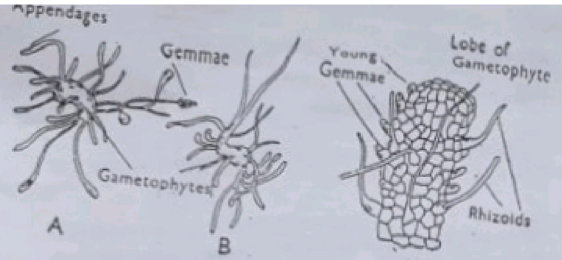


Fig. 48. Lycopodium phlegmaria, showing vegetative propagation by gemmae
A & —Complete gametophytes bearing appendages. In A. gemmae are seen.
C—A tip of the prothallial branch with rhizoids and gemmae.

Sexual Reproduction

Sex Organs

The **gametophyte**, the prothallus, of *Lycopodium*, is **monoecious**. The numerous **antheridia** and **archegonia** are borne on the crown or at the base of its lobes or arms when they are present. The antheridia usually develop first.

Antheridia

The **antheridia** are somewhat indefinite structures varying in size, shape, and number of sperms, even in the same plant. They are either wholly sunken or they project slightly. The mature **antheridium** is a **capsule** consisting of a wall of a single layer of cells enclosing a large number of spermatocytes.

Development of the Antheridium

The antheridium develops from a **single superficial cell**. It it the **antheridial initial**. The **antheridial initial** cell divides transversely into two cells, the **outer cell** and the **inner cell**. The **outer cell** is the **jacket initial** and it ultimately gives rise to the **single-layered** wall of the antheridium. In the jacket initial, only anticlinal divisions occur and there is formed for the antheridium a small one-layered wall. At the apex of the jacket a small triangular cell becomes differentiated. It is the **opercular cell**. The **inner cell**, the **primary androgonial cell** and redivides,

to form a large number of **androgonial cells**, the last generations of which give rise to the **androcytes** or **spermatozoid mother cells**. Metamorphosis of the spermatozoid mother cells into bi-

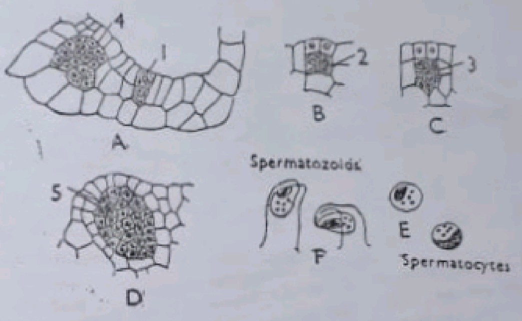


Fig. 49. Lycopodium clavatum
A-D—Stages in the development of the antheridium
E—Spermatocytes
F—Biflagellate spermatozoids.

flagellate spermatozoids is not clearly followed in detail but according to Lang (1899) it is said to follow the same changes as in other Pteridophytes. The **spermatoziods** are **fusiform with flagella at the anterior end**. The biciliate spermatozoids of *Lycopodium* resemble more of the Bryophytes rather than of those of the vascular plants. Again, in the antheridia of *Lycopodium* the *number* of spermatocytes varies a good deal in various species and may be *considerable*.

Archegonia

The **archegonia are sunken**, with only the *necks projecting* from the prothallus.

Development of the Archegonium

The **archegonium**, just like the antheridium, also develops from a **single superfical cell**. It is the **archegonial initial**. The **first division** of an archegonial initial is **transverse** and results in two cells, an outer cell, the **primary cover cell** and an inner

Fig. 35. Lycopodium sp.
In advanced species of Lycopodium, the cones are borne on long erect axes with an intervening zone covered with scale-like leaves.

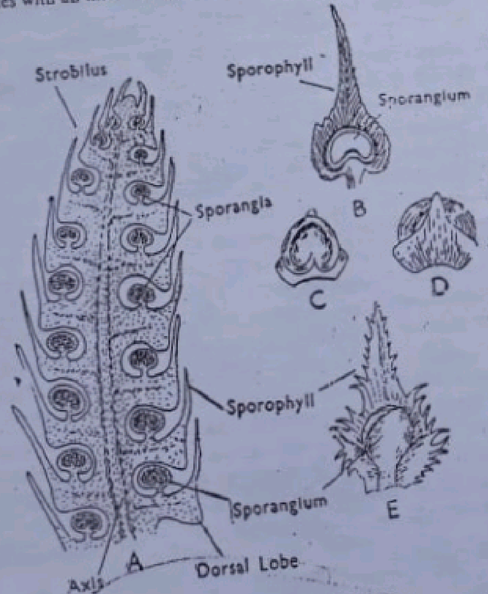


Fig. 36. Lycopodium clavatum
A—V.S. of strobilus. B—E—Sporophyll in various views, bearing a single sporangium on adaxial face.

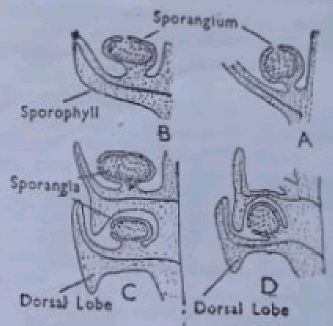


Fig. 37. Locopodium.

In species where there is no cone formation there is no special protection afforded to the sporangia (A and B.)

In species where a definite cone formation occurs the sporangia become protected in different degrees by the overlapping dorsal lobes of the sporophylls (C and D).

L. lucidulum. But in species where a definite cone formation occurs the sporangia become protected in different degrees by the overlapping dorsal lobes of the sporophylls above.

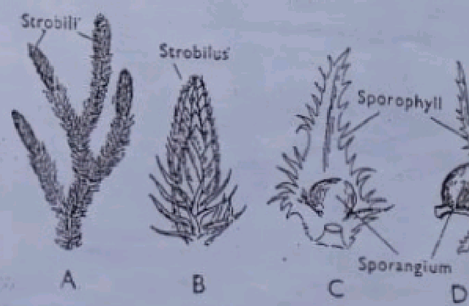


Fig 38. Lycopodium cornuum.
A—Branch apices showing strobili
B—Strobilus
C—Sporophyll with a sporangium, as seen from above.
D—Sporophyll, as seen from the side.

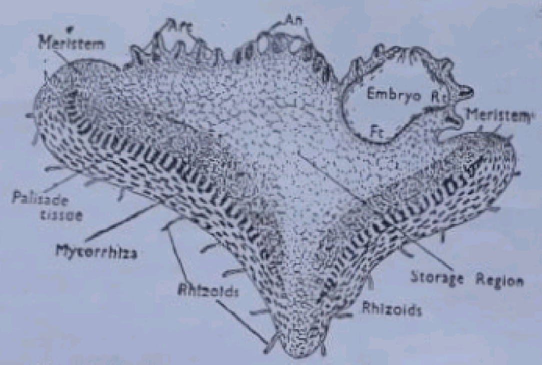


Fig. 46. Median section through the young prothallus of Lycopodium clavatum.
An—Antheridia Arc—Archegonia
Rt—Root Ft—Foot

lived. The other type, which is non-green and **subterranean**, is **tuberous and much larger**, often 1–2 cms, long and wide. In shape, it is, in some species, like a top or a carrot, in others it resembles a disc or a kernal of maize. The germination of spores in this group is long-delayed, in some species from 3 to 5 years or more. The gametophyte grows slowly, requiring several years more, as many as 6 to 15 years, to mature, and is long-lived, living over a period of years after maturity and even nourishing sporophytes for several years.

