definite wall of venter. At maturity the neck canal cell and the ventral canal

cell disorganize and absorb water which creates a pressure to separate apart the cover cells (Fig. 16 F) through which the antherozoids enter the archegonium and reach the egg.

Fertilization:

- Water is necessary to carry out the process of fertilization. The swimming antherozoids reach the egg through the neck of archegonium and the nucleus of antherozoid fuses with the egg nucleus thus forming a zygotic nucleus. The fertilized egg secretes a wall around it forming a diploid structure known as zygote or oospore (2x). Thus the gametophytic generation ends and the initial stage of sporophytic generation is formed.
- In some species e.g. *S. intermedia* the egg develops into embryo without fertilization. This phenomenon is known as parthenogenesis.

Embryo Development (Young Sporophyte):

Development of embryo:

- Oospore is the initial stage of sporophytic generation. During development of the embryo, the oospore first divides by a transverse division into an upper suspensor initial (epibasal) and a lower embryo initial (hypobasal) (Fig. 17 A, B).
- Later on by further divisions it forms a multicellular structure which gets differentiated into foot, rhizophore, stem and cotyledons (Fig. 17 E-J).
- In some species of *Selaginella* (e.g., *S. apus* and *S. rupestris* the megagametophytes are never shed from the megasporangium and remain on the strobilus. The oospore completes its development within the megasporangium and the young embryo grows into a seedling, develop primary root and then falls on the ground (Fig. 18).

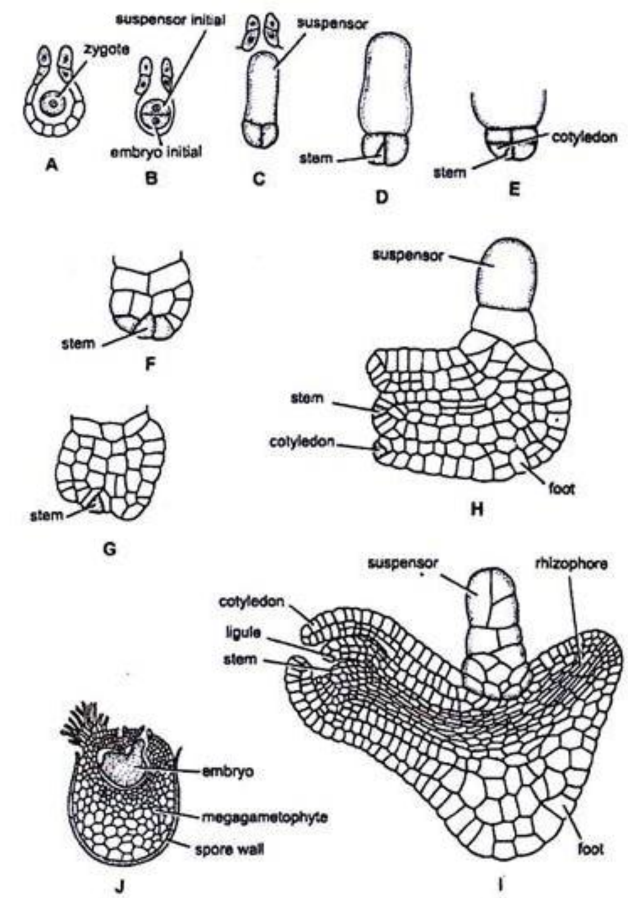


Fig 17 (A–J). ***Selaginella* : Development of embryo.**
A–I various stages in the development J. Longitudinal section of female gametophyte bearing embryo.

Life Cycle Patterns of *Selaginella*:

- *Selaginella* is a sporophytic plant (2x) and produces two different types of spores i.e., microspores and megaspores. In other words we may call it as heterosporous plant. These spores on germination produce male and female gametophytes (x) respectively which in turn developing upon the strobilus of parent produce antherozoids and egg in antheridia and archegonia respectively.

- These reproductive structures after fertilization produces zygote (2x) which again on germination gives rise to a sporophytic plant (2x). In this way the sporophytic and gametophytic generations alternate with each other although the sporophytic phase is dominant over gametophytic phase (Figs. 19, 20).

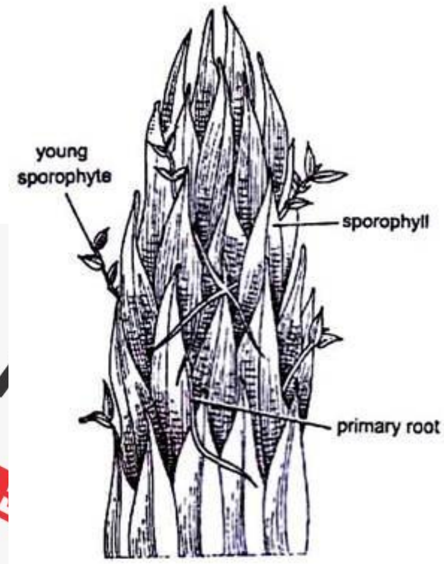


Fig. 18. *Selaginella.* Young sporophytes developing upon the strobilus of parent plant in *Selaginella rupestris.*

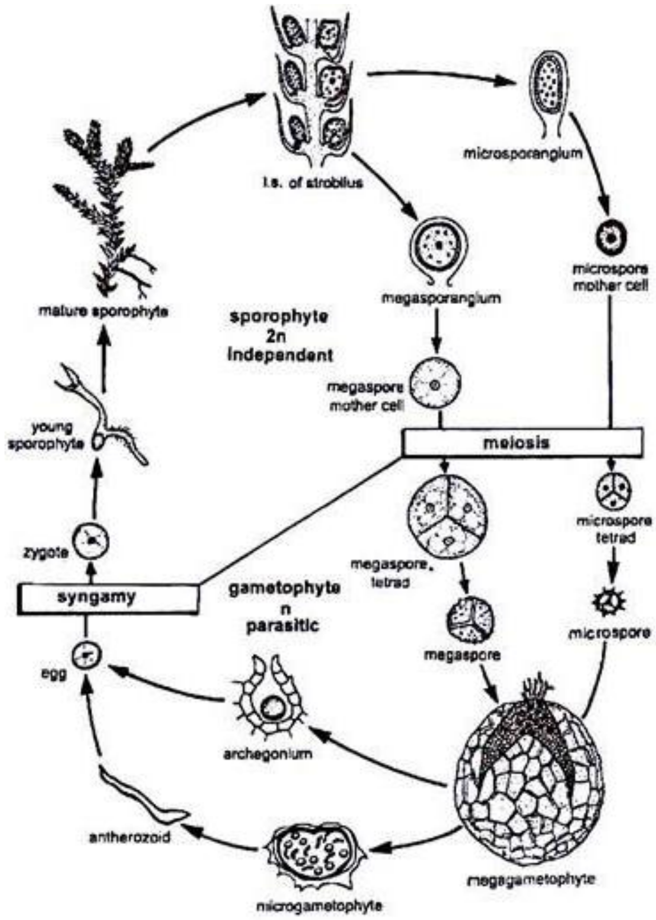


Fig. 19. Diagrammatic life cycle of *Selaginella*

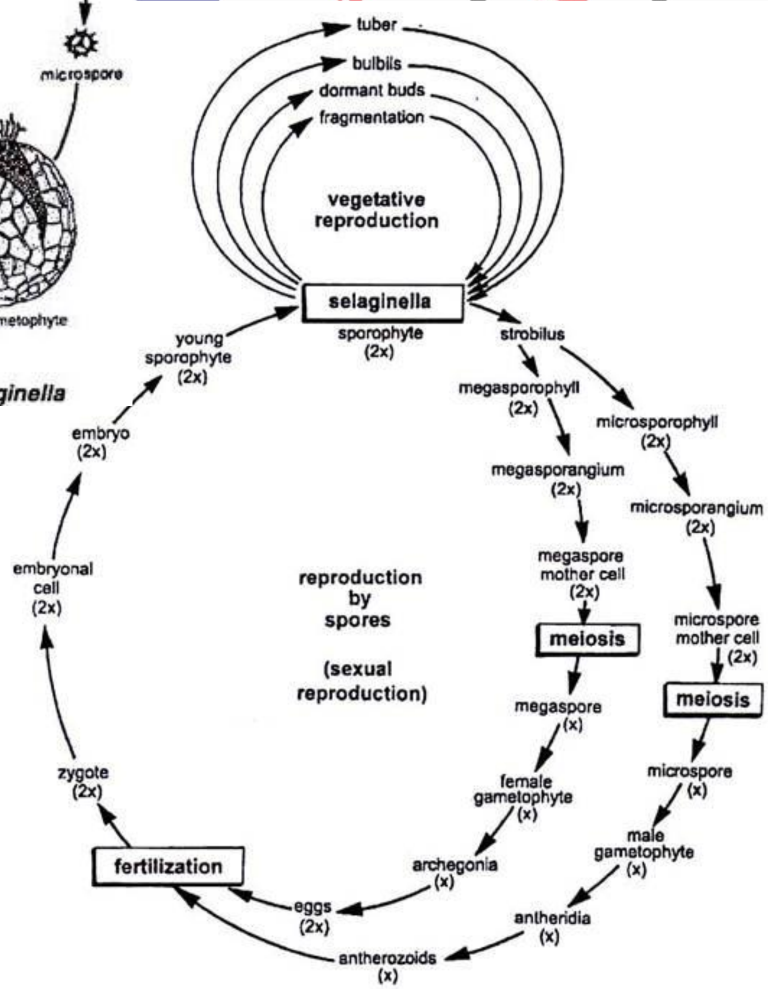


Fig. 20. *Selaginella* : schematic life cycle

Marsilea

SYSTEMATIC POSITION:

Division : Filicophyta (Pterophyta)
Class : Leptosporangiopsida
Order : Marsiliales
Family : Marsiliaceae
Genus : *Marsilea*

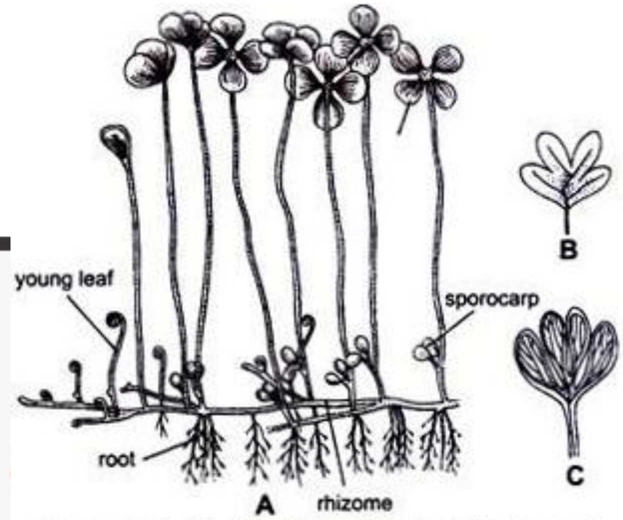


Fig. 1: (A–C). *Marsilea*. External features. A. External morphology; B. Leaf showing arrangement of segments as a result of three dichotomies, C. Pinna showing venation.

Habit and Habitat of Marsilea:

- *Marsilea* is commonly known as "pepper wort" or "water fern" (although it is a fern but hardly resembles a true fern). It is represented by about 53 species which are cosmopolitan in distribution but abundantly found in tropical countries like Africa and Australia. About 9 species have been reported from India.
- Either the species are hydrophytic or amphibious i.e., they grow rooted in mud or marshes and shallow pools or are completely submerged or partially or entirely out of water in wet habitats. *M. hirsuta* is an Australian xerophytic species. *M. hirsuta* and *M. quadrifolia* are two most common Indian species usually found growing in marshy places, wet soil or near muddy margins of ponds and are commonly found in U.P., Punjab, Bihar, Delhi etc.

External Features of Marsilea:

The mature sporophyte is an herbaceous plant. Its underground rhizome spreads in a diameter of 25 meter or more. The plant body is distinctly differentiated into rhizome, leaves and roots (Fig. 1 A).

1. Rhizome:

- All the species possess a rhizome which creeps on or just beneath the soil surface. It is slender, dichotomously branched with distinct nodes and internodes and is capable of indefinite growth in all directions as a result of which it occupies an area of 25 metre or more in diameter.
- In aquatic species the internodes are long while in sub-terrestrial species they are short. Usually from the upper side at nodes, the leaves are given out while from their lower side, the roots.

2. Leaves:

- They are borne alternately on upper side of rhizome at nodes, in two rows. Young leaves show circinate vernation (like ferns) (Fig. 1 A). In some species young leaves are covered with multicellular hairs. The leaves are compound, with basal petiole and terminal lamina.
- In submerged plants the petiole is a long and flexible structure and the lamina floats over the surface of water but in muddy or marshy plants the petiole of the leaf is short and rigid with short lamina spreading in the air.
- The lamina consists of 4 leaflets (pinnae) which are present at the apex of petiole. The 4 leaflets arise as a result of 3 dichotomies of the lamina in close succession to each other i.e., 2 leaflets arise slightly higher than other two (Fig. 1B).
- Pinnae have got a dichotomously branched vein system with cross connections (Fig. 1C). The veinlets at the margin are connected with loops thus forming a reticulum. The shape of pinna varies from obovate to obcuneate and margin also varies from entire to crenate or crenate to lobed.
- Sometimes the pinnas are once or twice deeply dichotomously lobed (*M. biloba*) or toothed (*M. minuta*). At night the pinna are folded upwardly. This is known as sleeping movement of pinna. Near the base of petiole the stalked bean-shaped sporocarps are borne.

3. Roots:

- The roots are adventitious, arising from the underside of the node of rhizome, either singly or in groups. In certain cases the roots are given out even from the internodes (*M. aegyptiaca*).

Internal Structure of Marsilea:

1. T. S. Rhizome (stem):

- A T. S. of the young rhizome shows a protostelic structure i.e., pith is absent and xylem is completely surrounded by phloem but in the old stem pith is developed in the centre and the stele is amphiphloic siphonostelic type.

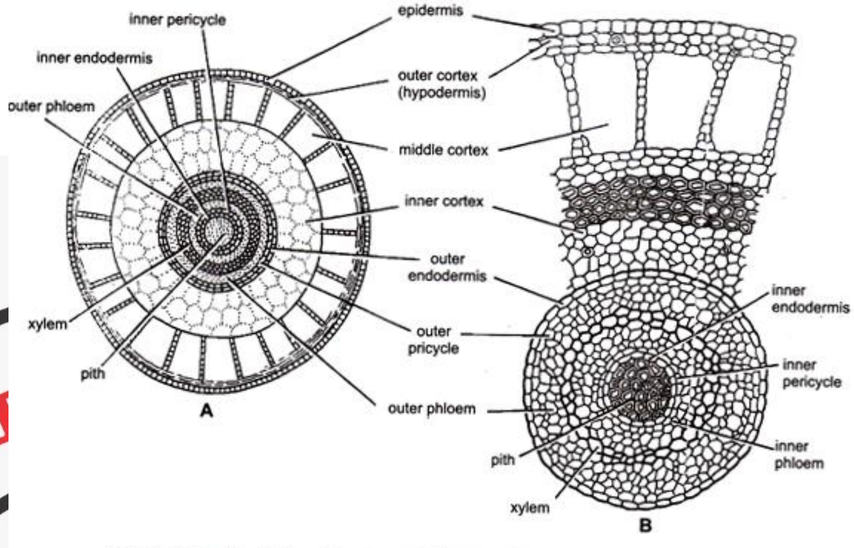


Fig. 2. A, B. *Marsilea*. Internal structure of rhizome. A. Diagrammatic, B. A part cellular.

