

B. SC. SEMESTER-II

BOTANY PAPER I

(PALAEOBOTANY, PTERIDOPHYTES, GYMNOSPERMS AND SOIL ANALYSIS)

UNIT-II:

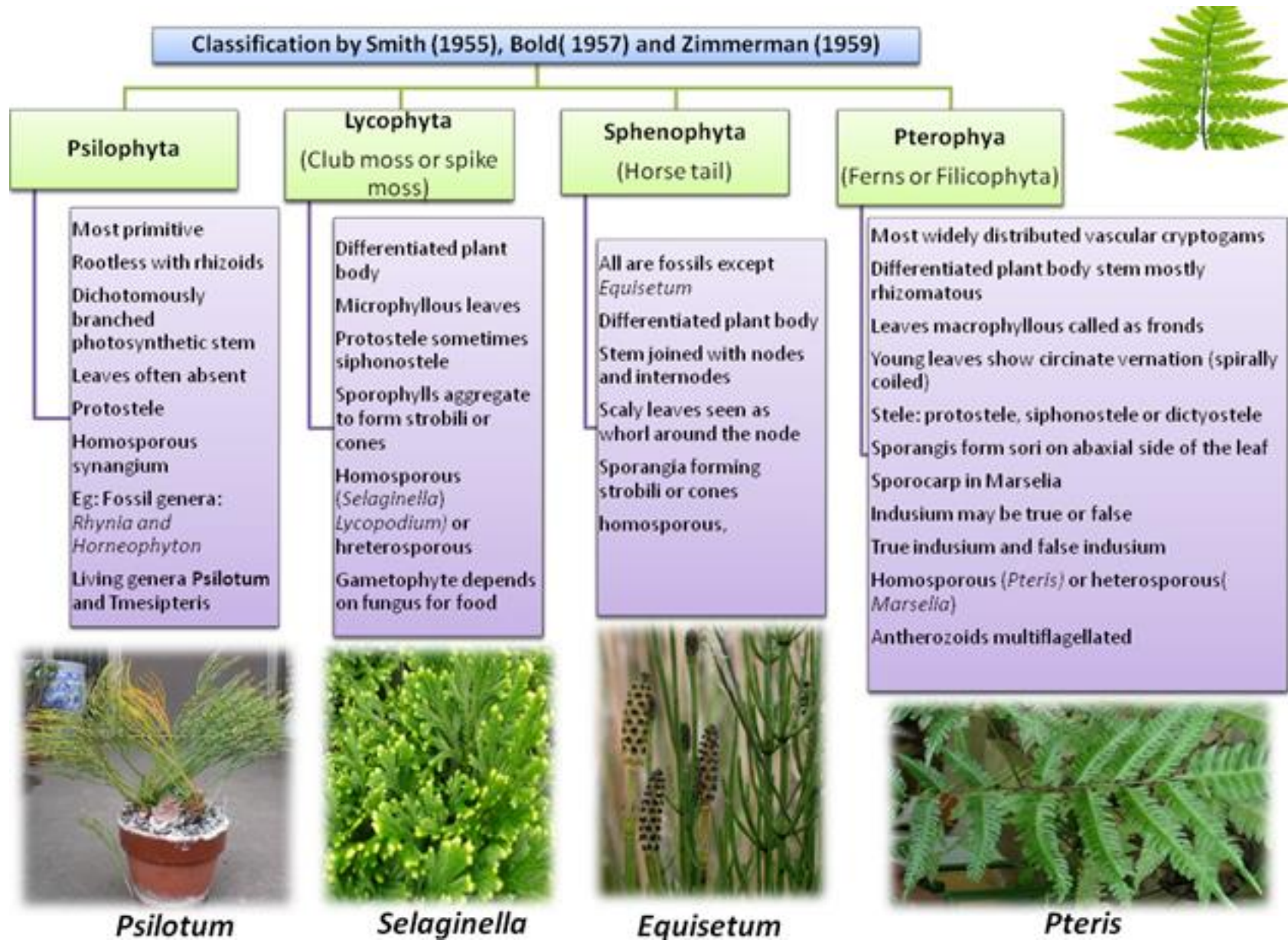
Pteridophytes:

- 1. Pteridophyta:** General characteristics, Classification (Smith, 1952),
- 2. Fossil Pteridophyte:** *Rhynia*
- 3. Life history of:** *Selaginella* and *Equisetum*.
4. Heterospory and seed habit.
5. Brief account of types of steles

1. Pteridophyta: General characteristics

- A vascular plant that generates and disperses spores is known as a pteridophyte.
- Because they do not produce blooms or seeds, pteridophytes are often referred to as "*cryptogams*," which means that their reproductive methods are hidden.
- They're the most rudimentary of the bunch.
- Pteridophytes live in wet, shaded, and damp environments.
- They can be found in bogs, swamps, tropical plants, and cracks in rocks.
- The Pteridophytes were among the first plants to actually live on land.
- They are vascular, seedless *cryptogams*.
- Pteridophytes are spore-reproducing, seedless plants.
- They lack xylem vessels and phloem companion cells but have vascular tissues.
- The majority of the leaves are missing, Homosporous synangium is the sporophyte.

Classification (Smith, 1952),



Smith (1955) divided the vascular cryptogams into four divisions :- Vascular Cryptogams (Pteridophytes)

Division (I) Psilophyta

Class - Psilophytineae

- Order 1. Psilophytales
- 2. Psilotales

Division (II) Lepidophyta

Class – Lycopodineae

- Order 1. Lycopodiales
- 2. Selaginellales
- 3. Lepidodendrales
- 4. Isoetales

Division (III) Calamophyta

Class - Equisetineae

- Order 1. Hyeniales
- 2. Sphenophyllales
- 3. Equisetales

Division (IV) Pterophyta

Class - Filicinae (Fern)

Subclass 1. Primofilices

Order 1. Protopteridales

2. Coenopteridales
3. Archaeopteridales

Subclass 2. Eusporangiatae

Order 1. Ophioglossales

2. Marattiales

Subclass 3. Leptosporangiatae

Order 1. Filicales

2. Marsileales
3. Salviniiales

2. Fossil Pteridophyte: Rhynia

Classification

Kingdom-Plantae

Division-Tracheophytes

Class-Rhyniopsida

Order – Rhyniales

Family – Rhyniaceae

Genus – *Rhynia*.

Introduction

They are simplest extinct vascular plant.

Discovered by **Sir William Dawson's** (**1858**) from Devonian period of Palaeozoic age.

Found at USA, Scotland, Norway and Belgium.

Some investigator Dr. Mackie(1913), Dr. Kidston and Prof. Lang

It has two species *R. major* and *R. gwynne-vaughani*.

- **External morphology**

- *R. Major* 50 cm in height and 1.5-6 mm in diameter. Aerial shoot are smooth
- *R. Gwynne-vaughani* 20 cm in height and 1-3 mm in diameter. Shoots with adventitious branches
- Root is absent
- Rhizoids are present instead of root
- Aerial stem was dichotomously branched and taper
- The tip of aerial branch bear solitary terminal sporangia

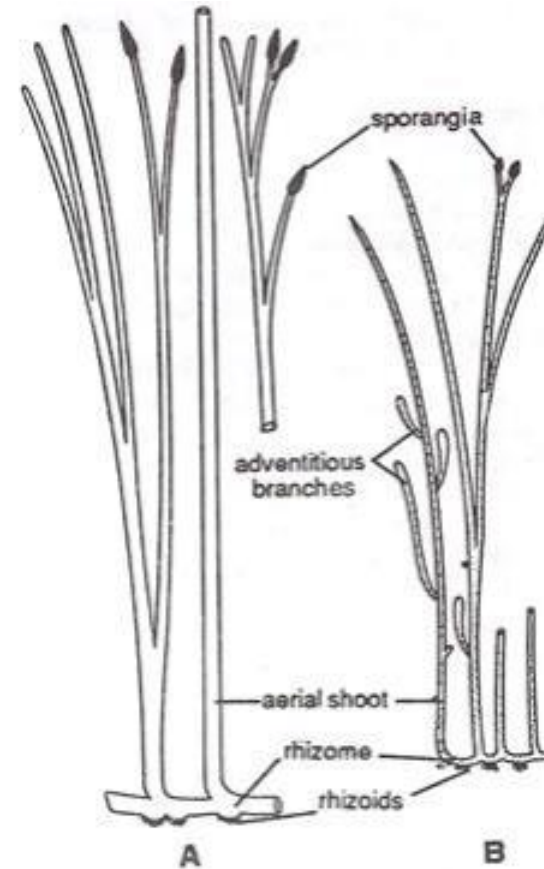
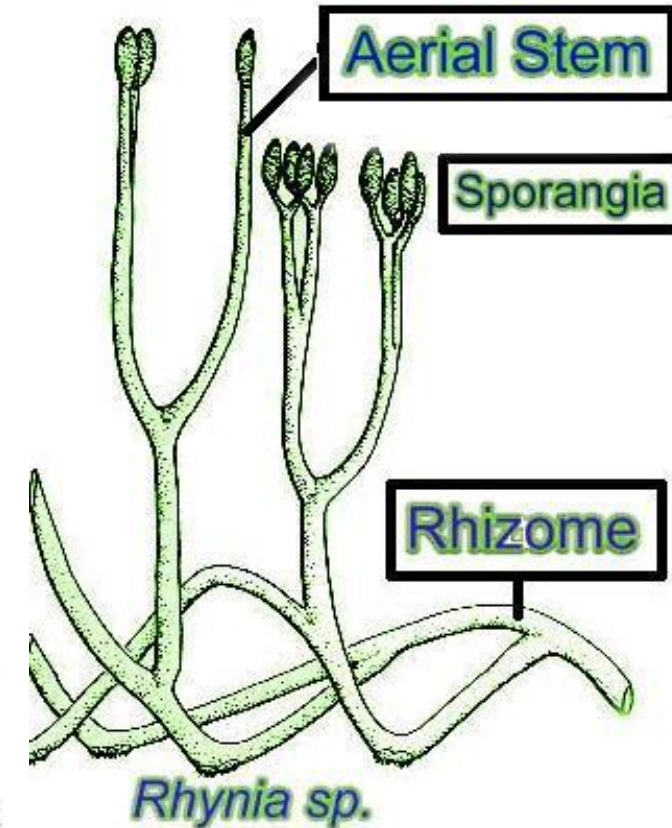


Fig. 206. *Rhytnia*, external features. A. *R. major*; B, *R. gwynne-vaughani*.



- **Internal structure**
- **Anatomy of stem**
- **Epidermis :-** 1} It is thick and covered by thick cuticle.
2} presence of stomata.
- **cortex:-** 1} Differentiated into outer and inner cortex.
2} Having intercellular spaces with chloroplast.
3} Endodermis and pericycle are absent.
- **Stele:-** 1} Presence of Protostele.
2} xylem made up of annular tracheids and no sieve element in phloem.

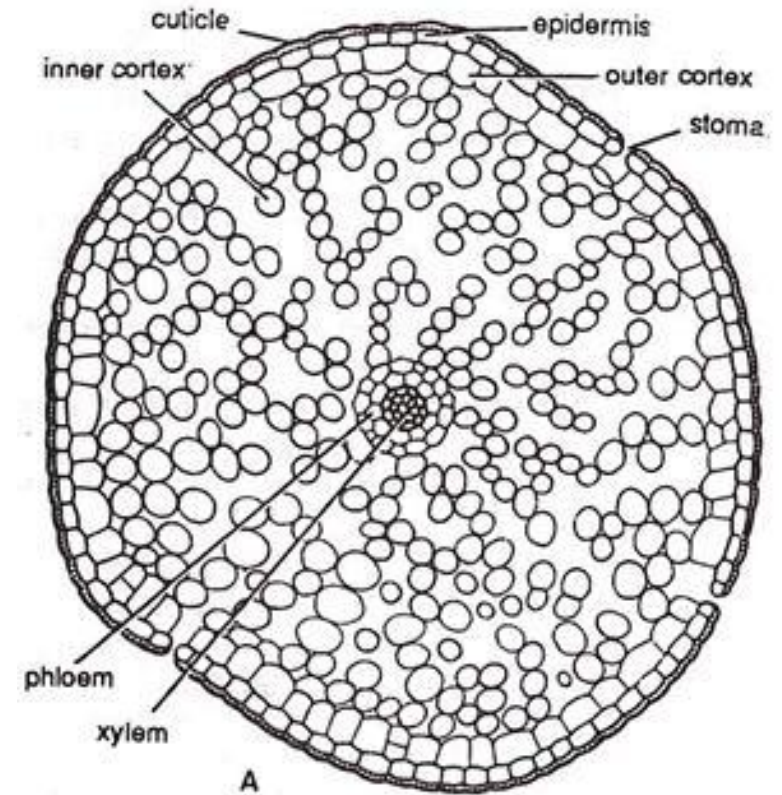


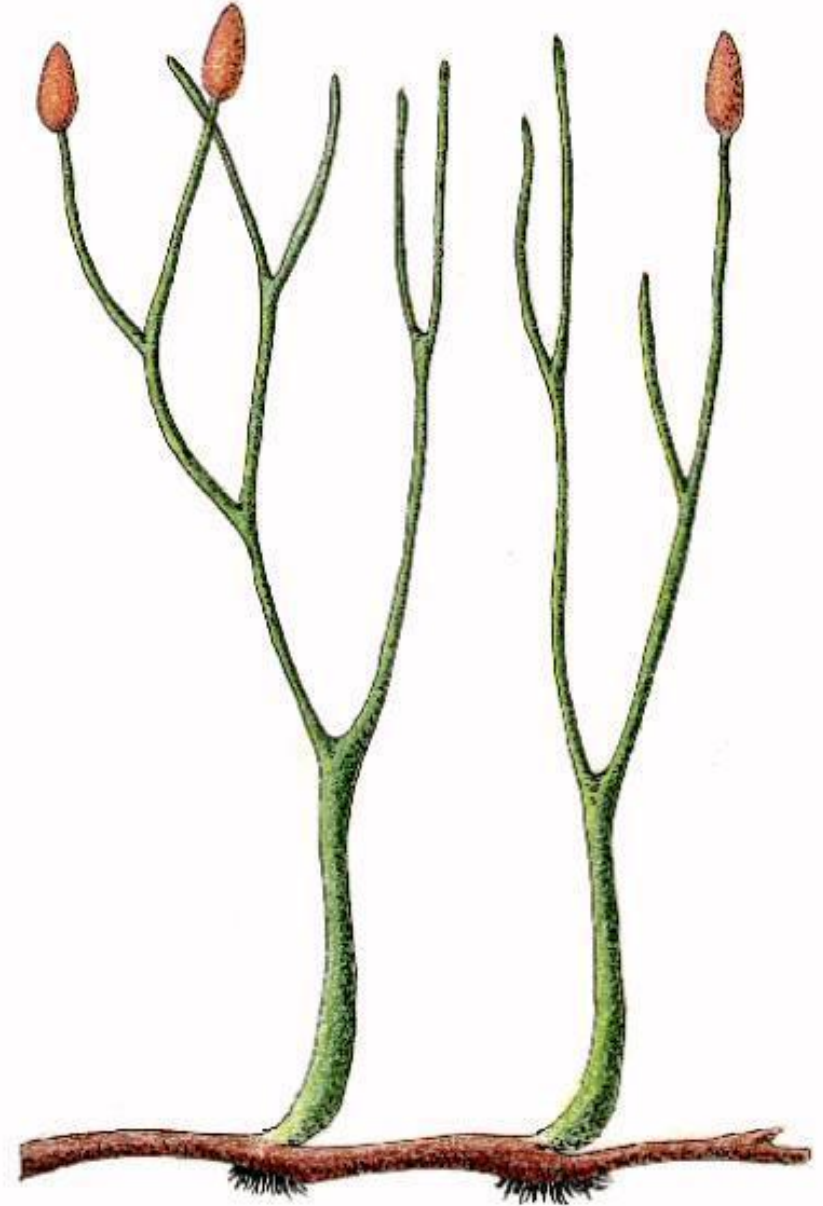
Fig. 207. *Rhynia*. A, T.S. rhizome; B,

Reproductive structure of Rhynia

- It takes place by sporangia formation.
- Born singly at apices of apical branches sporangia is oval and cylindrical and 12 mm long 4mm breadth.

L.S of Sporangium

- Outer most layer having thick epidermis.
- Presence of tapatum layer.
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- Having tetrahedral homospore.
- No evidence of gametophyte.



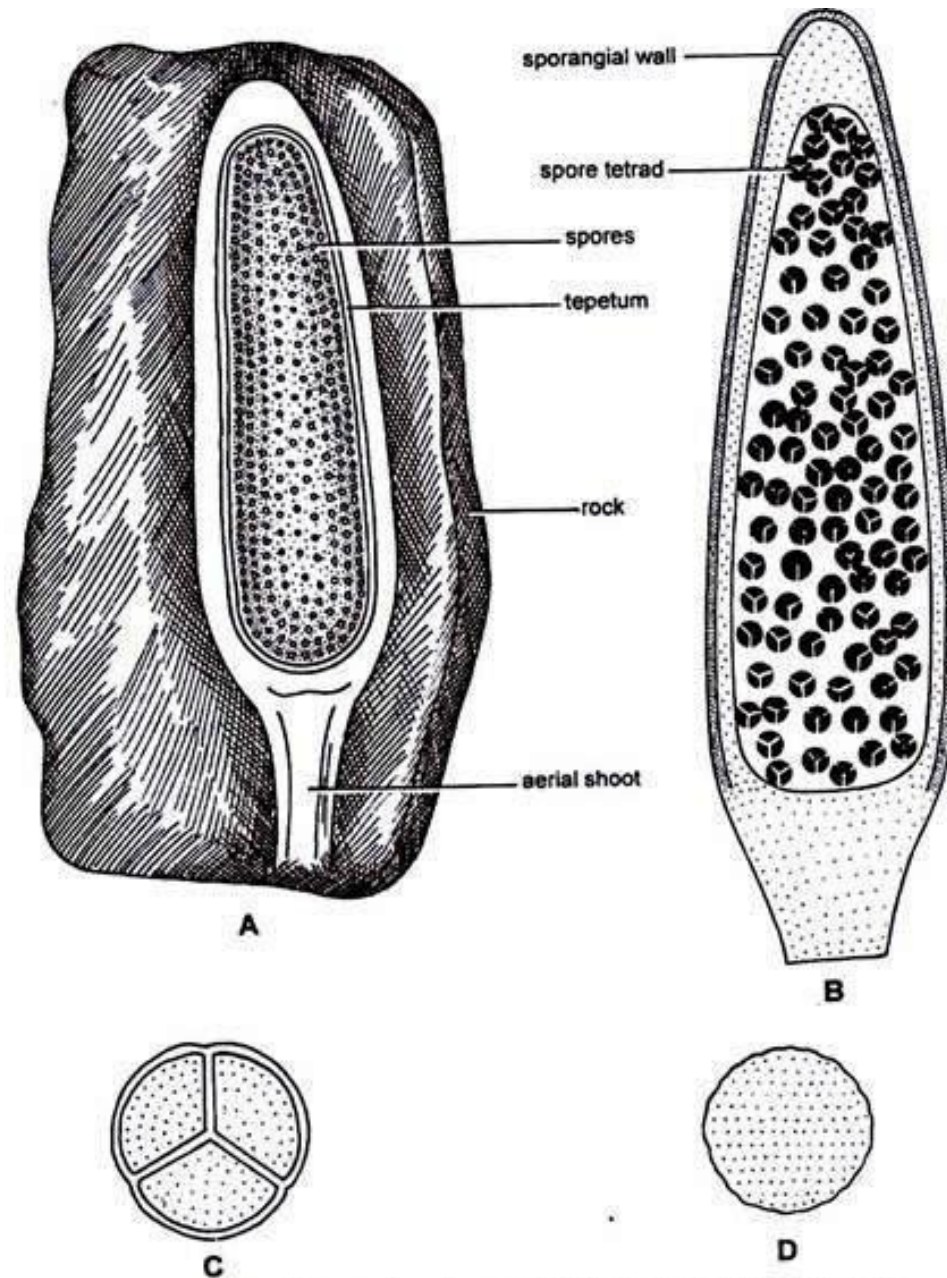


Fig. 3 (A-D) *Rhynia*. Sporangia and spores A. L.S. of sporangium of *R. major*, B. L.S. of sporangium of *R. gwynne-vaughani*, C. Sporetetrad, D. Spore

3. Life history of: *Selaginella*.

Systematic position

Division - Lycophyta

Class - Liliopsida

Order - Selaginellales

Family - Selaginellaceae

Genus – *Selaginella*

Habit and Habitat of *Selaginella*:

- *Selaginella* is the only living genus of the order Selaginellales and 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. oregana* It is found growing on tree trunks.