In both types an **endophytic fungus** is found in association with the tissues, occupying a definite position. Though some species, in the first group, may be without the fungus, the *mycorrhizal condition is characteristic* and, in **subterranean types,** *a prominent feature.*

The gametophytes of *Lycopodium* are not so well-known as are those of ferns and horsetails. They cannot readily be cultivated because in most species the spores do not germinate for a very long time and the gametophytes require years to mature. Gametophytes are not commonly found wild because in most species they are subterranean and those found on surfaces are extremely small.

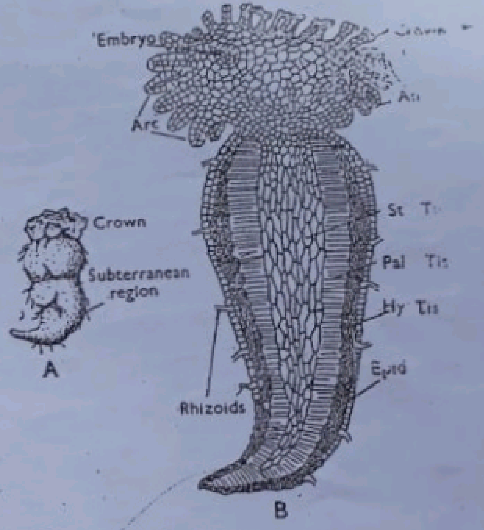


Fig. 47. Gametophytes of Lycopodium complanatum, a subterranean type.
A—A gametophyte entire, showing the aerial crown and the subterranean tuberous region
B—Vertical section of mature gametophyte of L. complanatum
An—Antheridia
Arc—Archegonia
St. Tis—Storage tissue
Pal. Tis—Palisade tissue
Hy. Tis—Hyphal tissue
Epid—Epidermis.

Vegetative Propagation of Gametophyte

In some species of *Lycopodium* vegetative propagation of the gametophyte occurs and it is suggestive of Bryophytes.

The gametophytes of epiphytic species, as in *Lycopodium Phlegmaria*, **Treub** has found that the prothallia sometimes propogate by special buds or gemmae. These reproductive bodies are of two types, minute ones which rest before development and larger ones which grow at once.

Professor **F. O. Bower** has studied in detail the development of the sporangium in a number of representative species of *Lycopodium*. It may develop either from a **single transverse row** of cells in *Lycopodium, selago*, or a **double row**, as in *L. inundatum* or **three rows**, as in *L. clavatum*.

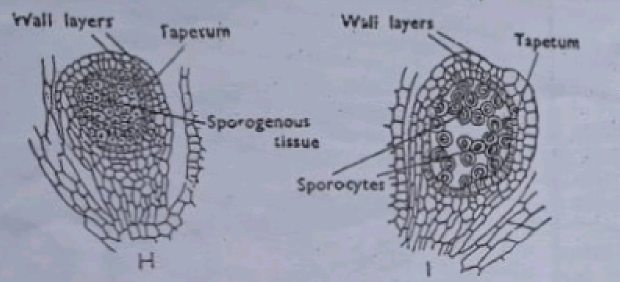


Fig. 41 Lycopodium selago.
H. A developed sporangium in radial section
L. Showing a sporangial wall the tapetum and sporocytes differentiated.

The **simplest type** is represented by *Lycopodium selago*. The
sporangium, in this type, develops from a *single transverse row*
of superficial cell at the base of the sporophyll, on the upper
surface. A radial section, at this stage, shows a single cell but
this is really only one of a series of cells. Each cell of this primary
row divides first into a large central cell and two peripheral cells.
The central cell then divides transversely to form a row of three
cells of which the middle one forms the **archesporium**. At this
stage, the young sporangium consists of a transverse row of arche
sporium covered above by a row of superficial cells called the pri
mary wall cells and below a layer of cells, the **subarchesporia**
cells. The archesporial cells, by rapid division, in various plane
form **spore mother cells** which by reduction division, form
number of **spores**. The **primary wall layer** above the archesp
rium, by pariclinal and anticlinal divisions, forms the **wall of the**
sporangium, enclosing the spores. The wall of the sporangi
finally consists only of **three layers**, of which, the innerm
layer abutting the sporogenous cells, forms the tapetem. T
tapetel cells contribute to the nourishment of the develop

spores. It does not, however disintegrate but remains permanently as part of the sporangial wall. The lower part of the tapetal layer of the sporangium is derived from the sub-archesporial layer.

In *Lycopodium selago* type, the archesporial tissue consists of a single transverse row of cells. In the more **specialised** species like *Lycopodium clavatum*, the primary archesporial cells consist of *three transverse rows* with a corresponding increase in the number of spores in the sporangium. *Lycopodium inundatum* froms an intermediate type, between *Lycopodium selago* and *L. clavatum*, with *two transverse rows* of archesporial cells.

Dehiscence of the sporangium

As the sporangium approaches maturity there is a differentiation of a narrow strip of cells, the **stomium**, at the apical portion of the sporangium, in the outermost layer of the wall. In the cells of the stomium, the inner wall of the cells become thickened and lignified whereas in the other cells the side walls alone become thickened and lignified. As the sporangium dries up, the apex of the sporangium splits along the stomium, into two *clam-shell-like valves* and the spores inside are scattered by wind. The position of the slit varies from apical to low on the other side, the opening is in the position most favourable for spore distribution.

Spores

The sporocytes, in the sporangium, by two successive divisions one of which is a reduction division, form tetrads of spores. The

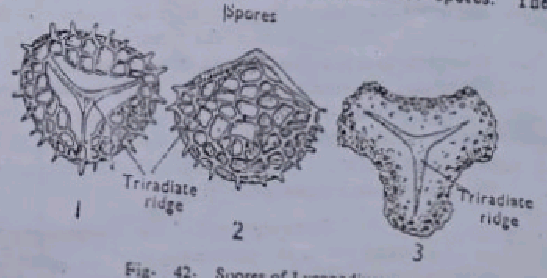


Fig. 42. Spores of Lycopodium
1. L. clavatum, top view.
2. L. complanatum, side view.
3 L. luciduium, top view.

into two cells. The basal cell (b), near the rhizoidal cell, und goes no further divisions, but the upper cell, by two success divisions, produces an apical cell with two cutting faces. Up this five-celled stage the growth of the prothallus is at t expense of the reserve material contained in the mature spo *Further growth of the prothallus is dependent on the symbiotic association and entrance of a Phycomycetous fungus at this stage into the basal cell.* All of the species with colourless gameto-phytes and most of those with chlorophyll have an entrance of this fungus into the basal cell. If there is no entrance of the fungus there is no further development of the gametophyte. Gametophytes developing beyond this early stage have the apical cell cutting off some half a dozen cells and then become replaced by a *group of meristematic cells*. Segments cut off by the apical cell, divide periclinally, and the outer cells thus formed become infected with the symbiotic fungus in the same manner as does the basal cell The apical group of meristematic cells differentiated early produces the major portion of the adult gametophyte,

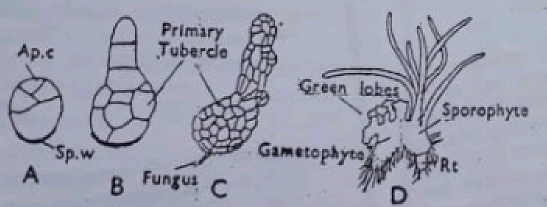


Fig. 44. Stages in the development of the gametophyte in Lycopodium cernuum

Early in development, the gametophyte forms a oval cell mass showing definite apical growth. This preliminary stage is called by Treub a primary tubercle.