A. T. S. of the old stem is somewhat circular in outline and shows the following structures:

(i) Epidermis:

- It is the outermost limiting layer of single celled thick parenchymatous cells. The stomata are absent.

(ii) Cortex:

- It is differentiated into three regions – the outer cortex, the middle cortex and the inner cortex.

(a) Outer cortex:

- It is present just below the epidermis (also called hypodermis). It is parenchymatous and may be one to several cells thick. Some of its cells contain tannin.

(b) Middle cortex:

- It is also called aerenchyma. It lies below the hypodermis. It consists of large air spaces (chambers) separated by one cell thick parenchymatous septa. In the xerophytic species e.g., *M. aegyptiaca* the air chambers are obliterated.

(c) Inner cortex:

- It is a solid tissue of several cells thickness. The outer layers are thick walled (sclerenchymatous) while the inner layer of cells is thin walled (parenchymatous) and compactly arranged. Some of these cells are filled with starch or tannin.

(iii) Stele:

- Stele is amphiphloic siphonostele i.e., in the centre there is a pith which may be either parenchymatous (aquatic species) or sclerenchymatous (terrestrial muddy species). Xylem is present in the form of a complete ring which is surrounded on both sides by a complete ring of inner and outer phloem, pericycle and endodermis.
- In this way the continuation of different tissues in the form of complete ring in stele is as follows—outer endodermis, outer pericycle, outer phloem, xylem, inner phloem, inner pericycle and inner endodermis. The protoxylem may be well defined exarch (*M. vestita*) or mesarch (*M. aegyptiaca*) or ill defined (*M. quadrifolia*).
- A T. S. of the nodal region shows an amphiphloic solenostelic condition and is provided with one leaf gap.

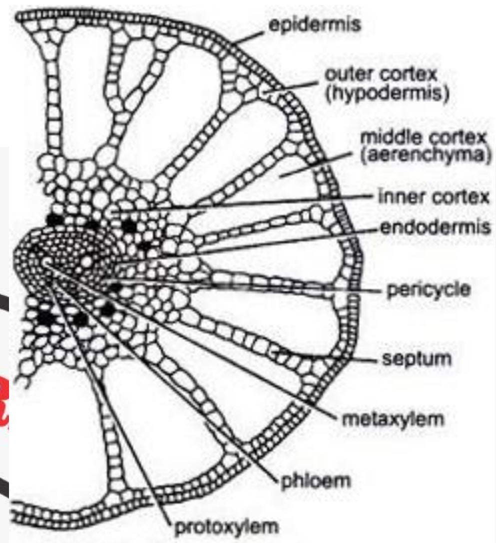


Fig. 3. *Marsilea quadrifolia.* T.S. of petiole

2. T. S. of Petiole:
- A T. S. of the petiole is somewhat circular in outline and is differentiated into epidermis, cortex and stele.

(i) Epidermis:
- It is the outermost layer of single cell thickness. The cells are parenchymatous and slightly elongated.

(ii) Cortex:
- It is differentiated into three regions: The outer cortex, the middle cortex and the inner cortex.

(a) Outer cortex:
- It is present just below the epidermis, (also called hypodermis). It is made of thin walled cells (parenchymatous).

(b) Middle cortex:
- It lies below the hypodermis and called aerenchyma. It consists a ring of air chambers. The air chambers are separated by single layered partitions of thin-walled parenchymatous cells.

(c) Inner cortex:
- It is a solid tissue of several cells thickness. The cell layers are parenchymatous and contain starch and tannin filled cells. In *M. minuta* few sclerenchymatous layers are also present just inner to middle cotex.

(iii) Stele:
- It is somewhat triangular in outline and is of protostelic type i.e. pith is absent. Xylem is "V" shaped with 2 distinct arms. Each arm is provided with metaxylem elements in the centre and protoxylem is situated at both the margins i. e., protoxylem is exarch.
- The xylem is surrounded on all sides by phloem. Phloem is externally surrounded by a single layer of parenchymatouspericycle which, in turn, is bounded by a single layered endodermis.

3. Transverse Section of Leaflet:
- T. S. of the leaflet shows epidermis, mesophyll and vascular bundles.

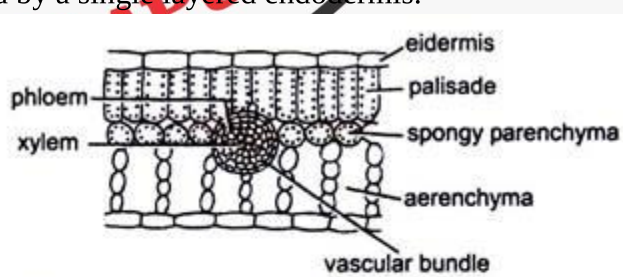


Fig. 4. *Marsilea quadrifolia.* V.S. of leaflet or pinna

(i) Epidermis:
- It is the outermost surrounding layer and is only one cell in thickness. It is differentiated into upper and lower epidermis. In floating leaflets the stomata are present on the upper epidermis but in case of plants growing in mud or moist soil where the leaves are aerial, the stomata are present both on upper as well as lower epidermis.

(ii) Mesophyll:
- It occupies a wide space between upper and lower epidermis. It is usually differentiated into an upper palisade tissue and lower spongy parenchyma. The palisade tissue is made up of elongated cells

provided with chloroplast. The spongy tissue is made up of loosely arranged parenchymatous cells with large air spaces separated by single layered septa. In submerged species, however, the mesophyll is not differentiated into palisade and spongy parenchyma.

(iii) Vascular bundles:

- In between the mesophyll tissue are present several vascular bundles. Each vascular bundle is concentric and amphicribal type i. e., made up of a centrally situated xylem, surrounded on all sides by phloem. The phloem is enclosed by a single layered thick endodermis.

4. T. S. Root:

- A T. S. of root is somewhat circular in outline and can be differentiated into epidermis or piliferous layer, cortex and stele (Fig. 5A, B).

(i) Epidermis:

- It is the outermost, parenchymatous, single layered covering.

(ii) Cortex:

- It can be differentiated into two parts: outer cortex and inner cortex. The outer cortex consists of large air chambers arranged in the form of a ring (parenchymatous). These chambers are separated from each other by longitudinal septa. The inner cortex is differentiated into outer parenchymatous and inner sclerenchymatous regions. The inner cortex is delimited by single layered thick endodermis.

(iii) Stele:

- It is of protostelic type and occupies the central position. It is devoid of pith. Xylem is situated in the centre which is diarch and exarch. It is surrounded by phloem. The phloem is bounded externally by a single layer of pericycle.

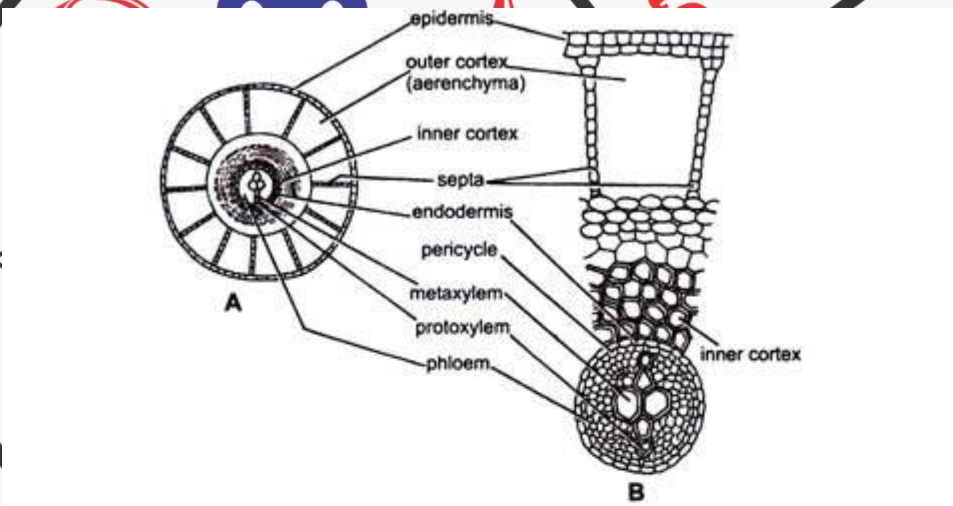


Fig. 5. (A, B) ***Marsilea quadrifolia.*** **Internal structure of root. A. Diagrammatic, B. A part cellular.**

Reproduction in Marsilea:

Marsilea reproduces by two methods:

(i) Vegetative reproduction & (ii) Sexual reproduction.

Vegetative reproduction:

- It takes place by means of tubers which are produced in dry conditions from the rhizome. First a branch is given out from the rhizome, which later on swells up due to the accumulation of food material. The structure is termed as tuber and is capable of tiding over the unfavourable conditions. On the return of favourable conditions it germinates to produce a new sporophytic plant, e.g., *M. hirsuta, M. quadrifolia*.

(ii) Sexual Reproduction:

1. Sporophytic Phase: Spore producing organs:

- *Marsilea* is heterosporous i. e., it produce two types of spores—microspores and megaspores. These spores are produced in microsporangia and megasporangia, respectively. These sporangia are borne in special type of spore producing organ called sporocarp. The sporocarp are born laterally on the short and lateral branches of the (called the peduncles or pedicels) petiole of leaf either near the base or a little higher up.
- They arise solitary or in clusters. The peduncle is usually unbranched but it may be branched also. Number of sporocarp differs in different species and varies from 1 to 20 or more. In *M. vestita*

Sporocarp arises single, in *M. quadrifolia* the peduncle is dichotomously branched bearing 2-4 sporocarps, in *M. polycarpa* several sporocarps arise in a linear row. The attachment of the pedicel sporocarp varies in different species.

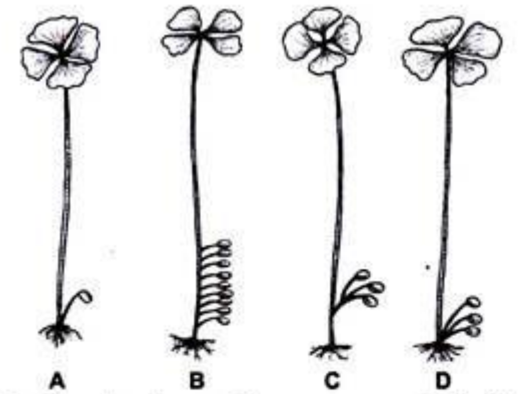


Fig. 6 (A-D) ***Marsileas.*** **Attachement of sporocarps on petiole in different species. A. *M. coromendelica*, B. *M. polycarpa*, C. *M. quadrifolia*, D. *M. minuta*.**

External Morphology of Sporocarp:

- Each sporocarp is an oval or bean shaped biconvex, flattened structure. It is green and soft when it is young but at maturity it becomes very hard and brown in colour. It is made up of a short stalk like structure known as peduncle and the body.
- The point of attachment of peduncle with the body is called raphe (Fig. 7A). Slightly above the raphe in a median plane are present 1 or 2 protuberances called tubercles. They are unequal in size and lower one is stouter than the upper one. In some cases the tubercles are absent e.g., *M. polycarpa*.

Internal Structure of Mature Sporocarp:

- The sporocarp is a bivalved structure. It can be split open in the dorsiventral plane into two halves (valves).

If we split open the sporocarp, we can see the following structures:

Wall of sporocarp:

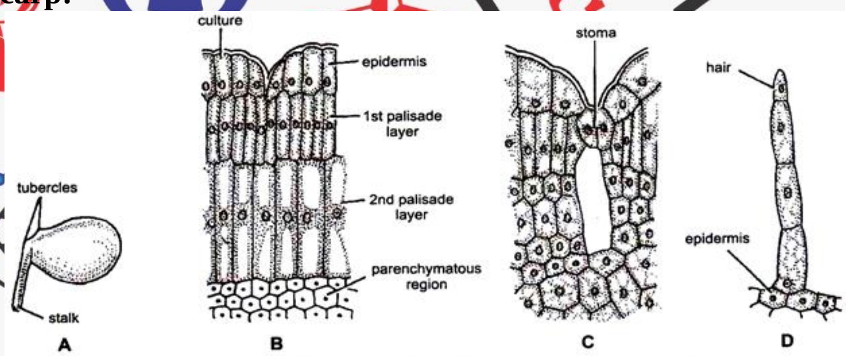


Fig. 7. (A-D). ***Marsilea.*** **Structure of sporocarp. A. sporocarp, B. Wall structure of sporocarp in T.S., C. sunken stoma in the wall of sporocarp, D. A multicellular hair.**

- It is very hard, thick and highly resistant to mechanical injury. It can be differentiated into three zones—outer epidermis, middle hypodermis and inner parenchymatous zone. Epidermis is single layered made up of broad and columnar cells. Its continuity is broken by the presence of sunken stomata (Fig. 7C).
- Some of the epidermal cells develop into multicellular hairs (Fig. 7D). Hypodermis consists of two layers of radially elongated palisade like cells. Both the layers are without intercellular spaces and have chloroplast in their cells. Next to hypodermal layers is the parenchymatous zone (Fig. 7B). In mature sporocarp the cells of this zone gelatinise and form a gelatinous ring which helps in the dehiscence of the sporocarp.

Cavity of sporocarp:

- The alternating rows of sori (sing, sorus, a group of sporangia is called sorus), one along each side lies transversely-dorsiventrally to the long axis of the sporocarp. The sori on either side alternate with each other. The number of sori inside the sporocarp varies from species to species. It may be from two (e.g., *M. aegyptiaca*) to twenty (e.g., *M. vestita*). Each sorus bears both microsporangia and megasporangia.
- Their number also varies from species to species. In *M. minuta* a sorus has 4-8 megasporangia and 8-13 microsporangia. In *M. aegyptiaca* each sorus has 5-16 megasporangia and 9-19 microsporangia.
- In *M. minuta*, *M. vestita*, *M. rajasthanensis*, sometimes megasporangia are absent in sorus. Each sorus arises on a ridge like placenta or receptacle formed on the sporocarp wall. Each sorus is surrounded by a thin, membranous two layered true indusium. The indusia of adjacent sori are partially fused.

