LYCOPODIUM

Structure

The main plant body is sporophytic. It consists of slender and branched stem, numerous small leaves (microphylls) and dichotomously- branched roots.

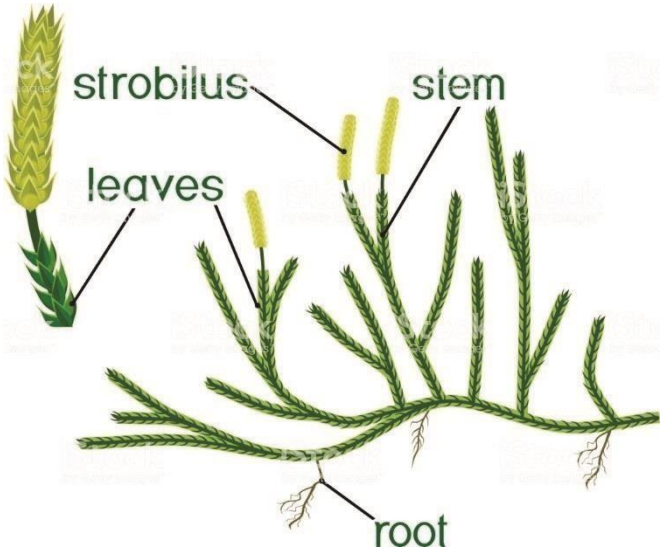

Fig.1.11. *Lycopodium* sporophyte

Internal structure of root

- The primary root or first formed root of the young sporophyte is ephemeral, shortlived. The older plants have dichotomously branched adventitious roots (the roots are endogenous in origin and are formed from the pericycle).
- In case of erect species like *Lycopodium selago* and *Lycopodium compactum,* the root arises from the basal part of the stem. However, the species with prostrate creeping stem e.g., *Lycopodium clavatum* and *Lycopodium cernuum,* bear roots all along its length.
- Anatomically, the root is divided into three parts — the outer epidermis, middle cortex and inner stele.
- The outer epidermis is made up of a single- layered thin-walled parenchymatous cells. Numerous root hairs are given out from the epidermal cells of the apical region of the root. A peculiarity of the root of *Lycopodium* is that the root hairs arise in pairs.
- Next to the epidermis is the cortex which is several layers in thickness. In older roots, the cortex is differentiated into outer and inner cortex. The outer cortex usually consists of heavily scarified cells. This sclerified region provides mechanical support to the root. The inner cortex is parenchymatous.

- The central portion of the root is occupied by protostele. The stele is monarch with one pro- toxylem group in young roots, but becomes diarch or triarch in older roots. The xylem is ‘C’ or ‘U’ shaped with the protoxylem at the tips of ‘C’ or ‘U’. The phloem lies in between the arms of the xylem.

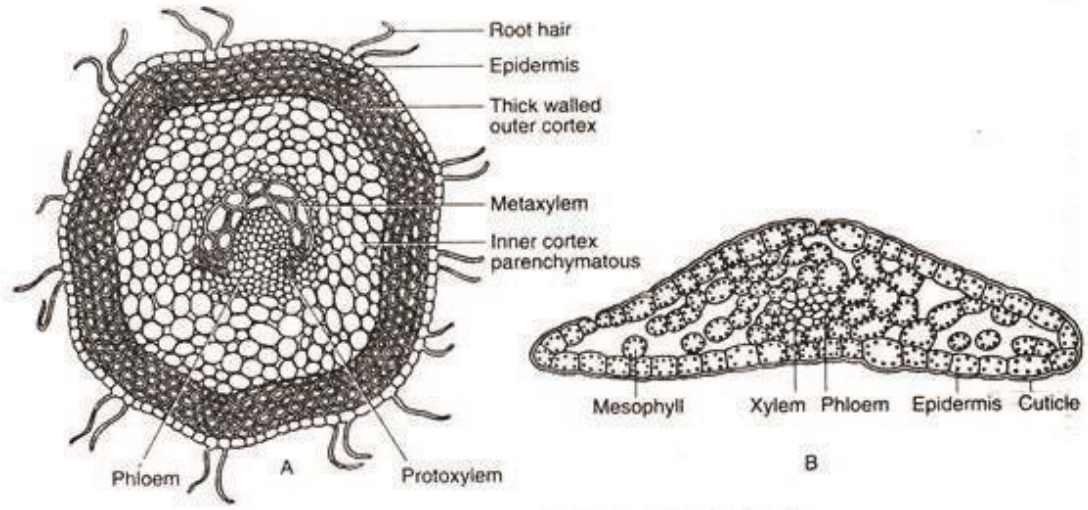

Fig.1.12. *Lycopodium* A-*T.S.* of root B- *V.S.* of leaf

Leaf:

- The leaves are simple, eligulate, sessile and small with a single unbranched mid-vein (microphyIIs). They are generally lanceolate in shape with a narrow apex and slightly broad base. The margins are generally entire but sometimes serrated in nature (e.g., *L. serratum).*
- Phyllotaxy is basically helical *(L. clavatum),* but the arrangement may appear to be opposite decussate *(L. complanatum, L. alpinum)* or whorled *(L. cernuum*), or even variable in different regions of the same plant. In some forms the leaf bases are decurrent (the leaf base is fused with and extends down the stem to varying degrees).
- The leaves are usually all alike and all of same size and shape (Isophylly or Homophylly). In some species, specially those with flattened stems, e.g., L. complanatum and *L. volubile,* the leaves show dimorphism (Anisophylly or Heterophylly) — particularly on lateral determinate branches.
- The anatomy of the leaf is very simple with a highly cuticularised one-layered epidermis, interrupted by stomata, a homogeneous parenchymatous mesophyll with large intercellular spaces and chloroplastids; and a median concentric vascular bundle with central xylem surrounded by phloem.