D—Gametophyte of the same with sporophyte

Ap.c—Apical cell; Sp.w—Spore wall; Rt-Root

In *Lycopodium cernuum* and some other species, variation may be found in the development of the gametophyte, in some details. The spores, in *L. cernuum*, lack chlorophyll but it develops just before the first cell division occurs, in the germination. The first **cell division is either vertical or horizontal and two cells of equal size are formed.** One of them usually does not divide further but

the other enlarges and divides by an oblique wall and for some time functions as an **apical cell with two cutting faces.** It cuts off cells alternately to the right and left. Each segment then divides by a periclinal wall into a peripheral and a central cell. Within a few weeks the developing gametophyte forms *an oval cell mass* showing definite apical growth. This preliminary stage is called by Treub a **'primary tubercle'**. According to **Treub**, the prothallus does not develop further unless it becomes associated with a symbiotic fungus. Then, from this primary tubercles is developed a cylindrical body with a distinct radial symmetry, which bears the lobes surrounding the apex of the adult thallus.

Adult Gametophyte

There is a great diversity in form and structure of the mature gametophyte in the various species of *Lycopodium*. Attempts have been made to group them into distinct types but the intergrading types make any arbitrary classification impossible.

However, **two distinct types** of gametophytes may be recognised. The first of the two types may be **green, except at base,** and **develops above ground.** They may be cylindrical or ovoid with a lobed or branching top and very *small*, only 2 to 3 mm. long. The spores in this type germinate in a few days and the gametophyte matures quickly, usually in one reason, and is short-

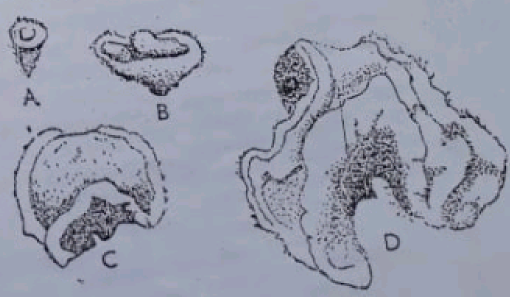


Fig. 45. Gametophyte of Lycopodium clavatum; an aerial type.
A-D – Stages in the development of the gametophyte.
D—Adult Gametophyte.

The **stem**, in the subgenus Urostachya, is either erect or pendent and is never creeping. It may be unbranched or branched. In the latter case, the branching is typically dichotomous and is usually with successive dichotomies at right angles to one another. In the other subgenus Rhopalostachya it is creeping and it bears the upright branches. The branching in this subgenus may be dichotomous in the earlier stages but is always monopodial in the later stages. But it may be possible that the monopodial branching is the result of unequal dichotomy.

The root system of *Lycopodium* is largely adventitious. The first root developed, as the young sporophyte becomes independent of the gametophyte, is short-lived. The roots of older plants are adventitious. In the subgenus Urostachya where stems are erect or pendent the adventitious roots arise primarily from the base of the stem. In the subgenus Rhopalostachya, the adventitious roots are borne along the entire length of the prostrate stem.

The branching of the roots strikingly dichotomous and generally has successive dichotomies at right angles to one another. In some species, the dichotomy is obscure. The roots do not become extensive and no endogenous lateral roots arise as in seed plants. Root hairs, in terrestrial forms, are abundant and persist over a long period.

The leaves are small, simple, sessile, usually with a broad base, and cover the stem closely. A few species may have somewhat larger leaves, at most 25—35 m.m., long. However, they are

A B C D E F

Fig. 28. Leaf form and arrangement is several species of Lycopodium.
A—L. rufescens B—L. mandioccanum
C—L. reflexum D—L. casuarinoides
E—L. cernuum F—L. volubile
(After Engler and Prant)

characteristically **microphyllous** in that they possess on unbranched midvein traversing from the base to the apex. The usual arrangement of the leaves is in close spirals (*L. clavatum* and *L. annotinum*) but they may be also in opposite pairs or somewhat irregular. Even where the arrangement is symmetrical it may vary from one part of the plant to another.

In most species, all the foliage leaves are alike in size but in a few, as in *Lycopodium volubile*, the leaves may be dimorphic and of two sizes, closely imbricated and arranged in definite vertical rows, like *Selaginella*.

Leaves of *Lycopodium* are **without a ligule**, so characteristic of the ligulate lycopods.

In some species, the foliage leaves bear each a sporangium, on the upper or adaxial face, near the base. Those leaves which bear the sporangia are known as the **sporophylls**. In those species where every leaf bears a sporangium the whole plant is likened to be a **strobilus**. In others, the foliage leaves and the sporophylls are distinct and separate and the latter are usuall/ restriited to the apex of the stem to form a **strobilus** or a cone. In those, where the sporophylls form definite strobili, they differ usually from the foliage leaves, generally in being smaller in size and paler in colour.

Internal Structure

STEM

The stem apex of *Lycopodium* grows by a mass of meristematice cells whereas in the case of most other Pteridophytes the stem grows only by a single well-defined apical cell. The apical meristem, an internode or two below, becomes differentiated into the three regions, the **epidermis**, the cortex and the stele in the mature stem.

Epidermis

The epidermis is single layered and covers the surface of the stem. Stomata, similar to those in the leaf, occur in the epidermis.

Cortex

The cortex is multilayered and varies greatly in its relative radial thickness from species to species. In some species, its radial thickness is several times that of the stele; in others, it may be of spores are very small, 0.03 mm., to 0.05 mm., in diameter, tetrahedral, i. e., four-sided like a tetrahedron, but with the base rounded or even hemispherical. The spores are light, with thin walls, which are smooth or pitted, or with honeycomb or net-like thickenings. Thickenings are most prominent on the rounded base and may be absent on the sides. Weak, **triradiate ridges** separate the three flat surfaces. Chlorophyll may be present in small amount.

Gametophyte

The spore germinates and produces the **gametophyte**, also called the **prothallus**.

Spores, in some species of *Lycopodium*, as *Lycopodium cernuum*, *L. inundatum*, etc., may begin germination within a few days after they are shed. The gametophyte, in these species, matures usually in one season and is also short-lived. But in other species, as *Lycopodium clavatum*, etc., the germination of the spore does not begin until after the spores are three to eight years old. Development of the gametophyte to the point where there are mature sexual organs, may correspondingly take 6 to 15 years and is usually longlived. In *Lycopodium selago* the first signs of germination were first observed only after three to five years. In this species and in *L. clavatum*, the first gametangia were found after six years and 12 to 15 years elapsed before mature gametangia were developed.

Development of the Gametophyte

For many years, the gametophyte of *Lycopodium* was practically unknown, and it was not until 1834 that the first comprehensive account was published by **Treub**. **Treub's** first paper described the gametophyte of *L. cernuum*, a common tropical species. In1878 an important memoir on the gametophytes of European Lycopodiaceae was published by **Bruchmann**. These studies of **Treub** and **Bruchmann** have been followed later by **Spessard** on some American species and by **Holloway** on several New Zealand ones.