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 :

(i) Stem:

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

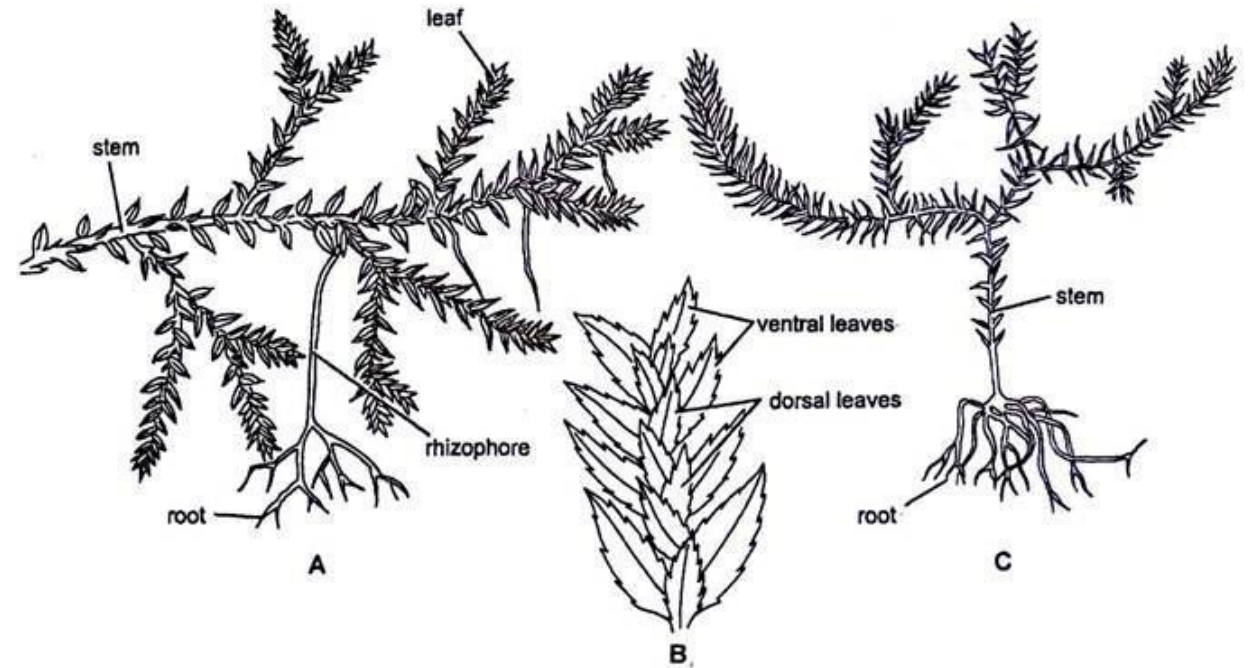


Fig. 1 (A–C). *Selaginella*. External features : A. *S. kraussiana*, B. Leaf arrangement in a branch of *S. kraussiana*, C. *S. spinulosa*

(ii) Leaves:

- They are usually small, simple and lanceolate with a pointed apex.
- Each leaf is provided with a single unbranched midrib.
- In the subgenus homoeophyllum all the leaves are of same size and are spirally arranged forming a dense covering.
- In the sub-genus 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).

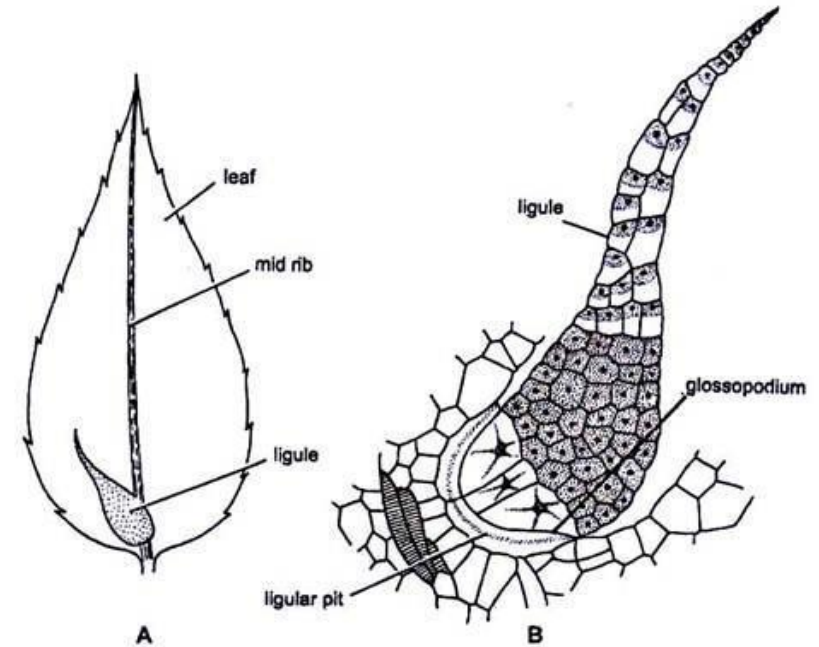


Fig. 2 (A, B). *Selaginella*. Structure of ligule : A. Leaf with ligule, B. Longitudinal section of ligule

- **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. krciussiana* 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.

Internal Structure of Selaginella:

1. Stem:

- A Transverse 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 hairs and 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.
- 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.

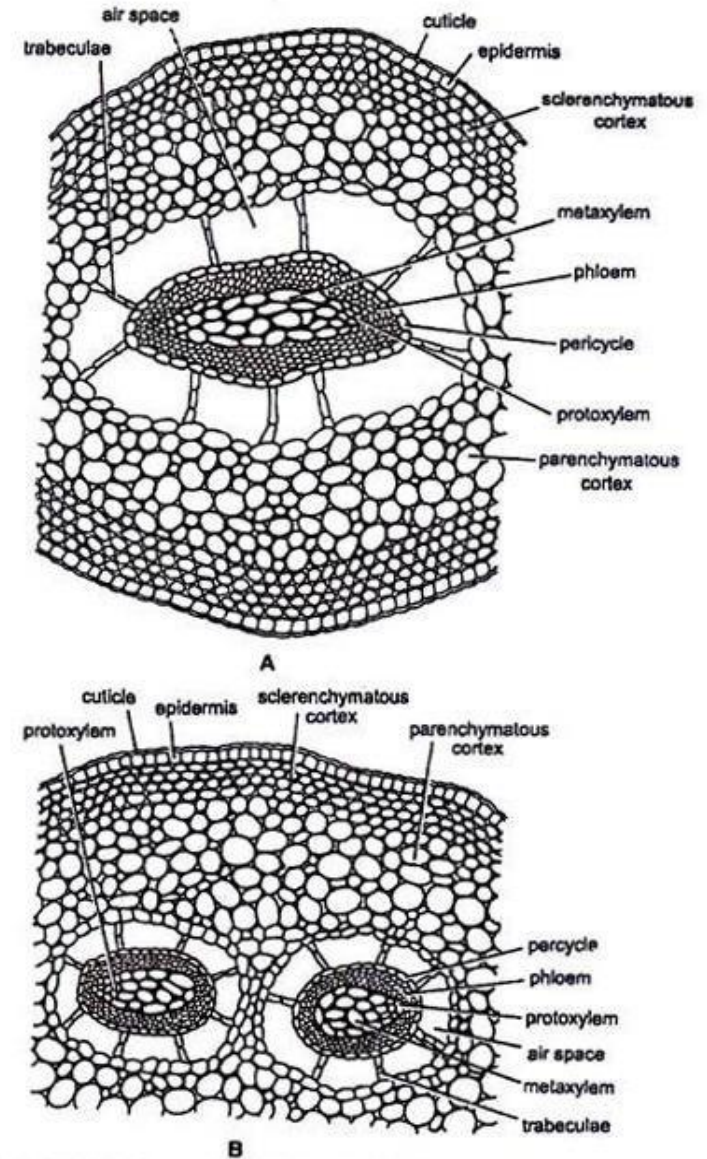


Fig. 3 (A-B). *Selaginella*. T. S. Stem. (A) T. S. monostelic stem, (B) T. S. distelic stem (a part cellular),

2. Root:

A T.S. of the root is somewhat circular in outline 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.

(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.

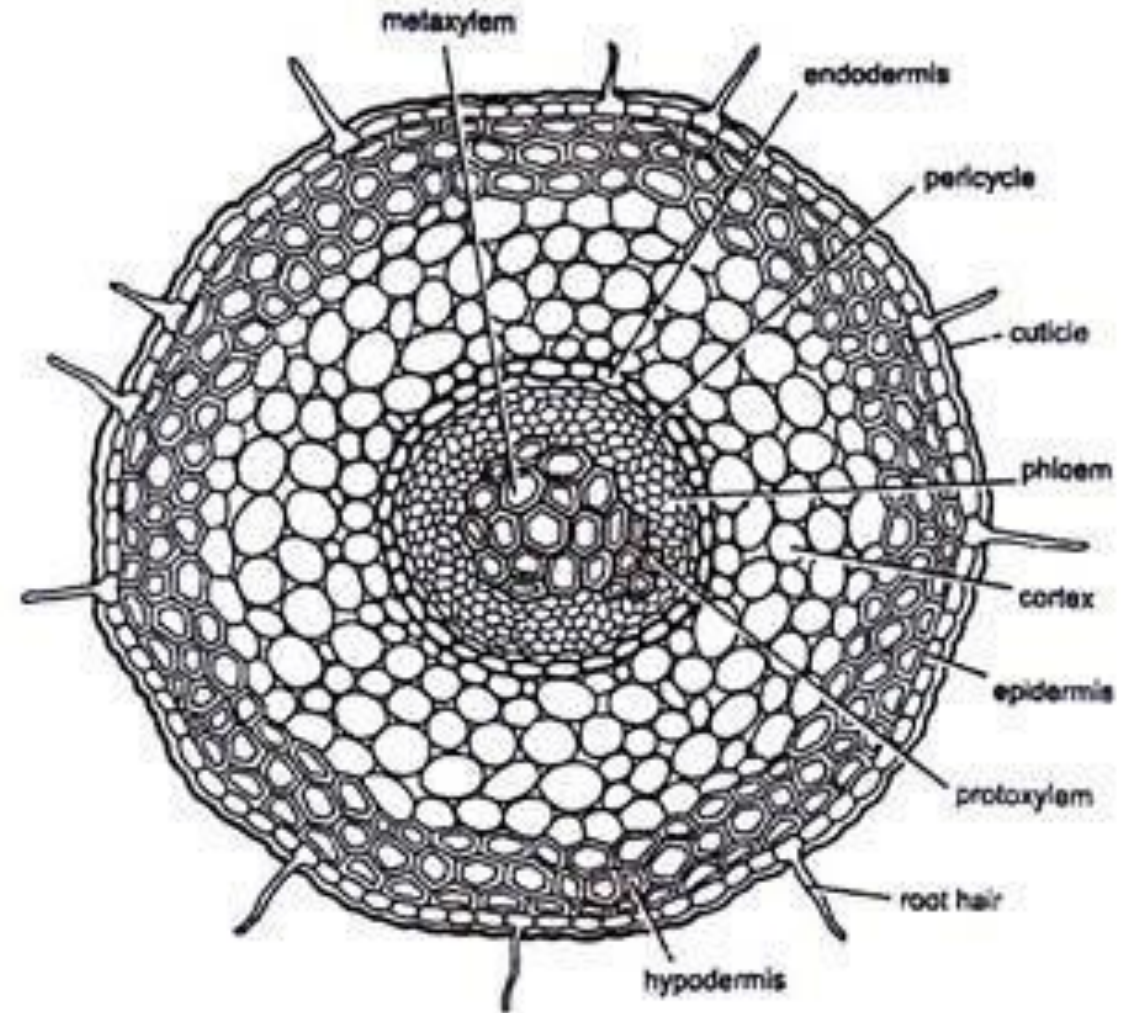


Fig. 4. *Selaginella*. T. S. of root

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 .

(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.

(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 crescentic with a number of protoxylem strands situated on the concave adaxial side.
- In *S. kraussiana*, *S. poulteri* etc. protoxylem is mesarch (centroxylic).

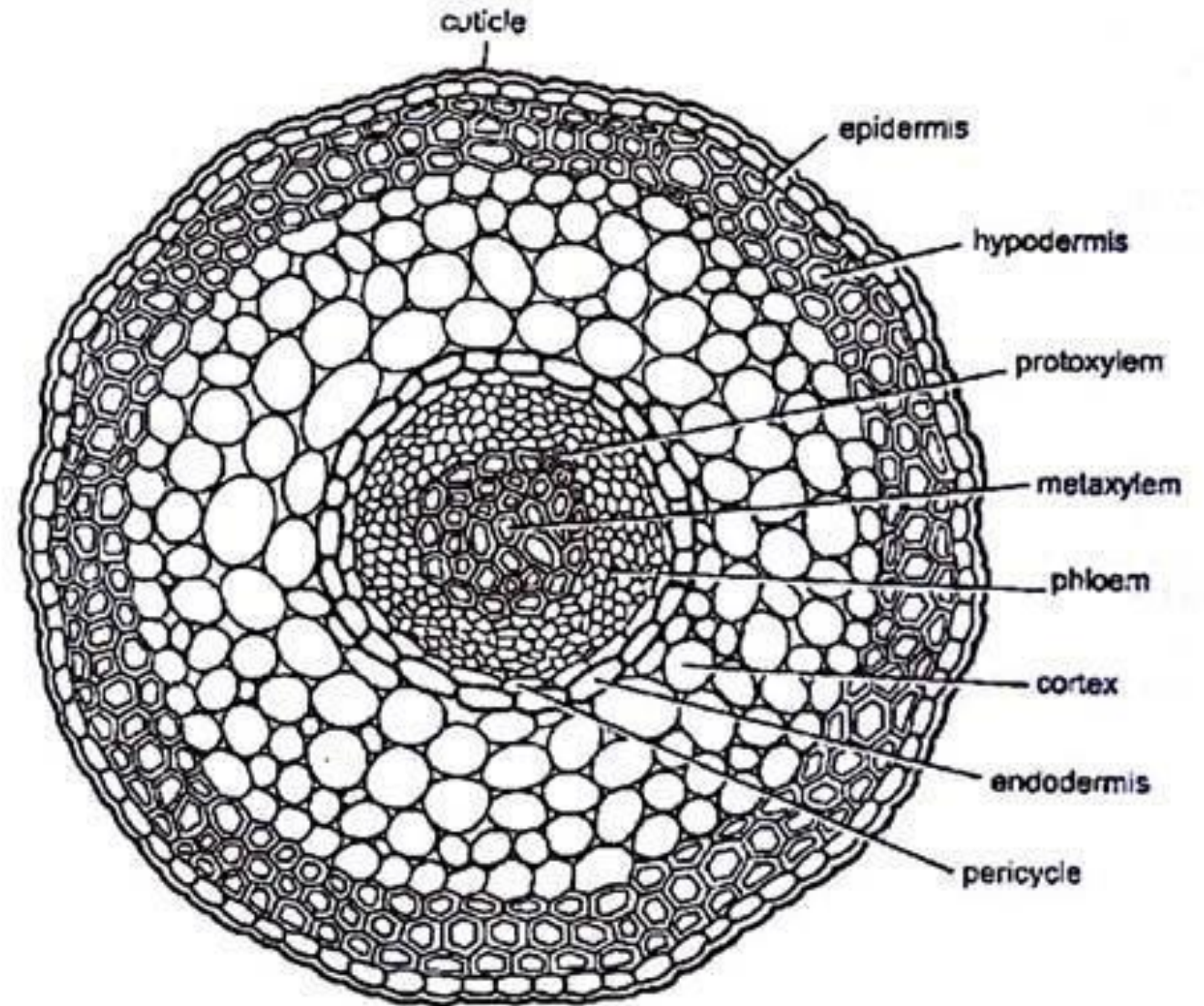


Fig. 5. *Selaginella* . T. S. rhizophore

4. Leaf:

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

(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., *willedenovii*) chloroplasts.
- Each chloroplast has several pyrenoid like bodies similar to order Anthocerotales (Bryophyta).
- 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.

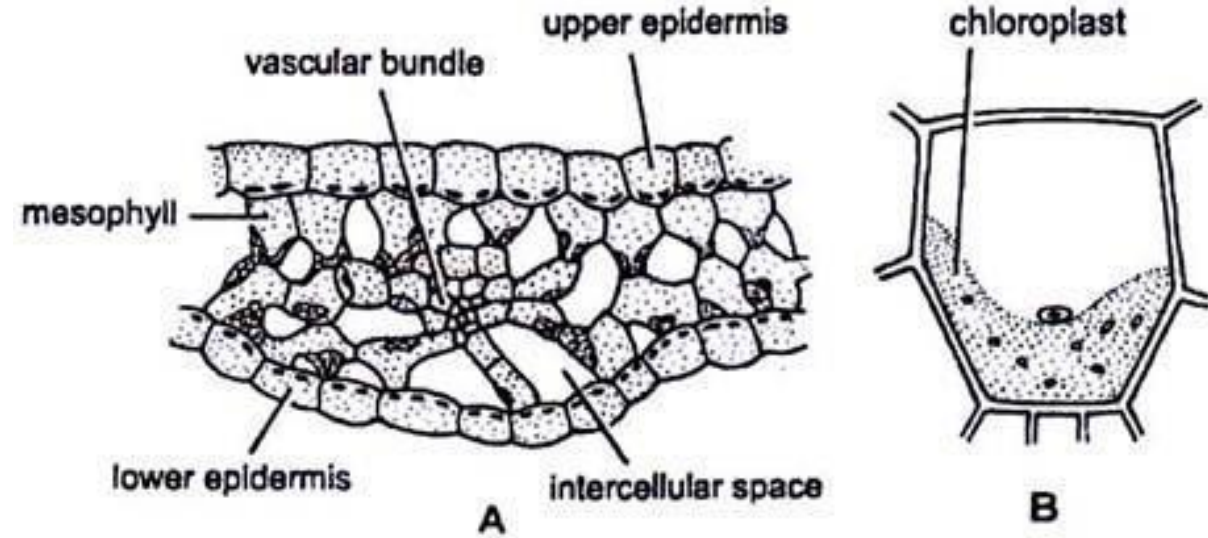


Fig. 6. (A–B). *Selaginella* : Internal Structure of leaf. A. T. S. of a part leaf of *S. kraussiana*, B. A mesophyll cell

Reproduction in Selaginella:

Selaginella reproduces by two methods:

Vegetatively and by formation of spores.

(i) Vegetative reproduction:

It 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.

(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.