- Stomata are distributed on both the surfaces of the leaf (i.e., amphistomatic) in most of species, but in some species (e.g., *L. complanatum* and *L. volubile*) stomata are confined to the lower surface only (i.e., hypostomatic).

Stem:

- The stem of all the species of *Lycopodium* are in general weak, slender and rhizomatous. It is usually erect (e.g., *L. selage*) or pendent (e.g., *L. phlegmaria*) in the sub-genus *Urostachya* and prostrate creeping in the sub-genus *Rhopalostachya*, which is sparsely (e.g., *L. annotinum*) or profusely branched (e.g., *L. obscurus*).
- In the members of the sub-genus Urostachya the branching is typically dichotomous, but in Rhopalostachya it is first dichotomous, which later becomes monopodia. The stem and branches are covered with small leaves (microphylls).
- Anatomically, the stem is differentiated into epidermis, cortex and stele. The outermost layer is a uniseriate epidermis, the walls of which are thick and cuticularised.
  The cortex is highly variable in thickness and structure.
- In some species it becomes homogeneous made up of parenchymatous cells (e.g., *L. phlegmaria, L. serratum),* and in others the cells of specific regions undergo sclerification. In some species, e.g., *L. clavatum*, the outer and inner portions of the cortex are composed of thick-walled sclerenchymatous cells whereas the middle portion consists of large, thin-walled parenchymatous cells.
- In *L. cernuum*, on the other- hand, the middle portion is sclerenchymatous in nature, while the inner and outer zones are parenchymatous.
- The endodermis is the innermost layer of the cortex showing characteristic casparian bands. The endodermis is followed by pericycle which is 2-6 layered thick.
- The transition from pericycle to cortex in some species (e.g., *L. clavatum*) is abrupt because the walls of the cortical cells are thick.

The Sporophyte of *Lycopodium:*

- In habit, all species vary widely, but all have slender, weak-stemmed, comparatively small, herbaceous or shrubby sporophytes. Many species are somewhat prostrate with stems creeping above or below the surface of the soil. Other terrestrial species have upright or semi-erect stems, which later on become more or less horizontal. Some species may also be epiphytic with pendent bodies, while still others are twining to some extent.

- In the simplest case, the sporophyte has a simple stem covered with numerous, mosslike leaves, each bearing a single large sporangium on its upper side. In this sense the whole sporophyte is a strobilus *(e.g. L. selago. L. pitheyoides, etc,).*

- In more complex types, the sporophytes have much-branched stems whose lower leaves are sterile and act as foliage leaves, and this gradual sterilization process can be traced to more than one form where the sporophyte is distinctly differentiated into a vegetative region bearing foliage leaves, and a reproductive region bearing the sporophylls.
- In such cases, the sporophylls are quite different in form from the foliage leaves and are localized and compacted to form a distinct strobilus (e.g., *L. clavatum*). These strobili are often separated from the vegetative body and are borne on slender stalks with rudimentary leaves.
- Branching of the stem is characteristically dichotomous. The two branches of a forking may be equal or unequal. The leaves are very numerous, simple and small (usually 210 mm. long, sometimes up to 25-30 mm.), arranged in close spirals, whorls or opposite pairs, or the arrangement may be somewhat irregular.
- The primary root is short-lived but many adventitious roots arise, singly or in acropetal clusters, from the under-side of the older parts of the stem and the branching is strikingly dichotomous. Root hairs are abundant and persistent in some terrestrial species and lateral roots do not develop.
- A cross-section of the stem shows two distinct regions, the cortex and the central cylinder of the stele. The cortex is bounded externally by an epidermis, one cell in thickness and with stomata. The cortex varies in thickness as well as in structure. In some species it is soft and parenchymatous throughout, in others the outer or the inner portion of the cortex undergoes sclerification, while in still others the entire cortex becomes sclerified.
- The cortex is limited internally by an endodermis with characteristic radially thickened walls. Lying within the endodermis is the pericycle 3-6 cells in thickness. Internal to the pericycle is the central core of vascular cylinder which is a protostele with xylem exarch. In the simplest case, the xylem appears as a star-like mass with a variable number of rays.

  In between the rays lies the phloem being separated from the xylem by narrow strip of parenchyma. In more advanced types of sporophytes, numerous furrows appear in the

- xylem cylinder so that the xylem breaks up isolated strands forming plate-like lobes or mesh-like mass, with included phloem bands.

1.2.1. Reproduction in *Lycopodium:*

Lycopodium reproduces both by vegetative and sexual methods.