The course of development of the gametophyte from the spore may vary in details in different species but the followi...

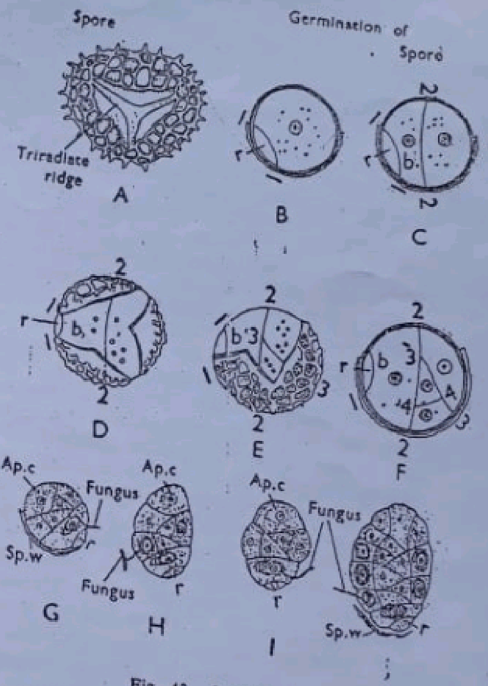


Fig. 43. Lycopodium

A - Spore
B-J—Stages in the development of the gametophyte
r—rhizoidal cell
b—basal cell
Ap-c—Apical cell
Sp. w—Spore wall

The **first division** of th...

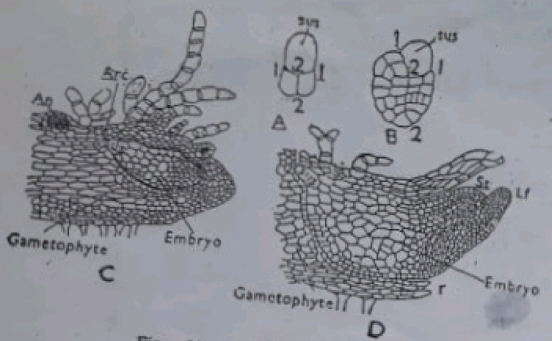


Fig. 54. Lycopodium clavatum
Development of the embryo.
A & B-The numbers indicate the sequence of divisions
C - Embryo enlarging downward and laterally in gametophyte
D - Embryo breaking through gametophyte laterally and upward
Sus - Suspensor An - Antheridium Arc . Archegonium St - Stem.
(After Bruchmann)

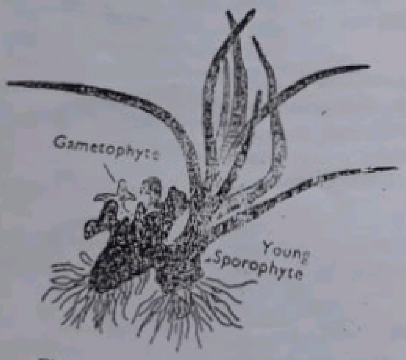
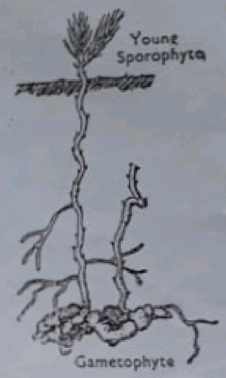


Fig. 55. Lycopodium cernuum
Gametophyte with young sporophyte
(After Treub)

development of *L. clavatum* etc. Now, in the further development of the embryo, a variation begins. The **two distal segments of the octant embryo develop into a massive globose structure, which Treub calls, a "protocorm".** It grows through the gametophyte, becomes green and develops rhizoids on its lower surface. From the upper surface of the protocorm arise a few to many, erect conical outgrowths, the **protophylls,** which are leaf-like in function and have stomata in their epidermis. There is fungus associated with it as in the gametophyte. No vascular tissue is present. After forming an indefinite number of protophyllus, the protocorm differentiates a meristematic region which develops into the stem of the adult plant, with normal leaves and adventitious roots. The protocorm is connected to the gametophyte by the foot The primary root develops from the surface of the



Gametphyte
Fig. 56. Lycopodium annotinum
Old prothallus with the young sporophyte projecting beyond the ground level.

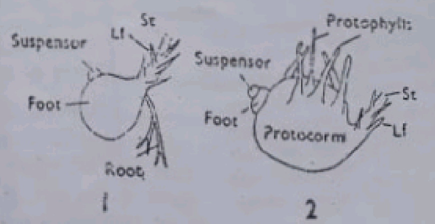


Fig. 57. Lycopodium
1. Embryo of species with subterranean gametophytes with a large foot attached directly to stem base.
2. Embryo of species with green surface-living gametophytes with small foot and the protocorm.
St—Stem. Lf—Leaf.

the surface of the ground, with erect leafy branches arising from the rhizome Some species are semi-erect with a short prortrate base and erect shoots as in *Lycopodium selago.* The ascending species, as in *Lycopodium volubile*, scramble over shrubs twining to some extent. *Lycopodium cernuum*, a species which occurs in all warmer parts of the world, has upright shoots which often 4 or 5ft. high, and form dense thickest. While most of the species are terrestrial, a good many species, as *Lycopodium phlegmaria* and *Lycopodium squarrosum* are epiphytic.

Prietzel (1900) divides the genus *Lycopodinm* into two sub-genera, based on the general habit, the **Urostachya** and **Rhopalostachya.** He includes all species without a creeping rhizome either terrestrial and erect or epiphytic and pendent, such as *Lycopodium selago, L. luciludum* and *L. phlegmaria*, in the former.

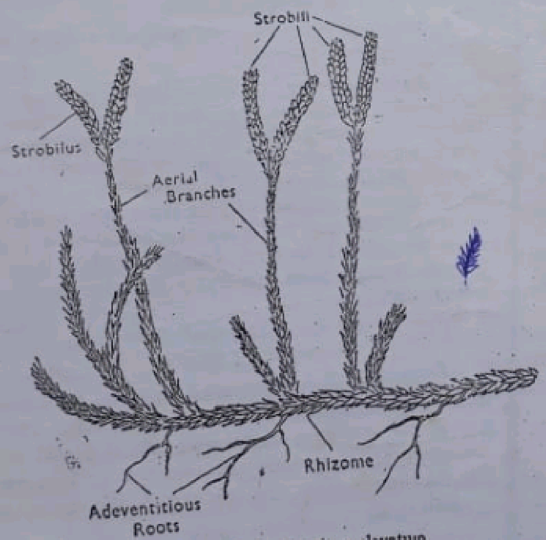


Fig. 26. Lycopodium clavatum

A species with a prostrate rhizome bearing erect aerial branches terminating in strobili, in some of the branches.

