Psilotum:

Distribution of Psilotum:

Though several species have been reported in Psilotum, all of them usually fall into two well defined species, viz., P. nudum (P. triquertum) and P.flaccidum (P. complanatum). The earlier reports of the existence of several species is probably due to the polymorphic nature of the sporophyte.

As has already been pointed out, Psilotum is distributed both in the tropics and the subtropics. Of the two species, P. nudum seems to enjoy a wider distribution being found in all the warmer regions of the world, including India.

In India it is found in Bengal, Assam and the hilly districts of Madhya Pradesh, Himachal Pradesh and Karnataka. P. nudum is also cultivated as a curiosity in botanical gardens. P. flaccidum is somewhat uncommon and is reported from tropical islands like Jamaica, Java etc., besides the Malayan peninsula and Mexico.

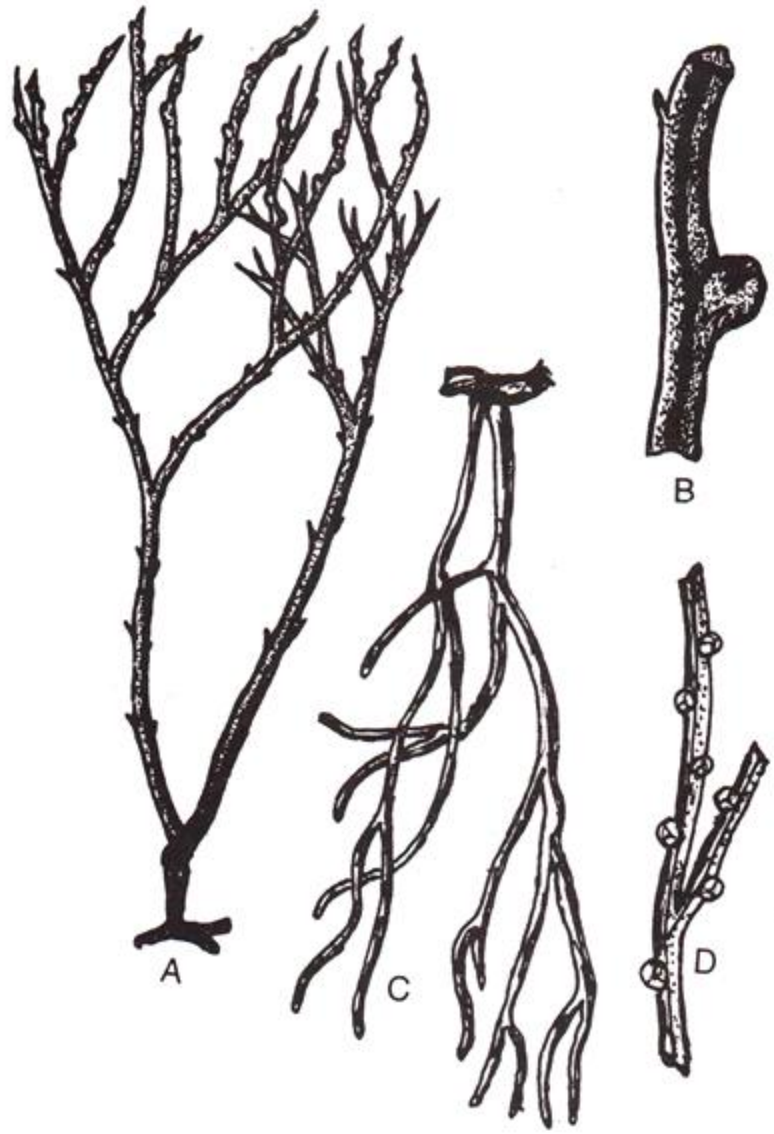

Fig. 19. *Psilotum* : Habit of *Psilotum nudum* (A) and a Part of the Shoot Bearing Synangia (B); Habit of *Psilotum flaccidum* (C) and a part of the Shoot bearing Synangia (D)

In their habitat they are either terrestrial or epiphytic. While P. nudum is predominantly terrestrial, P. flaccidum is mainly epiphytic growing in the humus packets of trees.

Sporophyte of Psilotum:
Morphology:
The plant body of Psilotum is differentiated into two parts viz., a horizontal underground rhizome and an erect aerial shoot. The rhizome is brownish in colour and dichotomously branched. There are

no roots. The rhizome is studded with a number of long, fine, thread like rhizoids. According to Bierhorst (1954 or 1958), the branching of the rhizome is irregular.

Some of the branches of the rhizome grow up and constitute the erect (P. nudum) or pendulous (P. flaccidum) shoot system. The aerial shoots are 20-75 cm long and are usually ribbed and multi-angular. The ultimate branches however are triquertous.

While the above description holds good for P. nudum, in P. flaccidum the base of the aerial shoot is triquertous while the tips are flattened. Unlike the rhizome, the aerial shoots are regularly dichotomously branched and are deep green in colour indicating their photosynthetic activity.