1. Vegetative Reproduction

Vegetative reproduction *Lycopodium* which take place by the following methods. **i.**

Gemmae or Bulbils:

- These are modified lateral branches which develop on the stem apex in the axils of leaves. Each bulbil consists of a short axis where several thick and fleshy leaves are arranged spirally and compactly.
- These leaves store food material. These bulbils fall on the ground and grow into new sporophytic plants, e.g., many *Urostachya* members like *L. selago; L. phlegmaria* and *L. lucidulum.*

ii. Fragmentation

- In this method, the progressive death and decay of older parts reach the region of branching; as a result the two branches separate and each branch develops into a new plant e.g., *L. incondatum* and other creeping species.

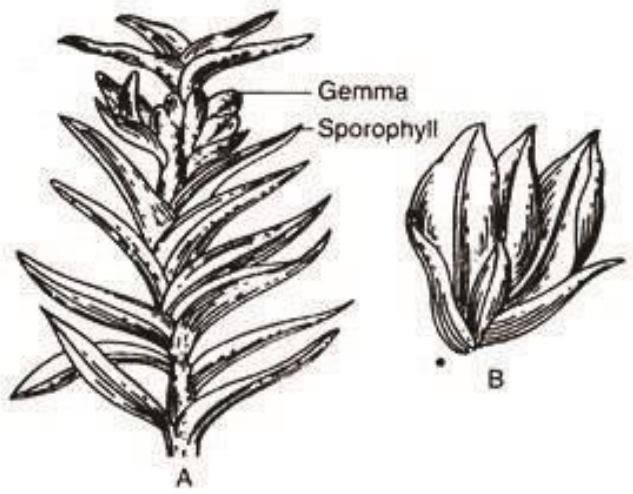

Fig.1.13. *Lycopodium* A. *A branch with gemmae* B. *A gemma*

iii. Adventitious Buds:

- The adventitious buds are formed near the base of the main stem and on separation from the main axis they are capable of forming new plants e.g., *L. phlegmaria, L. reflexum.*

iv. Root Tubercles:

- Bud-like tubercles are formed in the apical region of the adventitious root by the proliferation of the parenchymatous cells. These tubercles on germination produce new sporophyte e.g., *L. ramulosum, L. cernuum.*

2. Reproduction by Spores:

The plant body is a sporophyte i.e., it bears spores. The spores are developed in the sporangia.

Sporangia — the Spore-Producing Organ

- Position of the sporangium and organisation of the strobilus.
- Sporangia always occur singly on the adaxial surface of the specialised leaves called sporophylls or fertile leaves. The sporophyll forms a protective covering around the sporangium. The sporophylls may be aggregated into a definite strobilus (aggregation of sporophylls is called strobilus).
- The sporophylls of such strobili are different from vegetative leaves in size, shape, and colour. These types of strobili may occur on leafy stems or may be erected on lateral branches having very small, scale-like leaves (e.g., *L. clavatum; L. digitatum; L. obscurum).*

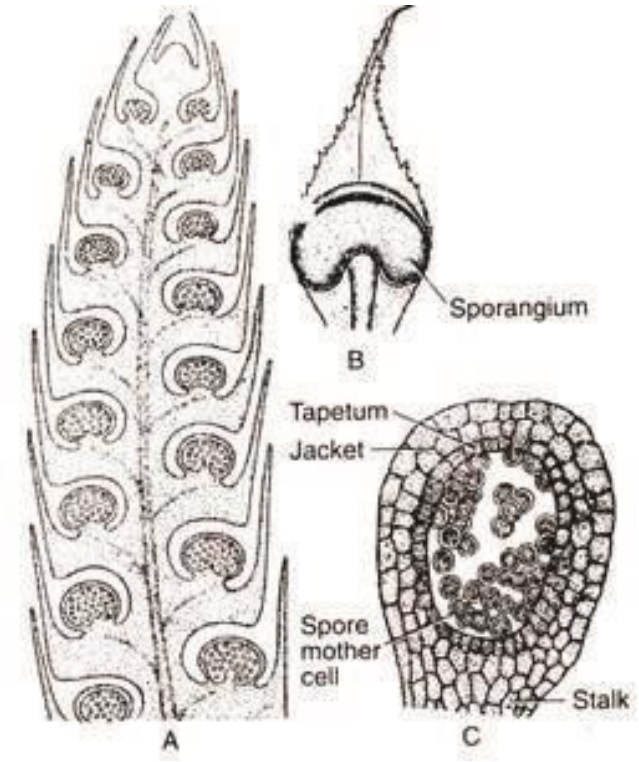

Fig.1.14. *Lycopodium clavatum :* A. L.S. of strobilus B. A sporophyll (adaxial view), C. L.S. of a mature sporangium

- In certain species of *Lycopodium (e.g., L. lucidulum and L. selago)* the sporophylls are similar to vegetative leaves. In these species no definite strobili are formed and the "fertile" areas alternate with "sterile" regions along the stem. Epiphytic species, viz., *L. phlegmaria,* has dichotomously branched pendulous strobilus.

Structure of the Sporangium:

- Mature sporangia of most species are unilocular, sub-spherical or reniform (kidneyshaped) in shape. The size of the sporangium varies from 1.0 to 2.5 mm in diameter and colour ranges from yellow to orange. The sporangium has a short and massive stalk.

Development of the Sporangium:

- Mode of sporangial development is of the eusporangiate type (originating from a group of superficial cells). A single transverse row of superficial cells at the adaxial (upper) surface of the sporophyll divides periclinally.