Vascular supply of the sporocarp:

- It is supplied by a main dorsal vein which runs along the narrow side facing the peduncle. From the dorsal vein, lateral branches are given alternatively right and left, at right angle to the dorsal vein which supplies laterally (Fig. 8). These lateral veins at their middle divide dichotomously. In the region here lateral vein forks, arises a placental bundle which too branches dichotomously. The first and the last lateral veins do not possess placental bundles.

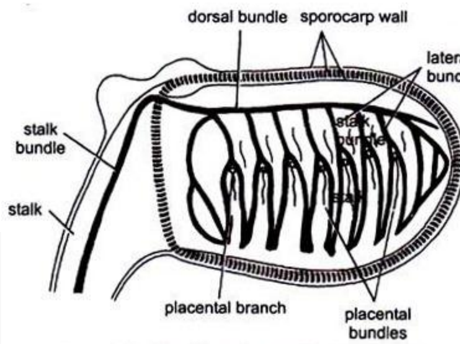


Fig. 8. *Marsilea.* Vascular supply of sporocarp.

The entire internal structure of the sporocarp can be best seen in section cut in three plains:

(i) Horizontal Longitudinal Section (H.L.S.): Section is cut horizontally but the sporocarp is cut longitudinally.

(ii) Vertical Longitudinal Section (V.L.S.): Section is cut vertically but the sporocarp is cut longitudinally.

(iii) Vertical Transverse Section (V.T.S.): Section is cut vertically but the sporocarp is cut transversely.

(i) Horizontal Longitudinal Section (H.L.S.):

- The section passes through the peduncle and cuts it transversely. Peduncle shows characteristic 'V' shaped xylem (Fig. 9 A, B). A H.L.S. of sporocarp shows the usual wall layers. The gelatinous ring is cut transversely and it appears in the form of dorsal and ventral mass at its proximal and distal ends.
- The dorsal mass is more prominent than

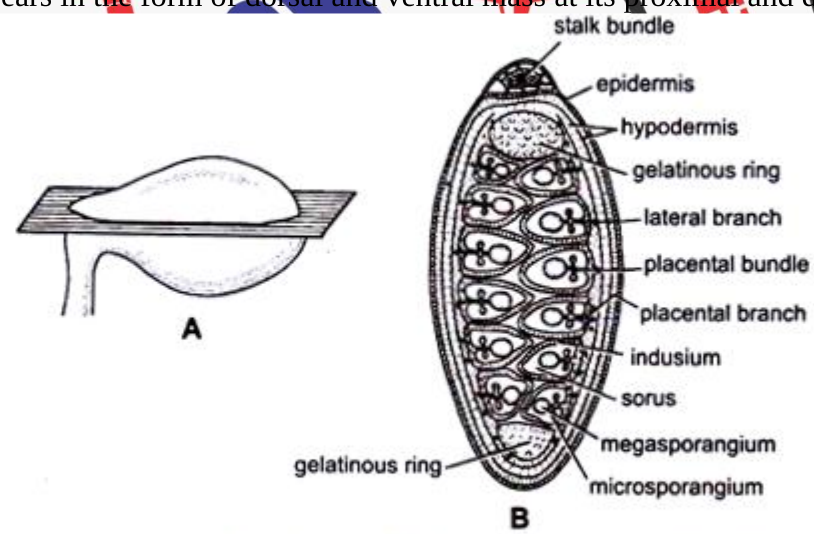


Fig. 9 (A, B). *Marsilea.* B. Horizontal longitudinal section (H.L.S.) of the sporocarp as shown in plane A.

transversely along with their two layered indusia. Sori show their alternate arrangement in the two rows. Each sorus has a receptacle which has a central terminal megasporangium and two lateral microsporangia, one on either side. The lateral bundle is also cut transversely below each sorus.

(ii) Vertical Longitudinal Section (V.L.S.):

- A V.L.S. of the sporocarp shows the usual wall layers. The peduncle along its vascular bundle is cut longitudinally. The entire gelatinous ring is cut vertically and it appears as a complete ring around the sori. The section cut the sori longitudinally, which are arranged in many vertical rows.
- If the section passes strictly through the median plane of sporocarp, only megasporangia are visible (Fig. 10A, B) but if it passes slightly away from the median line, only microsporangia are visible (Fig. 10C).

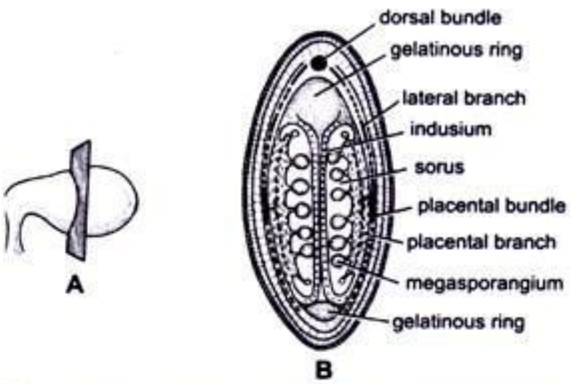


Fig. 11. ***Marsilea.*** **(A, B). B. vertical transverse section of the sporocorp as shown in plane A.**

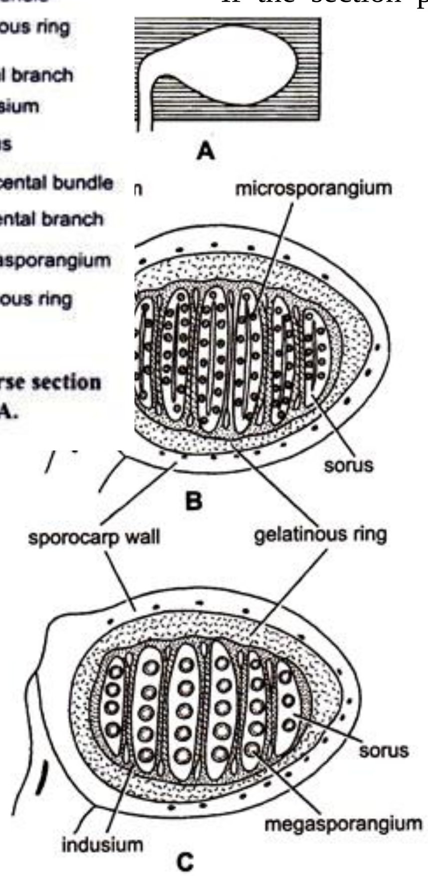


Fig. 10 (A-C). ***Marsilea.*** **Vertical longitudinal section (V.L.S.) of the sporocarp as shown in plane A., B. Section passing slightly away through the median plane (showing microsporangia), C. Section passing strictly through the median plane (showing megasporangia).**

(iii) Vertical Transverse Section (V.T.S.):

- A V.T.S. of the sporocarp shows the usual wall layers. Peduncle is not cut in the section. The gelatinous ring appears in the form of dorsal and ventral mass (as in H.L.S.). The gelatinous mass on the dorsal side is much more prominent.
- In V.T.S. only two sori covered with indusia are visible on the inner side and attached to the placental ridge on the outer side (Fig. 11 A, B). The sori reveal many megasporangia and only two or three microsporangia at the sides. The dorsal bundles, the lateral bundles and the placental bundles are clearly visible.

Structure of Microsporangium:

- It is somewhat oval structure with a long stalk and is present laterally on the receptacle. It is smaller in size. It has a single layered jacket followed by two layers of tapetal cells. In the centre is present a cavity filled with microspore mother cells (Fig. 14H).
- At maturity the tapetal cells disintegrate and each microspore mother cell divides reductionally forming 4 haploid microspores (Fig. 14I). The microspores are usually 32-64 in number and are liberated by the disintegration of the microsporangial wall (Fig. 14J).

Structure of Megasporangium:

- It is a spherical structure with a short stalk and is present on the top of the receptacle (Fig. 14A). It is bigger in size than the microsporangium (Fig. 14A). Its structure is similar to microsporangium except that only one megaspore is present per megasporangium at maturity. The megaspore is liberated by the disintegration of the megasporangial wall.

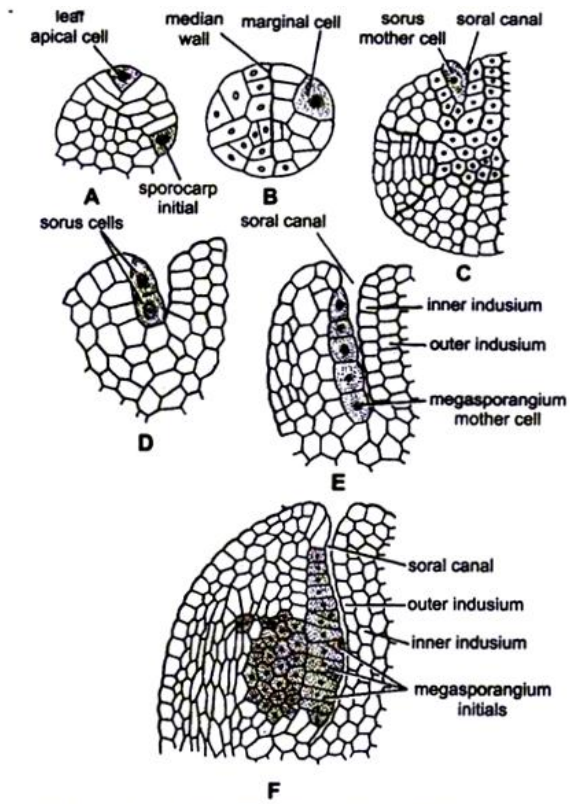


Fig. 13. (A-F). ***Marsilea.*** **Successive stages in the development of sporocarp.**

Dehiscence of Sporocarp and Liberation of Spores:

- The decaying of the wall of the sporocarp takes place due to bacterial action and thus the sporangia and spores are liberated. The sporocarp bursts open only in water in valvecular manner along the ventral side and apex. The gelatinuous ring absorbs water and extends greatly through the open margins of the sporocarp thus dragging out sori along with it.

It straightens and behaves as sporophore. The gelatinous ring bears two alternating rows of sori. The delicate mucilage wall of the sporangia (micro-or mega) opens in water and the spores (micro-or mega are liberated which germinate soon (Fig. 15 A, E).

2. Gametophytic Phase:

The microspores and the megaspores are the unit of male and female gametophytes respectively.

They germinate to produce the respective gametophyte in the following ways:

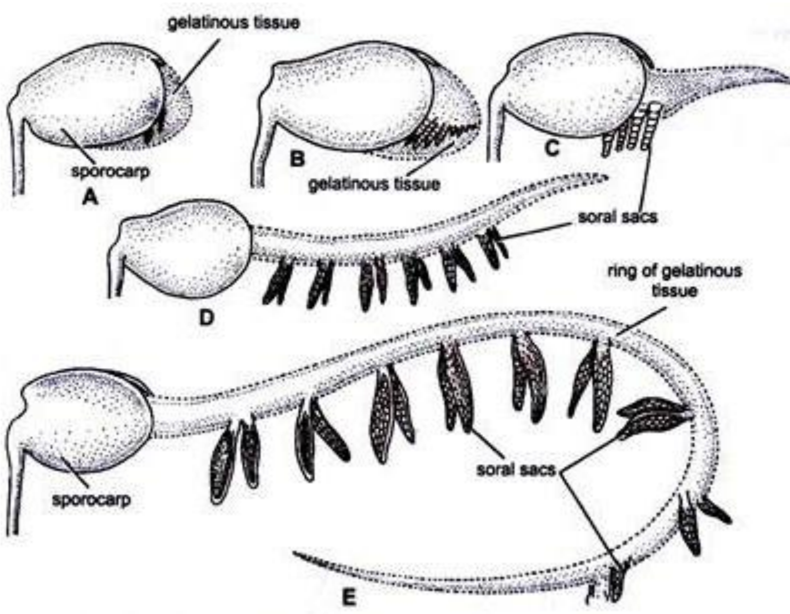


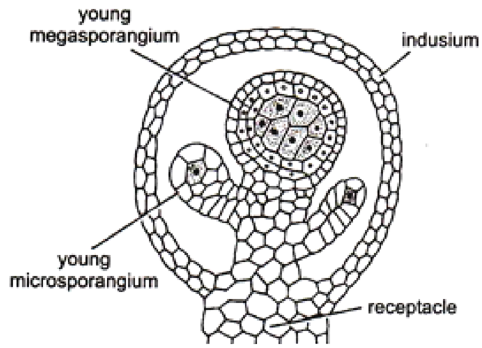
Fig. 15. (A-E) *Marsilea.* Successive stages in the dehiscence of the sporocarp

Fertilization:

- The free swimming antherozoids are attracted chemotactically towards the neck of a mature archegonium but only one enters the neck and reaches the egg. The male and female nuclei fuse to form a diploid structure called oospore or zygote. Thus the gametophytic generation ends and the unit of sporophytic generation is formed. In some species e.g., *M. drummondii*, parthenogenesis has been observed.

Development of embryo:

- Oospore is the initial stage of sporophytic generation. The first division of the oospore is in a vertical plane (parallel to the long axis of archegonium) to form 2 unequal cells. The bigger one is known as epibasal cell and the smaller one as hypobasal cell (Fig. 18 A, B). This is followed by a second transverse division to form 4 cells (quadrant stage) (Fig. 18C).



- The epibasal half gives rise to shoot and leaf whereas the hypobasal half gives rise to root and foot. The cell of epibasal half near the neck gives rise to cotyledon and other away from the neck, to the stem.
- In the same way the cell of the hypobasal half near the neck gives rise to root and other away from the neck, to the foot. Simultaneously, the tissue surrounding the archegonium divides to form a 2 or 3 celled thick calyptra which protects the embryo in young stage. The embryo later on gives rise to an adult plant.

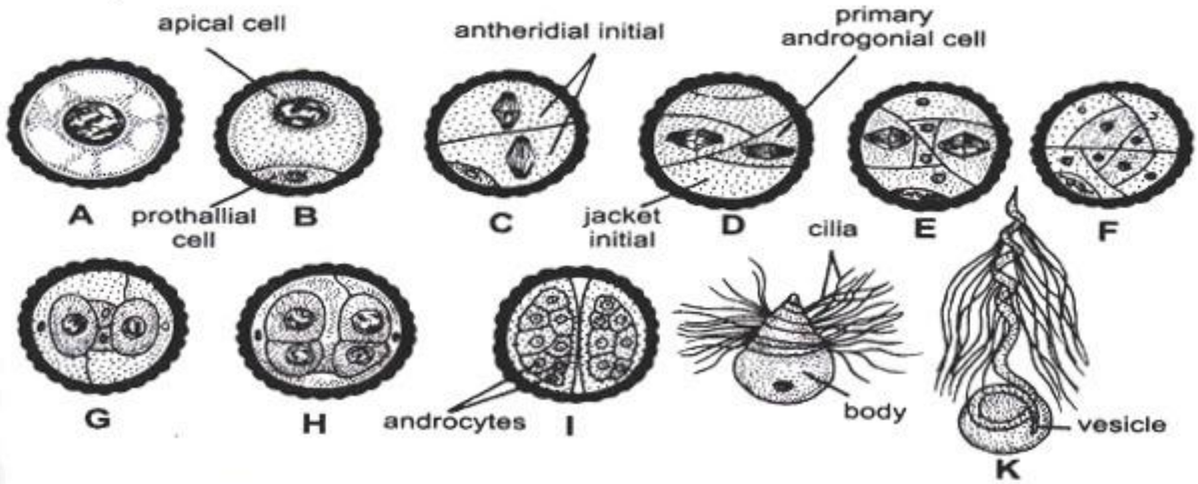


Fig. 16. (A-K). *Marsilea.* A-I. Successive stages in the development of male gametophyte, J.K. Antherozoids.