Here and there on the aerial shoot are found a number of scales or appendages which are often called leaves. These are of two types viz., sterile and fertile.

The sterile ones are found all along the length of the aerial shoot while the fertile ones are generally restricted to the upper portions and bear in their axils a trilobed spore bearing structure which is often called a Synangium. The leaves whether fertile or sterile are devoid of any vasculature and could be regarded as only emergences.

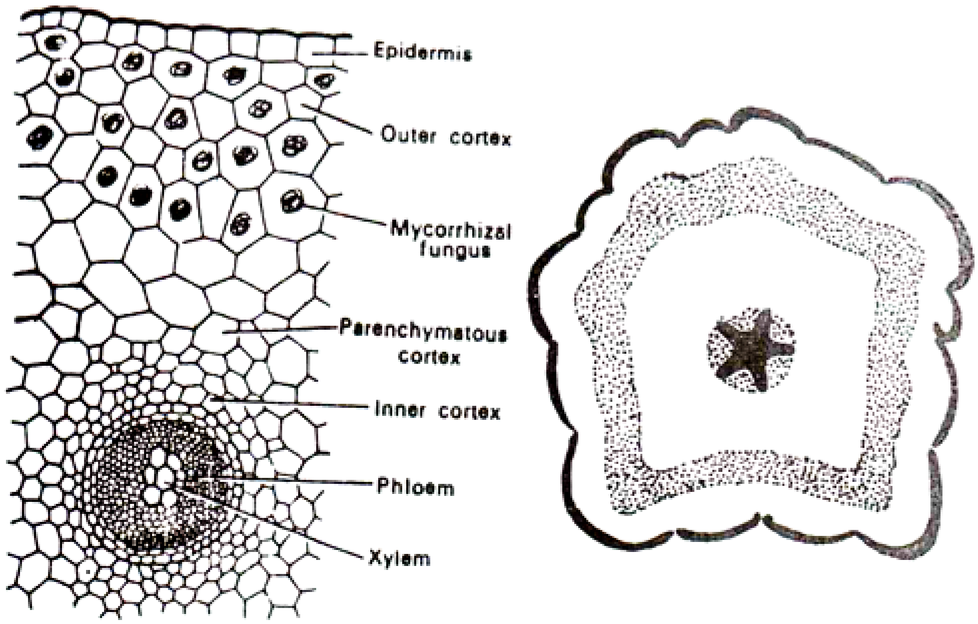

Fig. 20. *Psilotum* : T.S. of Rhizome.
A. Sector Enlarged, B. Ground Plan.

Internal Structure:

1. Aerial shoot:

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

The cortex is divided into three zones. The outer zone is chlorenchymatous and is made up of 2-5 layers of cells. The cells are loosely arranged with intercellular spaces. As the leaves are reduced, this constitutes the chief photosynthetic tissue of the plant.

The presence of thick cuticle, sunken stomata, photosynthetic stem and reduced leaves indicate the xerophytic nature of Psilotum. The middle region of cortex consists of 4-5 layers of sclerenchyma offering mechanical support to the stem. The inner cortex is made up of a few layers of closely packed parenchyma cells.

The stele occupies the central region of the stem. The outermost layer of the stele is endodermis. Next to the endodermis is an ill defined pericycle. The nature of the stele varies in the ultimate branches and in the basal portion. In the ultimate branches the stele is an actinostelic protostele with a solid core of stellate xylem mass in the centre. In the basal portion however, the central region of the stele consists of a sclerotic pith (Fig.21).