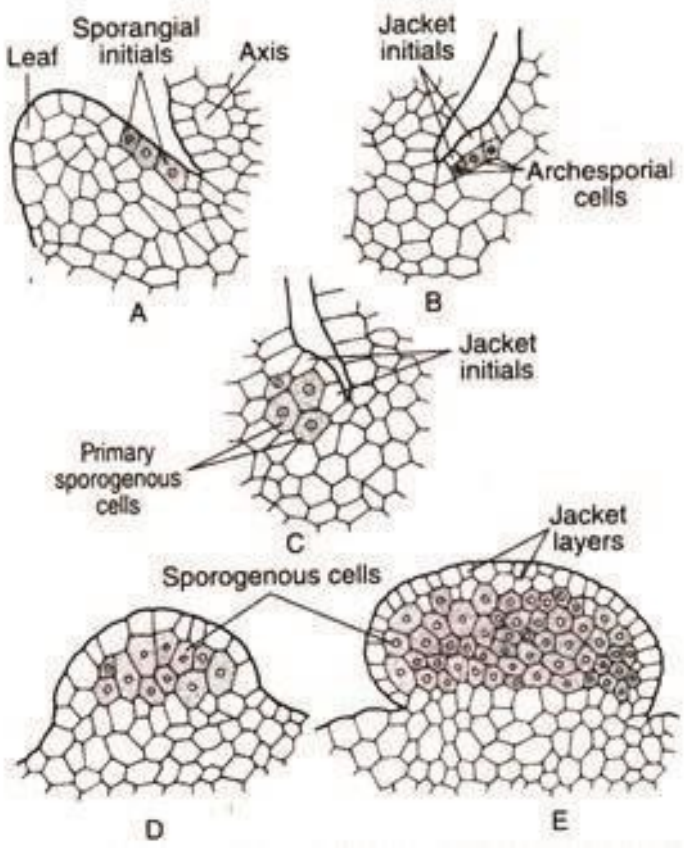

Fig.1.15. ***Lycopodium clavatum :*** **A- Stage in the sporangium development**

- The outer cells form the multilayered wall and the sporogenous tissue/cells derived from the inner cells of such divisions. The innermost layer of the sporangial wall functions as tapetal layer (i.e., nourishing tissue).
- The sporogenous tissue undergoes repeated mitotic divisions and ultimately gives rise to spore mother cells. As the sporangium matures, spore mother cells separate from each other and undergo meiotic division (reductional division) to form numerous spore tetrads (i.e., group of four cells produced by a meiotic division of a spore mother cell).
- Spores are triangular in shape with triradiate ridge, present on the inner (proximal) face.
- *Lycopodium* is a homosporous pteridophyte i.e., it produces spores of equal size and shapes. The mature spores are yellow in colour. The spore wall is divisible into two layers viz., the inner wall, called the intine, and an outer layer, the exine. The exine displays ornamentation that varies with the species.

Gametophyte:

- *Lycopodium* is homosporous, therefore, spore germinates exosporically to produce gametophytic prothallus, which bears both male and female sex organs (i.e., monoecious and homothalic). The germination of the spores may be immediate in some species (e.g., *Lycopodium cernuum, L. inundatum)* or after a delay of several years *(L. clavatum, L. complanatum).*
- The spores absorb water before germination. The first division of the spore is asymmetric to produce one small biconvex rhizoidal cell and a large cell. Soon after this division, the exine ruptures along the triradiate ridge. The rhizoidal cell disintegrates, while the large cell again divides by a vertical wall to form two cells.
- Of these two cells, the one nearer to rhizoidal cell is called basal cell which does not divide further. The other cell, by further divisions, forms apical cell with two cutting faces. The further development of gametophyte does not proceed if there is no infection into the basal cell by the mycorrhizal fungus.

  Three main types of mature prothalli (singular prothallus) may be distinguished in Lycopodium:

1. Cernuum Type

- These types of gametophytes are found in most of the tropical species (e.g. *L. cernuum, L. innunda- tum*). Here spore germinates immediately and the gametophyte completes its growth in one season. The prothalli are small, green and aerial with a lower conical basal region buried in the soil. Rhizoids occur in the colourless subterranean (basal) region.
- The subterranean region always contains an endophytic fungus. The entire plant body may not be over 3 mm long and are annual in nature. The upper green part is exposed and has a number of irregular leaf-like lobes (photosynthetic) forming a crown. Nutritionally, the prothallus is both autotrophic and saprophytic. The sex organs (antheridium and archegonium) generally occur near the bases of the aerial lobes.

2. Clavatum Type

- In this type, the spore germination is delayed for a long time (one to many years), thus the prothallus has a longer lifespan. Here the prothalli are fleshy, non-green, totally saprophytic and completely subterranean and perennial in nature. Development takes place beneath the surface of the ground or within a layer of humus.

The prothalli are large and may be up to 2 centimeters in length. They may be topshaped with a convolute margin *(L. clavatum*), or carrot- shaped *(L. complanatum* and *L. annotinum).* The top of the prothallus are lobed and the sex organs and the growing embryos are located on these lobes. Although all the gametophytic cells are parenchymatous, the tissue differentiation is noted in the lower portion.