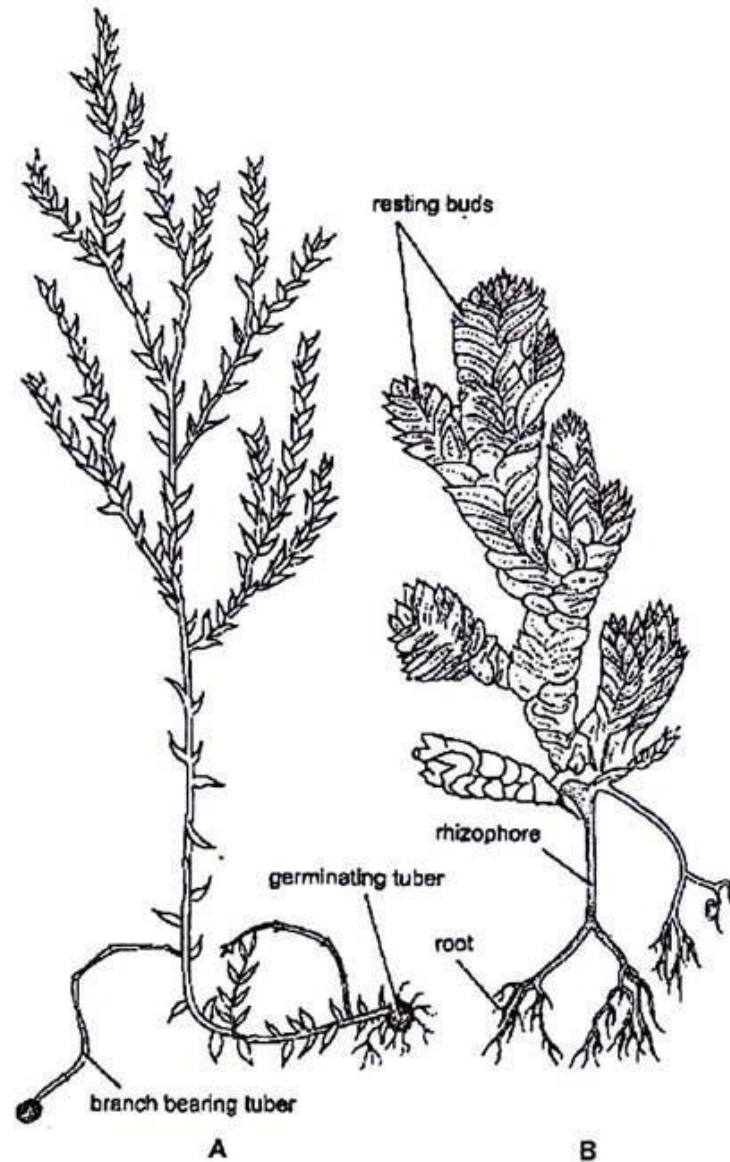


Fig. 7 (A-B). *Selaginella*. Vegetative reproduction, A. Tubers, B. Resting buds

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).

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).

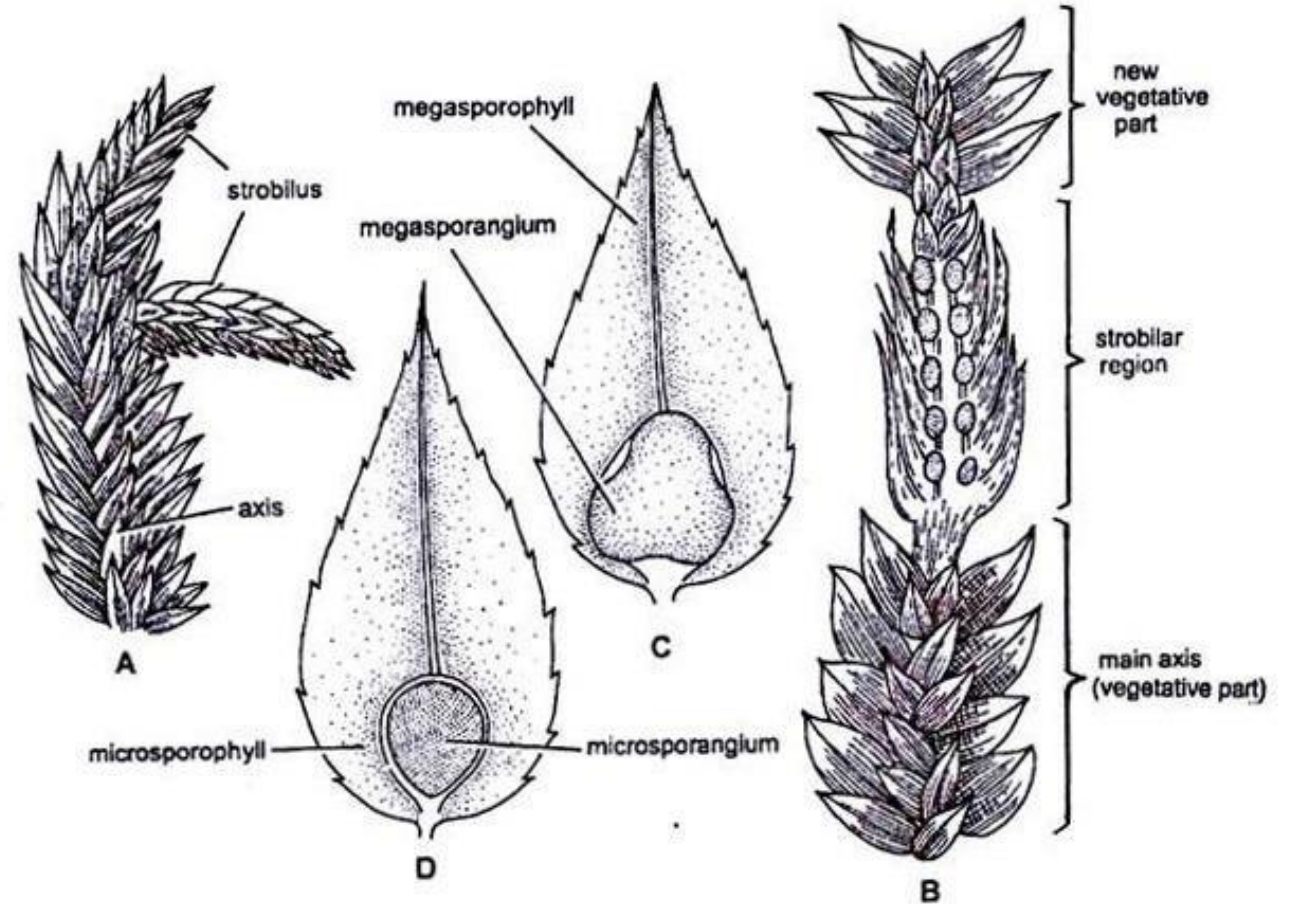


Fig. 8 (A–D). *Selaginella*: Structure of strobilus. A. A branch bearing strobilus, B. A branch after formation of strobilus region again changing into vegetative region, C. A megasporophyll, D. A microsporophyll

The Longitudinal section (L.S.)

- 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.
- 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.

Microsporangium:

- Each microsporangium is a stalked, globular or elongated structure.
- Its colour varies from red, yellow to brown in different species.
- The wall is 2 layered thick which is followed by a conspicuous tapetum.
- 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.

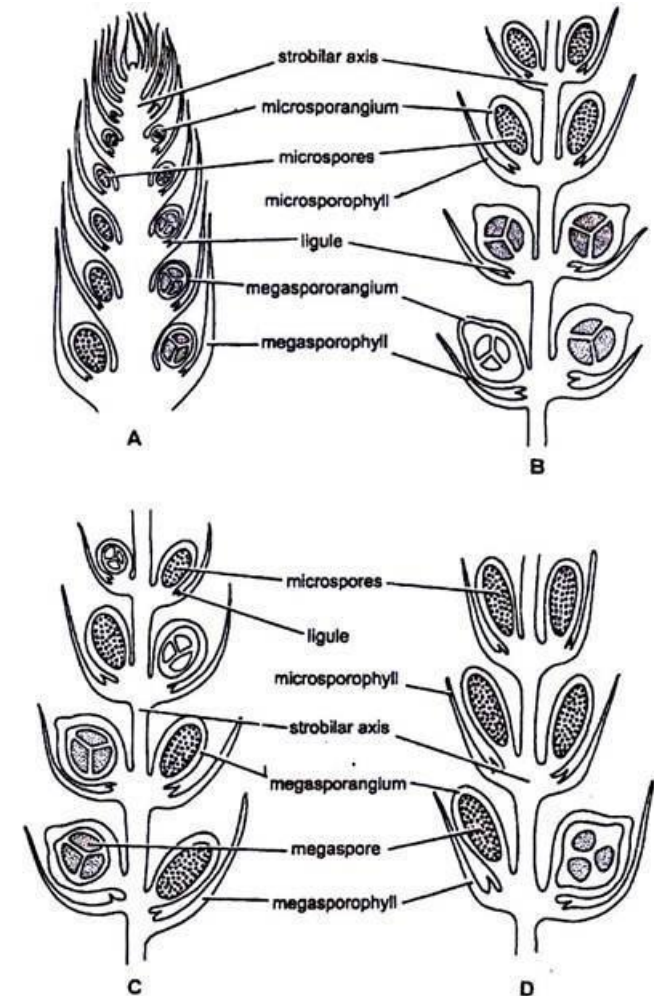


Fig. 9. (A-D). *Selaginella*. Longitudinal sections of strobili of different species showing position of microsporangia and megasporangia A. *S. inaequalifolia*, B. *S. rupestris*, C. *S. martensii*, D. *S. kraussiana*

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 .
- 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 except 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 .
- 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:

- 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 . These cells divide periclinally forming outer jacket initials and inner archesporial initials.
- The jacket initials by further periclinal and anticlinal divisions form the jacket which is 2 celled thick.
- The archesporial initials divide in all directions forming a group of cells known as sporogenous tissue.
- The cells of the outer most layer of sporogenous tissue divides periclinally forming a single layered tapetum just inner to wall of sporangium.
- It is a nourishing layer. Tissue at the base of sporangium divides to form the sporangial stalk.
- The cell of sporogenous tissue in case of microsporangium finally gives rise to microspore mother cells and in case of megasporangium gives rise to megaspore mother cells.

- In microsporangium all the microspore mother cells are functional and each one divides reductionally forming a tetrad of 4 haploid microspores, as a result of which a large number of tetrads of microspores are formed inside microsporangium.
- Later on these microspores separate from each other.
- The mature microsporangium dehisces by a vertical slit in the apical region.
- By the drying of unsplitted portion, the spores are forced out and then they are dispersed away by wind.
- In megasporangium all the megaspore mother cells degenerate except one which divides reductionally forming a tetrad of 4 haploid megaspores.
- The dehiscence of megasporangium is similar to that of microsporangium.

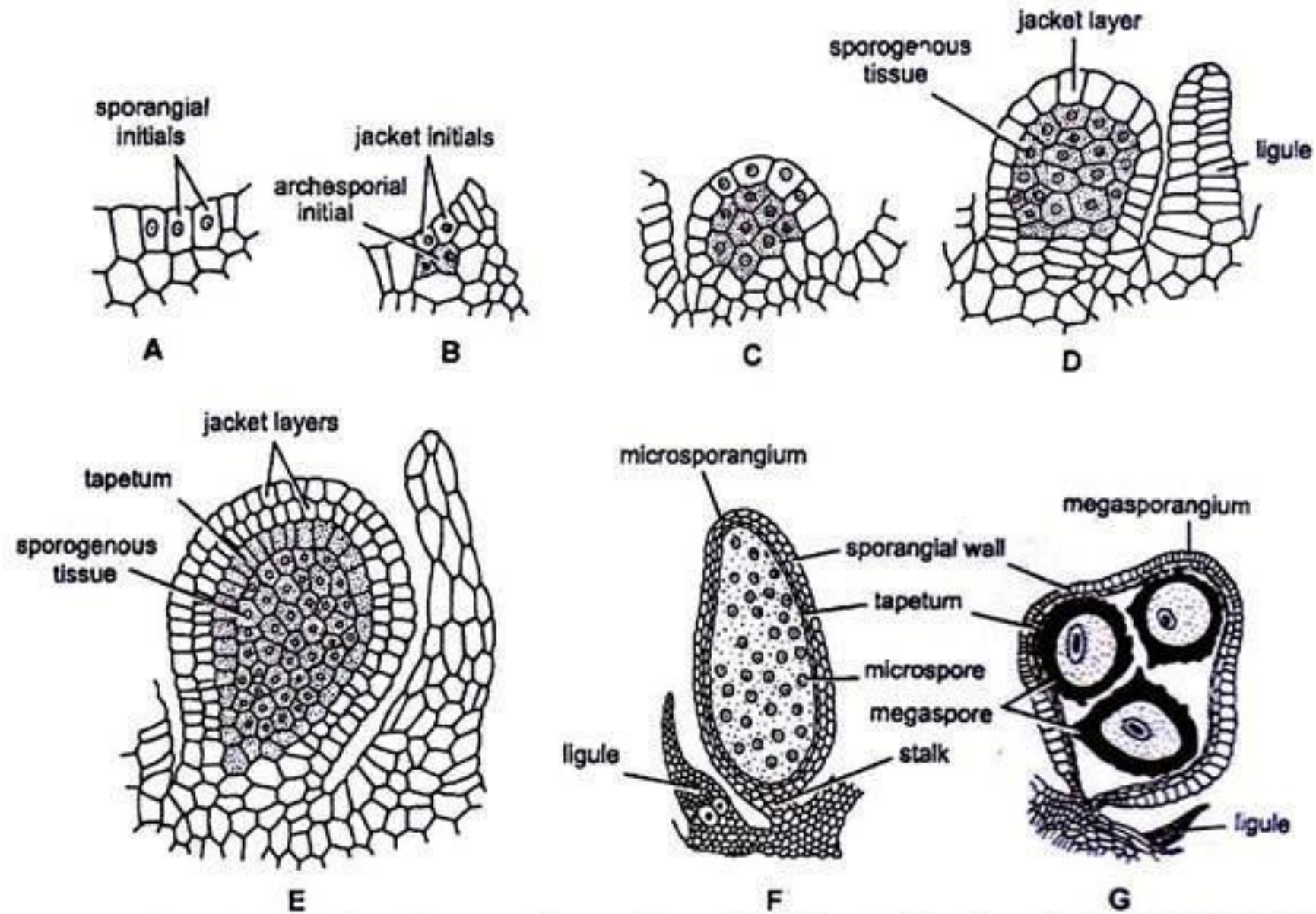


Fig. 10. (A–G). *Selaginella*. Development of sporangium. (A–E). Successive stages in the development of microsporangium in *S. kraussiana*, F. Mature microsporangium, G. Mature megasporangium

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 gametophytes, 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.
 - 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 exospore, mesospore and endospore.
 - The microspores on germination give rise to male prothalli and megaspores to the female prothalli.

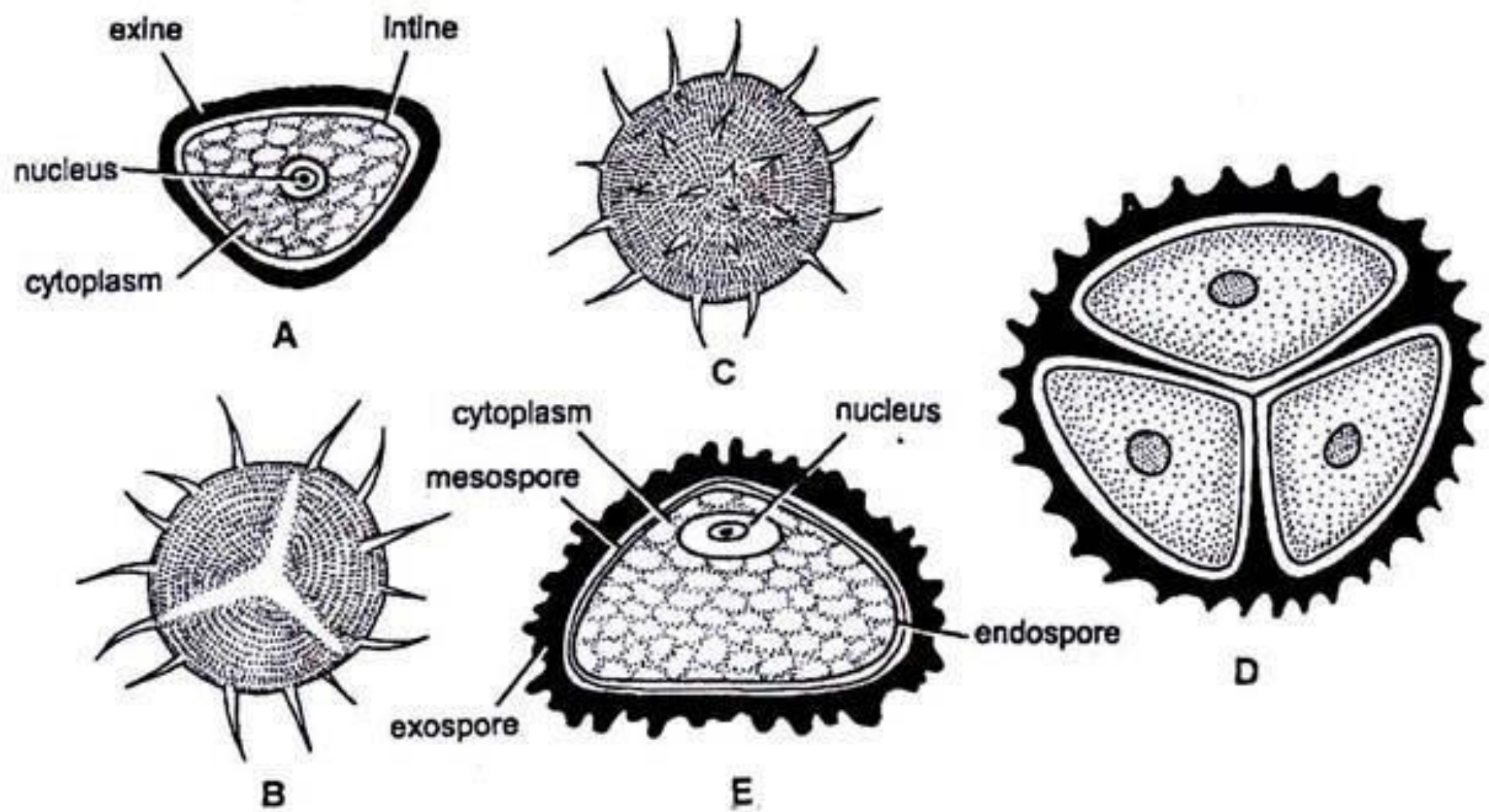


Fig. 11 (A–E). *Selaginella*. Structure of spores : A. A single microspore showing detailed structure, B. Apical view of spore, C. Basal view, D. Megaspore in tetrad, E. A single megaspore.

Development of male gametophyte: Microgametophyte

- 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.
- Generally a 13- celled microgametophyte is formed before the microsporangium dehisces.
- The gametophyte consist 13 cells (1 prothallial cell + 4 androgonial cells + 8 jacket cells). In *S. kraussiana* the gametophyte is shed at this stage. Further development takes place after shedding.
- Each microspore is a unicellular, uninucleate, rounded or spherical, haploid structure with outer spiny thick exosporium and inner thin endosporium.
- The rest of the development proceeds when they fall on a suitable substratum.
- 4 Primary androgonial cells divide and redivide to form 128 or 256 androcytes or antherozoid mother cells which float in mucilage filled cavity of the microspore.

Antherozoid

- Each antherozoid mother cell finally metamorphosis into a single antherozoid 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.