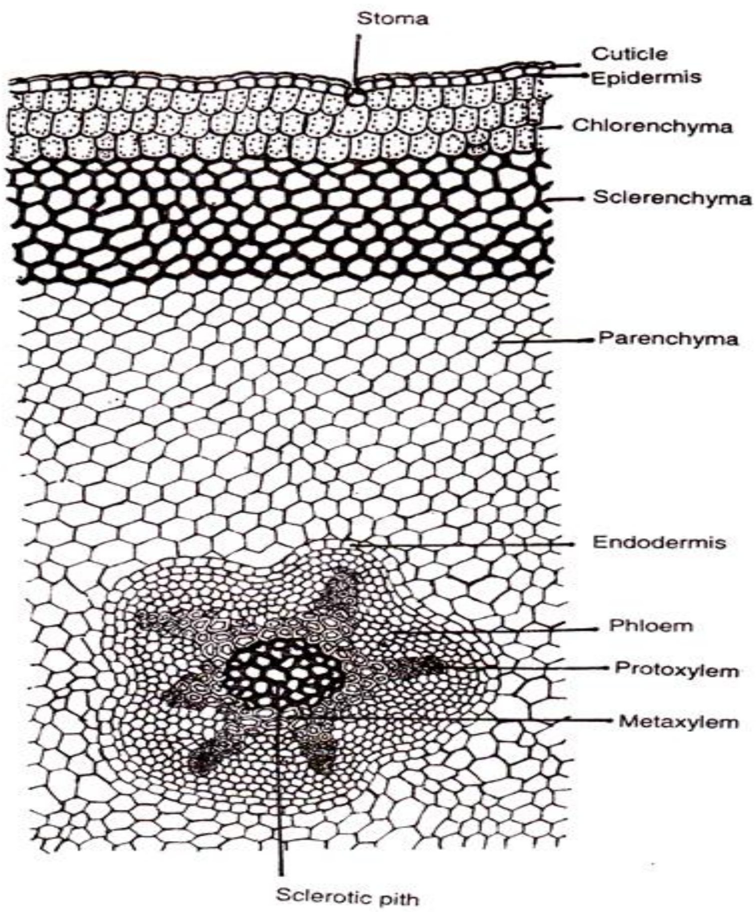

Fig. 21. *Psilotum* : T.S. of Aerial Shoot (a sector enlarged)

The xylem is exarch with the protoxylem points located at the lips of the rays. The xylem consists of scalariform pitted or annular tracheids. Sometimes spiral tracheids are also found. Surrounding the xylem is the phloem. According to Parihar (1965) the nature of phloem is difficult to determine because the distribution of sieve areas in these cells is imperfectly known.

In the ultimate branches the xylem may be smooth instead of the usual stellate nature. At the extreme base of the aerial stem between the xylem and phloem some, scattered xylem elements are found. Boodle (1904), Ford (1904) and others regard it as secondary xylem. According to Schoute (1938) however, these are primary xylem elements differentiating a little later in ontogeny. His opinion is, based on the absence of a definite cambium.

2. Rhizome:

This also shows an epidermis, a cortex and stele. The epidermis is ill defined. The cortex is divided into three zones. The outer cortex is parenchymatous and the cells have mycorrhizal fungus. The middle cortex has parenchyma cells rich in starch grains.

The innermost region of the cortex also consists of parenchyma that are usually dark brown in colour due to the deposition of a substance called phlobaphene. This is believed to be an oxidation product of tannins.

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

3. Leaf:

Anatomically the leaves show epidermis and the mesophyll. The epidermal cells are cutinised. The mesophyll has chlorophyllous cells which may be loosely or closely packed. The stomata are absent in the epidermis as such the chlorophyllous cells have no means of gaseous exchange. There is no vascular supply to the leaf. But in P. flaccidum a leaf trace which starts from the stem terminates at the leaf base.

The absence of stomata and the lack of vascular supply make the chlorophyllous cells of the leaf ineffective in photosynthesis.

Apical growth: A single wedge shaped apical cell contributes to the growth of the stem.

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

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

2. Spore Production:
The sporophyte reproduces asexually by the formation of spores. Spores are produced in special trilobed structures called synangia which are generally restricted to the upper portions of the aerial shoots where they are borne in the axils of minute bifid scales. Rouffa (1971) has reported that appendages are absent in the shoots of Psilotum plants growing in Japan. Here synangia are borne at the tips of branches.

Development of the Synangium:
Our knowledge of the development of synangium is mainly due to the work of Bower (1935). The development is apparently of the eusporangiate type, even though each sporogenous mass appears to originate from a single cell. According to Bower (1935) the synangium arises as an outgrowth on the adaxial face of the appendage.

According to Bierhorst (1934) however the synangium arises earlier than the appendage. In many cases the first division of the synangial initial produces an outer jacket initial and an inner archesporial cell (Fig.22). The jacket initial undergoes a number of anticlinal and periclinal divisions to produce the multilayered wall of the synangium.