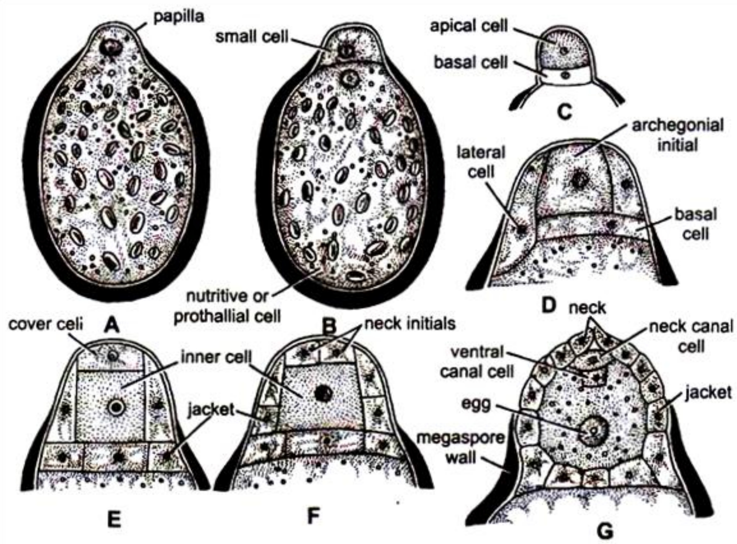


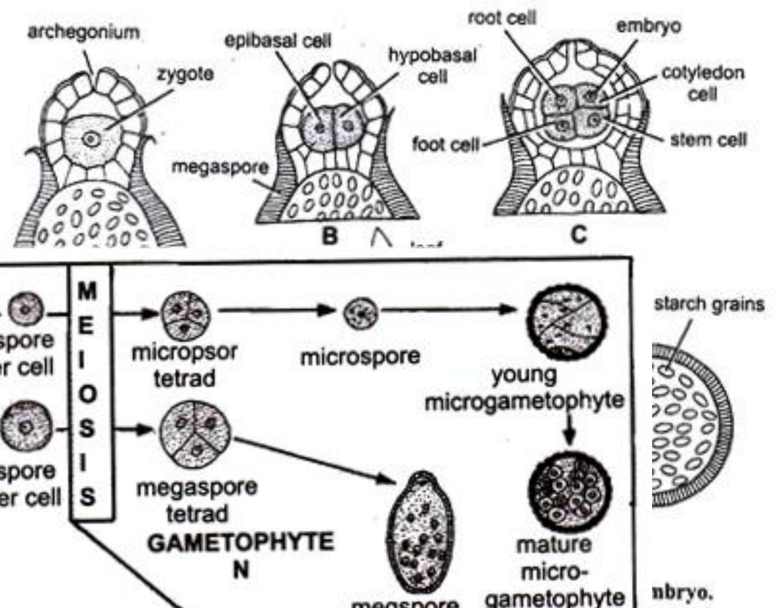
Fig. 17. (A-G). *Marsllea.* A-F successive stages inthe development of female gametophyte G. a mature archegonium.

angium and megasorangium,
n with microspores.

Life Cycle Patterns of Marsilea:

- Mature plant of Marsilea is diploid. Marsilea is a heterosporous fern because it produces 2 different types of spores i. e., microspores and megaspores. Micro- and megaspore mother cells are produced inside micro- and megasporangium respectively which represents the late stage of sporophytic generation. After reduction division microspores and megaspores are produced which represent the initial stage of gametophytic generation.

- Microspore gives rise to make gametophyte which, in turn, produces archegonium and egg. Both antherozoid and egg fuse to from a diploid oospore (2x).The oospore is the initial states of sporophytic generation. Hence, in the way the sporophytic and gametophytic generation alternate with each other although the sporophytic phase is dominant over gametophytic phase (fig 19,20).



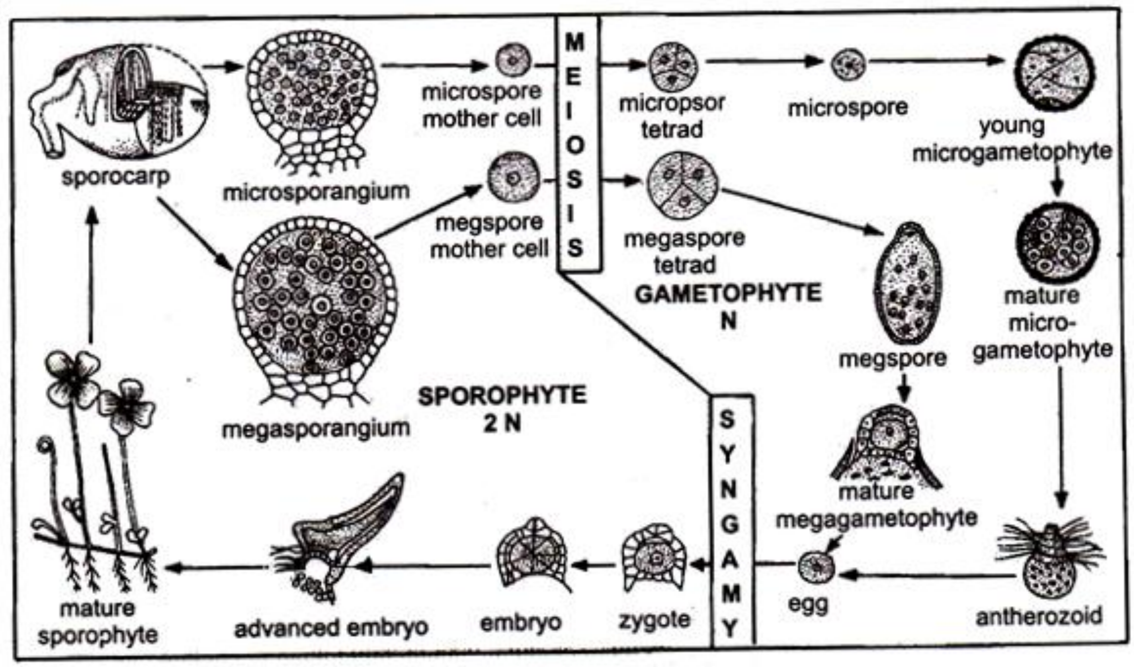


Fig. 19. *Marsilea.* Diagrammatic life cycle.

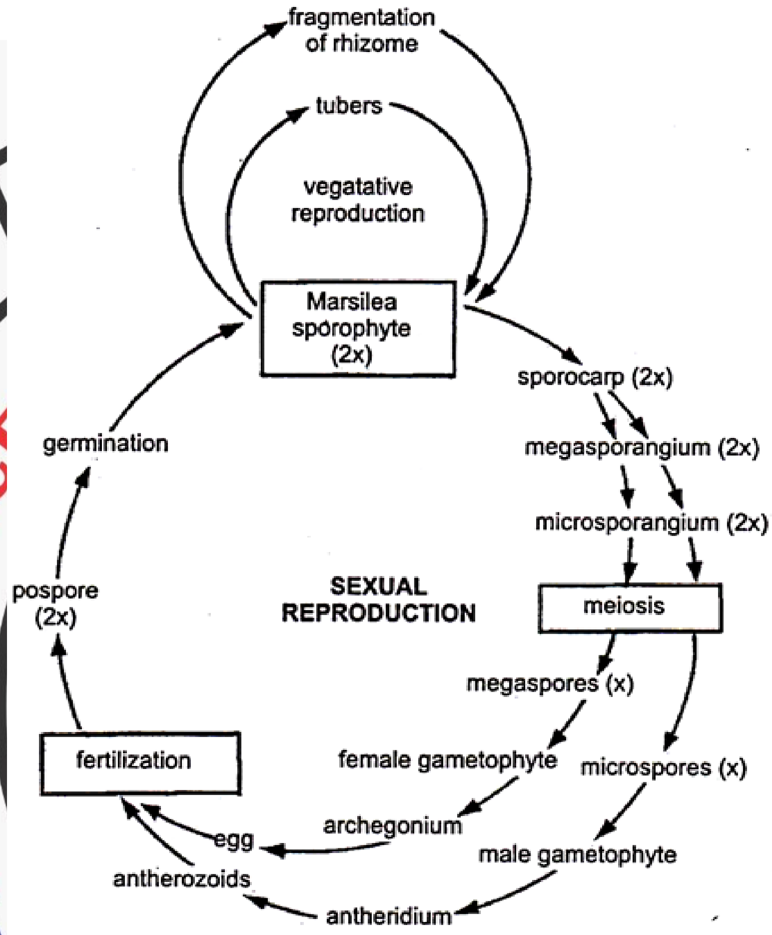


Fig. 20. ***Marsilea.*** **Schematic life cycle.**

Brief account of Evolution of Stele or Stelar Evolution

- Stele (= Greek word meaning a column) can be defined as the unit of vascular system that is made up of xylem, phloem, interfascicular tissues, medullary rays, pericycle and pith (if present).
- The term stele refers to the central core of plant axis and is restricted only to primary tissues. The term is used in case of Pteridophytes and is seldom applied in case of angiosperms and gymnosperms. Endodermis delimits a stele on the peripheral side.

There are two basic types of stele:
1. Protostele, and
2. Siphonostele.

1. Protostele:

- A protostele is composed of a solid core of xylem mass surrounded by phloem, which in turn remains encircled by pericycle. Endodermis delimits protostele on the peripheral side. In protostele pith is absent and the protoxylem is exarch. There is no leaf gap. Some dicotyledonous roots have radial stele where pith is completely absent. Such radial stele is also referred to as protostele.

There are three types of protostele (Fig. 15.1) which are as follows:

(A) Haplostele:

- Haplostele has a cylinder of phloem that surrounds a smooth core of xylem. The xylem mass appears circular or oval in outline as seen in cross-section. Protoxylem is exarch. Ex. *Selaginella*, *Lygodium*, the extinct psilophytes *Rhynia* and *Homeophyton* etc.

(B) Actinostele (Figs. 15.1 & 15.3A):

- Actinostele has a cylinder of phloem that surrounds a star-like mass of xylem. As seen in cross-section, the xylem mass has radiating ribs of varying number. Protoxylem occurs at the tip of radiating ribs. Phloem also occupies the position between the xylem lobes and furrows. Ex. *Psilotum* and the extinct psilophyte *Asteroxylon*.

(C) Plectostele:

- Plectostele has masses of xylem that are in the form of plate-like lobes. As seen in cross-section the plates are of different sizes and some of the plates are united at one end. Cylinder of phloem surrounds xylem masses and phloem also occurs between xylem plates. Ex. *Lycopodium clavatum*.
- *Lycopodium* cernuum has mixed protostele (Figs. 15.1 & 15.3B). In this type of stele as seen in cross-section the xylem is mesh-like mass that is uniformly distributed and appears to be embedded in the ground mass of phloem.

2. Siphonostele:

- Siphonostele, where xylem is in the form of a hollow cylinder, has parenchymatous pith at the central region of xylem. The xylem is surrounded by phloem that in turn remains encircled by pericycle. The whole stele is limited outside by a continuous endodermis. In siphonostele xylem and phloem are in the form of a continuous or split vascular cylinder.

The following two types are recognized (Fig. 15.1) on the basis of position(s) of phloem in relation to xylem in siphonostele:

(a) Ectophloic siphonostele:

- Ectophloic siphonostele has a continuous cylinder of phloem surrounding the peripheral side of xylem. Parenchymatous pith occurs at the central region of xylem. The whole stele is delimited outside by a continuous endodermis. Sporne (1976) defines ectophloic siphonostele as 'medullated protostele'. Leaf gap is absent in ectophloic siphonostele. Ex. ferns like *Osmunda*, *Schizaea* etc. and dicotyledonous angiosperm like *Phlox*, *Lindenbergia* etc.

(b) Amphiphloic siphonostele (Figs. 15.1 & 15.3C):

- Amphiphloic siphonostele has cylinders of phloem on the peripheral and inner side of xylem. The peripheral phloem is termed as outer phloem and the other as inner phloem. Pericycle and endodermis appear both outside and inside of vascular tissues. To distinguish them the terms outer and inner pericycle, and outer and inner endodermis are used.