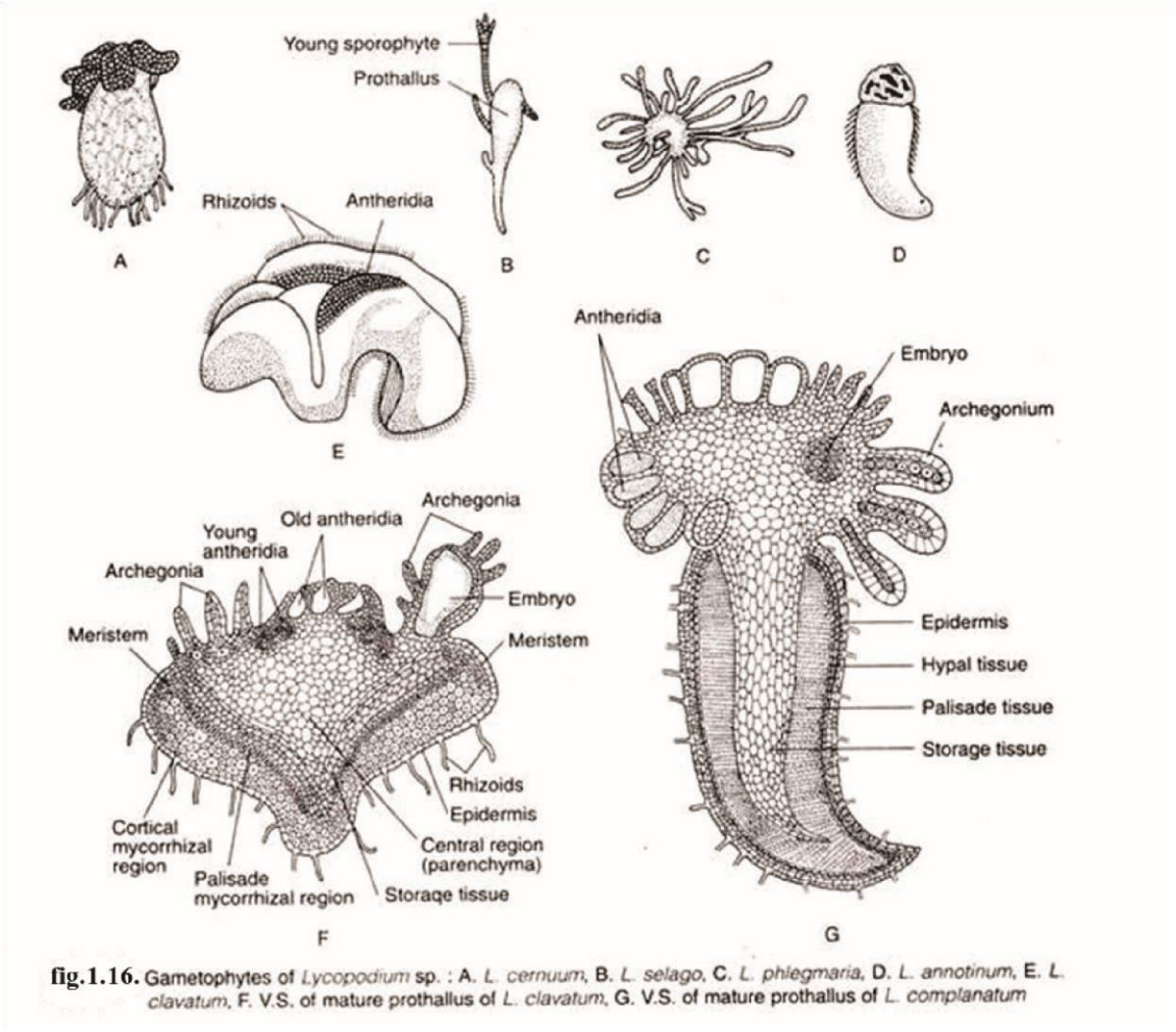

fig.1.16. Gametophytes of *Lycopodium* sp. : A. *L. cernuum*, B. *L. selago*, C. *L. phlegmaria*, D. *L. annotinum*, E. *L. clavatum*, F. V.S. of mature prothallus of *L. clavatum*, G. V.S. of mature prothallus of *L. complanatum*

- The central region constitutes storage tissue made up of vertically elongated cells. The radially elongated, closely packed chlorenchymatous cells constitute the palisade mycorrhizal layer. External to the palisade tissue is the cortical mycorrhizal region. The epidermis is present outside the cortical mycorrhizal region, some of the epidermal cells produce rhizoids.

3. Phlegmaria Type

- Here the prothalli are aerial but saprophytic in nature, grow on tree trunks below a coating of humus. This type is found in epiphytic species of *Lycopodium* (e.g., *L. phlegmaria).* Here the spore germination is immediate and the gametophyte grows for only one season.
- The prothallus consists of a short, tuberous central part from which a number of colourless, slender and cylindrical branches develop in an irregular fashion. These branches bear sex organs and they are usually surrounded by glandular hairs called paraphysis.
- There are also some intermediate types in between these forms. For example, the gametophyte of *L. selago* is in-between the Cernuum and Clavatum types. Here spore germination and gametophyte development take place immediately like Cernuum type.
- However, the spores germinate after a long resting period if the spores are deeply buried in the soil. As a result a subterranean saprophytic Clavatum type of gametophyte is formed. Hence more than one type of prothalli may occur in the same species.