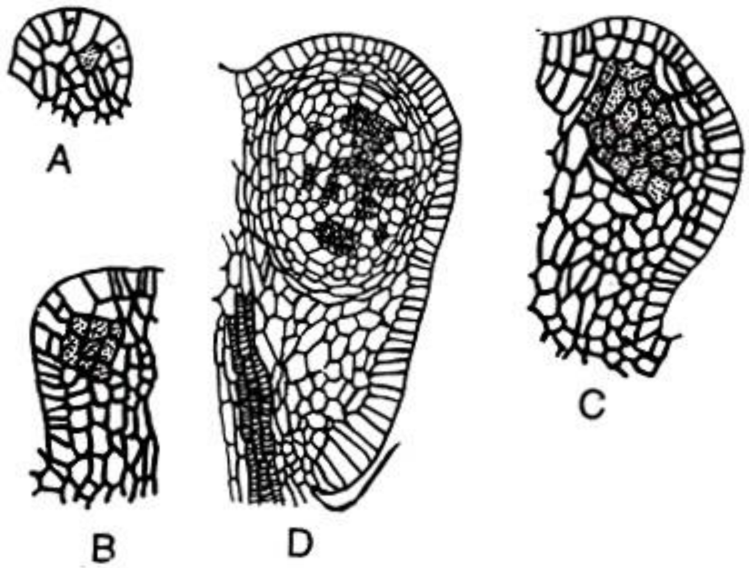

Fig. 22. *Psilotum*, Stages in the Development of Sporangium

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

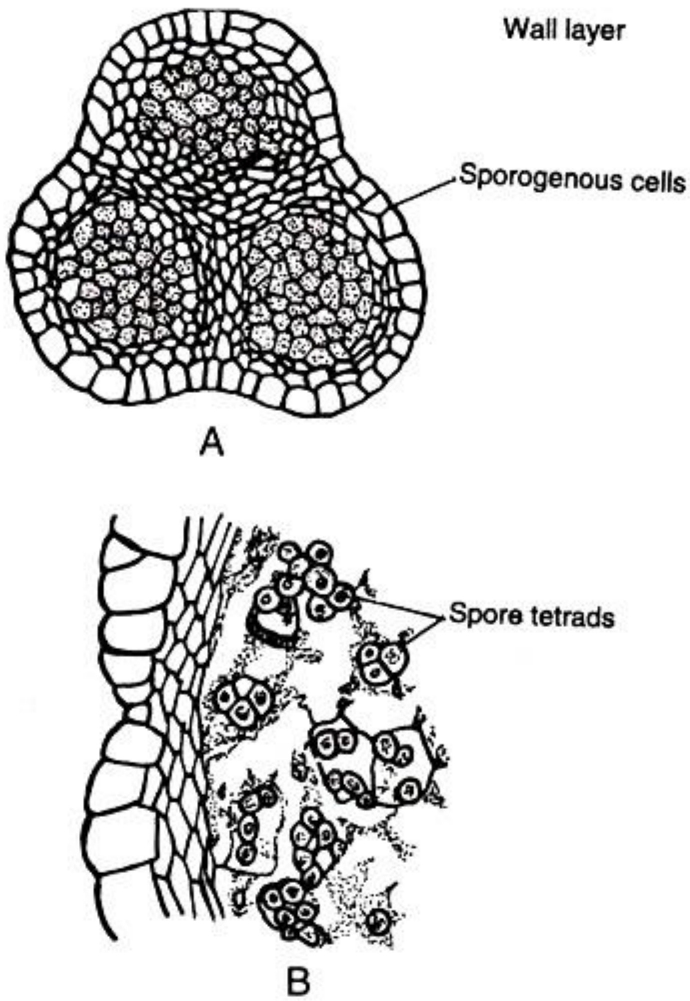

Fig. 23. *Psilotum*
A. T.S. of Young Synangium, B. Sectional View (a portion) of Synangium with Spore Tetrads

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

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

Dehiscence of the Synangium:
When the spore mother cells are undergoing reduction division some of the wall cells thicken except in a small vertical row marking the

future line of dehiscence. The synangium splits open along this line liberating the spores.