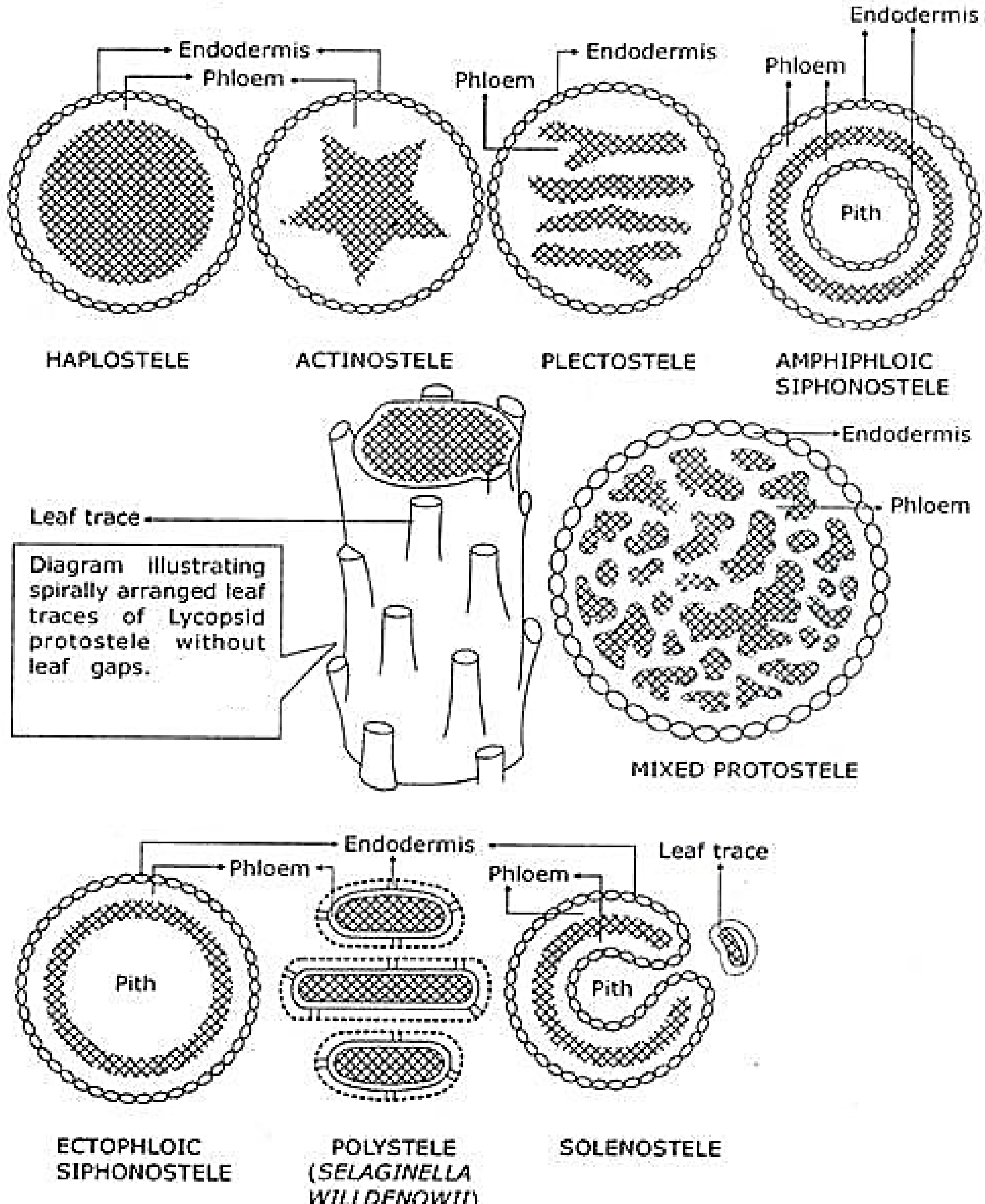


Figure 15.1

Diagrammatic illustration of different types of stele in t.s. view. Xylem = crosshatched.

Lycopodium cernuum has mixed protostele (Figs. 15.1 & 15.3B). In this type of stele as seen in cross-section the xylem is mesh-like mass that is uniformly distributed and appears to be embedded in the ground mass of phloem.

- The outer pericycle occurs surrounding the peripheral side of outer phloem whereas the inner pericycle is situated on the inner side of inner phloem. Outer endodermis delimits the whole stele and occurs between cortex and outer pericycle. Inner endodermis occurs between inner pericycle and pith. Ex. *Marsilea* and *Adiantum* etc.
- Ectophloic and amphiphloic siphonostele may be cladosiphonic or phyllosiphonic. In cladosiphonic siphonostele the vascular tissues, in cross section, appear as continuous cylinder as the leaf traces are without gaps (e.g. *Selaginella*). The traces of phyllosiphonic siphonostele are with gaps and so the vascular tissues appear as isolated bundles in transverse section (e.g. *Polypodium*).

i. Solenostele:

- Solenostele can be defined as a type of amphiphloic siphonostele with non-overlapping leaf gap. The leaf gaps are distantly spaced. Solenostele consists of two vascular strands-the small leaf trace and the large principal vascular strand as seen in a cross-section of stem at node. The principal vascular strand appears horse-shoe-shaped due to the presence of parenchymatous leaf gap.
- In the vascular strands phloem appears both outside and inside of xylem. The two vascular strands have individual continuous endodermis. The vascular strand is in the form of a continuous cylinder between leaf gaps. The vascular cylinder is interrupted at the places corresponding to the origin of leaf traces. Ex. Anemia, *Adiantum pedatum*, *Davallia* etc. It is to note that ectophloic siphonostele with non-overlapping leaf gap is also referred to as solenostele.

ii. Dictyostele:

- Dictyostele can be defined as a type of amphiphloic siphonostele with overlapping leaf gaps. The upper part of a leaf gap overlaps the lower part of the upper adjacent leaf gap. The gaps are not distantly spaced from each other and occur in parallel manner. As a result a longitudinal cylindrical network of interconnected vascular strands (Fig. 15.1C) is formed when viewed as three- dimensional object.
- The vascular strand is perforated as seen in cross-section. The vascular strands are arranged in a ring-like manner and parenchyma occurs in between the vascular strands. Each vascular strand is composed of xylem surrounded by phloem.
- This amphicribral vascular strand is surrounded by a pericycle and the whole being bounded on the outside by a continuous endodermis. Ex. *Mohria*, *Polypodium falcatum*, *Ophioglossum*, *Dryopteris* etc. Each vascular strand of dictyostele (Fig. 15.2) is referred to as meristele.

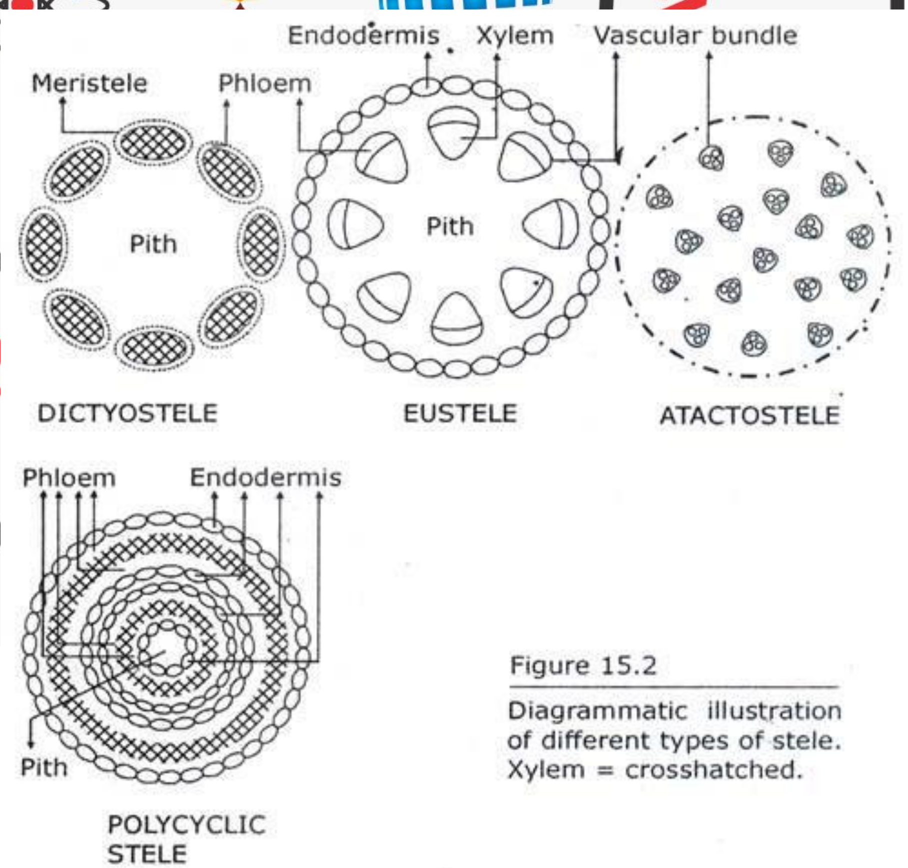


Figure 15.2
Diagrammatic illustration of different types of stele. Xylem = crosshatched.

iii. Eustele:

- Eustele can be defined as a type of ectophloic siphonostele with overlapping leaf gaps. The leaf gaps occur parallel to each other and are not distantly spaced. The upper part of a gap overlaps the basal part of the upper adjacent gap. When viewed as three-dimensional object the vascular strands form an interconnected network. The vascular strands are separate as seen in cross- section. Each vascular strand, also called vascular bundle, is conjoint and collateral.

- Parenchyma occurs at interfascicular region. All vascular bundles are arranged in a ring like manner. Pericycle surrounds the vascular bundles on the peripheral side, the whole being bounded by a continuous endodermis. Eustele is the characteristic of gymnosperm and dicotyledonous stem. Ex. *Helianthus*, *Xanthium* etc. Eustele with bicollateral vascular bundle is observed in the families Cucurbitaceae, Solanaceae etc.

iv. Atactostele:

- Atactostele can be defined as a type of eustele where collateral vascular bundles are arranged in an irregular manner (Fig. 15.2). It is the characteristic of monocotyledonous stem where there is no distinction between pith and cortex.
- Parenchyma bounded by epidermis is designated as ground tissue in monocotyledons. The vascular bundles are scattered on the ground tissue as seen in cross-section of stem. The vascular strands form an interconnected network when viewed as three-dimensional object. Ex. stem of *Zea mays*, *Asparagus* (Fig. 15.3E) etc.

v. Polystele (Fig. 15.3D):

- Polystele can be defined as having more than one protostele as observed in the cross-section of a stem. In *Selaginella willdenowii* (Fig. 15.1) three protosteles occur. Each protostele has xylem surrounded by phloem, the whole being bounded by endodermis.

- In angiosperm polysteles occur in the families like Acanthaceae, Nymphaeaceae, Palmae etc. In cross-section polysteles appear to be scattered or organized into a ring. In longitudinal section it is revealed that individual steles, by anastomosis among themselves, form a network.

vi. Polycyclic stele:

- Polycyclic stele can be defined as having two or more coaxial cylinders of vascular strands as observed in the cross-section of a stem. The individual cylinders are interconnected at the base of inner stele. Polycyclic steles are also referred to as polycyclic siphonostele where the innermost vascular cylinder is amphiphloic siphonostele (Fig. 15.2). The other cylinders remain separated by parenchyma. Ex. *Matonia pectinata*.

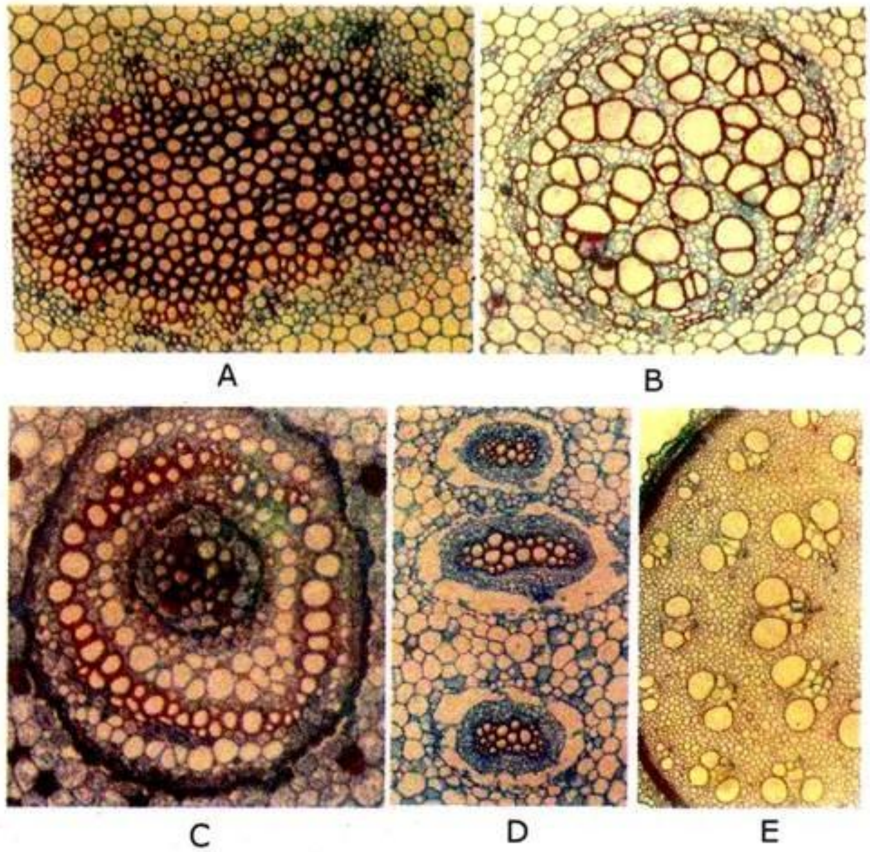


Figure 15.3

Microphotograph of different types of stele. A. Actinostele of *Psilotum* stem. B. Mixed protostele of *Lycopodium* stem. C. Amphiphloic siphonostele of *Marsilea* stem. D. Polystele of *Selaginella* stem and E. Atactostele of *Asparagus* stem.

HETEROSPORY IN PTERIDOPHYTES:

Most of the Pteridophytes produce one kind of similar spore. Such Pteridophytes 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.

According to Rashid (1976) or modern Pteridologists only 9 genera of Pteridophytes are heterosporous. These are *Selaginella*, *Isoetes*, *Stylites*, *Marsilea*, *Pilularia*, *Regnellidium*, *Salvinia*, *Azolla* and *Platyzoma*.

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. A number 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, 1958 Lepidocarpon 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 megasporangium 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 retorted and it produced microsporangia. By sudden lowering of the temperature, the size of the microspores in the sporocarp of *Marsilea* increases by six times.

Biological Significance of Heterospory:

The phenomenon of heterospory is of great biological significance on account of the following facts:
(i) The development of the female gametophyte starts while the megaspore is still inside the megasporangium.
(ii) Same is true of microspores i.e., they also start germinating into male gametophytes while they are still inside microsporangium.
(iii) The female gametophyte derives its nourishment from the sporophyte i.e., female gametophyte is dependent on sporophyte for its nourishment.
(iv) The dependence of female gametophyte on sporophyte for its nourishment provides better starting point for the development of new embryo than an independent green prothallus which has to manufacture its own food.

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 gametophyte.
4. Archegonium.
5. Egg.

Lower Spermatophytes (Gymnosperms):
1. Nucellus of ovule.
2. Megaspore (Embryo sac).
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.

PALEOBOTANY- GEOLOGIC TIME SCALE

The geologic time scale is an essential tool for understanding the history of Earth and the evolution of life. Geologists have divided Earth's history into a series of time intervals. These time intervals are not equal in length like the hours in a day. Instead the time variables are variable in length. This is because geologic time is divided using significant events in the history of the earth. The first principal subdivision is called the eon. An eon, the largest division of the geologic time scale, spans hundreds to thousands of millions of years. Geologists generally agree that there are two major eons: the Precambrian eon and the Phanerozoic eon. The Precambrian goes from the formation of the earth to the time when multicellular organisms first appeared - that's a really long time - from 4,500 million years ago to just about 543 million years ago. Then begins the Phanerozoic eon, which continues up to today. Eons are made up of eras, divisions that span time periods of tens to hundreds of millions of years. The three major eras are the Paleozoic, the Mesozoic, and the Cenozoic. The Cenozoic era is the one we are in today. It began 65 million years ago, right about the time that the dinosaurs went extinct. Eras are subdivided into periods. The events that bound the periods are wide-spread in their extent but are not as significant as those which bound the eras. Subdivision of periods into epochs can be done only for the most recent portion of the geologic time scale. This is because older rocks have been buried deeply, intensely deformed and severely modified by long-term earth processes. Evidence of the length of geologic time comes from three sources i.e., sedimentation, saltiness of the ocean and the disintegration rate of uranium. Estimation of time by carbon dating are limited to the last 45,000 years.