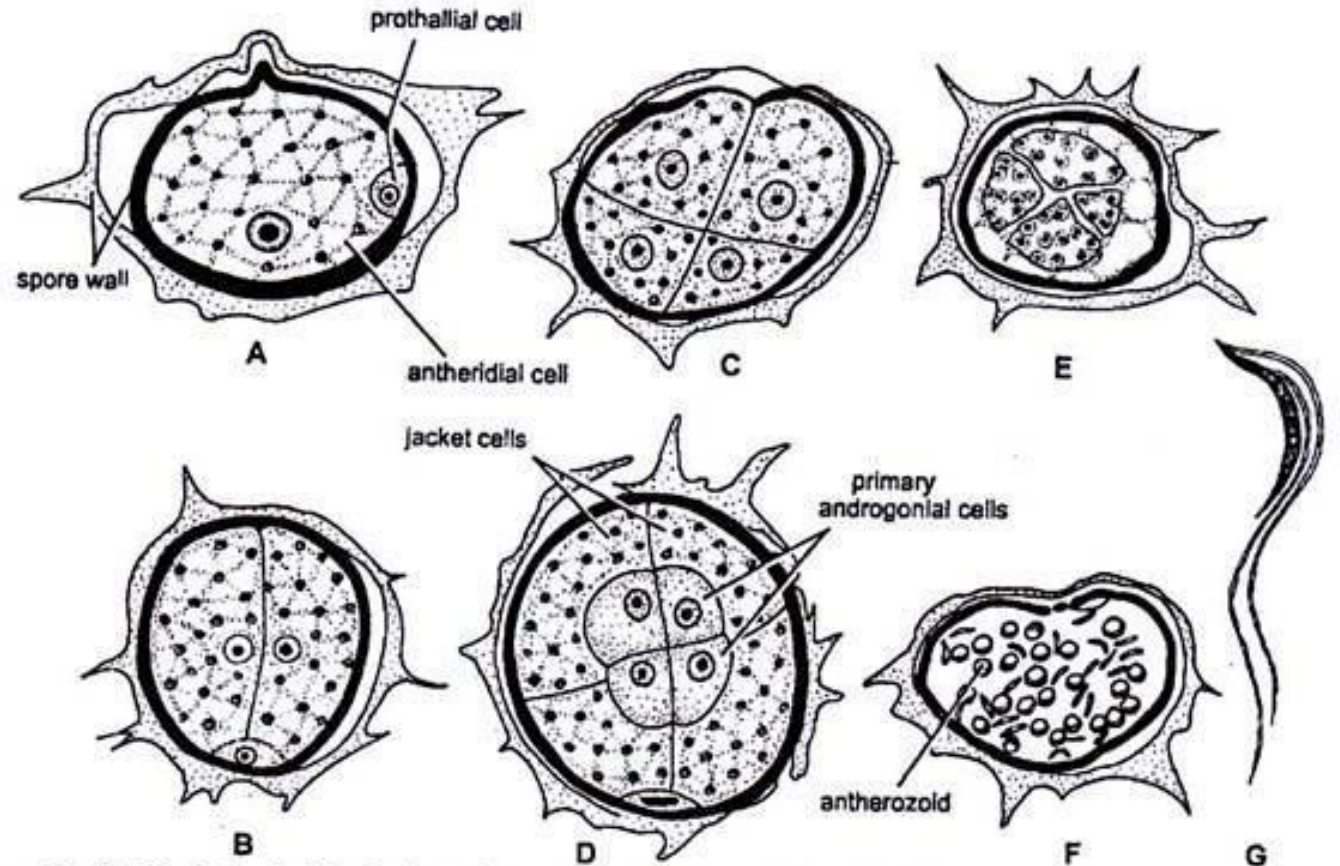


Fig. 13. (A–G) *Selaginella*. Schematic representation of the development of male gametophyte

Development of female gametophyte: megaspores

- The megaspores are much bigger in size than the microspores and range in diameter from 1.5-5 mm.
- When they are in tetrad the spores have a triadial shape but become subspherical on separation.
- The wall of the megaspore is very thick and consists of a sculptured exine, a middle mesospore and a thin intine.
- The cytoplasm consists of reserve food in the form of oil globules and nitrogenous material. The amount of nitrogenous material present is considerably less in comparison with the microspore.
- Chemical analysis of the stored food in megaspores of *Selaginella* reveals that they have 48% fats, 0.43% nitrogenous matter and 1.26% mineral material.

Archegonium:

- A few cells near the apex of female prothallus behave as archegonial initials which by further divisions, give rise to archegonia.
- Each archegonium develops from a single superficial cell of the female prothallus situated near the apical region and is termed as archegonial intitial.

Structure of Mature Archegonium:

- The archegonium is a short flask shaped structure embedded in female gametophytic tissue.
- 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 .
- 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 through which the antherozoids enter the archegonium and reach the egg.

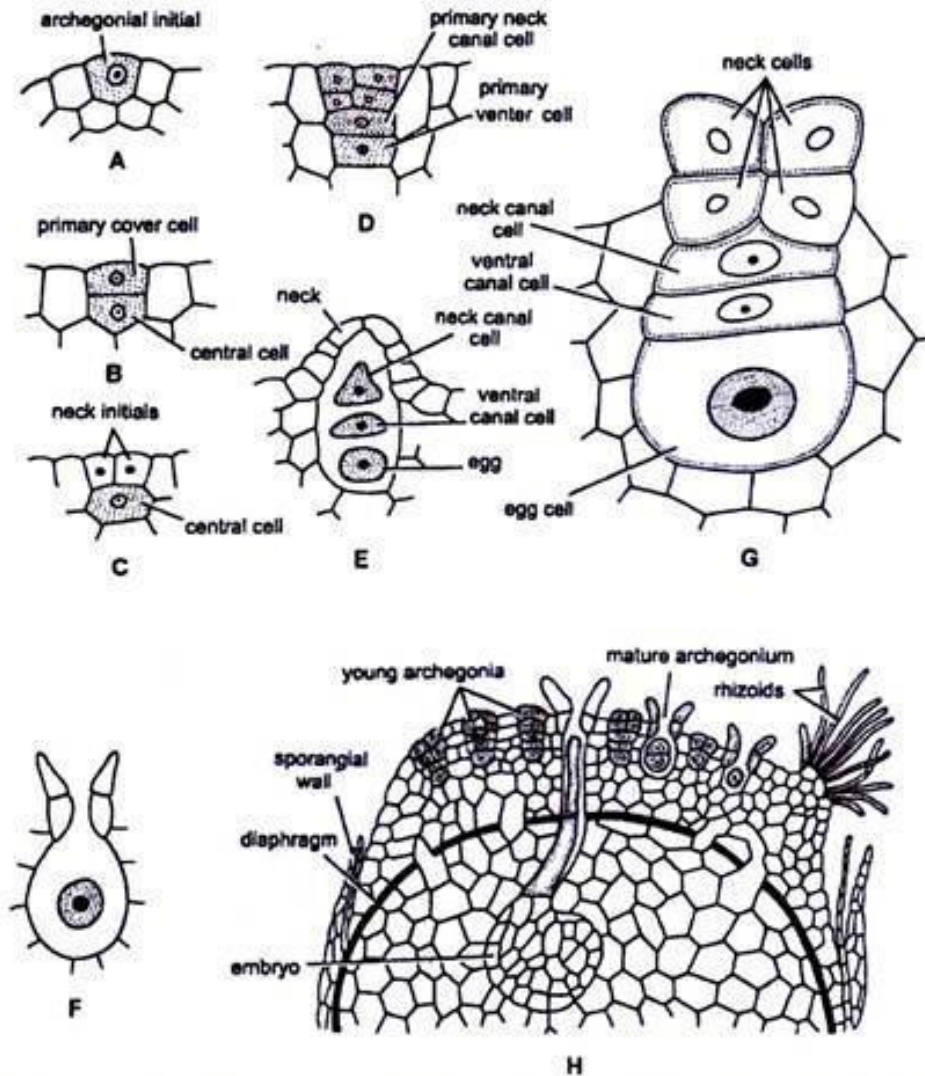


Fig. 16 (A–G). *Salaginella* : Development of archegonium. A–F. Various stages in the development, G. A mature archegonium before fertilization, H. A nearly median section of a mature prothallus showing various stages in the development of archegonium.

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.

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).
- The suspensor initial further divides in all directions forming a multicellular suspensor which thrusts the developing embryo deep into the female gametophytic tissue to absorb food for further development of embryo.
- The embryo initial divides by 2 vertical divisions at right angle to each other thus forming 4 cells.
- One of these 4 cells divides by an oblique wall forming a shoot initial.
- Now the cells except the shoot initial divide sporophyte transversely forming 2 tiers of 4 cells each.
- Later on by further divisions it forms a multicellular structure which gets differentiated into foot, rhizophore, stem and cotyledons .

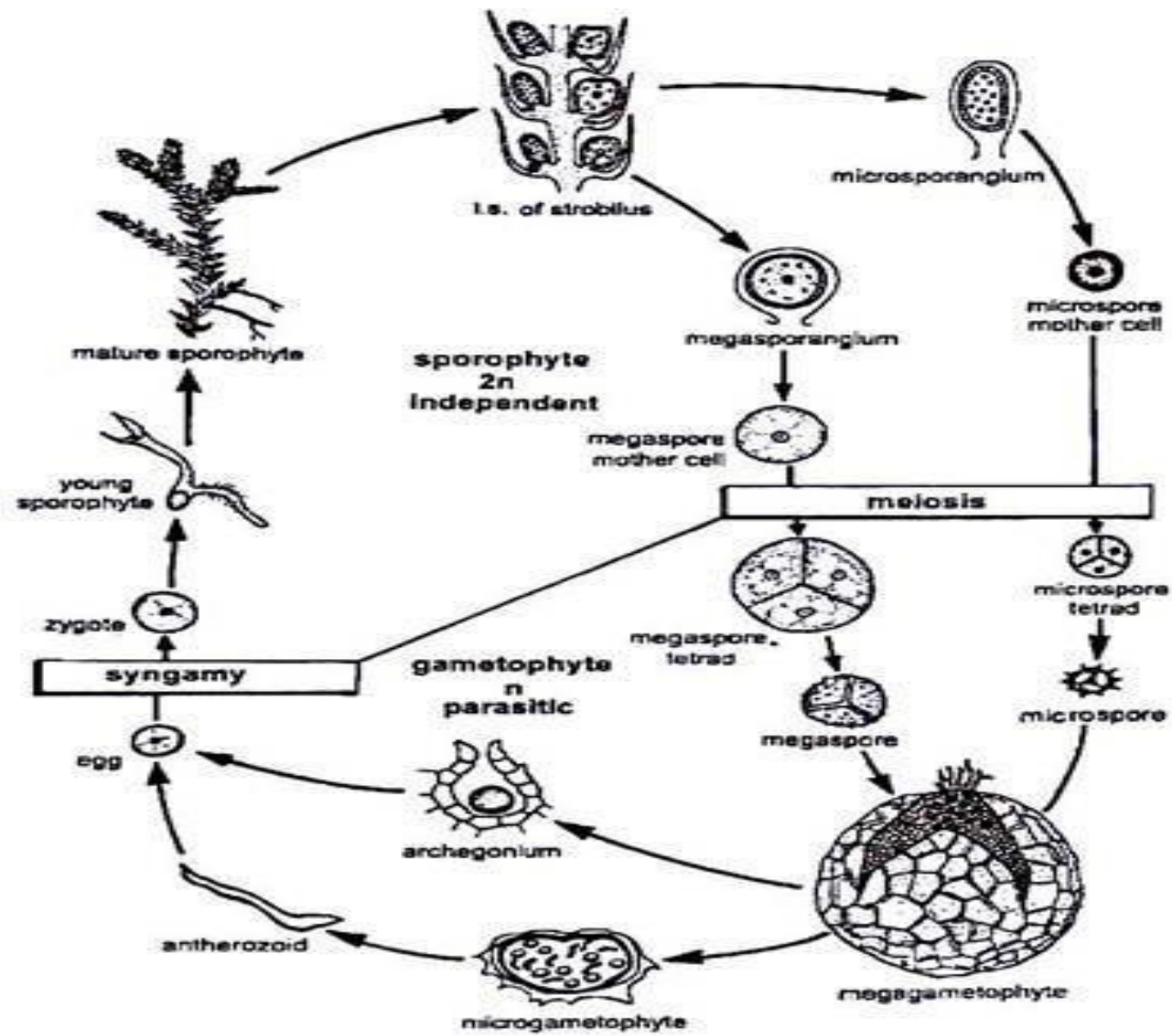


Fig. 19. Diagrammatic life cycle of *Selaginella*

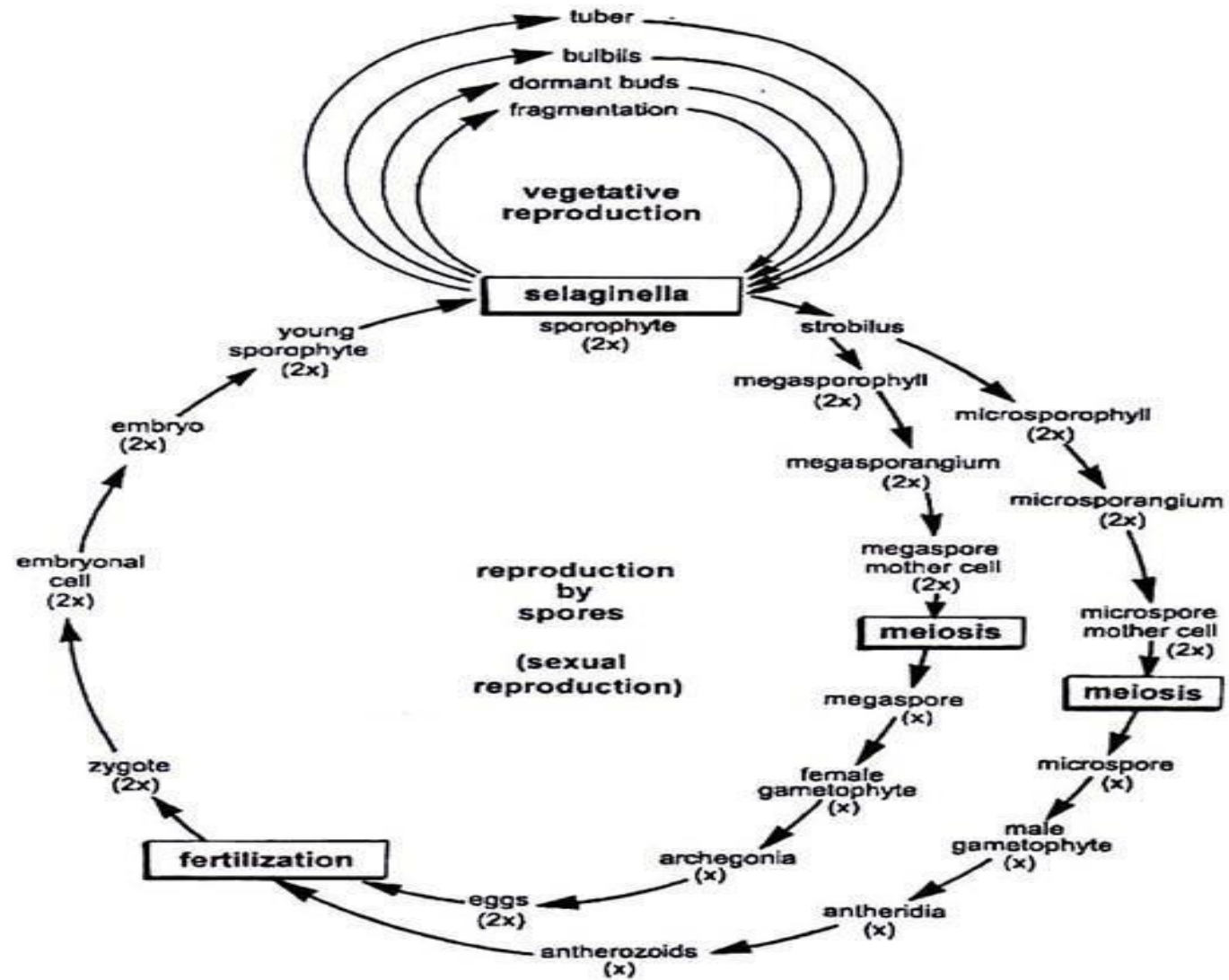


Fig. 20. *Selaginella* : schematic life cycle

3. Life history of: *Equisetum*

SYSTEMATIC POSITION

Division: Pteridophyta

Class: Sphenopsida

Order: Equisetales

Family: Equisetaceae

Genus: *Equisetum*

- *Equisetum* (**horsetail, snake grass, puzzlegrass**) is the only living genus in Equisetaceae, a family of vascular plants that reproduce by spores rather than seeds.
- **Habit and Habitat of *Equisetum*:**
- The plant body of *Equisetum* has an aerial part and an underground rhizome part.
- The rhizome is perennial, horizontal, branched and creeping in nature.
- The aerial part is herbaceous and usually annual.

- Majority of the species are small with a size range in between 15 and 60 cm in height and 2.0 cm in diameter.
- Some species grow up in higher heights [e.g., *E. giganteum* (13 m), *E. telmateia* (2 m); *E. ramosissimum* (4 m), though their stem are relatively thin (0.5-2.0 cm in diam.)] showing vine like habit and climb over adjacent forest trees.
- *Equisetums* generally grow in wet or damp habitats and are particularly common along the banks of streams or irrigation canals (*E. debile*, *E. palustre*).
- However, some species are adapted to xeric condition (e.g., *Equisetum arvense*). Some common Indian species are: *E. arvense*, *E. debile*, *E. diffusum*, *E. ramosissimum*)
- Some species of *Equisetum* are indicators of the mineral content of the soil in which they grow.
- Some species accumulate gold (about 4.5 ounce per ton of dry wt.), thus they are considered as ‘gold indicator plants.
- Hence these plants help in exploration for new ore deposits. In *Equisetum*, silica is deposited on the outer wall of the epidermal cells giving the characteristic rough feeling, thus it provides a protective covering against predators and pathogens.

Structure of *Equisetum*:

- **The Sporophyte:**

- The sporophytic plant body of *Equisetum* is differentiated into stem, roots and leaves.

- **Stem:**

- The stem of *Equisetum* has two parts: perennial, underground, much-branched rhizome and an erect, usually annual aerial shoot.
- The branching is monopodial, shoots are differentiated into nodes and internodes.
- In majority of the species, all the shoots are alike and chlorophyllous and some of them bear strobili at their apices (e.g., *E. ramosissimum*, *E. debile*).
- Sometimes shoot shows dimorphism (two types of shoots i.e., vegetative and fertile) e.g., *E. arvense*. Some shoots are profusely branched, green (chlorophyllous) and purely vegetative.
- The others are fertile, unbranched, brownish in colour (achlorophyllous) and have terminal strobili.
- The underground rhizome and the aerial axis appear to be articulated or jointed due to the presence of distinct nodes and internodes.