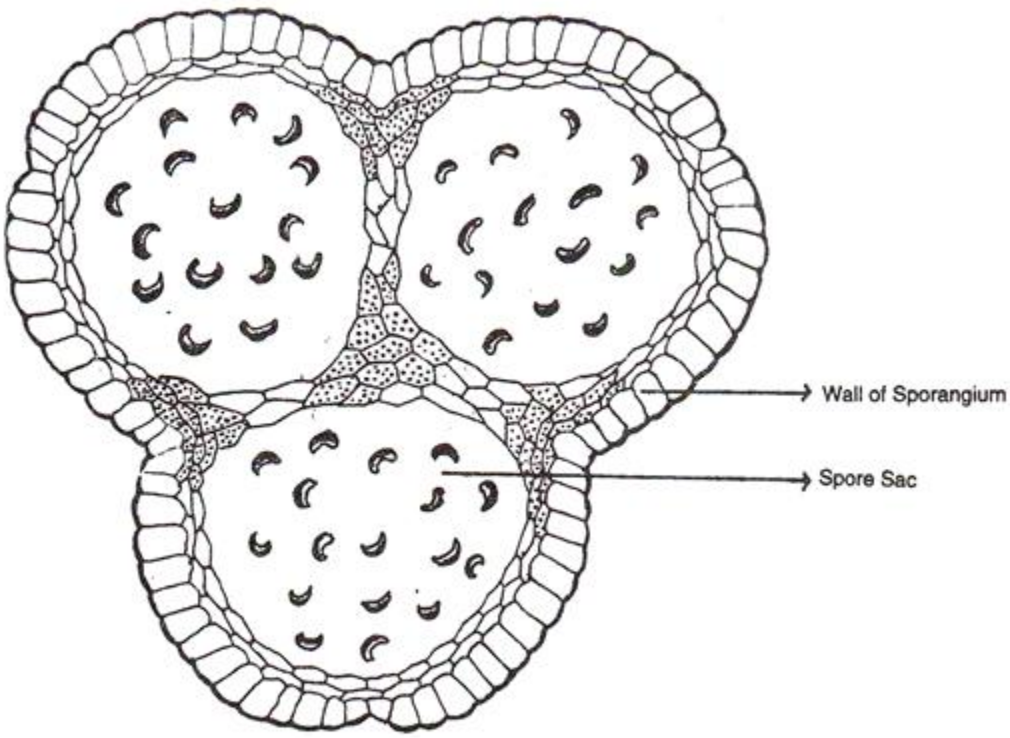

Fig. 24. *Psilotum*, T.S. of Mature Synangium with Spores

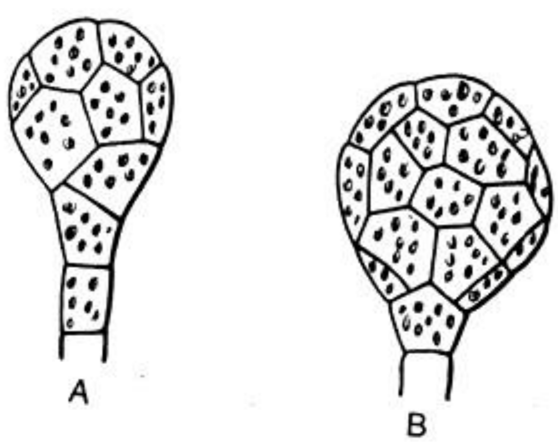

Fig. 25. *Psilotum* : Sporophytic Gemmae (Note the starch grains in cells)

Structure of the spore: Spores vary in shape from bilateral to tetrahedral type. Their average size is 0.065 x 0.032 mm.

Gametophyte of Psilotum:
Germination of the Spore and Development of Gametophyte:

The spores were germinated and the development of the gametophyte was studied for the first time in 1947 by Darnel-Smith. Germination starts after four months on placing the spores on a suitable substratum. The first sign of germination is the splitting of the outer spore wall and the projection of a small tubular outgrowth.

Later a cross wall cuts off the outgrowth from the remainder of the spore. In this way two cells are formed. Of the two cells, the upper by further divisions establishes an apical cell which produces a mass of tissue. Early in the development, the gametophyte gets infected by the fungus.

Structure of the Mature Gametophyte:

The gametophyte is partly or totally subterranean. It is usually cylindrical in shape with dichotomous branches. The branching however need not be always dichotomous. In size, the gametophyte ranges from 0.5 to 2 mm. The colour of the gametophyte is usually dark brown. This is due to the presence of endophytic fungus.

The gametophyte is wholly parenchymatous with strongly cutinised cell walls. The outermost layer of the cells gives rise to a number of rhizoids. In the hypodermal region the cells have the endophytic fungus. According to Beirhorst (1953) the fungus is probably Cladochytrium tmesepteridis. The cells are achlorophyllous and the nutrition of the gametophyte is saprophytic.

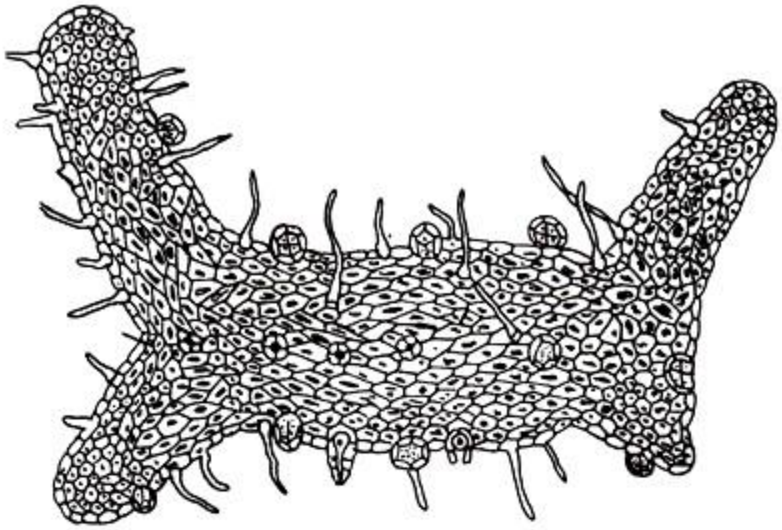

Fig. 26. *Psilotum*, Gametophyte of *P.nudum*

Internal Structure of the Gametophyte:

A transverse section of the mature gametophyte shows that it is wholly parenchymatous. Some of the superficial cells give rise to rhizoids. The outer walls, radial walls and even the inner corner of the walls of the peripheral cells are highly cutinised. Mycorrhizal association is found in some of the cells. The central region of the gametophyte also consists of parenchyma with no trace of any vasculature.

In some of the abnormal gametophytes of P. nudum found in the volcanic island of Ranjitoto near New Zealand, Holloway (1939) described certain unusual features. These gametophytes were much bigger than the normal ones and had a diameter of 1 mm. The interesting feature in these gametophytes was the presence of a central vascular strand.