3. Sexual reproduction

The gametophytic prothallus of *Lycopodium* is monoecious (homothallic) i.e., male (antheridia) and female (archegonia) sex organs are developed on the same prothallus. The antheridia and archegonia are generally intermingled near the bases of the upright lobes in those species where gametophytes are of the green annual type. In subterranean perennial forms, the sex organs are segregated into definite groups. In both types, antheridia generally appear first near the middle of the crown of the gametophyte.

Antheridium:

- The antheridium develops from a single superficial cell called antheridial initial of the prothallus. The initial cell divides transversely forming an upper jacket initial and a lower primary androgonial cell.
- The jacket initial divides anticlinally to form one-layered jacket. The lower androgonial cell forms a mass of androcytes through many irregular divisions. Each androcyte matures into a biflagellate sperm resembling the sperms of certain bryophytes or algae.

A sperm is a blunt-ended, fusiform cell, 8-10 μm long and 4-5 μm wide. There are two flagella, each one is about 38 μm long. The antheridia are almost wholly embedded in the gametophytic tissue. The sperms are released by breaking down the operculum at top.

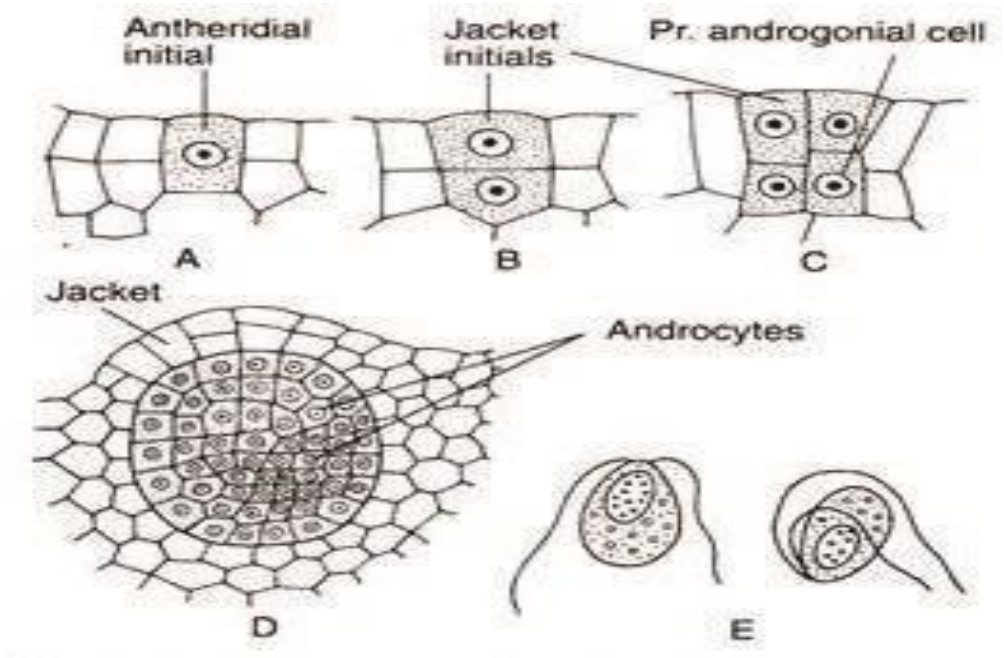

Fig . 1.17. *Lycopodium* : A-D. Stage in the development of antheridium E. Antherozoids

Archegonium:

- The archegonium develops from a superficial archegonial initial cell. The first periclinal division of archegonial intial gives rise to an upper primary cover cell and a lower central cell. The central cell divides by a transverse wall to form a lower primary venter cell and an upper primary canal cell.
- The primary canal cell, by repeated divisions, forms 4-8 neck canal cells (exception, one neck canal cell in *L. cernuum*, 14 in *L. complanatum*). The venter cell forms the egg often after cutting off a ventral canal cell. The upper primary cover cells divide and redivide to form neck of archegonium. Venter is embedded in the gametophyte tissue and the neck of the archegonium protrudes out.