In the latter are included species which are creeping and prostrate with upright branches arising from prostrate stems as *Lycopodium cernuum, L. inundatum. etc.*

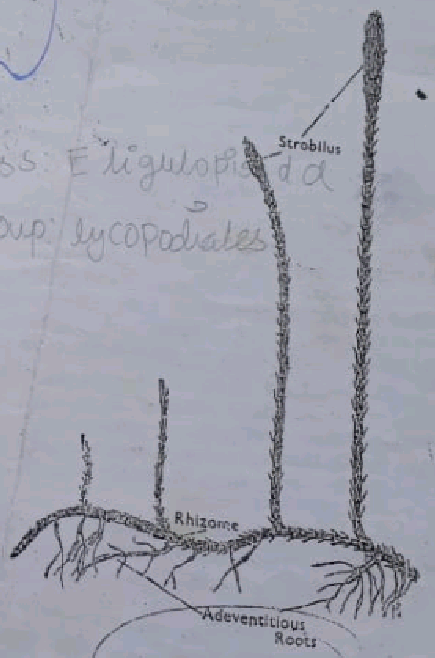


Fig. 27. Lycopodium inundatum.

A species included in the subgenus Rhopalostachya with a creeping rhizome bearing erect branches.

External Structure

Lycopodium plant is the **Sporophyte** and is differentiated into **root, stem and leaf.**

protocorm exogenously unlike the later ones. The wh
corm separates from the prothallus as soon as the first
are formed.

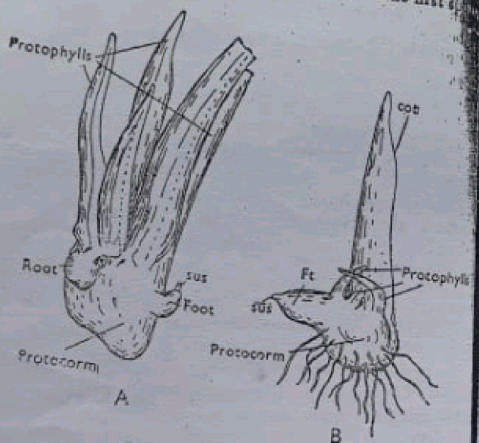


Fig. 58. *Lycopodium cernuum*
A & B-Protocorm Cot-Cotyledon
Sus-Suspensor Ft - Foot
(After Treub)

The Protocorm Theory

The **protocorm** has been *variously interpreted*. Around protocorm, a theory known as "**Protocorm Theory**" has sprung

Treub (1890) regards the protocorm as a *structure of antiquity* and it is a *phylogenetic precursor of stem*. Others, **Bower** (1908) and **Holloway** (1910) hold that it is a *late phylog tic specialisation* and represents a "*gouty interlude*" in the e ontogeny of the sporophyte.

This protocorm is unlike a typical young sporophyte in lack of roots and of vascular tissue and suggests a gametoph in shape and appearance, in its parenchymatous mass

its rhizoids and endophytic fungus. Though it bears green af-like lobes, the "prophylls" or "protophylls", these are indefi- te in position and of the simplest structure without vascular ssue; they resemble the lobes of prothallium rather than true aves. The young plant at this stage, though a sporophyte morphologically, looks and lives like a gametophyte. After the protocorm has lived for sometime, nourished, in part, by the foot embedded in the gametophyte, a growing point arises laterally, or possibly internally, and a stem apex develops bearing true leaves and a root. It is looked upon as a primitive sort of sporophyte, as yet rootless, without conducting tissue and partly dependent upon the gametophyte, the *evolutionary forerunner of the leafy vascular sporophyte*.

The "**Protocorm Theory**" which assumes in the protocorm a step in the origin of the independent sporophyte of the Pteridophytes find an evidence of support in *Phylloglossum*, for, in this small and simple clubmoss, there is seen a permanent protocorm stage. In other words, this plant is regarded still to be in the most primitive stage of sporophyte independence and complexity. According to this theory, *Phylloglossum* is regarded as a permanently embroynic lycopod.

In opposition to the view of **Treub** (1890), where the protocorm is considered as a structure of great antiquity and of phylogenetic significance, **Goebel** (1904) and **Bower** (1908) contest this view and state that the protocorm is to be looked upon merely as an organ of perennation having only a physiological significance. **Holloway** (1917-20), in researches on the prothalli of New Zealand species of the genus *Lycopodium*, observes that this organ is of great use in perennation and also is capable of dividing dichotomously and can bear bulbils as are found on the sporophyte of *Lycopodium*. He comes to the conclusion that the organ may not be an organ of mere physiological importance but also of phylogenetic significance.

Confirmation of **Treub's** view that the protocorm is a structure of great antiquity, according to **T. S. Mahabale** (1946), comes from the discovery of the Psilophytales by Kidston and Lang (1917). In the morphology of these primitive land plants there is a swollen portion at the base, specially in *Hornea*

Lignieri, which bears a close resembalance to the protocorm of lycopods Mahabale observes "This means that we are able to telescope the existence of the protocorm of modern lycopods in the Devonian plants, a period of not less than 300 million of years". He suggests that this protocorm is a vestigial structure of great antiquity. He adds further that it is quite possible that this structure might have arisen as an organ *sui generis* which might have had in the remote past adapted itself secondarily to a function of perennation but for which it has not become well suited. Hence, in course of time, it may have become partly vestigial and partly useful as Holloway (1910) thinks. Eames (1936) argues that the protocorm is lacking in the more primitive species of *Lycopodium* where it should be found if it is of any significance. It is merely a resting stage in embryonic development related to environmental conditions. The analogy with *Phylloglossum* does not apply because *Phylloglossum* is a reduced plant and the fact that it possesses vascular tissue throughout, that it bears roots, and that its leaves having vascular traces and veins are not prophylls, is sufficient proof that it is not a permanent protocorm. The "Protocorm Theory" according to Eames, is now merely of historical interest only.

Hornea Lignieri

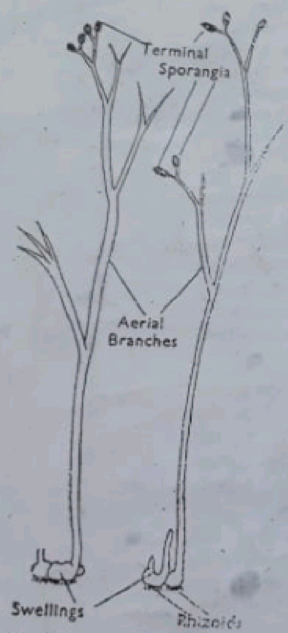


Fig. 59. Hornea Lignieri
Shows a swollen base that bears a close resemblance to the protocorm of lycopods.

Life cycle

Lycopodium, with about 180 species, is the largest genus, in the Lycopodiaceae.

Sporophyte

All species of *Lycopodium* are herbaceous perennials. The terrestrial species may be erect or prostrate with creeping rhizome on or below the surface of the ground. A few are epiphytes with pendent branches. The sporophyte is differentiated into root, stem and leaf. The roots are adventitious, the stem is dichotomously branched, and the leaves are microphyllous with an unbranched midvein.

Lycopodium is homosporous and the spores are produced in sporangia borne singly on the adaxial face of the leaf at the base. The sporophylls may not differ in some from ordinary vegetative leaves, or they may be modified in size and colour. Every leaf may bear a sporangium and be a sporophyll in some species but in others the sporophylls may aggregate at the apices of main stem or its branches to form definite strobili or cones.

The sporangia, in *Lycopodium*, are relatively large, kidney-shaped and are borne singly on the adaxial face of the leaves near their bases or in their axils. The development of the sporangium is eusporangiate.

Lycopodium is homosporous and produces only one kind of sporangia and one kind of spores. The spores are very small 00.3 m m. to 00.5 m. m. in diameter, tetrahedral but rounded or hemispherical at the base and with weak triradiate ridges at the top.