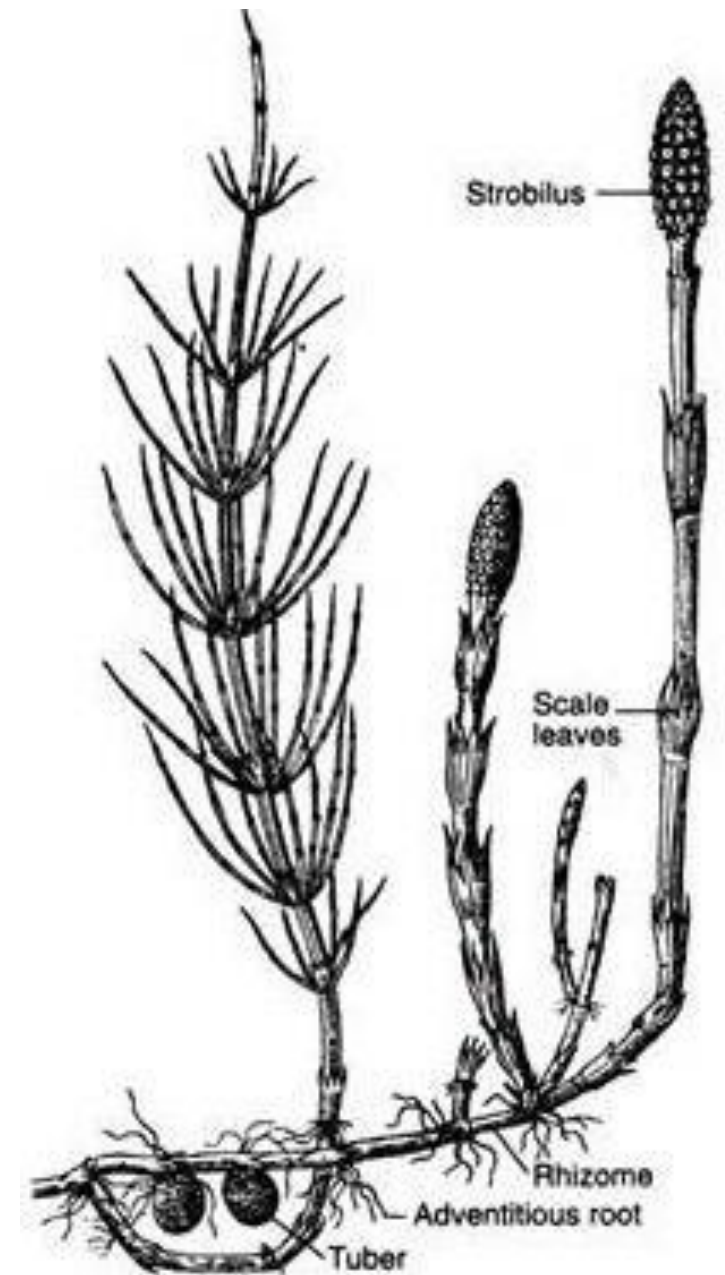


Fig. 7.83 : *Equisetum arvense* sporophyte

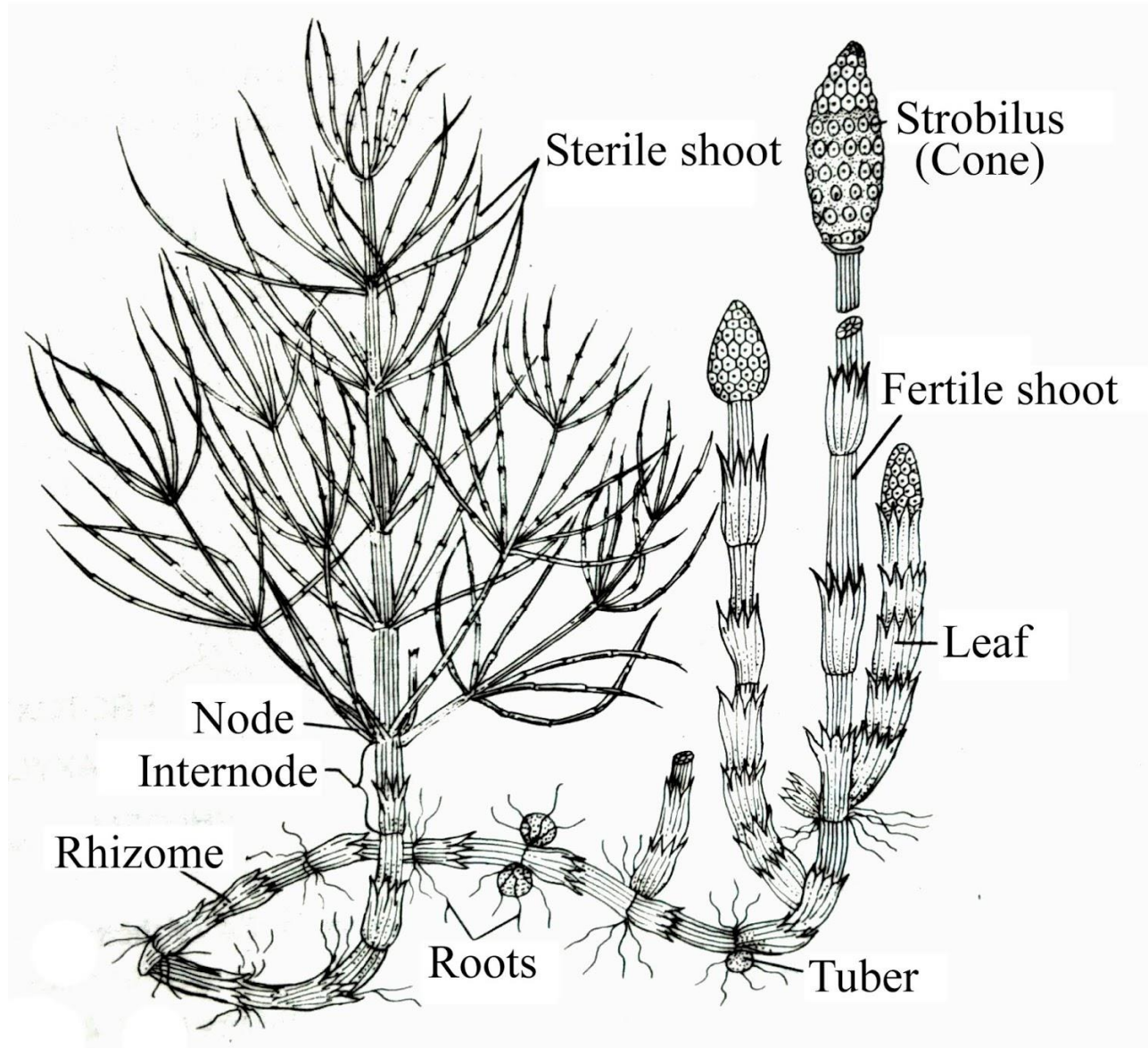


Fig: *Equisetum* spp. Sporophytic plant body showing habit.

- **Leaves:**

- The leaves of *Equisetum* are small, simple, scale-like and isophyllous; they are attached at each node, united at least for a part of the length and thus form a sheath around the stem.
- The sheath has free and pointed teeth-like tips.
- The number of leaves per node varies according to the species.
- The species with narrow stems have few leaves and those with thick stem have many leaves .
- The number of leaves at a node corresponds to the number of ridges on the internode below.
- The leaves do not perform any photosynthetic function and their main function is to provide protection to young buds at the node
- **Root:**
- The primary root is ephemeral. The slender adventitious roots arise endogenously at the nodes of the stems.

Internal Features of Stem:

T.S., the stem of *Equisetum*

In T.S., the stem of *Equisetum* appears wavy in outline with ridges and furrows.

Epidermis

- The epidermal cell walls are thick, cuticularised and have a deposition of siliceous material.
- Stomata are distributed only in the furrows between the ridges.

Hypodermis

- A hypodermal sclerenchymatous zone is present below each ridge which may extend up to stele in *E. giganteum*.

cortex

- The cortex is differentiated into outer and inner regions.
- The outer cortex is chlorenchymatous, while the inner cortex is made up of thin-walled parenchymatous cells.
- There is a large air cavity in the inner cortex corresponding to each furrow and alternating with the ridges, known as vallecular canal.

Stele

- Innermost layer of cortex is the endodermis, the cells of which contains casparian strips. In *E. litorale*, each vascular bundle contains its individual endodermis.
- Below the endodermis is present a single-layered pericycle.
- Vascular bundles are present below the ridges, i.e., alternate to the vallecular canals of the cortex.
- They are present in the ring.
- The number of vascular bundles and vallecular canals is equal to the number of ridges and grooves, respectively
- Stele is of ectophloic siphonostelic type.

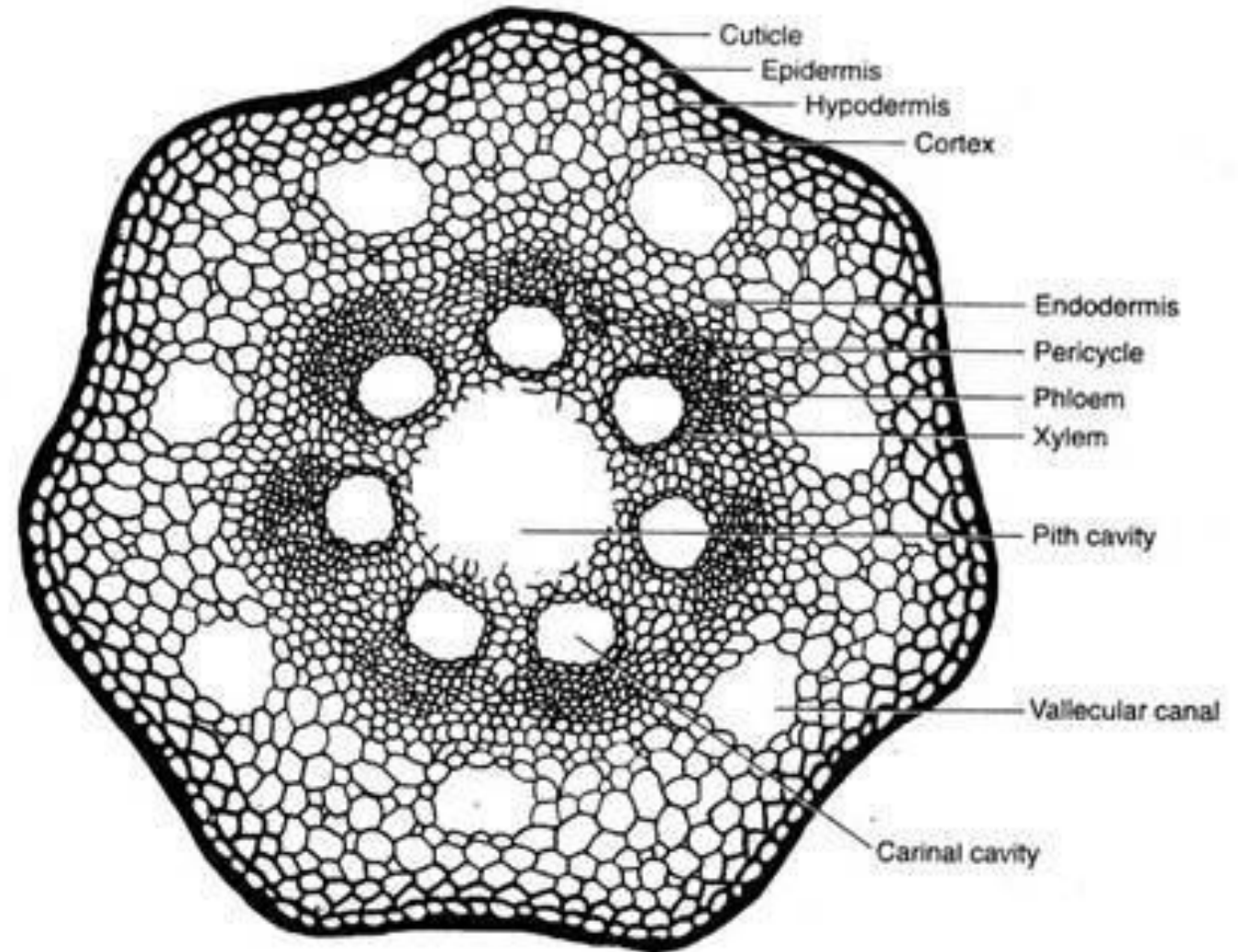


Fig. 7.84 : *Equisetum* T.S. of stem (rhizome)

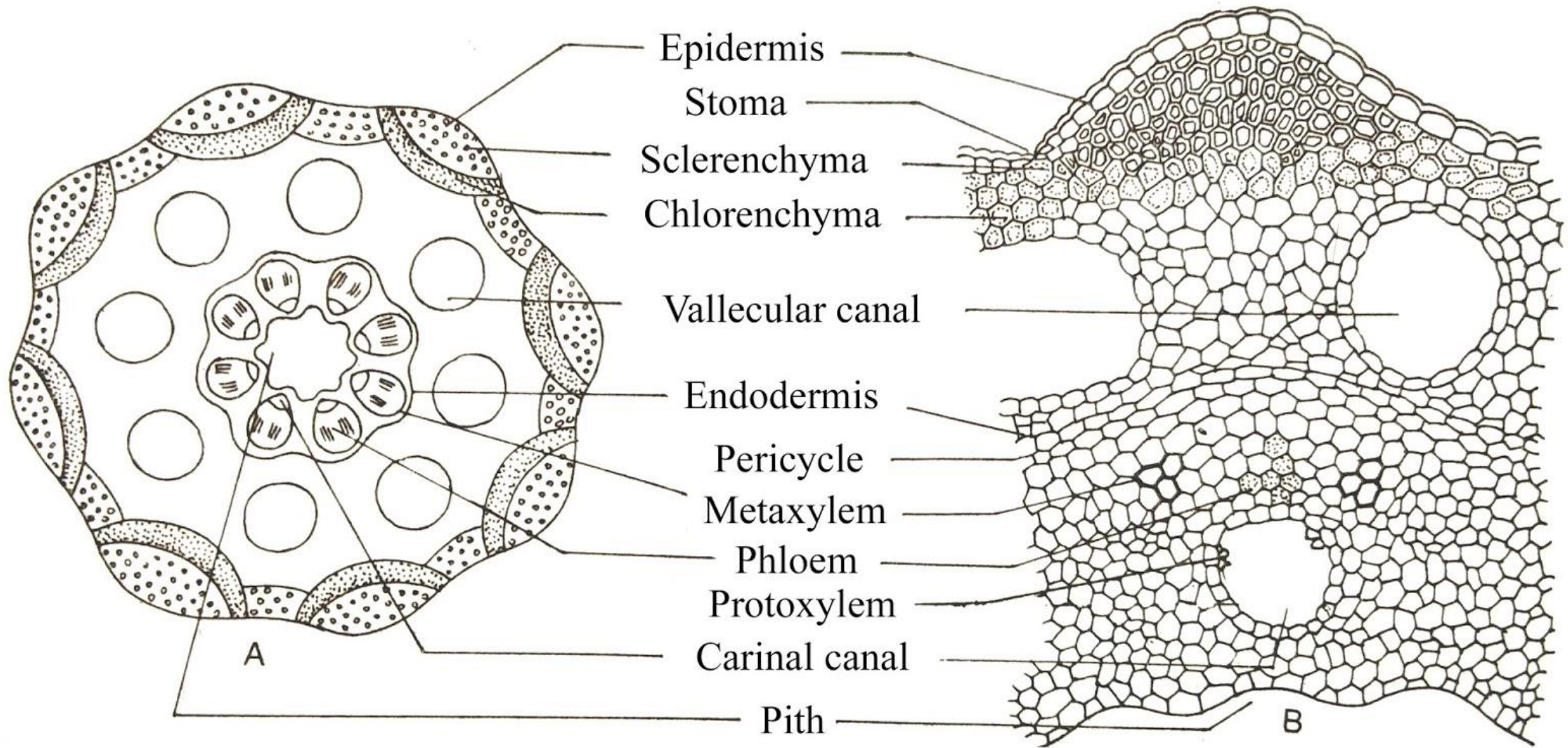


Fig: *Equisetum spp.* TS of aerial branch through an internode, (A) Diagrammatic; (B) Cellular.

T.S. Internode of Rhizome:

1. Ridges and grooves are not so much well-marked as in sterile shoot.
2. Absence of stomata.
3. Absence of chlorenchymatous region.
4. Sclerenchyma is poorly developed.
5. Hollow pith cavity is not well-developed and sometimes it becomes solid.

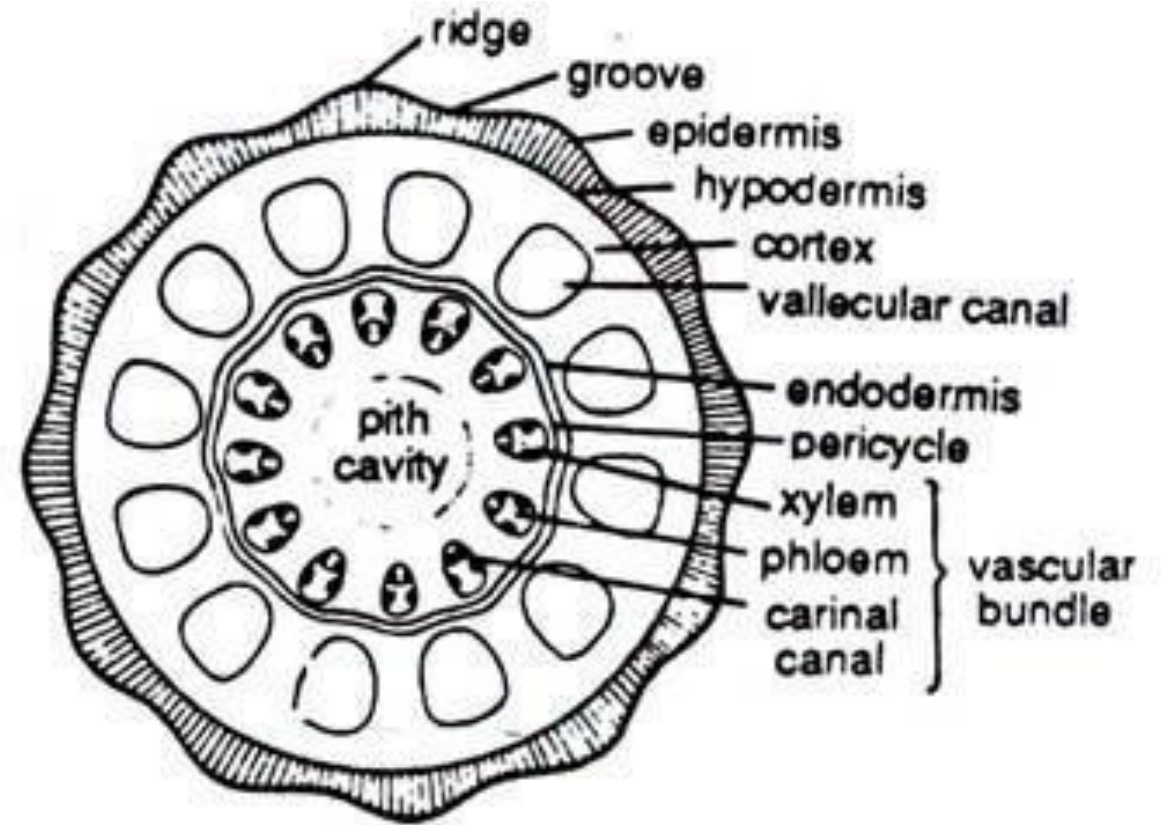


Fig. 240. *Equisetum*. T.S. internode of rhizome (diagrammatic).

T. S. Adventitious Root:

1. Outermost layer is epidermis, from which arise many root hairs.
2. Cortex is thick and multi-layered.
3. Outer zone of cortex consists of 3 to 4 celled thick exodermis. 4. Inner zone is parenchymatous with many intercellular spaces.
5. Endodermis is two-layered
6. Pericycle is absent.
7. Stele is a protosteles, which is triarch or tetrarch.
8. In the centre is present a large metaxylem tracheid having many protoxylem groups towards the periphery.
9. Phloem is present in between the angles of protoxylem.