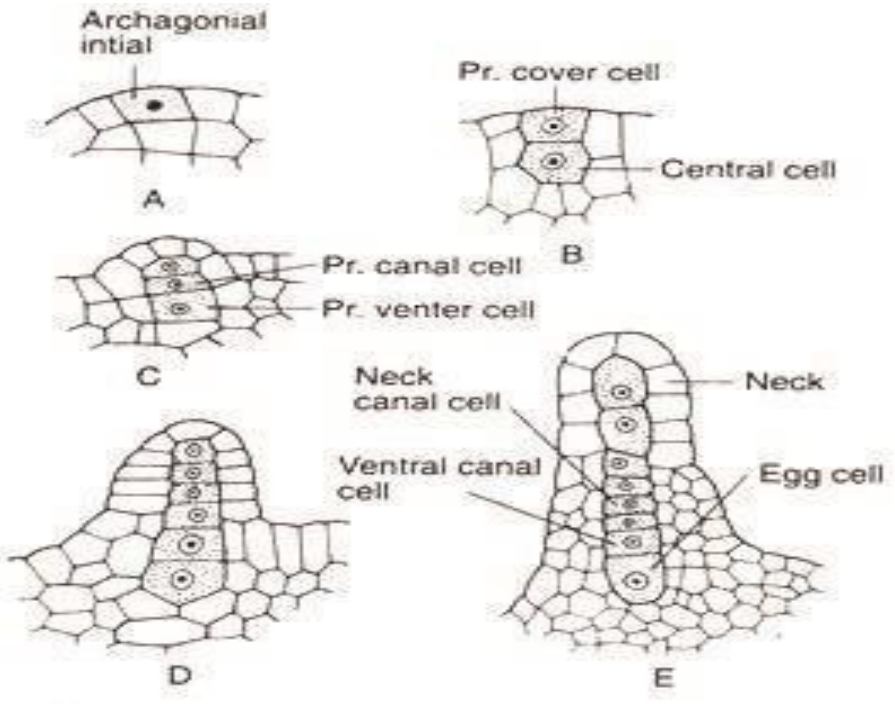

Fig . 1.18. *Lycopodium* : A-D. Stage in the development of archegonium, E. A mature archegonium

Fertilisation:

- Fertilisation takes place in the usual way. The neck canal cells and the ventral canal cell disintegrate to form a passage for the entrance of the motile biflagellate sperms. The sperm reaches the archegonium by swimming through a film of water on the surface of the gametophyte.
- Free citric acid or salts of citric acid, available in the canal as a by-product of disintegration of canal cells, may play a role in the attraction of sperms to the archegonia.

Only one sperm eventually fertilises the egg that develops into the zygote.

Embryo (New Sporophyte):

- The early stages in the development of zygote reveals a common basic plan in all the species, but later stages differ according to the species.
- In species with subterranean gametophyte.
- The first division of the zygote is transverse to right angle to the long axis of the archegonium which produces an outer suspensor cell and an inner embryonic cell (Fig.

7.33A). The outer cell may or may not enlarge but it does not undergo further divisions and becomes a suspensor.

Subsequent divisions of lower cell produces a multicellular embryo. The embryo in *Lycopodium* is endoscopic in nature (where the future shoot apex is directed away from the mouth of the archegonium). Further development of the embryo produces shoot apex and foot. The shoot apex grows laterally and upward Suspensor and the foot develops along the lower side of the embryo.

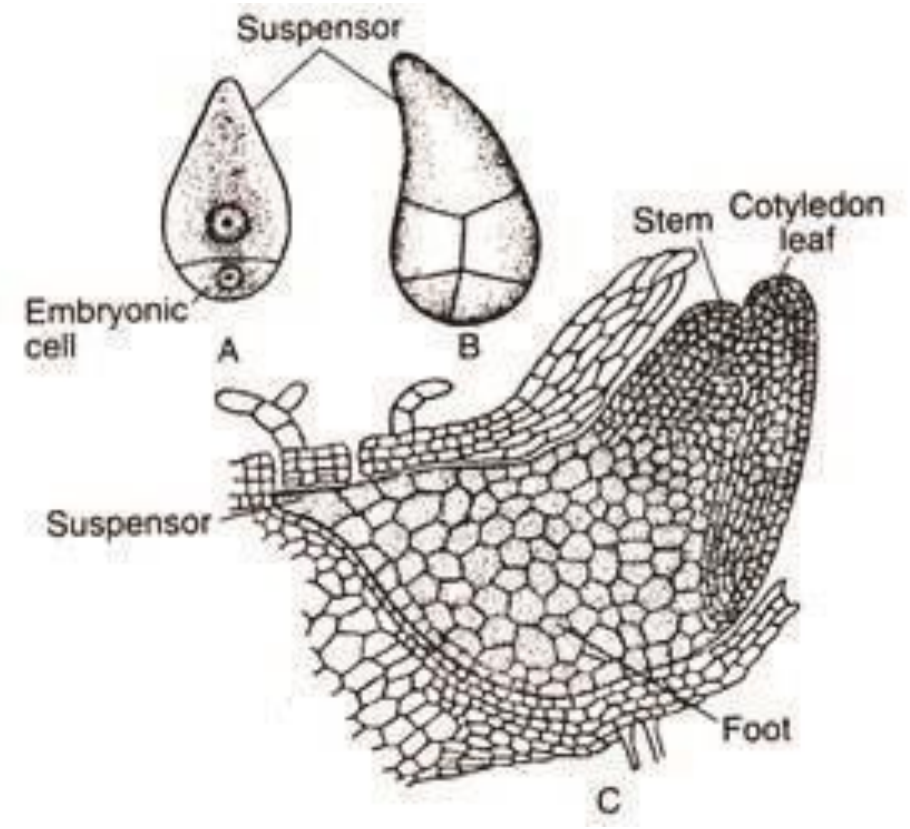

Fig . 1.19. *Lycopodium* : A-C. Stage in the development of embryo

- The roots generally come out from the areas between the first leaf and foot. The foot enlarges, and with the help of the foot the embryo remains embedded in the gametophyte. The foot acts as a haustorial structure until the sporophyte becomes physiologically independent e.g., *L. clavatum; L. anno-tinum; L. phlegmaria; L. selago; L. complanatum.*
- In species with green surface-living gametophytes.