Gametophyte

The spores, on liberation, germinate to give rise to the gametophyte, also called the prothallus. Spores, in some species, as *Lycopodium cernuum* and *L. inundatum*, may begin germination within a few days after they are shed. The gametophyte, in these species, matures usually quickly, in one season, and also is short-lived. But in other species, as *Lycopodium clavatum*, etc., the germination of the spore does not begin until after the spores are three to eight years old. Development of the gametophyte to the

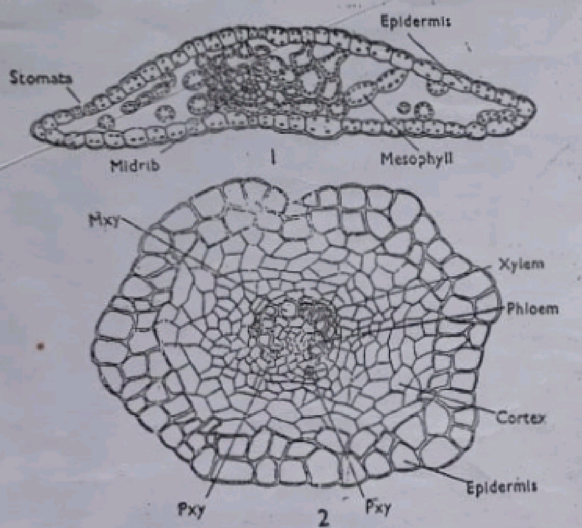


Fig. 33. Lycopodium.
1. Lycopodium volubile : T.S. of Leaf.
2. Lycopodium serratum : T.S. of Root.

Thus, defferentiated from the apical meristem, the matur root shows the three regions **epidermis, cortex** and the stele typical of other vascular plants.

Epidermis

The epidermis, that covers the surface of the root, is sing layered. It gives rise to root hairs. The root hairs are peculi in that they *occur in pairs*. The occurrence of the root hairs in pairs results from the fact that hair initials are formed by oblique or anticlinal division of a young epidermal cell.

Cortex

The cortex is several cells in thickness and often the ou layers become heavily sclerified as the root becomes old.

Stele

The roots of *Lycopodium* may be, in some instances, **monarch** with the protoxylem in one mass; in others, it may be either **diarch** with two protoxylem masses, or *hexarch to decarch* with six to ten radial xylem plates, sometimes joined at the centre of the stele. But most roots are **diarch** and have a C-, or U-shaped mass of xylem, with the protoxylem at the tips of the curved xylem mass with intervening metaxylem. Diarch roots have generally one mass of phloem that lies between the points of C or U.

Leaf

The leaves of all species of *Lycopodium* are sessile and small and are typically **microphyllous** in the sense that they contain each an unbranched **Midvein** traversing from the base to the apex.

A **mature leaf** shows the three regions, the **epidermis, mesophyll** and the median **midvein**.

Epidermis

The **epidermis** is single-layered and there is no difference between the upper and lower epidermis. The epidermal cells are closely arranged without intercellular spaces. They contain chloroplasts, typical of shade plants. Stomata occur in the epidermis generally equally distributed on both the surfaces but in dimorphic leaves they may be restricted to one face only.

Mesophyll

The **mesophyll** is not differentiated into the palisade and the spongy tissues but consists of uniform parenchymatous cells which may be angular in outline without intercellular space or they may be rounded enclosing intercellular spaces. The mesophyll cells possess chloroplasts.

Midvein

The leaf possesses a single unbranched median vein, the **midvein**, in the centre of the leaf embedded within the mesophyll. It is concentric having a central strand of narrow annular and spiral tracheids surrounded by a phloem composed of parenchyma with scattered narrow sieve tubes. The vein may be ensheathed by an endodermis or it may be lacking.

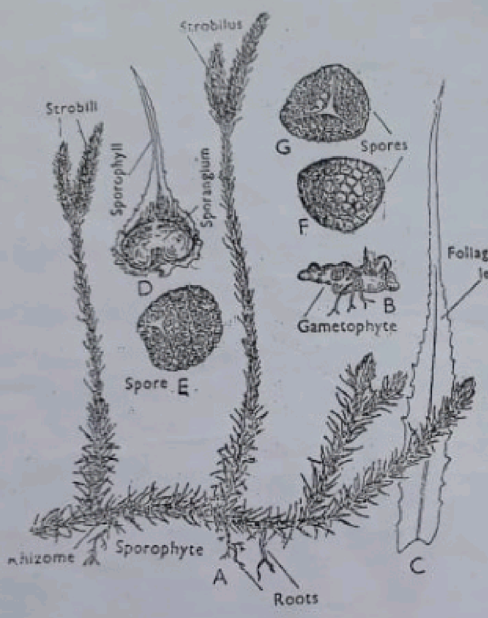


Fig. 39. Locopodium clavatum.

A—A part of the sporophyte. B—Prothallus of an allied species. C—Foliage leaf. D—Sporophyll with sporangium. E, F, & C-Spores

Sporangia

The Sporangia are relatively large, 1.0 to 2.5 mm., in diameter, reni form, or in some species spherical, yellowish when mature and attached by a short stalk or pad-like base to the sporophyll.

Lycopodium is homospororous and produces only one kind of sporangia and one kind of spores. A ripe **sporangium** consists of a short multicellular stalk and capsule consisting of a wall of

three layers in thickness, the innermost of which is transformed into a tapetum. The sporangium encloses inside numerous small spores.

Development of the Sporangium

In *Lycopodium*, a *single sporangium* develops *adaxially* near the base of the leaf. The sporangial initials, which are superficial, may form on the upper surface of the leaf near the base of it. The sporangial initials, which are superficial, may form on the upper surface of the leaf near the base or in fome species may be differentiated a little above the axil, on the stem. During growth, the position of the sporangium initials may be shifted from leaf to the axis or form the axis to the leaf. The mature *sporangium* may therefore be *foliar* or *axillary* in position.

The development of the sporangium, in *Lycopodium*, is **eusporangiate**. The method of sporangium formation, where a *group of cells, superficial in position*, by periclinal division, forms an *inner and an outer layers of cells*, the *inner forming the sporogenous cells* and *outer, the sterile wall of the sporangium*, is called the eusporangiate method.

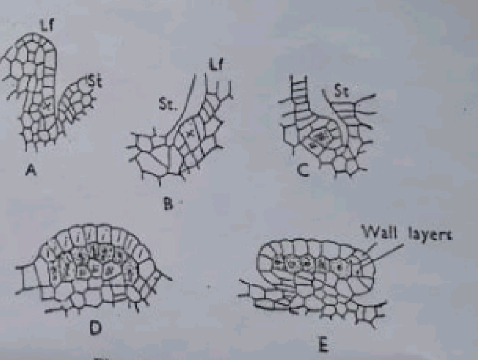


Fig. 40. Lycopodium selago.

A- E. Developmental stages of the sporangium.
A, B and C. Radial sections of young sporangium showing a single transverse row of sporangial initials.
D. Tangential section of the same.
E. A sporangium in transverse secti-

protocorm exogenously unlike the later ones. The wh
corm separates from the prothallus as soon as the first
are formed.