Cenozoic - Quaternary	**Holocene** 1000yrs ago till now	Little Ice Age. Major habitat changes and deforestations caused by humans. A major extinction wave due to introduced pests and habitat destruction. The last major ice age ends and the sea level rises by 80-110m worldwide, causing new continental margins, dunes and beaches. Climate still fluctuates in ten little ice ages.
	Pleistocene 1.6-0.01 Mya	Climate fluctuating cold to mild. The era of ice ages. Numerous glacial advances, deserts on large scale; Sahara formed. Planetary spread of *Homo Sapiens* over Eurasia;
Cenozoic -- Tertiary 66.4-1.6 Mya	**Pliocene** 5-2 Mya	Cooler climate; continued uplift and mountain building, with widespread glaciation in Northern Hemisphere.
	Miocene 25-5 Mya	Moderate climate; extensive glaciation begins again in Southern Hemisphere. Moderate uplift of Rocky Mountains. Spread of grasslands as forests contract.
	Oligocene 38-25 Mya	Rise of Alps and Himalayas. Lands generally low. Volcanoes in Rocky Mountains. South America separates from Antarctica. Forests decline to make way for grasslands. Origin of many modern families of flowering plants.
	Eocene 55-38 Mya	Mild to very tropical climate. Australia separates from Antarctica; India collides with Asia. Formation of grasslands.
	Paleocene 65-55 Mya	Mild to cool climate. Wide, shallow continental seas largely disappear. First known primitive primates and Mammal carnivores.
	65 Mya	**Mass extinctions**

	Cretaceous 144-66.4 Mya	Tropical to subtropical climate. Elevation of Rocky Mountains at end of period. Africa and South America separate. Flowering plants become abundant. At end of period extinction of most cycads. Angiosperms dominate the land flora, colonize most land and diversify.
Mesozoic 245-66.4 Mya	**Jurassic** 208-144 Mya	Mild climate. Continents low, with large areas covered by seas. Mountains rise from Alaska to Mexico. Gymnosperms, especially cycads and ferns. First flowering plants (angiosperms).
	208 Mya	**Mass extinctions**
	Triassic 245-208 Mya	At first, deserts stretched out over most of the land, slowly giving way to a mild, moist climate with great areas of forested plains. Continents and mountainous joined in one mass. Large areas arid. Eruptions in eastern North America. Appalachians uplifted and broken into basins. Forests of gymnosperms and ferns.
	248 Mya	**Mass extinctions**
Precambrian 3960-590 Mya	**Proterozoic** 2500-540 Mya	Dry and cold climate to warm and moist. Eukaryotic cells and multicellularity by close of era.
	Archean 3960-2500 Mya	Extensive mountain building. Shallow seas. Accumulation of free oxygen. Origin of life. Prokaryotes, bacteria, blue-green algae.
Azoic 4500-3960 Mya		Planet forms from accumulation of cosmic dust and from meteorite impacts. These impacts and the heat caused by compression melt the interior of the planet. The heat melts the Earth's interior to enable heavy elements to migrate to its centre, while light elements migrate to its crust. 4400 Mya the liquid core with the mantle appeared. Planet cools. Formation of Earth's crust (4200 Mya). Extensive volcanic activity prevents life from forming.
	sun's planets 4560 Mya	
Formation of universe 15 - 4.5 Gya	**sun and solar system** 5000 Mya	Universe is 2/3 its present size. From a left-over dust cloud originating from a supernova explosion, the sun forms, attracting most of the material. But rotational momentum has kept enough debris in space to form the planets. The sun's interior heats to 15 million degrees, hot enough for nuclear fusion: protons fuse into helium
	Unknown period	The exact age of the universe is not known (15 to 9 Gya). Below this line, all time is relative to the Big Bang; above it, time is relative to the present
	first galaxies 1000 Mya	Universe has expanded to 1/5 its present size. Nuclear reactions inside stars (supernovas) have made most of the heavy elements from which terrestrial planets are made and the elements necessary for life. The Milky Way, our galaxy, was formed 10,000 Mya. The universe cools further to 3ºK, its temperature today
	Universe becomes transparent 300,000 y	Matter clusters into ever larger units. Stars are formed. The universe becomes transparent. Its radiation, the background radiation, is still observable today.

Note: Mya = million years ago. Gya = billion years ago. kya= thousand years ago.

CONTRIBUTION OF PALEOBOTANIST - BIRBAL SAHNI

- **Birbal Sahni** (14 November 1891 – 10 April 1949) was an Indian paleobotanist who studied the fossils of the Indian subcontinent.
- He also took an interest in geology and archaeology. He founded the Birbal Sahni Institute of Paleobotany at Lucknow.
- His major contributions were in the study of the fossil plants of India and in plant evolution. He was also involved in the establishment of Indian science education and served as the President of the National

Academy of Sciences, India and as an Honorary President of the International Botanical Congress, Stockholm.

- Birbal Sahni was the first botanist to study extensively the flora of Indian Gondwana. Sahni also explored the Raj Mahal hills in Bihar, which is a treasury of fossils of ancient plants. Here he discovered some new genus of plants. A model of the extinct plant *Williamsonia sewardiana* which thrived in Rajmahal, Bihar about 140million years ago. This model is based on the reconstruction envisaged by Birbal Sahni.
- *Pentoxylon* was an important discovery of the group Pentoxylae from Nipania in Dumka district, Rajamahal hills, Bihar (age 110-114 million years ago). Reconstruction of plant with leaves, stem, flowers. The tongue shaped *Glossopteris*, represents a unique group of extinct vascular plants (age: Permian, 250-280 million years ago) was described by Sahni.
- *Birbal sahni divyadarshanii*, a fossil of an enigmatic flower like organ of the extinct plant discovered from Hura coalfield, Santhal Pargana, Bihar (age 250-280 million years) by Sahni and Prof. Divya Darshan.
- Sahni worked on living plants species including *Nephrotepsis*, *Niphobolus*, *Taxus*, *Psilotum*, *Tmesipteris* and *Acmopyle* examining evolutionary trends and geographical distributions. 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. He recorded foreign pollen in the

Paleozoic 540-245 Mya	**Permian** 286-245 Mya	Extremely violent climate changes: deserts, swamps, ice. Extensive glaciation in Southern Hemisphere. Seas drain from land; worldwide aridity. Appalachians formed by end of Paleozoic. Age of the seed plants. Origin of Conifers, Cycads and Ginkgos; possible origin of flowering plants; earlier forest types wane.
	Carboniferous 360-286 Mya	Slower earth movements. Sea beds began to rise. Climate warm; conditions like those in subtropical zones; little seasonal variation, water plentiful. Lands low, covered by shallow seas or great coal swamps. Great swamps; forests of ferns, Gymnosperms (naked seed plants) and Horsetails.
	367 Mya	**Mass extinctions**
	Devonian 408-360 Mya	Violent change in the Earth's landscape by volcanic activity and crustal movements, folding and mountain forming. Sea covers most of land. Climate became drier. Extinction of primitive vascular plants. Origin of modern groups of vascular plants with true leaves, roots and stems. The Earth started to look green. Some plants started to produce seeds, rather than spores.
	Silurian 438-408 Mya	Mild climate. Continents generally flat; again flooded. Mountain building in Europe. Earliest vascular plants (Psilopsids, Lycophytes). Modern group of algae and fungi.
	438 Mya	**Mass extinctions**
	Ordovician 505-438 Mya	Mild climate. Shallow seas; retreating from land and spreading back; teeming with life. Continents low; sea covers US. Limestone deposits. All plants and animals still restricted to the water. First fungi. Possible invasions of land by plants.
	Cambrian 540-505 Mya	Mild climate; extensive seas, spilling over continents. Plants only as algae.

	Formation of nucleotides 10^{-3} to 10^{-2} s	All forms of particles are formed: neutrons, protons, electrons, etc. The universe expands to 1/1000 present size, temperature cools to 3000°K. The light elements hydrogen and helium are formed.
	Moment of inflation 10^{-12} -	The universe has cooled to 10^{15} degrees, being a soup of matter (quarks) and radiation, a dense plasma gas under very high pressure. As the universe continues to expand, it cools further and matter wins over antimatter. The universe inflates rapidly to almost 1/1000 present size.
	Moment of [illegible]	The very moment of the big bang is shrouded in mystery because scientists believe that conventional physics won't apply at the very high temperatures in excess of a million

	temperature $0\text{-}10^{-12}$ s	billon degrees 10^{15o}C. Electromagnetic radiation and matter are indistinguishable.

ovules of living *Gingko 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*. Another major contribution was in the studies on the morphology of the Zygopteridaceae. 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*.

PALEOBOTANY

- Paleobotany refers to the study of plant Fossils, which lived some millions of years ago and are now extinct (not present). If they exist even now in living form they are called living fossils. It requires thorough study of paleontology or the study of rocks.
- Fossils are the firm portions or parts or whole organisms of plant or animal preserved in various forms inside the earth's crust by nature. The word fossil owes its derivation from Latin verb 'Fodere' which means 'to dig'. Therefore, basically fossil means any organic remains obtained from earth and excludes inorganic objects or objects fashioned by humans. It can also be defined as imprints of nature in the womb of mother earth.

Process of Fossilization or Formation of Fossils:

- Most fossils are found in sedimentary rocks, those rocks produced by the accumulation of sediment such as sand or mud. Soil, minerals, even huge rocks, boulders and other materials will be broken down into smaller pieces through rainfall, streams, rivers, wind other weathering conditions and wash away sediment on land, depositing it in bodies of water. Heavier particles settle down, whereas finer and lighter particles stay suspended in water. All these are ultimately carried to the sea or oceans by the rivers and are deposited in the form of a layer. Similar layers are continuously deposited at the bottom of seas, lakes etc. These layers are laid down one above the other. As the time pass on the lower layers with the weight of upper layers and upper layers under the pressure of the water above gets compressed and gradually harden into stony rocks. Since these are made of numerous layers or strata they are called sedimentary rocks.
- During flow of waters it also carries plant materials such as leaves, fruits, seeds etc., that falls for various reasons and are deposited at the bottom of the water bodies and are covered by sediments, which prevent oxidative decomposition and disintegration. As layers of sediment harden into layers of rocks, the plant material will be embedded and preserved. Rarely the plant body may be preserved intact. Generally, separation of plant parts happened during this process.

Important factors for fossilization are:

- Nature of tissues
- Conditions to which the tissues are subjected before and during fossilization.
- Hard tissues such as fibers, sclerenchyma, xylem are well preserved than soft tissues of flowers and leaves (rarely preserved).
- After embedding if there are no destructive agents (high oxygen, microorganisms etc.,) fossilization begins.
- Ideal conditions for fossil formation is an enclosed body of water such as a lake or swamp in which only fine grained sediments accumulate with sufficient speed to bring about quick burial.
- Low oxygen content and high concentration of toxic substances prevents decay. Then perfect fossilization takes place.

Types of Fossils: There are different types of fossils depending upon process of fossilization. Compression, Impressions, Petrifactions, Molds, Incrustation, Casts, Paper Coal, Coal Balls, Compactations or mummified plants etc.,

Petrification:

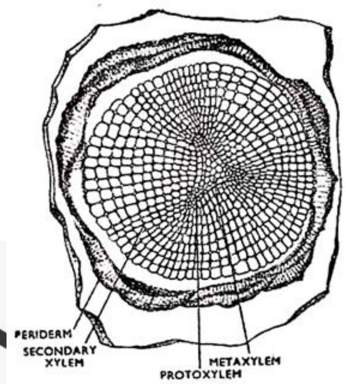


Fig. 504. Section of a coal ball showing t.s. of a petrified *Sphenophyllum* stem.

- Petrification is the best but perhaps the rarest type of fossilization. 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' (around 20 minerals such as iron, pyrites, silicates, carbonates, sulphates, phosphates, calcite, dolomite, etc.) takes place.
- Water is full of dissolved minerals. It seeps through the layer of sediments to reach the dead organism. When water evaporates only the hardened, materials are left behind. 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.
- External, internal, anatomical structures and cellular details 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. Coal balls (Figs. 504 & 505) are irregularly rounded masses ranging in diameter from a few millimeters to a meter. 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.

Fig. 505. A. A mass of coal showing coal balls. B. Section of A showing petrified stems within coal balls.

- Even delicate parts remain intact in the coal balls so that the anatomy as well as the morphology is clear. *Calmopityacea* is known for its cellular details due to existence of petrifactions but morphological structure and habit are not understood. *Rhynie* plants are example. *Callixylon* logs is upper Devonian black shale in east Pennsylvanian age in Colorado.

Compression:

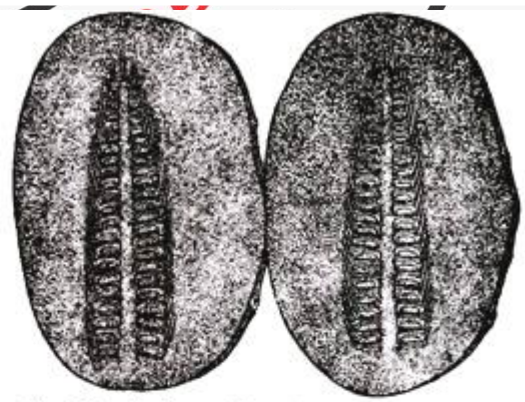


Fig. 509. A clay nodule split open showing a *Lepidostrobus* cone compression inside.

- This type of fossil is most common in the sedimentary deposits of rocks. The whole plant or plant part gets buried and the sediments go on accumulating over the plant. As the name itself suggests the buried specimen gets flattened and is retained as a carbonaceous film with outlines of external features.

- The growing pressure of the sedimentary rocks removes the air and the watery contents of the fragment out and causes the plant tissue to compress.
- The compression shows the original outline of the plant or plant parts but the original thickness of the plant material cannot be determined. Although sometimes the cell pattern of cutinized epidermis is retained. Often coalified plant structures with variable amount of cellular organization preserved, may be removable intact from matrix using mineral acids.
- Various types of sediments are involved for compression and are shale, sandstone, volcanic ash, diatomaceous earth etc., Useful for external morphological studies and to relate evolution. 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. On splitting open this nodule the organic remains are found very much intact (Fig 509) although not as perfectly as in a petrified fossil.
- Attractive fossil flora enriched with compressions of liverworts, ferns, *Ginkgo* leaves and conifers has been observed in Yorkshire coast of England. A shale deposit formed under formed under simulating conditions exists in Puryear. Abundance of organic remains marks the features of this fossil flora.
- Large number of epidermal cells, spores and cellular details of fossilized specimen are observed. Big Horn Mountains in the northwest corner of this park is an area carpeted with silicified woods and stumps affixed in their natural position.