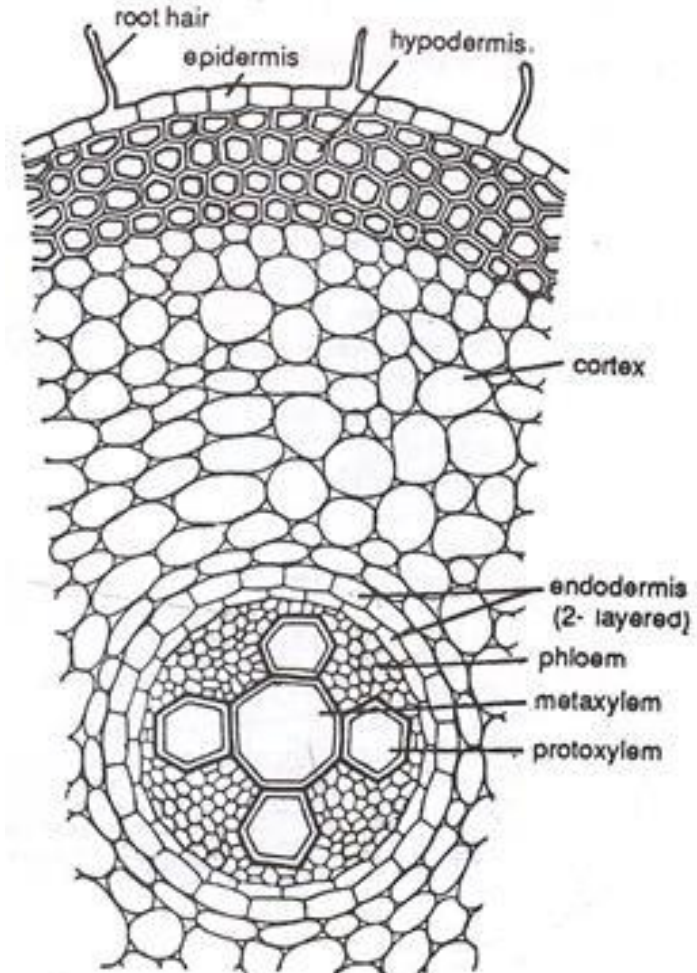


Fig. 242. *Equisetum*. T.S. root (a part cellular).

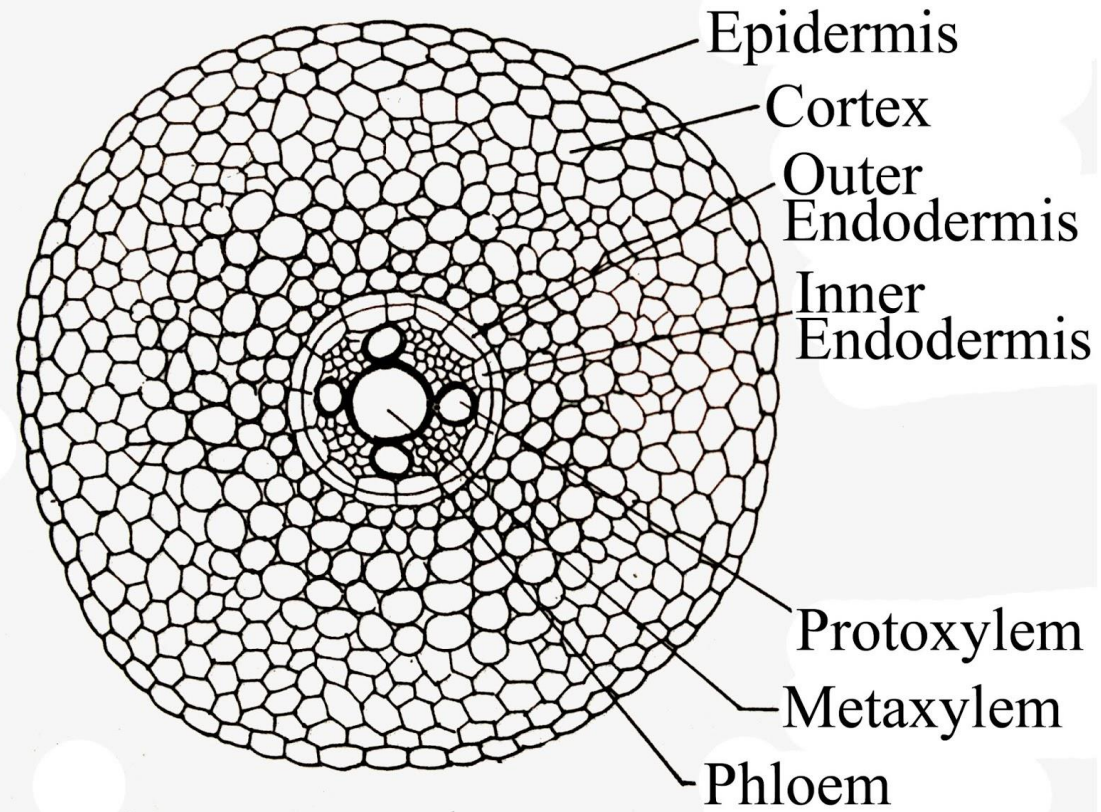


Fig: *Equisetum* spp. TS of root.

Reproduction in Equisetum:

Equisetum reproduces vegetatively and by means of spores.

i. Vegetative Reproduction:

- The subterranean rhizomes of some species (e.g., *E. telmateia*, *E. arvense*) form tubers which, on separation from the parent plant, germinate to produce new sporophytic plants.
- The tubers develop due to irregular growth of some buds at the nodes of the rhizomes.

ii. Reproduction by Spores:

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

Strobilus:

- The strobilus are terminal in position and generally are borne terminally on the chlorophyllous vegetative shoot .
- However, they may be borne terminally on a strictly non- chlorophyllous axis (e.g., *E. arvense*). The strobilus is composed of an axis with whorls of sporangiophores .
- Each sporangiophore is a stalked structure bearing a hexagonal peltate disc at its distal end .
- On the under surface of the sporangiophore disc 5-10 elongate, cylindrical hanging sporangia are borne near the periphery in a ring.
- The flattened tips of the sporangiophores fit closely together which provide protection to the developing sporangia.
- The axis bears a ring-like outgrowth, the so-called annulus immediately below the whorls of sporangiophores which provide additional protection during early development.

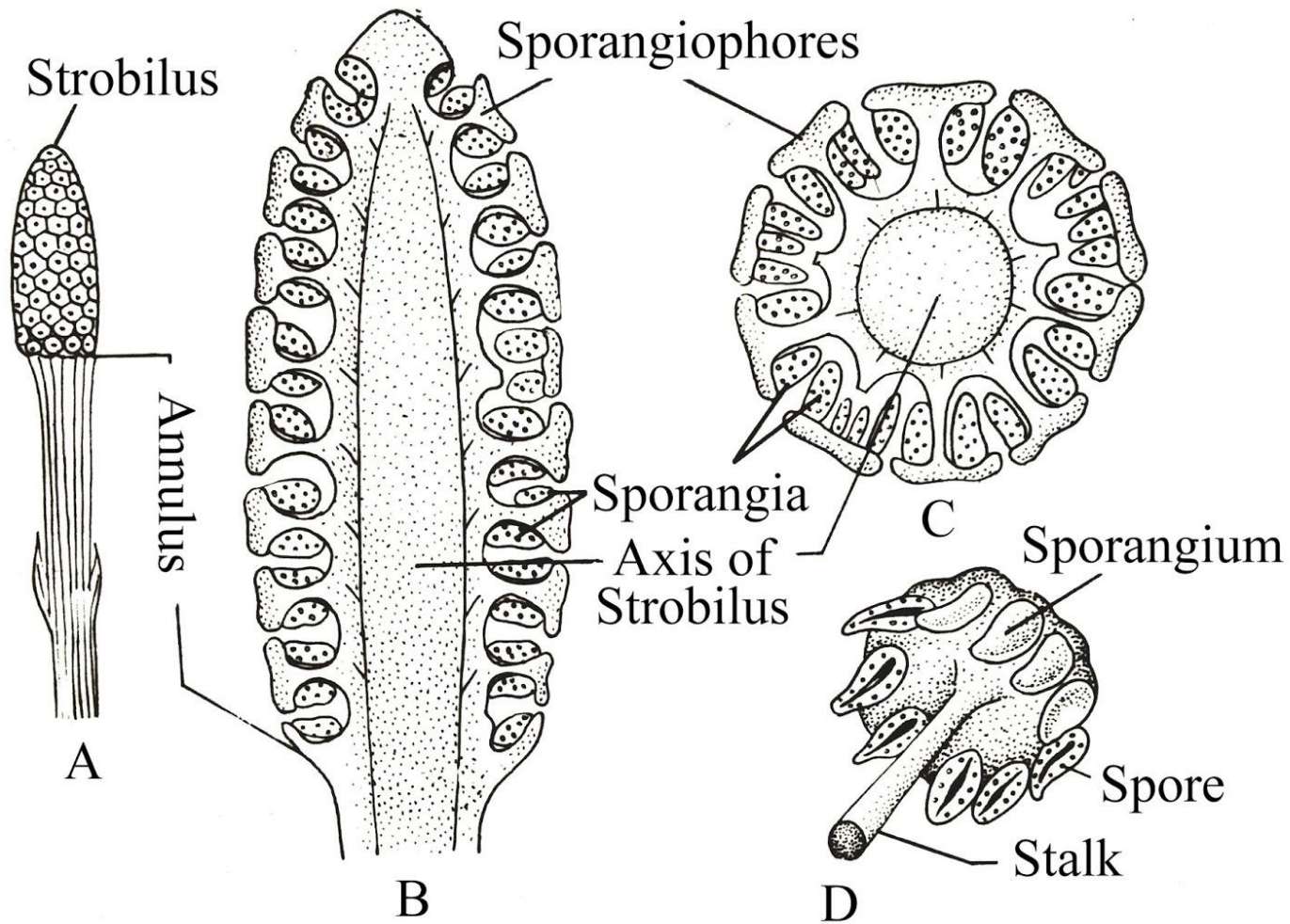


Fig: *Equisetum* spp. (A) A part of fertile shoot bearing strobilus; (B) LS of strobilus; (C) TS of strobilus; (D) Single sporangiophore.

Structure of Mature Sporangium:

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

Dehiscence of Sporangium:

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

Spores:

- The spores are spherical and filled with densely packed chloroplasts.
- The spore wall is laminated and shows four concentric layers.
- The innermost is the delicate intine, followed by thick exine, the middle cuticular layer and the outermost episporium or perispore.
- The intine (endospore) and exine (exospore) are the true walls of the spore.
- The outer two layers i.e., cuticular layer and episporium are derived due to the disintegration of the nonfunctional spore mother cells and tapetal cells.
- At maturity, the episporium (the outermost layer) splits to produce four ribbon like bands or strips with flat spoon-like tips.
- These bands are free from the spore wall except for a common point of attachment and remain tightly coiled around the spore wall until the sporangium is fully matured.
- These are called elaters. The elaters are hygroscopic in nature.
- The spores remain moist at early stages of development, thus the elaters are spirally coiled round the spore.
- The spores dry out at maturity and consequently the elaters become uncoiled.
- These uncoiled elaters become entangled with the elaters of other spores.
- Through these actions the elaters help in the dehiscence process and also the dispersal of spores in large groups from the sporangium.
- The elaters of *Equisetum* are different from those of the bryophytes .

Gametophyte Generation:

- Equisetum is a homosporous pteridophyte.
- The haploid spores germinate to form gametophyte.
- The germination takes place immediately if the spores land on a suitable substratum.
- If the spores do not germinate immediately, their viability decrease significantly.
- The spores swell up by absorbing water and shed their exine.
- The first division of the spore results in two unequal cells: a small and a large cell.
- The smaller cell elongates and forms the first rhizoid.
- The larger cell divides irregularly to produce the prothallus.
- The prevailing environmental conditions determine the size and shape of the prothallus.
- If a large number of spores are developed together within a limited space, then the prothalli formed are of thin filamentous type. But a relatively thick and cushion-shaped prothalli are formed from sparsely germinating spores.
- Mature gametophytic plants may range in size from a few millimeters up to 3 centimeters e.g., *E. debile* in diameter.
- They are dorsiventral and consist of a basal non-chlorophyllous cushion-like portion from which a number of erect chlorophyllous multicellular lobes develop upwards.
- Unicellular rhizoids are formed from the basal cells of cushion.
- The prothallus bears sex organs and reproduces by means of sexual method

Sex organ in Equisetum:

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

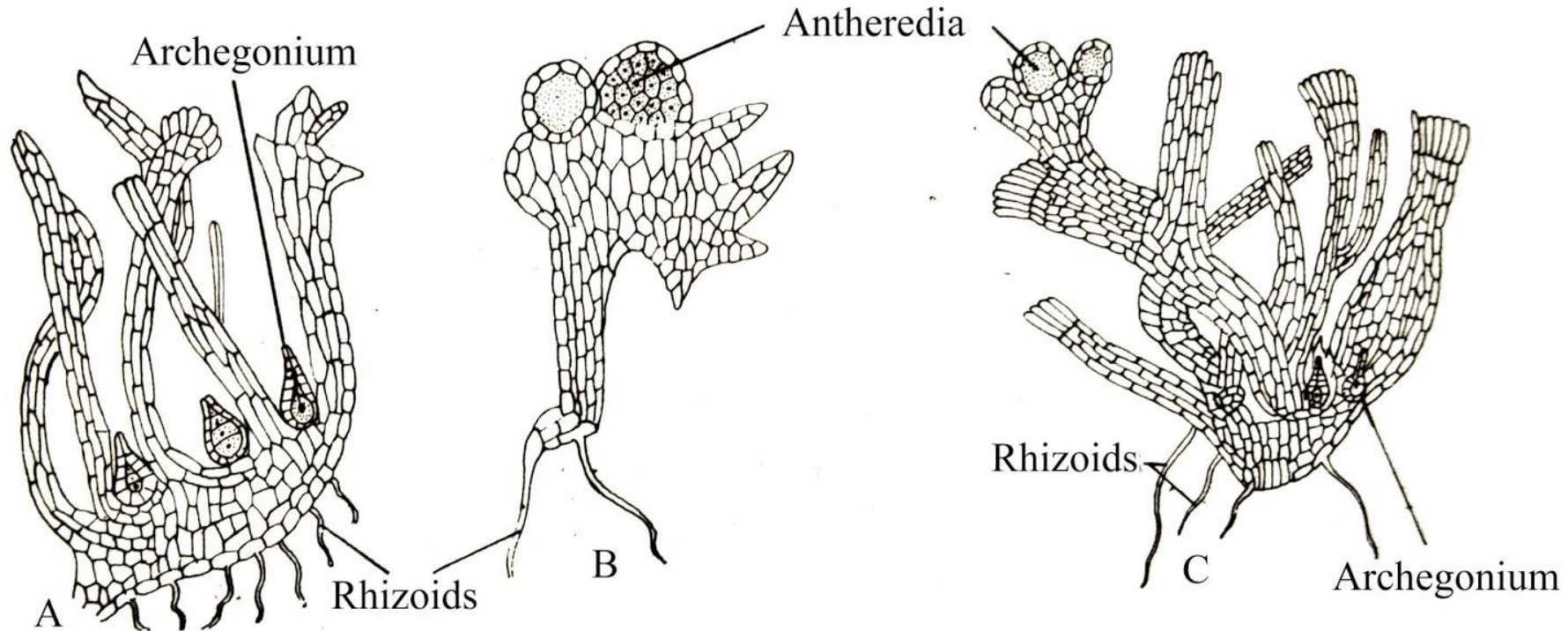


Fig: *Equisetum* spp. Dioecious (A) Female and (B) Male gametophytes; (C) Monoecious gametophyte

Sex Organs of Equisetum:

1. Antheridium:

- In monoecious species, antheridia develop later than archegonia.
- They are of two types — projecting type and embedded type.
- Antheridia first appear on the lobes of the gametophyte.
- The periclinal division of the superficial antheridial initial gives rise to jacket initial and an androgonial cell.
- The jacket initial divides anticlinally to form a single-layered jacket.
- The repeated divisions of androgonial cells form numerous cells which, on metamorphosis, produce spermatids/antherozoids.
- The antherozoids escape through a pore created by the separation of the apical jacket cell.
- The apical part of the antherozoid is spirally coiled, whereas the lower part is, to some extent, expanded.
- Each antherozoid has about 120 flagella attached to the anterior end.

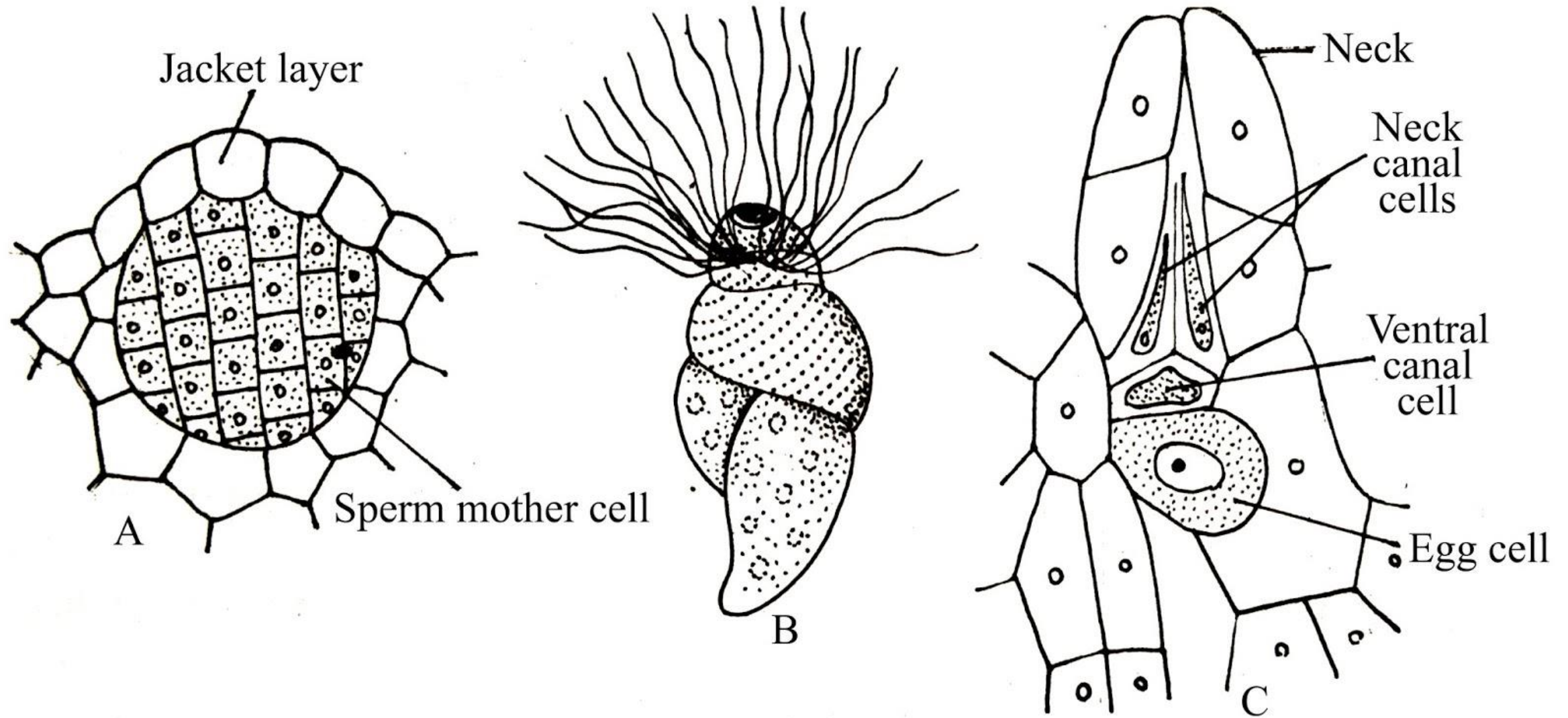


Fig: *Equisetum spp.* (A) Single antheridium (immature); (B) Single spermatozoid; (C) An archegonium (mature).

ii. Archegonium:

- Any superficial cell in the marginal meristem acts as an archegonial initial which undergoes periclinal division to form a primary cover cell and an inner central cell.
- The cover cell, by two vertical divisions at right angle to each other, forms a neck.
- The central cell divides transversely to form a primary neck canal cell and a venter cell.
- Two neck canal cells are produced from the primary neck canal cell.
- While, the venter cell, by a transverse division, forms the ventral canal cell and an egg.
- At maturity, an archegonium has a projecting neck comprising of three to four tiers of neck cells arranged in four rows, two neck canal cells of unequal size, a ventral canal cell, and an egg at the base of the embedded venter.
- The archegonia are confined to cushion region in- between the aerial lobes.