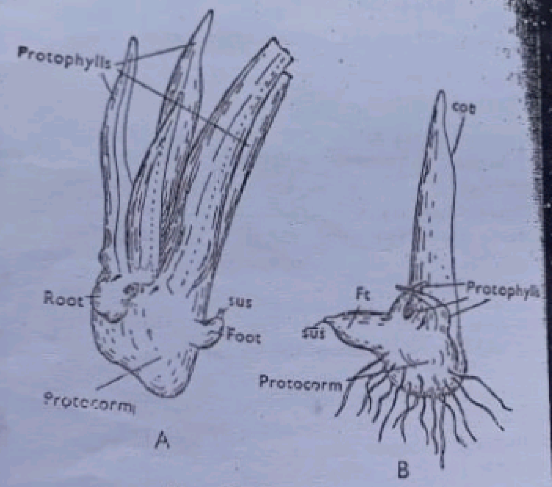


Fig. 58. Lycopodium cernuum

A & B-Protocorm Cot-Cotyledon
Sus-Suspensor Ft - Foot

(After Treub)

The Protocorm Theory

The **protocorm** has been *variously interpreted*. Around protocorm, a theory known as "**Protocorm Theory**" has sprung

Treub (1890) regards the protocorm as a *structure of g antiquity* and it is a *phylogenetic precursor of stem*. Others, **Bower** (1908) and **Holloway** (1910) hold that it is a *late phylog tic specialisation* and represents a "*gouty interlude*" in the e ontogeny of the sporophyte.

This protocorm is unlike a typical young sporophyte in lack of roots and of vascular tissue and suggests a gametoph in shape and appearance, in its parenchymatous mass o

its rhizoids and endophytic fungus. Though it bears green af-like lobes, the "prophylls" or "protophylls", these are indefi- te in position and of the simplest structure without vascular ue; they resemble the lobes of prothallium rather than true aves. The young plant at this stage, though a sporophyte orphologically, looks and lives like a gametophyte. After the rotocorm has lived for sometime, nourished, in part, by the foot embedded in the gametophyte, a growing point arises laterally, or possibly internally, and a stem apex develops bearing true leaves and a root. It is looked upon as a primitive sort of sporophyte, as yet rootless, without conducting tissue and partly dependent upon the gametophyte, the *evolutionary forerunner of the leafy vascular sporophyte.*

The "**Protocorm Theory**" which assumes in the protocorm a step in the origin of the independent sporophyte of the Pterido- phytes find an evidence of support in *Phylloglossum*, for, in this small and simple clubmoss, there is seen a permanent protocorm stage. In other words, this plant is regarded still to be in the most primitive stage of sporophyte independence and complexity. According to this theory, *Phylloglossum* is regarded as a perma- nently embroynic lycopod.

In opposition to the view of **Treub** (1890), where the proto- corm is considered as a structure of great antiquity and of phylo- genetic significance, **Goebel** (1904) and **Bower** (1908) contest this view and state that the protocorm is to be looked upon merely as an organ of perennation having only a physiological signifi- cance **Holloway** (1917-20), in researches on the prothalli of New Zealand species of the genus *Lycopodium*, observes that this organ is of great use in perennation and also is capable of dividing dichotomously and can bear bulbils as are found on the sporo- phyte of *Lycopodium*. He comes to the conclusion that the organ may not be an organ of mere physiological importance but also of phylogenetic significance.

Confirmation of **Treub's** view that the protocorm is a stru- cture of great antiquity, according to **T. S. Mahabale** (1946), comes from the discovery of the Psilophytales by **Kidston** and **Lang** (1917). In the morphology of these primitive land plants there is a swollen portion at the base, specially in *Hornea*

... (or the upper cell next to ... neck) though, it may enlarge to some extent,

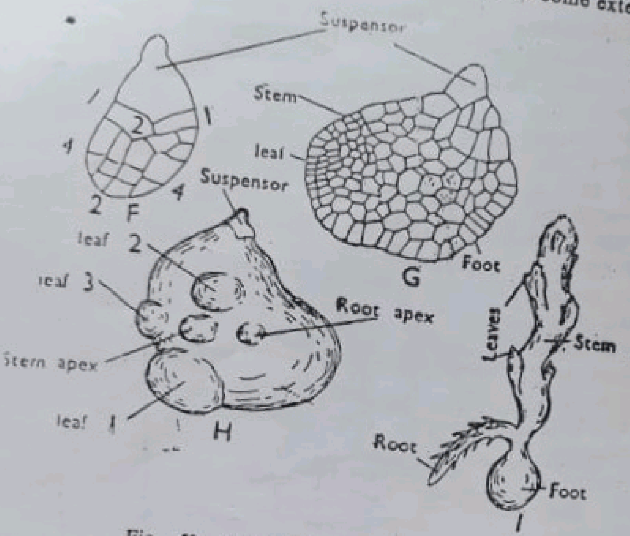


Fig. 52. Lycopodium annotinum
Showing developmental stages of the embryo (After Bruchmann).

usually *remains undivided* or it *may divide transversely* to form a two or three-celled **suspensor**, a *structure characteristic of Lycopodineae.* The lower cell or the **hypobasal cell**, is the **embryonic cell**, because it develops eventually the **embryo pro-**...r.

The **hypobasal cell**, the **embryonal cell**, first divides somewhat obliquely or vertically and this is followed by another vertical division of the two daughter cells thus formed. Transverse division of each of these cells results in an **8-celled embryo**. The embryo now consists of nine cells or **1+8 cells. At this stage** quadrants are obscurely evident in the body of the embryo ...r development shows that these quadrants seem to bear ...irly definite relation to the organs of the young plant.

...o **quadrants** next to the suspensor enlarge laterally and ...ard into the tissue of the gametophyte and form a sub...al foot, an organ for the absorption of the food from the ...ophyte. The two **lower quadrants** give rise to the **stem**, and ...and the root) of the sporophyte. Of the two quadrants, one ... the **stem** and the other forms the first **leaf or cotyledon**.

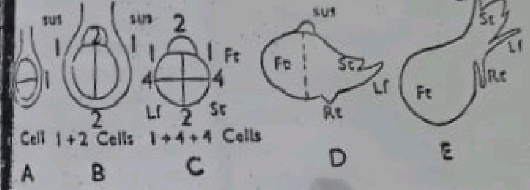


Fig. 53. Lycopodium
Showing stages of embryo development in subterranean species
Sus-Suspensor Ft-Foot Rt-Root
Lf - Leaf St - Stem

...e is no **segment for the root** and *it is developed* **later** *from* ...*same quadrant as the leaf.* The stem and the leaf segments enlarge ...ther laterally and upward. After a time, the first root appears ...n the base of the enlarged leaf quadrant. The stem grows ...idly upward with other leaves developing and the root ...nches but does not become extensive.

The first root and the first stem are short-lived in some ...cies, new roots arising adventitiously and endogenous in ...gin. A horizontal stem of the adult plant arises from the base ...he erect one. The whole process of development is very slow ...several years may elapse before the young sporophyte reaches ...surface of the soil.

In species, with **green prothallia**, as in *Lycopodium cernuum* ...*L. laterale*, etc., an important variation occurs, in embryo ...elopment.

The early development of the embryo upto the **9-celled stage**, ...1 (sus) +8 (octant) stage, s similar to that as in the embryo

The root system of lycopodium

REPRODUCTION

Vegetative Propagation of the Sporophyte

Reproduction, by vegetative means, is of much frequence, in the various species of *Lycopodium*, so much so, often stands of considerable extent form from one original individual.