Impression:

- These fossils are just impression of plants or plant parts on sediments. It is a negative of compression, both compression and impression leave two halves, an obverse and a reverse.
- While sediments increase in thickness, they bury, compress and flatten tender compressible plant fragments to a fraction of its original thickness. But non-compressible leafy structures get entombed in sediments, on decay of organic matter, leave imprints of its form and venation.
- Impressions found in fine grained matrices exhibit better details. 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. These fossils are useful in studying the external features of various plant parts and venation pattern of leaves (Fig. 508).

Fig. 508. Impression of *Neuropteris* leaf.

- 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.
- Deposit of Puryear in western Tennessee (United States) is a treasure of a large number of impressions in brown clay which is overlapped by a light coloured clay deposit. The former bears a variety of specimens of leaves, seeds, large number of pollen grains and fruits from lower Eocene comprising Wilcox group. Clay dug may be separated along bedding plane to expose fine leaf impressions.

Amber: Transparent golden-brown resin fossil formed from hardened pine tree sap.

Cast: Fossil formed when a mold is later filled in by mud or mineral matter.

Mold: Fossil formed when acidic water dissolves a shell or bone around which sand or mud has already hardened.

Pseudo fossils: Sometimes watery solutions of various minerals speed through the sediments and it takes the shape of some plant part or animal. Their study shows that they are neither plants nor animals. Such fossils are called pseudo fossils.

The following points highlight six main sophisticated techniques which are employed these days to study the fossils in laboratory.

1. Ground Thin Section Technique:

The specimen to be studied is cut into small-sized sections. Its surfaces are smoothed with 400-carborundum. The smooth surface of the section of the specimen is mounted on a glass slide. It is warmed and coated with melted resin. The latter hardens upon cooling. The fastened specimens are cut to form very thin slices which are ground on revolving 100-carborundum lap. Liquid resin-mounting medium is used for mounting the sections.

2. Peel Technique:

The first step of this technique involves the etching of the fossil surface with the help of some mineral acids (e.g., hydrofluoric acid) and the final step involves transfer of the exact fossil structure. Another mixture usually used for etching is prepared by mixing butyl acetate (1000ml), nitrocellulose (115gm), toluol (10ml), amyl alcohol (200ml) and dehydrated castor oil (5ml). Before using for etching purposes, this mixture is aged for at least two weeks. After etching the specimen surface is washed with water, dried and covered with nitrocellulose. Wait for a few hours. The so formed film will dry during this period. It is peeled off from the specimen and studied.

3. Transfer Technique:

Delicate fossil materials are studied by this technique. Several methods are used in the form of transfer technique. In the Ash by cellulose film transfer method, peel solution is coated on the delicate fossil material adjoining the rock surface. When the solution dries, the portion of the rock having fossil material is removed. 25% hydrofluoric acid is then used for dissolving the rock material.

4. Maceration Technique:

In the usual method of maceration technique, the fossil material is immersed in a mixture of 5% KOH and Conc. HNO_3 for one week. The material is then washed thoroughly with water so that the acid is completely removed. It is then incubated with the solution of NaOH. Hydrofluoric acid is used for cleaning the thus separated cuticularized parts of the fossil material.

5. X-ray Technique:

Highly sensitive celluloid films are used to obtain X-ray photographs of the fossil specimens.

6. Microtomy Technique:

Fossil specimens, specially their macerated tissues, are embedded in celloidin or wax before microtomy. Sectioning of the embedded material is done by usual process of microtomy. The sectioned materials are stained and studied.

Rhynia

- Class : Psilotopsida
- Order : Psilotales
- Family : Rhyniaceae
- Genus : *Rhynia*

External Structure of *Rhynia*:

- The plants of *Rhynia* were herbaceous. R. major was 50 cm. in height and 1.5 to 6 mm in diameter whereas *R. gwynne-vaughani* was only about 20 cm. in height and 1 to 3 mm in diameter.
- The plant body was differentiated into a subterranean rhizome with an abruptly turned upright photosynthetic aerial shoots. Roots were absent but at places rhizome was provided with tufts of unicellular rhizoids (Fig. 1 A, B). The aerial shoots were cylindrical and leafless with a tapering dichotomously branched system.

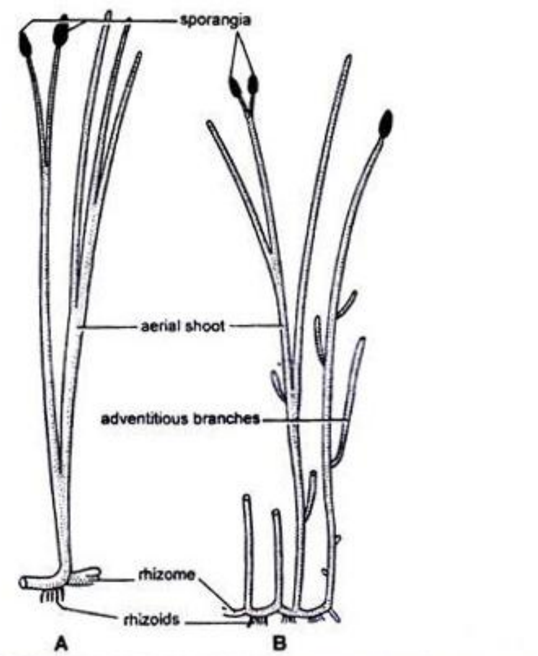


Fig. 1 (A–B). *Rhynia*. External features. A. *R. major*, B. *R. gwynne-vaughani*

- In *R. major* the aerial shoots were smooth (Fig 1 A) but in case of *R. gwynne-vaughani* many adventitious branches were present on the aerial shoots as well as rhizome (Fig. 1 B). These branches perhaps help in vegetative propagation.
- The tip of the aerial branch usually bears a solitary terminal sporangium which was about 12 mm in length and about 4 mm in diameter.

Internal Structure of *Rhynia*:

Transverse section (T.S.) of Aerial shoot and Rhizome:

- Anatomically, the aerial shoots and rhizome are almost similar. T. S. of aerial shoot can be differentiated into three parts: epidermis, cortex and stele (Fig. 2 A).

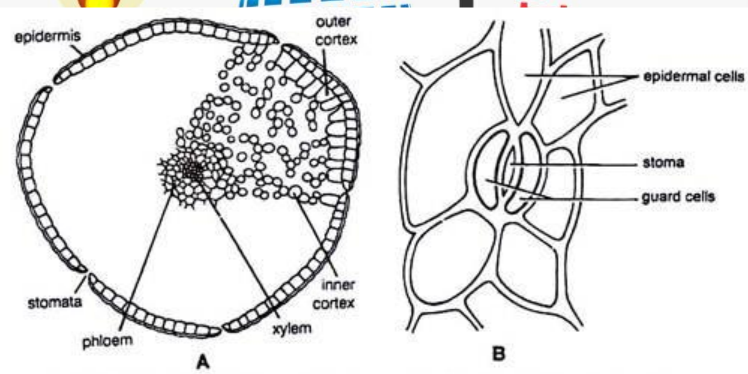


Fig. 2 (A–B). Rhynia. Internal Structure : A. T. S. of aerial shoot, B. a stoma

(a) Epidermis:

- It was the outer-most surrounding layer. It was one cell thick and covered by thin cuticle. In aerial shoots it was interrupted at certain places by stomata but stomata (Fig. 2 B) were absent in rhizome.

(b) Cortex:

- Epidermis was followed by cortex. It is differentiated into outer cortex and inner cortex. The outer cortex was only 1-4 cells thick, thin walled and without intercellular spaces. The inner cortex had large intercellular spaces and its cells had chloroplast. It is thought that this was the chief photosynthetic region of the plant. The endodermis and pericycle layers were absent.

Stele: The centre of the aerial shoot/rhizome was occupied by stele. The stele was a protostele (haplostele). The xylem was made up of annular tracheids and there were no sieve plates in phloem.

Reproductive Structures of *Rhynia*:

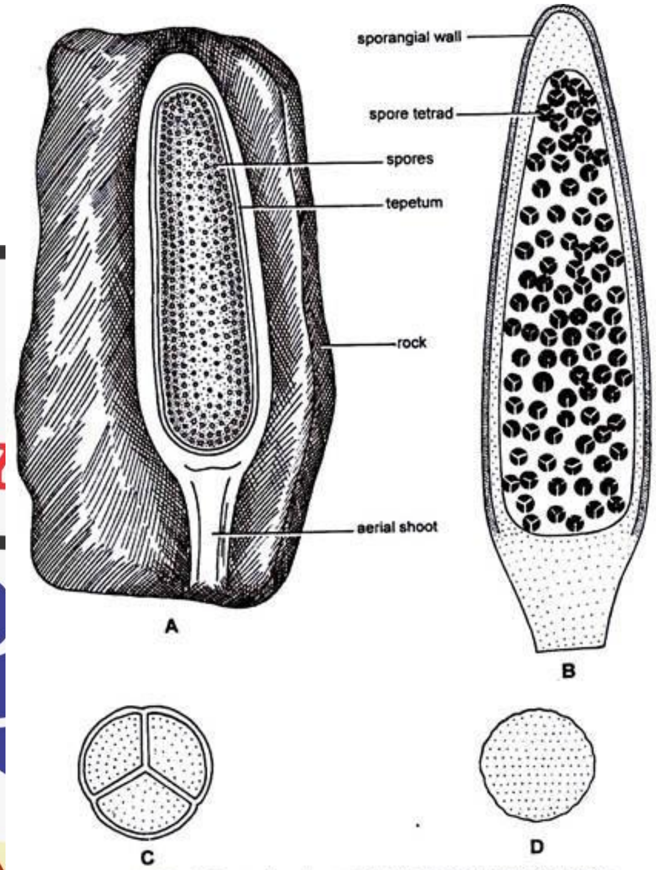


Fig. 3 (A–D) *Rhynia.* Sporangia and spores A. L. S. of sporangium of *R. major*, B. L.S. of sporangium of *R. gwynne-vaughani*, C. Sporetetrad, D. Spore

- The sporangia were borne singly on the apices of some aerial branches, each sporangium being oval or slightly cylindrical structure with a little greater diameter than that of aerial branch on which it is developed. They were 12 mm long and 4 mm in breadth in *R. major* and 4 mm long and 1 mm broad in *R. gwynne-vaughani*.
- A longitudinal section (L.S.) of sporangium shows that it had a five cells thick wall. The outermost layer was 1 cell thick cuticularized epidermis. It was followed by 3 cells thick middle layers of thin walled cells.
- The inner-most layer was 1 cell thick tapetum. The wall was surrounding a spacious sporangial cavity which was without columella and contained large number of spores. The spores were of same size and measured up to 60 μ in diameter.
- It means that *Rhynia* was homosporous. In many specimens the sporangium contained tetrahedral tetrads of spores (Fig. 3 B, C) which suggest that they were formed by reduction division and the plant bearing them represented the sporophytic generation.
- There was no special mechanism of sporangium dehiscence. The liberation of spores seems to have taken place by disintegration of the sporangial wall. Nothing definite about the gametophyte of *Rhynia* is known.

Cycadeoidea

- Class : Cycadopsida
- Order : Cycadeoideales
- Family : Cycadeoideaceae
- Genus : *Cycadeoidea*

History of *Cycadeoidea*:

- *Cycadeoidea*, also called Bennettites by several European palaeobotanists is represented by about 30 species. The name *Cycadeoidea* was put forward in 1827 for petrified trunks from Isle of Portland. Though Bennettites is still employed for plant fossils from the Isle of Wight, *Cycadeoidea* is now the valid name of the genus. It has been reported from Upper Jurassic to Upper Cretaceous rocks of America, India, Russia and several European countries. It occurs in the form of a large number of petrifactions in different parts of the world.

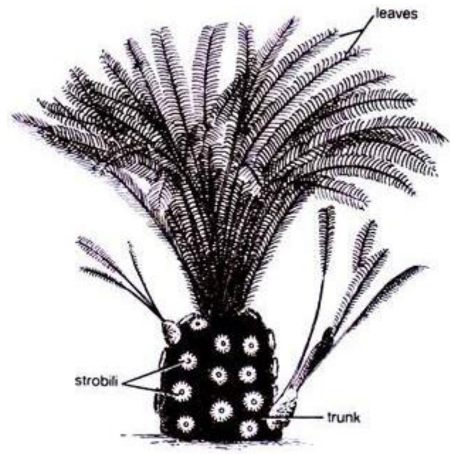


Fig. 6.1. *Cycadeoidea dacotensis*. External features. (after Macbride)

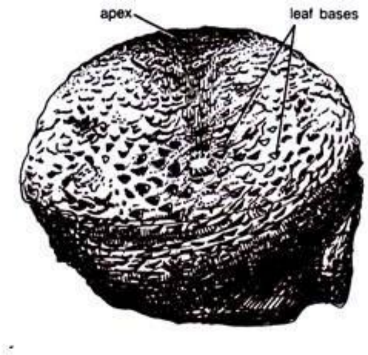


Fig. 6.2. *Cycadeoidea colossalis* showing almost completely spherical stem. (after Wieland).

Morphological Features of *Cycadeoidea*:

- The *Cycadeoidea* trunks were short, stout, spherical to sub-spherical (Figs. 6.1, 6.2) and un-branched or branched. The trunks and leaves of many of its species show remarkable resemblance with those of living Cycads.
- Some of the species were short while others (*Cycadeoidea jenneyana*) attained a height of 3 to 3 .6 meters. The trunk generally attained a diameter of about 50 cm, and had many, persistent, rhomboidal leaf bases (Figs. 6.2, 6.3). A compact crown of Cycad-like, large, pinnately compound leaves was present at the apex. The leaflets had many parallel veins.

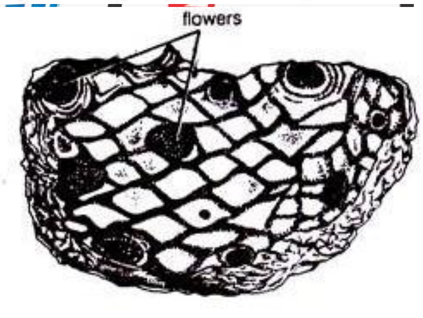


Fig. 6.3. *Cycadeoidea gibsonianus*. Tangential section through leaf base and flowers.

Anatomy of *Cycadeoidea*:

- The stem was roughly circular or oval in outline. It remained covered by heavy armour of leaf bases.
- The epidermis was not very distinct.
- The cortex was parenchymatous and possessed many mucilage canals and leaf traces. M
- any conjoint, collateral, open and endarch vascular bundles constituted the primary vasculature of the stem (Fig. 6.4).