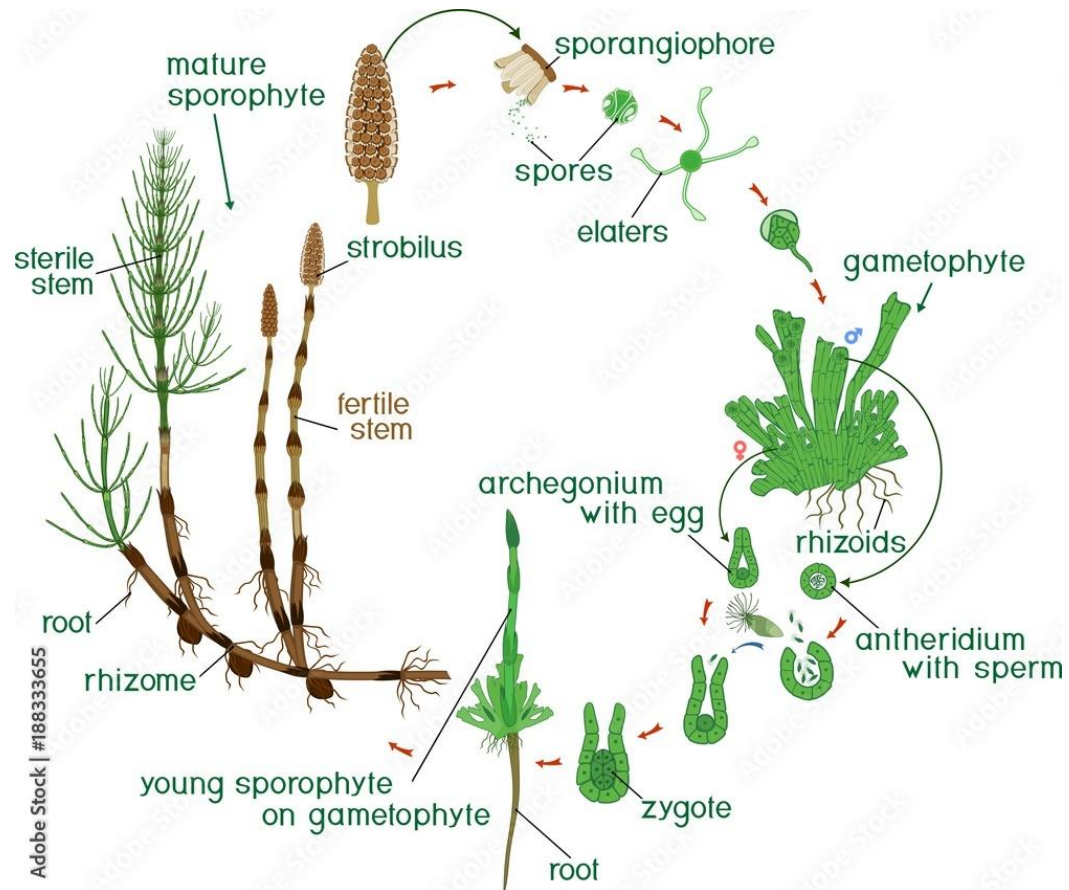
Fertilization:

- Water is essential for fertilization.
- The gametophyte must be covered with a thin layer of water in which the motile antherozoides swim to the archegonia.
- The neck canal cells and ventral canal cell of the archegonia disintegrate to form a passage for the entry of antherozoids.
- Many antherozoids pass through the canal of the archegonium but only one of them fuses with the egg.
- Thus diploid zygote is formed.
- Generally more than one archegonia are fertilised in a prothallus.

Embryo (The New Sporophyte):

- The embryo is the mother cell of the next sporophytic generation.
- Unlike most pteridophytes, several sporophytes develop on the same prothallus.

Life Cycle of Equisetum:



Heterospory and seed habit.

- Heterospory is a phenomenon in which two kinds of spores are borne by the same plant.
- The spores differ in size, structure and function.
- The smaller one is known as microspore and larger one is known as megaspore.
- Such Pteridophytes are known as heterosporous and the phenomenon is known as heterospory.
- Most of the Pteridophytes produce one kind of similar spores, Such Pteridophytes are known as homosporous and this phenomenon is known as homospory.
- The sporangia show greater specialization.
- They are differentiated into micro and megasporangia.
- The microsporangia contain microspores whereas megasporangia contain megaspores.
- The production of two types of spores with different sexuality was first evolved in pteridophytes.
- Even though, the condition of heterospory is now represented by 9 genera viz. *Selaginella*, *Isoetes*, *Stylites*, *Marsilea*, *Pilularia*, *Regnellidium*, *Salvinia*, *Azolla* and *Platyzoma*.

Origin of Heterospory

- A detailed study of homosporous forms has revealed that heterospory originated due to reduction in number of spores within sporangia i.e., if more number of spores are functional than there is more competition for nutrition and limited nutrients are provided to developing spores.
- In this way microspores are formed, they are smaller in size and more in number.
- On the other hand, if some of the spore mother cell in a sporangium disintegrates during development, the remaining ones get sufficient nutrients.
- These are megaspores; they are larger in size but less in number.

Evidences of Heterospory

Paleobotanical evidences:

- These were concluded on the basis that earlier vascular plants were heterosporous eg. *Lepidocarpon*, *Lepidostrobus* etc.
- According to Scott (1894) an indication of heterospory can be traced in *Calamostachys binneyana* and *C. casheana*.
- In former the sporangia were with large number of small spores in tetrads.
- In later two distinct types of sporangia microsporangia and megasporangia occurred.
- A similar disintegration was observed in some species of *Lepidocarpon*, *Calamocarpon* and *Stauropteris*.
- The above example indicates that: Heterospory has not only evolved in living forms but was present in the fossil plants.
- It originated due to integration of spores in a sporangium.
- However, the reduction in number of spores or spore mother cell was achieved but it cannot be determined as there is no information regarding the development of sporangia and spore.

Evidences from developmental studies:

- Developmental studies in pteridophytes, during the formation of sporocytes, meiosis and maturation of spore provide a real insight in the understanding of heterospory.
- In *Selaginella*, *Isoetes*, *Marsilea*, *Salvinia* etc. early development of microsporangium and megasporangium is similar till the formation of sporocytes.
- In *Selaginella* all the sporocyte in microsporangia undergoes meiosis as a result a large number of microspores is formed.
- On the other hand all the megasporocytes except one abort and the surviving megasporocyte undergo meiosis to form four large functional megaspore of same or variable size.
- Developmental studies have thus, showed that the process of heterospory becomes operative either before meiosis (e.g. *Selaginella*) or after meiosis (e.g. *Marsilea*)

Evidences from Experimental studies:

- On the basis of experimental studies on Selaginella and Marsilea it has been found that heterospory originated due to nutritional factors.
- It was observed that if the photosynthetic activity of Selaginella was slowed down by keeping it in low light intensity, then only microsporangia developed.
- Due to the low photosynthetic activity, nutrition became a limiting factor and spores could not grow in size.
- Thus, under such conditions only microspores were produced. Similar experiments were performed on Marsilea by Shattak (1910).
- In variable conditions of light, temperature and nutrients, he found that in plants growing in favourable conditions the microsporangium contains aborted microspore and microsporangium showing microspore abortion developed spore that were 16 times larger than the original size.
- In extreme cases of abortion only a single spore survived and looked alike a megaspore and showed all structural features of megaspore.
- Under unfavourable conditions of light, temperature and nutrients, he was able to induce the formation of the larger number of smaller spore in megasporangia.
- However, it was not possible to germinate these altered spores therefore; no conclusive results can be achieved.

Advantage of heterospory

- Heterospory expresses sex determining capability of plant.
- In homosporous species, differentiation of sex takes place at the gametophytic stage, whereas in heterosporous species difference in size of the spore is related to the sex of the gametophyte.
- A microspore always gives rise to male gametophyte and megaspore gives rise to female gametophyte. Therefore, in heterosporous forms sex can be predicted at the spore stage.
- The biological significance of heterospory is that in heterosporous forms the development of gametophyte is endosporic (spore germinate within the sporangium) and its nutrition is derived from the sporophyte hence is not affected by the ecological factors as in the case of independently growing gametophytes which has to manufacture not only its own food but also for the developing embryo.
- It is an evolutionary step towards seed habit.

Heterospory and Seed habit

- In seed bearing plants, there are two kinds of spores (microspores and megaspores) which grow to form male and female gametophyte respectively, In these plants the single megaspore is not shed from the megasporangium but retained within it while still attached to the mother plant.
- It germinates within the megasporangium producing the much reduced female gametophyte (nucellus) bearing archegonia. Later the nucellus and the gametophyte are protected by a covering known as integument and the whole structure is known as ovule.
- After fertilization zygote within ovule give rise to the embryo and the rest of the gametophyte including endosperm and integument thickens to form a seed coat.
- This entire structure (integumented ovule) is known as seed.

Thus, the important features leading to the development of seed habit are:

- The evolution of heterospory i.e. production of two kinds of spores The retention and germination of megaspore to form female gametophyte, fertilization of the egg and embryo formation within the megasporangium.
- Elaboration of the apex of the megaspore for receiving microspores or pollen grains.
- Envelopment of the megasporangium (nucellus) by an integument except at the apex thus forming micropyle. Selaginella shows a remarkable approach to seed habit because of the following features: It is heterosporous.
- The megaspore starts germinating within the megasporangia and their time of release varies with species. The number of megaspore in *S. rupestris* and *S. monospora* is reduced to one.

- In *S. rupestris* the megaspore is never shed and the fertilisation and the development of embryo takes place while megaspore is enclosed within the megasporangium.
- However the seed development in these species cannot be called as true seed habit because-:
- The megasporangium is not covered with integuments.
- The retention of megaspore permanently within the megasporangium has not become established.
- Histological union between the megaspore and megasporangium is absent.
- Absence of resting period after the development of embryo.

Life Cycle of *Equisetum*

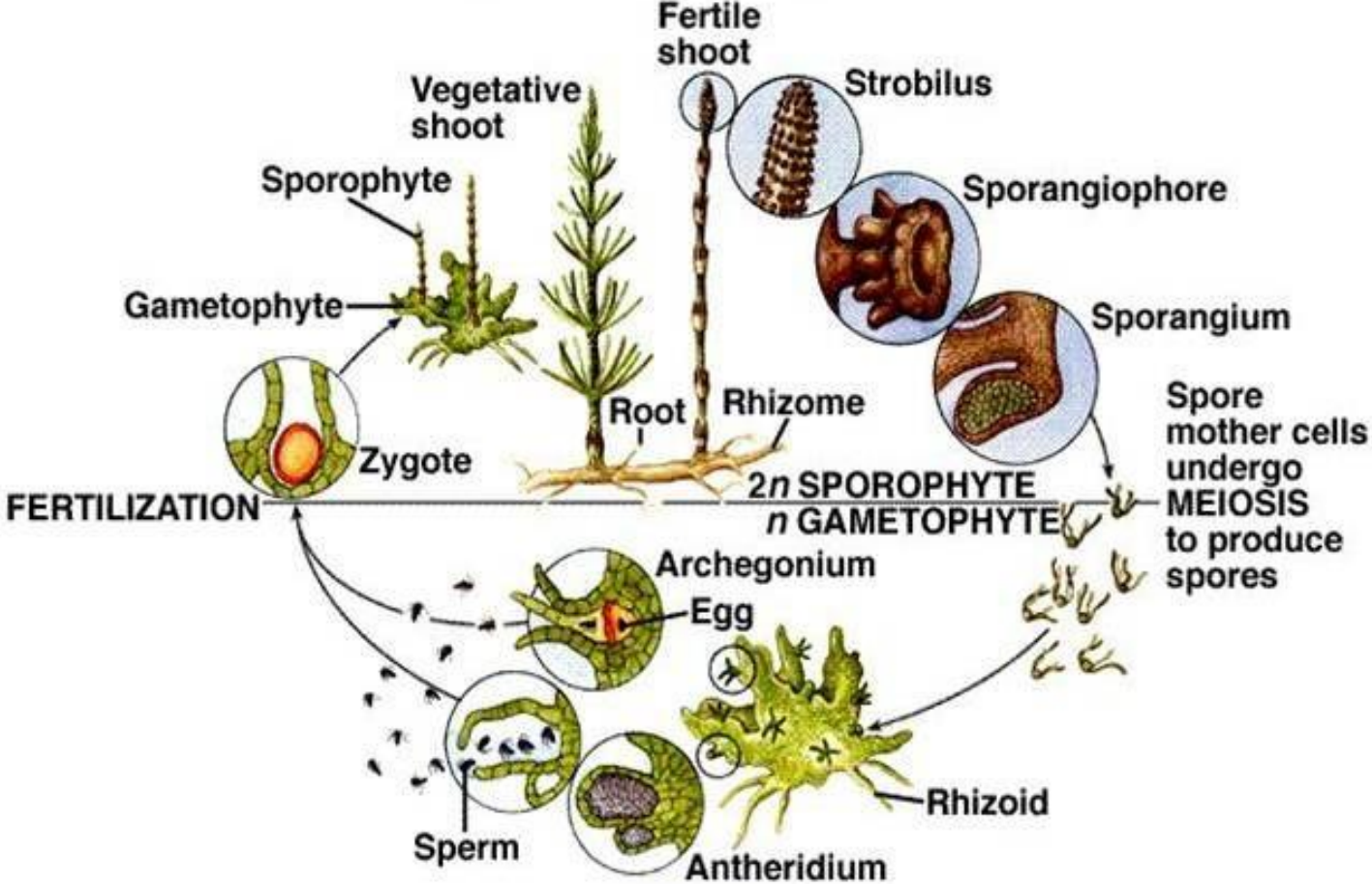


Diagramme showing different stages in Life cycle of a homosporous pteridophyte (*Equisetum*)

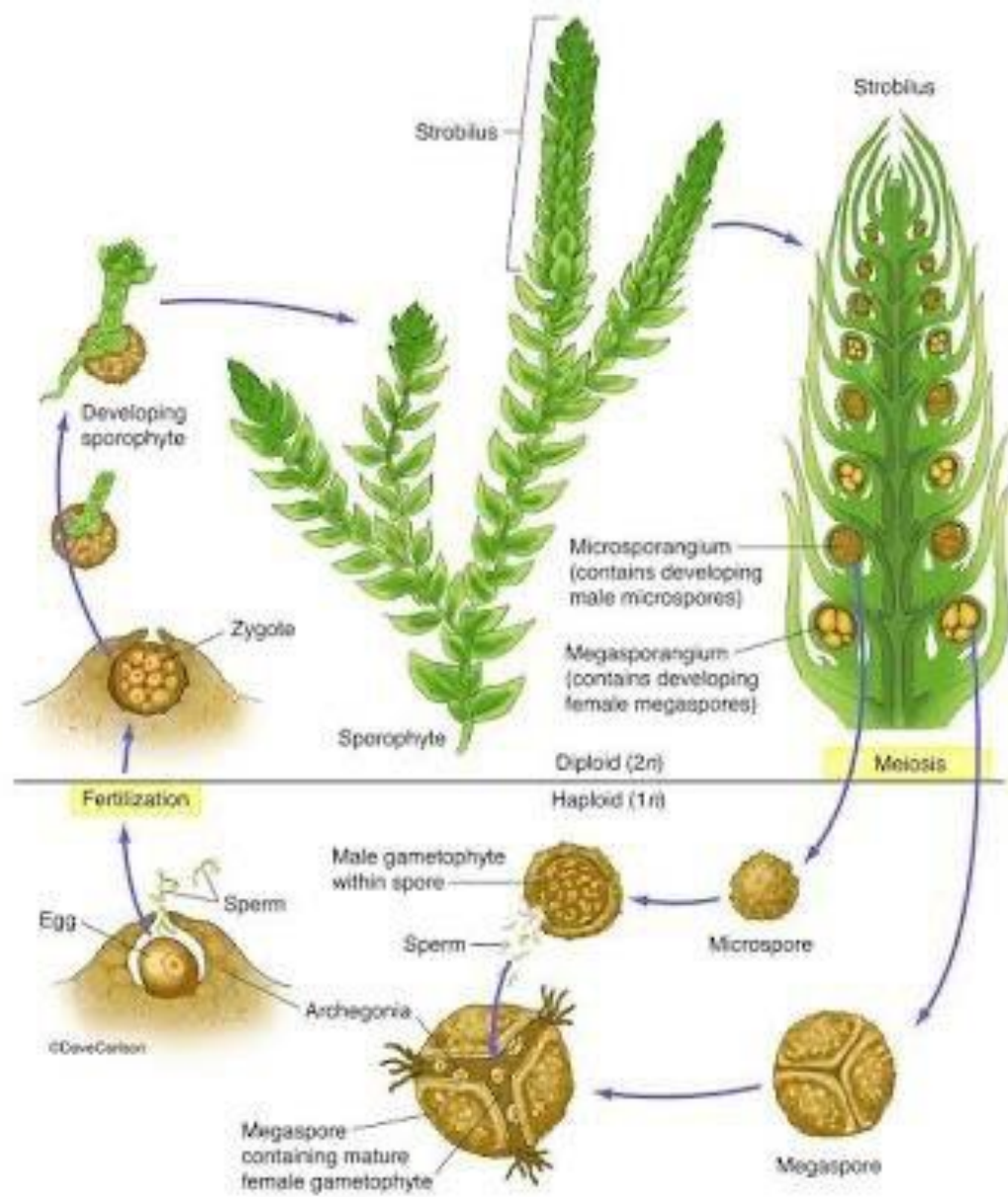


Diagram showing different stages in Life cycle of a heterosporous pteridophytes (*Selaginella*)

5. Brief account of types of steles

Stelar Evolution

- The stele (Greek word meaning pillar or column) is defined as a central vascular cylinder, with or without pith.
- Endodermis is the boundary between cortex and stele.
- The central cylinder or core of vascular tissue, consisting of xylem, phloem, pericycle and sometimes medullary rays and pith, is technically called the stele.
- The concept of the stele as the fundamental unit of vascular system was put forward by Van Tieghem and Douliot (1886) who proposed and developed Stelar theory.
- The stele of stem was connected with that of leaf by a vascular connection known as leaf trace.

Types of stele in pteridophytes

The stele in pteridophytes can be differentiated into two major groups.