The vascular strand consisted of a few annular and scaliriform or scalariform reticulate tracheids. The tracheids were surrounded by phloem. There was even a clearly recognizable endodermis. In these prothalli there was a cortex of parenchyma cells between the vascular strand and the superficial layer.

The occurrence of vasculature in these gametophytes is something unusual and Holloway (1939) gave the following interpretations to account for their presence:
1. Abnormal nuclear conditions- possibly diploid condition.

2. Some special physiological conditions of the gametophyte.

3. The remnants of an archaic feature. Regarding the first point, Manton (1942) observed that the vascularized gametophytes from Rangitoto were diploid instead of being haploid.

The sporophytes were tetraploid. Bierhorst (1953) has done cytological work on the gametophytes and sporophytes of P. nudum and according to him the chromosome number (n) of the gametophyte ranges from 100 to 105. P. nudum plants growing in Ceylon have a chromosome number of n = 52-54.

The existence of polyploidy seemed to be a sufficient evidence to account for the presence of vasculature. However, as Parihar (1965) observes diploid gametophytes have been noticed in many instances, e.g. in Osmunda regalis, but there is no trace of abnormality in them.

The presence of vasculature and certain similarities in the general plan of the sporophyte and gametophyte give credence to the view that the sporophyte and gametophyte are basically similar and that the former is nothing but the modification of the latter.

Regarding the observation that the presence of vasculature is an archaic feature, Pichi-Sermolli (1958) observes ‘a vestige of archaic feature in a plant like Psilotum which possesses many primitive characters is logical and need not surprise us’.

Reproduction:
The gametophyte reproduces by two methods
(1) Vegetative propagation and

(2) Sexual reproduction.

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

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

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

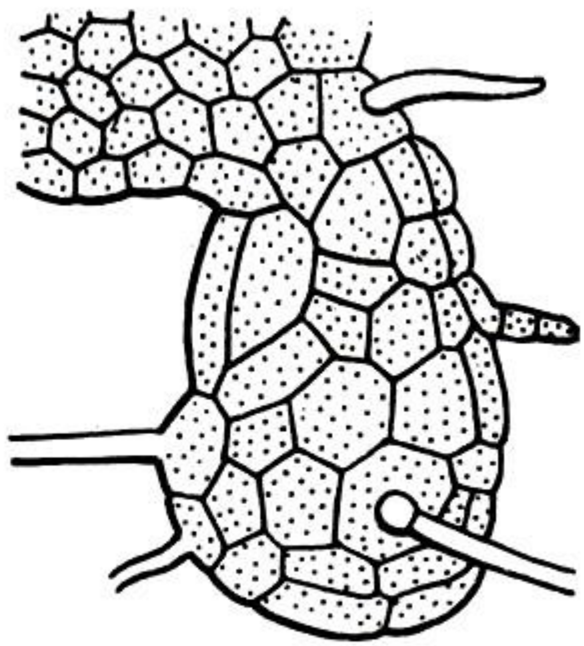

Fig. 27. *Psilotum* : Gametophytic Gemma of *P.nudum*

Development and Structure of the Antheridium:
The antheridium develops from a superficial cell called and anthcridial initial. This undergoes a periclinal division to form two superposed cells (Fig.28a). Of the two cells the outer cell is called the jacket initial

and the inner cell is called the primary androgonial cell. The primary androgonial cell divides in all the planes to form a large number of cells (Fig.28d). Meanwhile, the jacket initial divides anticlinally to form a jacket layer, one cell in thickness.

The androgonial cells divide further to form the androcytes. These androcytes metamorphose themselves into spirally coiled multi-ciliate antherozoids. When the antheridium is reaching maturity it bulges out from the surface of the gametophyte.

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

Development and Structure of the Archegonium:
The archegonia are also produced from the superficial cells of the gametophyte. A superficial cell which is destined to form an archegonium is called an archegonial initial. This undergo periclinal division to form an outer primary cover cell and an inner central cell.

The primary cover fell divides twice vertically where the second division is at right angles to the first one to form four quadrately arranged cells called the neck initials. A long sectional view at this stage however, reveals two neck initials and a central cell (Fig.28). The central cell subsequently extends in between the neck initials so as to form an elongated structure. The neck initials divide several times transversely to form an archegonial neck 4-7 cells in height.

As the archegonial neck is elongating the central cell keeps pace with it by extending into the neck. After sometime the central cell divides transversely to form an upper primary neck canal and a lower primary venter cell (Fig.28g). The primary canal cell divides once to form two neck canal cells, whereas the primary venter cell divides once transversely to form an upper short-lived venter canal cell and a lower egg cell with a prominent nucleus.