- A large centrally located pith was present. The xylem and the phloem have been studied in detail by Wieland (1906) (Fig. 6.5 A, C) Most of the tracheids were rectangular in shape. They were scalariform. The tracheids of protoxylem were spiral.
- The secondary xylem and the secondary phloem were traversed by secondary medullary rays, which were either uniseriate or bi-seriate.
- Cambium was clearly visible. A leaf trace developed singly from the primary vascular strand. It divided into many mesarch strands upon entering into the cortex. At the place of its origin the leaf trace was C-shaped.

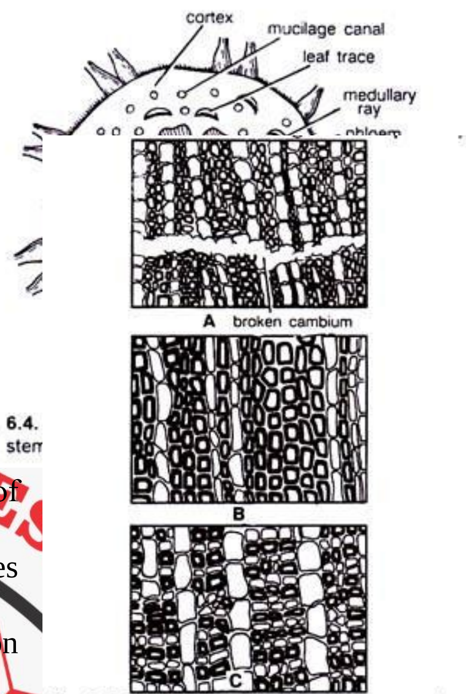
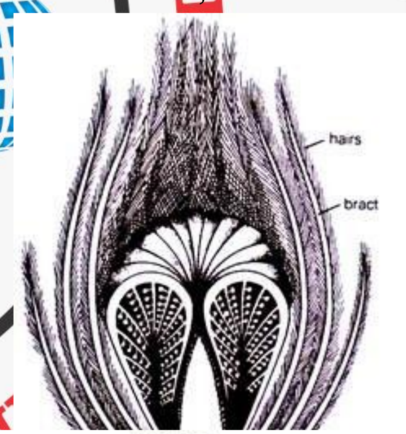


Fig. 6.4. T.S. stem

Fig. 6.5. *Cycadeoidea wielandii.* A, T.S. stem passing near cambium; B, T.S. secondary wood; C, T.S. phloem showing thin-walled and thick-walled tracheids. (all after Wieland).

Reproductive Organs of *Cycadeoidea*:

- The Bennettitalean reproductive organs are designated as "flowers ". The flower buds in the plants were present in the axil of leaf bases.
- As many on 500 flower buds were present on a single trunk in species such as *Cycadeoidea dartonii* (=*Monanthesia dartonii*).
- In several species of *Cycadeoidea* all the flower buds were present on a trunk at almost the same stage of development.
- Some palaeobotanists believe that such a plant might have flowered only once during its lifetime. Except a few species (e.g. *C. wielendii*) the flowers in *Cycadeoidea* were bisexual. Hermaphrodite flower developed on a short pedicel. They were surrounded by as many as one hundred bracts, which were hairy and protective (Fig. 6.6).
- Flowers in different species were of different size. In *Cycadeoidea dartonii* they attained a length of about 2 cm and a diameter of about 1.5 cm while in *C. dacotensis* each flower was about 8 cm long and 3 cm in diameter. In *C. dacotensis* the lower two-third portion of the floral axis had about 100-150 bracts.
- A whorl of stamens was present above the bracts. Each stamen was pinnately branched (Fig. 6.7) and each pinna had a double row of purse-shaped sporangia. Each sporangium resembled with a synangium. A conical floral axis was present just above the whorl of stamens. The entire compact structure resembled with a strobilus.



Microsporophyll in *Cycadeoidea*:

- According to Wieland (1906, 1916), the androecium or pollen-bearing region consisted of about 20 pinnate, microsporophyll's. These were somewhat fixed or united at the base.
- Bean-shaped pollen capsules were arranged in two rows on each pinna of the sporophyll. This microsporophyll's remained folded round the gynoecium when young, but probably at maturity they expanded.
- Delevoryas (1963), however, opined that the microsporophyll's never expanded. He further concludes that synangia-bearing structures, described as pinnae by Wieland (1906), were similar to the trabeculae. These trabeculae established a connection between outer and inner walls of the androecium.

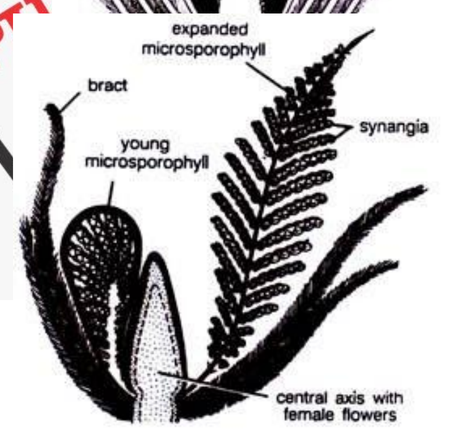


Fig. 6.7. *Cycadeoidea dacotensis.* Apical part with expanded and curved microsporophylls and a central conical axis. (after Wieland).

- Pollen capsules or synangia were borne along these trabeculae. Several (20-30) pollen sacs or microsporangia were present in a pollen capsule or synangium. The wall of a synangium consisted of outer palisade-like, thick-walled cells followed by thin-walled layer and then a tapetum. The tapetum was not clearly demarcated (Figs. 6.8, 6.9). The pollen grains were oval in shape and measured up to 68fi in length. Multicellular pollen grains in *Cycadeoidea* have been reported by Taylor (1973).

Gynoecium of *Cycadeoidea*:

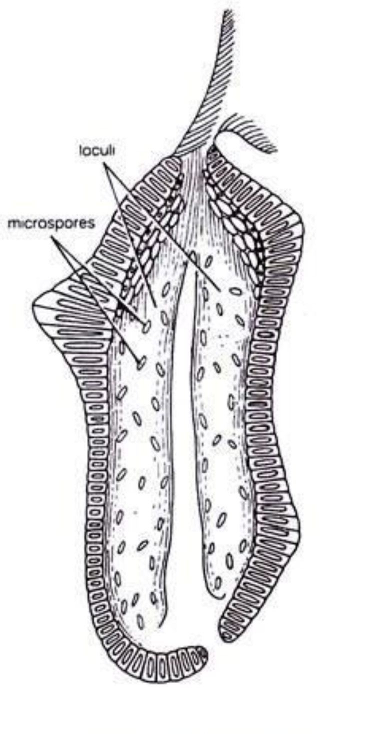


Fig. 6.8. *Cycadeoidea dacotensis*. L.S. sporangium showing stalk and two loculi with microspores. (after Wieland, 1906).

- The gynoecium receptacle was spherical or conical in shape. Hundreds of the stalked ovule along with an approximately equal number of inter-seminal scales were present on the receptacle (Fig. 6.10).
- Each ovule was about 1 mm in length. The integument of the ovule was fused with the nucellus, except at the apex.
- The ovule was orthotropous with a long micropylar beak. A pollen chamber and a nucellar beak was present in each ovule (Fig. 6.11).
- The seed was somewhat elongated or oval in shape and possessed two cotyledons (Fig. 6.12). Crepet and Delevoryas (1972) reported a linear tetrad in the nucellar region of *Cycadeoidea*.

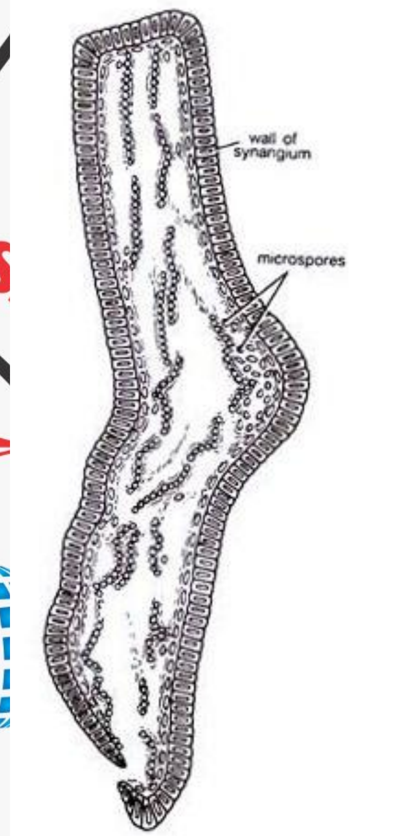


Fig. 6.9. *Cycadeoidea dacotensis*. T.S. of a synangium. (after Wieland, 1906).

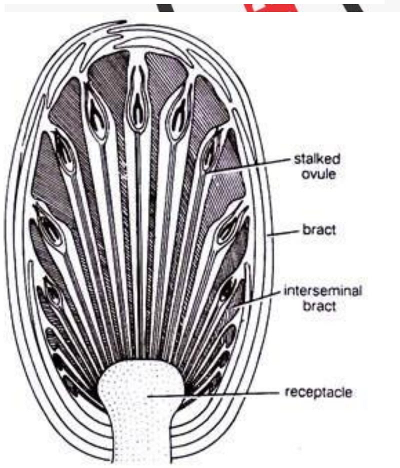


Fig. 6.10. *Bennettites gibsonianus*. A female strobilus showing terminal seed with dicotyledonous embryos

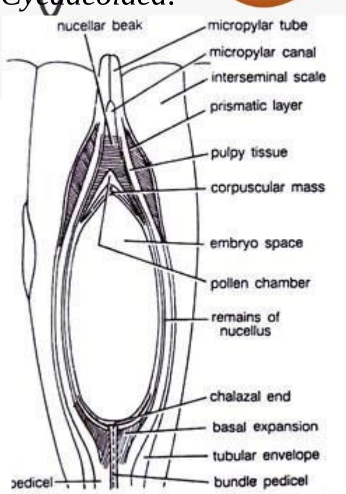


Fig. 6.11. *Bennettites morieri*. L.S. seed. (after Wieland, 1906).

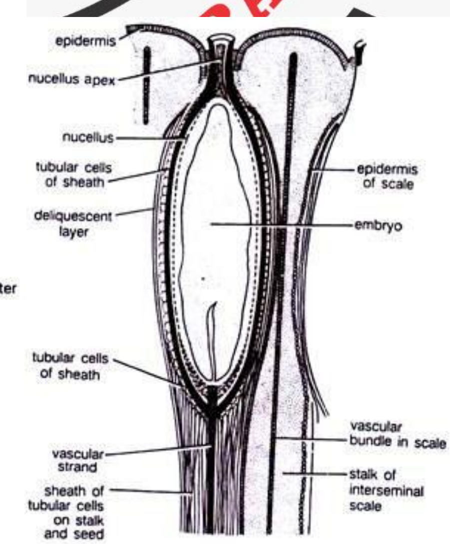


Fig. 6.12. *Bennettites albianus*. L.S. seed along with two surrounding interseminal scales. (after Stopes)

Pentoxylales

- Stem Genera of Pentoxyleae:
- ***Pentoxylon Sahnii:*** *Pentoxylon sahnii* and *Nipanioxylon guptai* are the stem genera of "Pentoxyleae". The stems of *Pentoxylon* sahnii attained a diameter from 3mm to 2cm. The stem has always been reported in association with the leaves called *Nipaniophyllum*.
- Presence of five steles in a cross- section of the stem has been the main reason for giving the name *Pentoxylon* to the genus. Many short lateral shoots or dwarf shoots were also present on the stem.
- Five steles (Fig. 7.1) occupied greater part of the stem in a cross-section. Each stele had its own cambium. The cambium was uniformly active in the young stems, but at maturity more secondary tissue developed towards the centre, and thus the secondary wood appeared eccentric.
- Primary phloem and primary xylem were present towards outer and inner sides of the cambium, respectively. Six steles have also been observed by Sahni (1948), although rarely.
- According to Vishnu Mittre (1953) the number of steles varied along the length of the stem. There were present five much smaller bundles just alternating with the main bundles of the stem i.e. five steles. Each such bundle had a large amount of secondary wood. These were probably the leaf trace bundles.
- Medullary rays of the main steles were uniseriate, and they lacked ray tracheids, wood parenchyma and resin canals. The secondary wood resembled greatly with that of *Araucaria*. Uniseriate or bi-seriate bordered pits were present on the radial wall of tracheids.

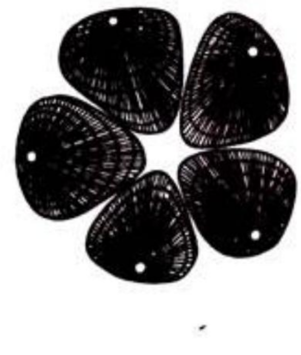


Fig. 7.1. *Pentoxylon sahnii.* T.S. stele. (after Sahni)

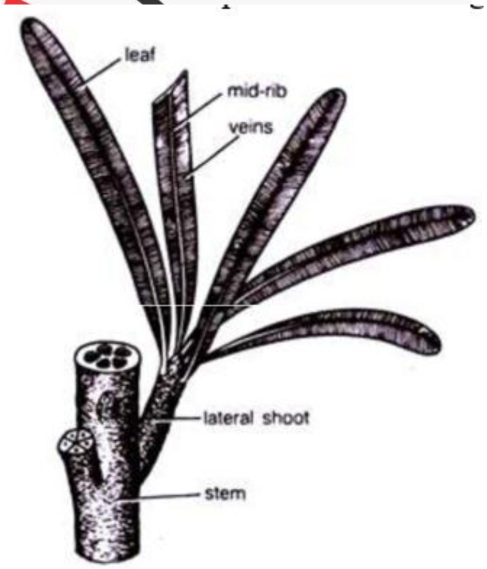


Fig. 7.2. *Pentoxylon sahnii.* Reconstruction of stem and leaves (*Nipaniophyllum raoi*). (after Sahni).

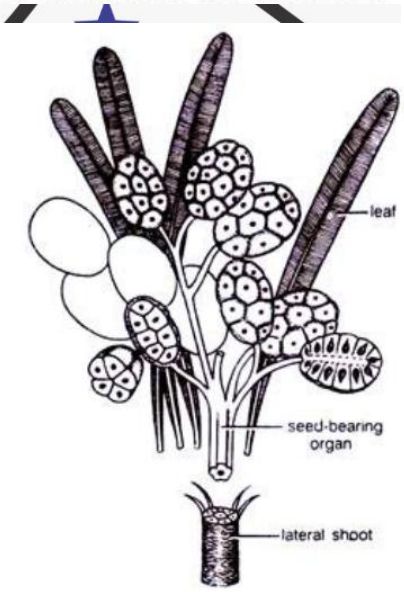


Fig. 7.3. *Carnoconites compactum.* Female cones. (after Sahni).