The several methods of vegetative reproduction are sa follows :

1. In species with creeping rhizo mes, vegetative propagation occurs by progressive growth, and d eath of the older parts, and new plants are formed.

2. In *Lycopodium inundatum*, during winter or the beginning of the season's growth, the entire plant dies except the tip of the rhizome which functions as a resting bud. At the return of the favourable season, the resting buds resume growth and develop into new plants.

3. In tropical epiphytic species, fragments of the plant body, when become detached, produce new plants rather freely.

4. In some species of *Lycopodium*, such as *Lycopodium selago*, special buds or *gemmae*, are formed. These gemmae are short branches formed in the axils of leaves. They consist of a short axis bearing several thickened fleshy leaves. Before becoming detached a root is formed at the base. When the gemma becomes detached and comes into contact with the ground, the root quickly fastens the young plant to the substratum.

5. In *Lycopodium cernuum and L ramulosum*, Holloway (1917) has recorded the formation of *root tubercles* produced from the cortical cells of the root. These root tubercles, when detached produce new plants.

6. The young protocorm of some species, as in *Lycopodium laterale* and *L ramulosum*, by budding and branching, may give rise to new plants.

Asexual Reproduction

Lycopodium plant is the sporophyte and reproduces asexually by the formation of **spores** in sporangia. *Lycopodium* is homosporous.

The sporangia, in *Lycopodium*, are relatively large, kidney shaped and are borne singly on the upper or adaxial face of the leaves near the base, in the leaf axil or on the stem just above the leaf.

Sporophylls

The leaf that bears the sporangium is the **sporophyll**. The sporophylls differ a great deal in the various species. In a few species, as in *Lycopodium selago*, all the leaves of the mature plant bear the sporangia. That is, every leaf is a sporophyll. Then the entire plant is likened to be a **strobilus**. Foliage leaves and sporophylls of most species in the subgenus Urostachya are approximately of the same size and both are green. In *Lycopodium* selago and *L. lucidulum*, the sporophylls are like the sterile leaves or differ from them only in their somewhat smaller size. In such species the fertile and sterile regions alternate on the stem, one of each developing annually and further elongation of the shoot is not effected. Sporophylls of this type continue to serve as photosynthetic organs after the spores are shed. An advance on this condition is seen in the subgenus Rhopalostachya where the sporophylls aggregated at the apices of the main stem or its branches into definite **strobili** or cones. In those cone-bearing species the leaves may pass through transition forms into sporophylls. In other more advanced species, as in *Lycopodium carolinum* etc., the cones are borne on long erect ... with an intervening zone covered with reduced scale-like leaves. The sporophyllus in the latter cases are distinctly reproductive in function and the sporangia in such cones are obviously more favourably placed for spore distribution by wind.

In species were there is no cone formation there is no special protection afforded to the sporangia as in *Lycopodium selago* and

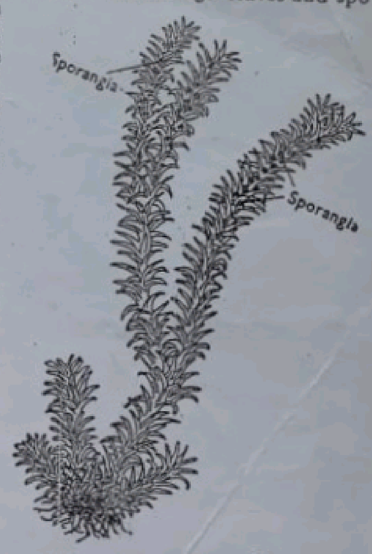


Fig. 34 Lycopodium lucidulum, a species in which the sporophylls differ little from vegetative leaves and the fertile and sterile regions alternate.

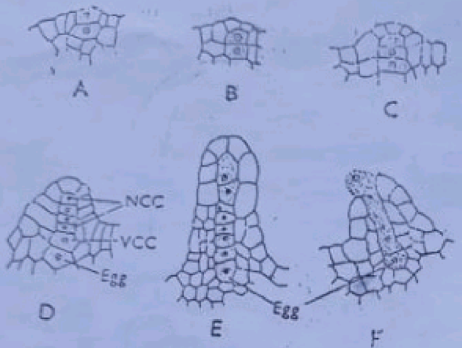


Fig. 50. Lycopodium clavatum
A-F—Stages in the development of archegonium (After Bruchmann)

cell, the central cell. The **primary cover cell** gives rise to the neck of the archegonium and the **inner cell** to the **axial row**.

The inner cell divides periclinally into a **primary canal cell** and a **primary ventral cell**. The **primary ventral cell** may divide transversely into two to form a **ventral canal** cell and an egg or it may enlarge and directly function as an egg. The **primary canal** cell, by transverse divisions, forms a variable number of **neck canal cells**. In *Lycopodium cernuum*, the neck is short and the neck canal cells may be not more than *two or three*. In *Lycopodium selago* the neck canal cells may be *seven*. In *Lycopodium complanatum*, the neck canal cells may be as many as *sixteen*. In this respect the arche-

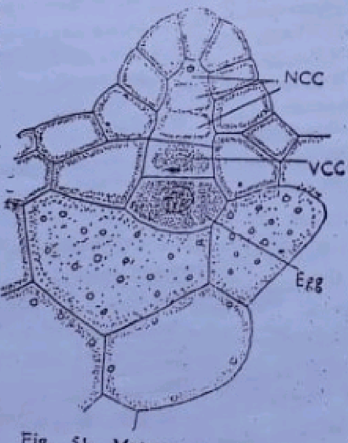


Fig. 51. Mature archegonium of Lycopodium cernuum, where there are only three neck canal cells

onium of this species has no counterpart anywhere among the teridophyta and it is comparable only to the mosses.

As the axial row is developing, the **primary cover cell** undergoes two successive anticlinal divisions at right angles to each other, to form four **neck initials**. Transverse divisions of the neck initials result in a **neck 3–4 cells in height** and typically composed **four vertical rows of cells**.

Thus, the **mature archegonium**, in *Lycopodium*, consists of an **axial row** consisting of an **egg, ventral canal**, and a **varying number of neck canal cells**, and a **neck** projecting above the prothallus, 3–4 cells in height, and composed of **4 vertical rows of cells**.

Fertilisation

As the archegonium is mature the neck cells at the tip of the archegonium separate and the neck canal cells and the ventral canal cell disintegrate leaving a passage free for the spermatozoids to enter the archegonium to fuse with the egg. The opercular cell, in the antheridium, also breaks open, in a ripe antheridium and the spermatozoids are set free, which may swim or be washed to the archegonium. They enter the archegonium and one of them fuses with the egg in the venter andfertilisation takes place. The fertilised egg is the **oospore** and by division it gives rise to the **sporophyte**.

Embryo and its Development

Treub, Bruchmann and Holloway have made most important investigations in the development of the several species of *Lycopodium*. All the species examined show a uniform development in the earlier stages but show a good deal of difference in later embryonic development.

Embryo development, in species with **subterranean prothallia**, as in *Lycopodium clavatum* and *L. annotinum*, is essentially as follows :—

The fertilised egg surrounds itself with a wall. In divides first by a **transverse** wall, transverse to the long axis of the