- The early developmental stages, until the differentiation into specialised parts, are similar to that of the subterranean species. In this case, foot is formed as usual, but, instead of shoot apex, a spherical parenchymatous body termed protocorm (extraprothalial undifferentiated tuberous body) is developed.
- No root is produced but rhizoids occur on the lower surface and leaf-like outgrowths, called Proto- phylls or prophylls, arise on the upper surface of the protocorm. The protocorm remains in this stage for some time and a shoot apical meristem becomes organised and a "normal" type of shoot is produced, e.g., *L. cernuum; L. corolinianum; L. inundatum; L. laterale etc.*

The Gametophyte of *Lycopodium:*

1. When the spores are mature, a narrow transverse strip of cells (stomium) is gradually differentiated at the apex of the sporangium, which ruptures transversely and liberates the spores. Each spore, under favourable conditions, germinates and produces the gametophytic plant. There are two main types of gametophytes.
2. In tropical species *(L. cernuum*) usually the spores after liberation germinate quickly and form short-lived gametophytes, on the surface of the ground, which are very small, green (excepting the basal portion), somewhat cylindrical to ovoid bodies with lobed apices.
3. In other cases, especially in creeping and epiphytic species *(L. clavatum),* the spores after a shorter or longer period of rest (3-8 years) germinate and form non-green, subterranean, somewhat tuberous or carrot- shaped, much larger gametophytes, sometimes much convoluted, and these grow to maturity very slowly, taking several years (6-15 years) and nourishing the young sporophytes.
4. In other species, transitional forms occur and these gametophytes are partly subterranean with a green, lobed, aerial portion (crown) bearing the sex organs. Usually, both types of gametophytes are associated with an endophytic fungus forming a mycorrhiza, which is a prominent feature of the gametophyte.
5. The gametophyte of *Lycopodium* is monoecious (homothallic) and numerous sex organs, antheridia and archegonia, are borne either on the crown, or in between its lobes, or on the central cushion in flattened types of the gametophytes.

6. The antheridia vary in size, shape and number of spermatozoids and either project slightly or remain wholly embedded within the gametophytic tissue. There are many spermatozoid mother cells within the single-layered antheridial wall and each gives rise to a biflagellate (rarely three) spermatozoid resembling the spermatozoid of Bryophyta.
7. The archegonia are either short or long and embedded in the tissue of the gametophytes with their necks protruding upwards. At maturity, each archegonium contains an egg cell, a ventral canal cell and 6, sometimes 10-13, canal cells (but only one neck canal cell in shorter archegonium).
8. When the archegonium attains maturity its neck canal cells and ventral canal cell disintegrate forming a passage open to the ovum for the spermatozoids to fertilize. The walls of the antheridium breaks up, the spermatozoids are set free, these are washed to the archegonium and one of them, finding its way through the neck, ultimately fertilizes the ovum.
9. The fertilized ovum soon covers itself with a wall and forms the oospore. With fertilization and formation of oospore, the sporophytic or diploid generation begins.

The New Sporophyte of *Lycopodium:*

• The oospore, by repeated divisions, gives rise to an embryo consisting of a suspensor cell, an absorbing organ called the foot, the stem, a leaf and a root belated in development. From this embryo the young sporophyte gradually develops and this may be supported and nourished by the gametophyte for several years. In some cases several young sporophytes may be borne simultaneously on the same gametophyte.

1.2.2. Life cycle

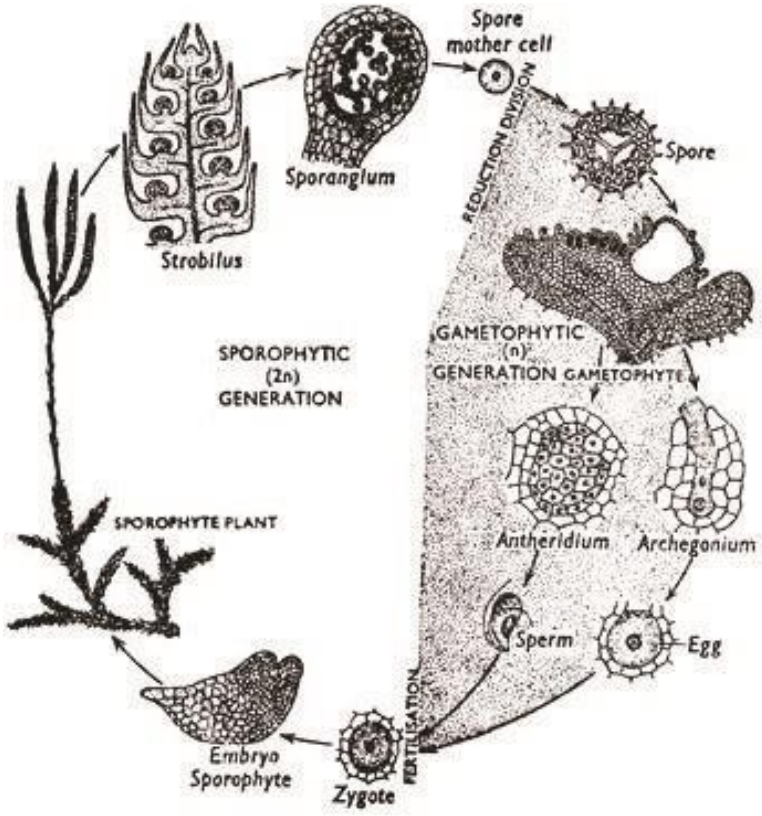

Fig. 1.20. Life cycle of *Lycopodium*