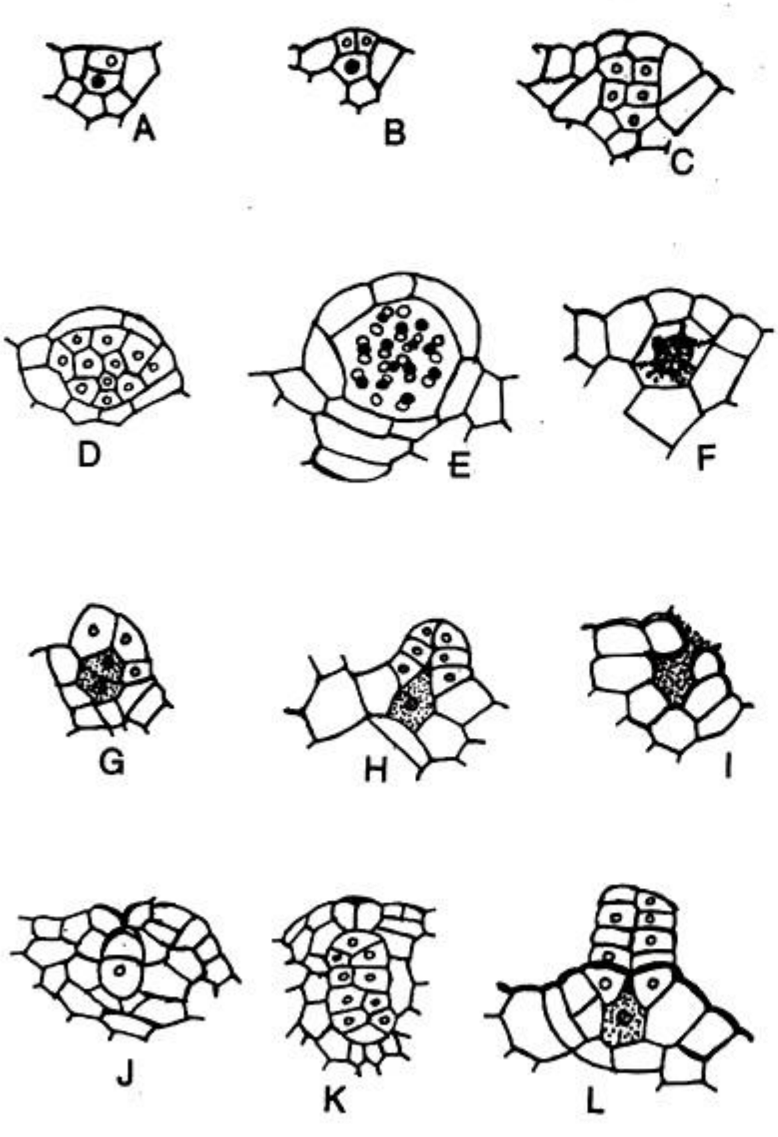

Fig. 28. *Psilotum* : Development of Sex Organs in the Gametophyte of *P.nudum*; A-E. Antheridium, F-J Archegonium, K-l. Archegonium and embryo respectively

As the archegonium is reaching maturity, the neck canal cells degenerate. In some cases they degenerate as soon as they are formed. In a mature archegonium; some of the terminal tiers of the neck slough off (Fig.28j) leaving only the basal one or two tiers. At this stage except for egg all other cells in the archegonium disintegrate.

Fertilization:

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

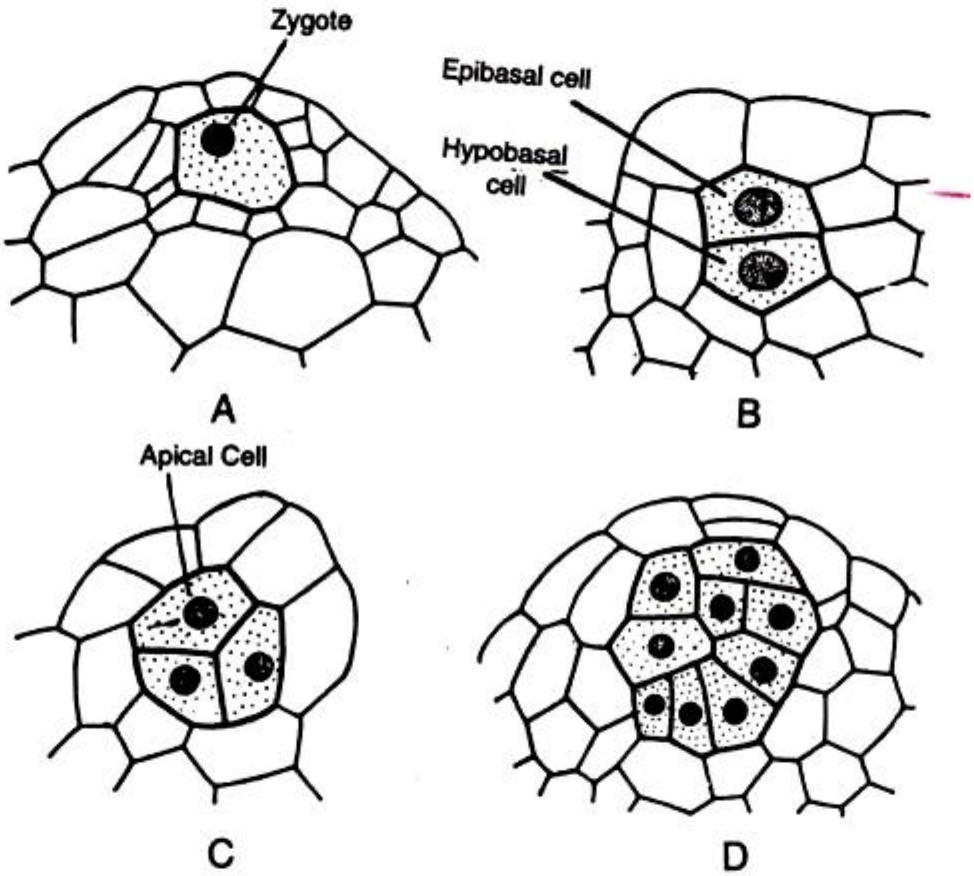

Fig. 29. *Psilotum* : Stages in early Embryogeny of *P. nudum*

Embryogeny:

Soon after fertilization, the zygote enlarges in the cavity of the venter. First division of the zygote is transverse and it results in forming an upper epibasal cell (cell nearer to the archegonial neck) and a lower hypo basal cell (cell away from the archegonial neck) (Fig.28k). The hypo basal cell gives rise to the foot and the epibasal cell gives rise to shoot.

This type of embryogeny, where the shoot apex is pointed towards the archegonial neck is called exoscopic. There is no formation of root or cotyledons. The hypo basal cell divides in all the planes to form a bulbous foot which gives rise to haustorial outgrowths into the gametophyte.

Meanwhile, the divisions in the epibasal cell result in the formation of a three sided apical cell. By the activity of this apical cell the shoot apex projects out of the gametophyte. At this stage it gets infected with the mycorrhizal fungus. This assures independent nutrition to the young sporophyte.

When the young sporophyte is about 8-10 mm long, it detaches from the gametophyte and leads an independent life. In the beginning it is subterranean, later some of the branches grow Apo geotropically and form the aerial shoots.

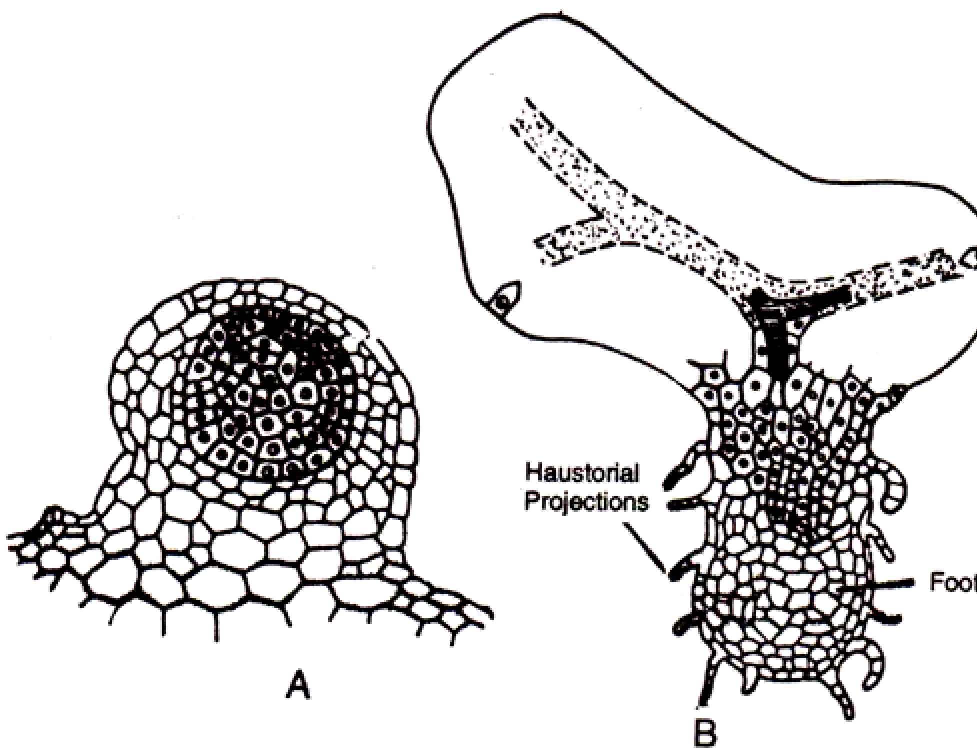

Fig. 30. *Psilotum* : Stages in Late Embryogeny of *P. nudum*