1. Protostele:

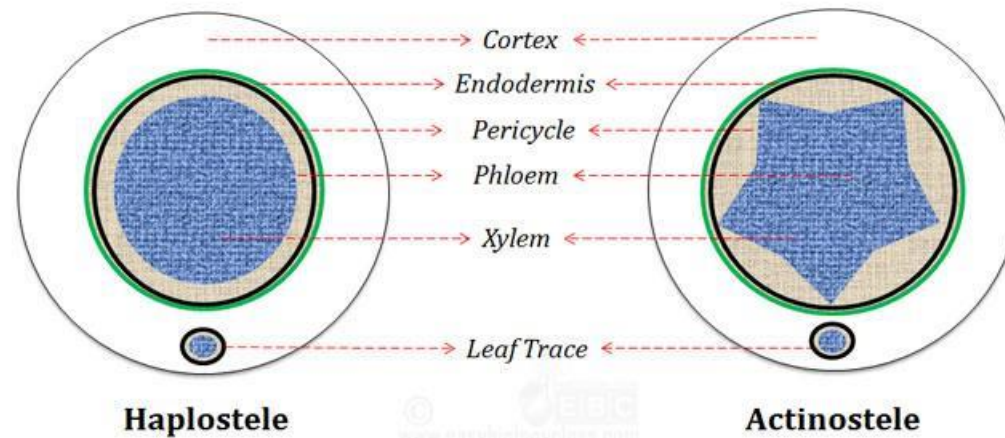
- It is the most simplest and primitive type of stele.
- In protostele, the vascular bundle is a concentric solid mass and the central core of xylem is surrounded by a layer of phloem and finally surrounded by a layer of pericycle.
- The protostele exists in following forms:

a). Haplostele:

- This is the most primitive type of stele.
- In this the xylem forms a solid, smooth and spherical central core which is surrounded by a continuous concentric layer of phloem e.g. *Lygodium*, *Selaginella*.

b) Actinostele:

- This is the modification of the haplostele and somewhat more advanced in having the central xylem core with radiating ribs and phloem is not concentric but present in between the radiating ribs of xylem e.g. *Psilotum*.
- The protoxylem is present at the tips of radiating arms.



c) Plectostele:

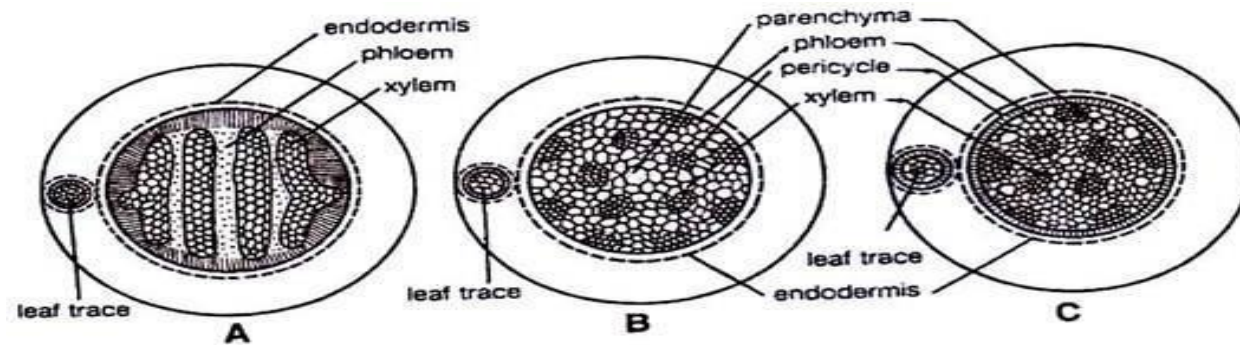
- In the stem of some species of *Lycopodium* the solid core of xylem gets broken in a number of plate-like lobes, more or less lying parallel to one another.
- The phloem alternates with xylem plates e.g. *Lycopodium volubile*.
- This specialized form of protostele is termed as plectostele.

d) Mixed protostele:

- In this type, masses of xylem and phloem are uniformly distributed.
- Scattered groups of xylem are embedded in the ground tissue of phloem e.g. *Lycopodium cernuum*.

e) Protostele with mixed pith:

- In the centre there is parenchyma cells associated alongwith the tracheids e.g. *Lepidodendron*.
- It may be derived from the transformation of the tracheids into parenchyma and may be first step in formation of pith.
- Such type of protostele is termed as mixed-protostele.



2. Siphonostele:

- Medullated protostele is called siphonostele.
- It is characteristic of Filicophyta.
- This is the modification of protostele.
- During the development the siphonostele the central core of xylem is replaced by parenchymatous cells so that definite pith surrounded by xylem appears in the centre.
- On the basis of branch and leaf gaps Jeffrey (1910), distinguished two types of siphonosteles, cladosisiphonic siphonosteles (leaf gaps not found) and phyllosiphonic siphonosteles (leaf and branch gaps are present).

Jeffrey (1898) classified Siphonostele into following two types, on the basis of position of phloem.

(a) Ectophloic siphonostele:

- The pith is surrounded by concentric xylem cylinder and next to xylem the concentric phloem cylinder.
- It means the phloem is restricted only on the external sides of the xylem. (e.g. *Osmunda* and *Schizea*).
- The pith is central in position.
- The phloem is externally surrounded by pericycle and endodermis.

(b) Amphiphloic siphonostele:

- The pith is surrounded by the vascular tissue.
- The concentric inner phloem cylinder surrounds the central pith.
- Next is the concentric xylem cylinder which is immediately surrounded by outer phloem cylinder.
- It means phloem is present both sides of xylem. (e.g., *Marsilea* rhizome)



Ectophloic Siphonostele

Amphiphloic Siphonostele

Other modification of Siphonostele

3. Solenostele

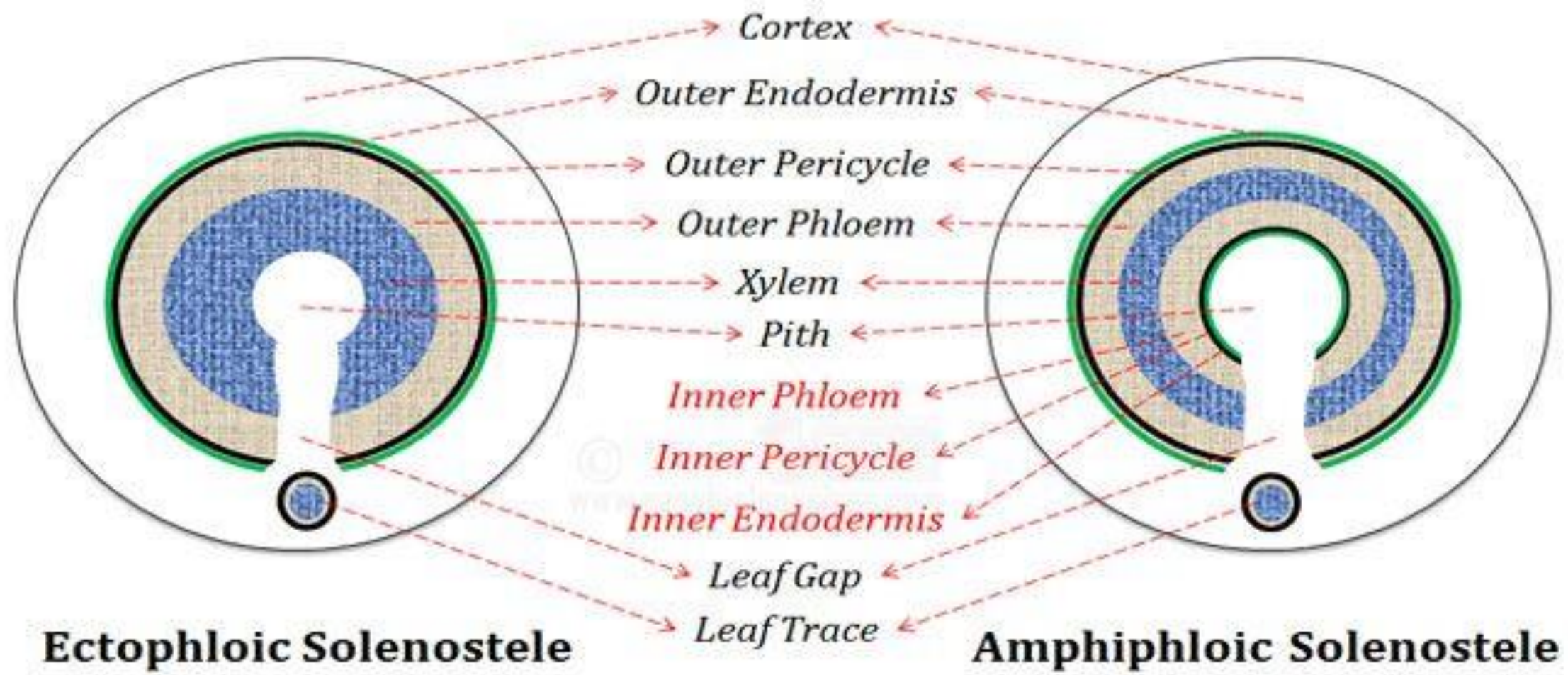
- If the siphonostele perforated at the place or places to the origin of the leaf trace, such a condition is known as Solenostele.

Ectophloic solenostele :

- This type of solenostele derived from the ectophloic siphonostele.
- So, here the phloem is present only side of xylem.

Amphiphloic solenostele :

- This type of solenostele derived from the amphiphloic siphonostele.
- So in this case the phloem is present on both the sides of the xylem.



4. Dictyostele

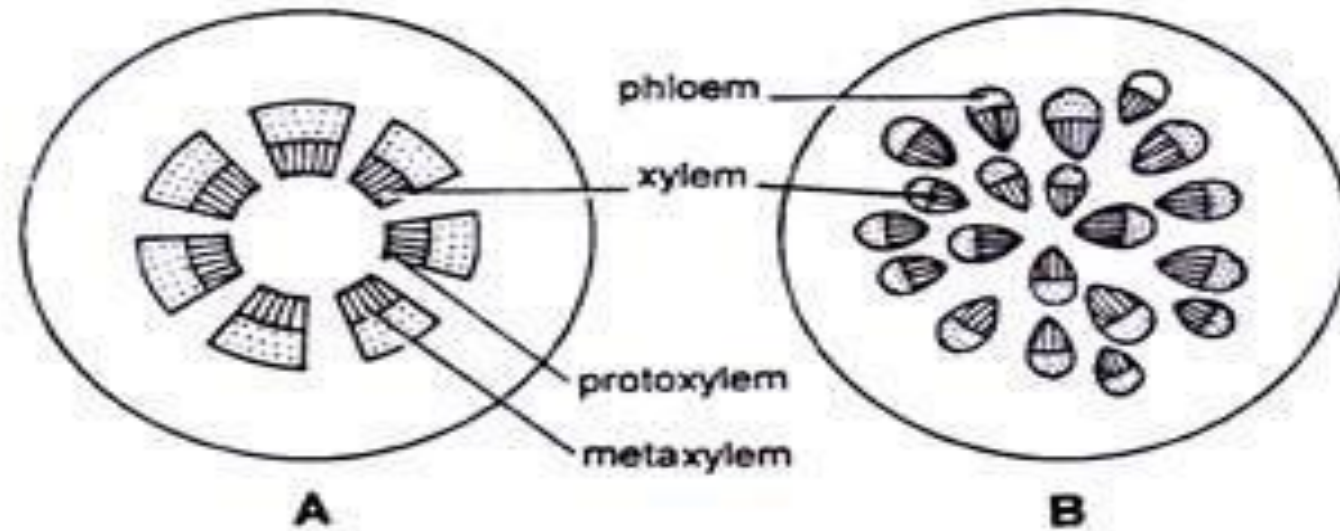
- In the more advanced siphonosteles of Pteropsida, the successive gaps may overlap each other.
- Brebner (1902) called the siphonosteles with overlapping gaps as dictyosteles.
- So, in this case the solenostele broken into a network of separate vascular strands, due to crowded leaf gaps.
- In such cases each separate vascular strand is known as meristele.
- Each meristele is of protostelic type.
- The dictyostele is a ring of many meristeles.

5. Eustele

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

6. Atactostele

- In atactostele the vascular strands are scattered.
- It occurs into monocotyledons.
- George Brebner (1902) coined the term atactostele (Greek atact-without order) for vein arrangement seen in transverse view which has been described later as “scattered” by Berg (1997).

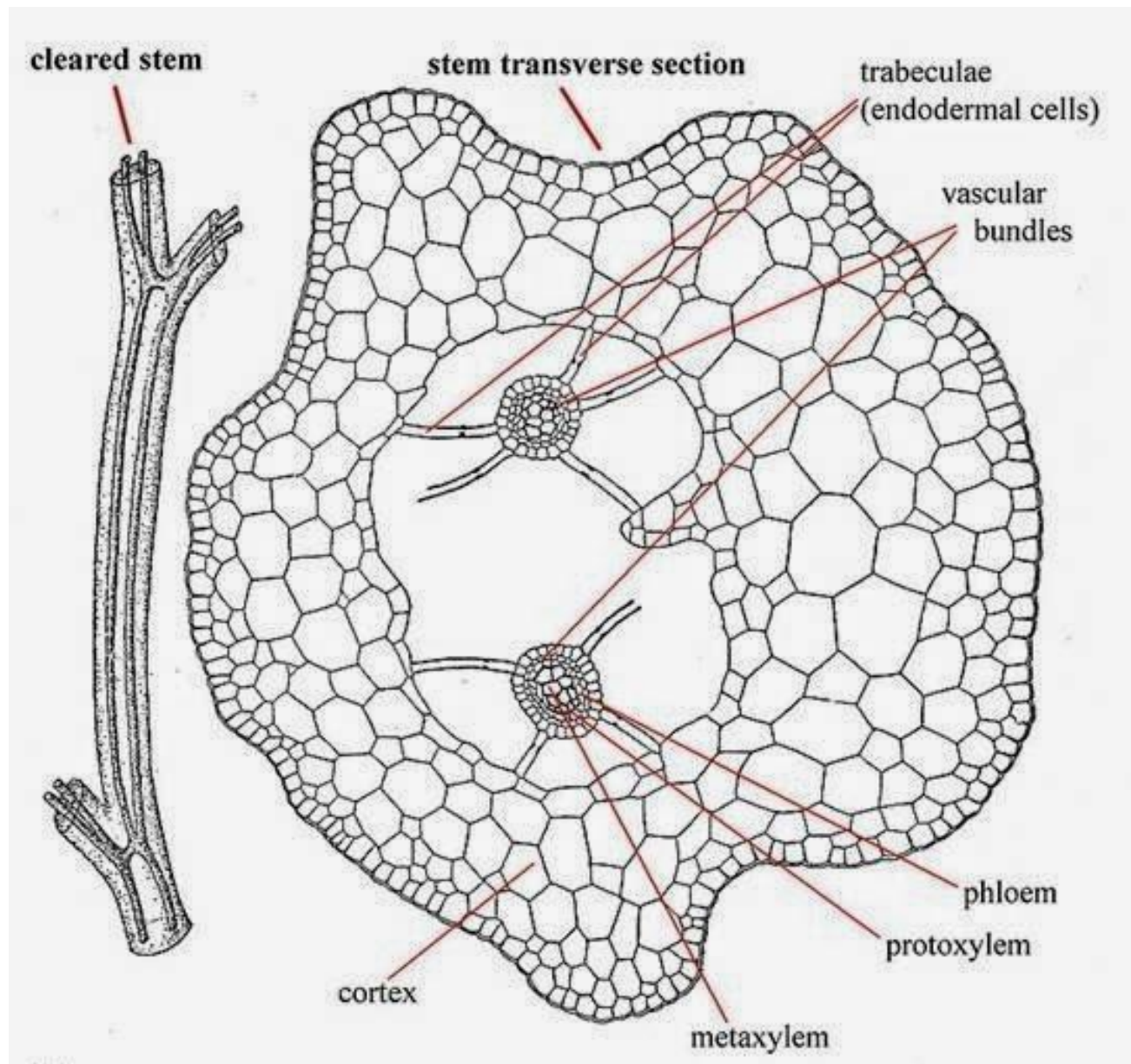


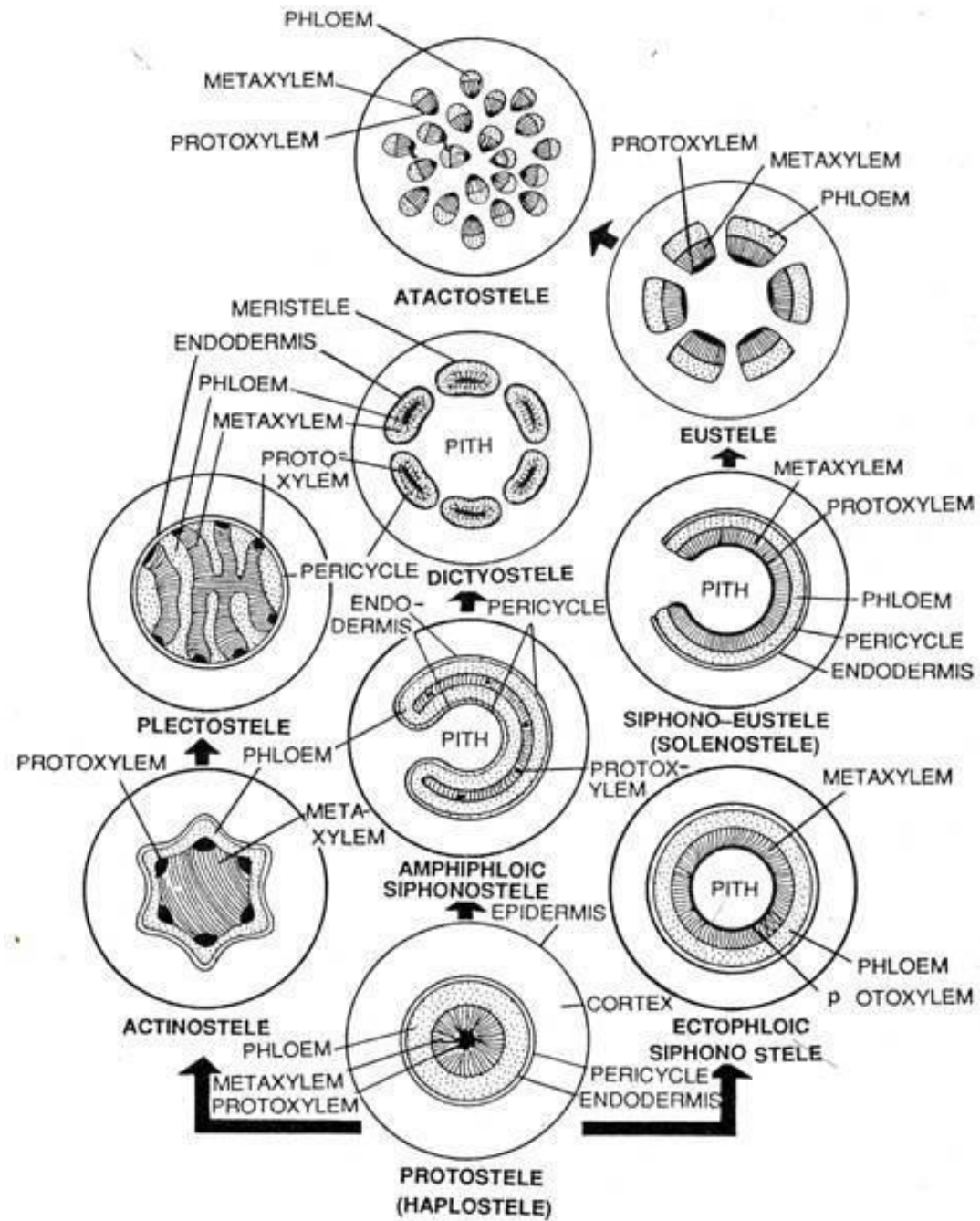
7. Polycyclic Stele

- When the vascular tissue present in the form of two or more concentric cylinders, such a stele is called polycyclic stele.
- A typical polycyclic stele possesses two or more concentric rings of vascular tissue.
- This may be a solenostele or a dictyostele.
- Two concentric rings of vascular tissue are found in *Pteridium aquilinum* and three in *Matonia pectinata*.

8. Polystele

- Some times more than one stele are present in the axis of some pteridophytes.
- Such a condition is called Polystelics.
- Such stele shows polystelic condition.
- Certain species of *Selaginella* have polystelic condition.





THE END