Class: Psilotopsida

Order: Psilotales

Family: Psilotaceae

Genus: *Psilotum*

The division **Psilophyta** is made up of living plants comprising one order, one family and two genera (*Psilotum* and *Tmesipteris*)

*Psilotum* consisting of two species *P. nudum* and *P. complanatum* (*P. flaccidum*) is pantropical and subtropical in distribution. (Psilotin, a specific phenolic substance/flavanoid, has been found in *Psilotum*).

*P. nudum* is an erect, slender, shrubby plants found in the crevices of rocks may attain a height up to 25cm. This plant is commonly known as whisk fern.

The sporophytes of *Psilotum* are dichotomously branched with an underground rhizome system and an upright system of branches. Rhizomes produce rhizoids which act as roots.

No roots are present (instead they have rhizomes with absorptive rhizoids infested with mycorrhizal fungi). The underground rhizome system anchors the plant and rhizoids serve as absorptive structure. The endophytic fungus within the cortical cells sends out hyphae that come through the rhizoids and probably help in the
function of absorption. The rhizoids are one to three cells in height and covered with cuticle. They arise from epidermal cells of the rhizome.

Psilotum rhizomes with rhizoids

Any one of the rhizome tips may turn upward and undergo several to many dichotomies that establish the basic plan of aerial branch organization.

The green aerial dichotomous branch is in three dimensions. The upright branch or stem doing virtually all the photosynthesis. The stem has mere emergences without any vasculature and spirally arranged on the aerial stem.

The sporophyte have only small, vein less, scale-like outgrowths (= enations) on the stems (these are usually not considered to be true leaves).

A portion of aerial branch showing three-lobed synangia and their associated forked appendages

The yellow synangia are present in the axils of the enations. The enations are Tiny, green, superficially scale like, vein less, photosynthetic flaps of tissue helically arranged on the upper part of the aerial stem.
Internally it is consist of photosynthetic parenchyma cells that are continuous, lower down, with similar tissue of the stem. A leaf trace ends at the base of this foliar structure. On the upper part of the stem short stalked trilobed structure associated with bilobed foliar appendages are present known as synangium, the fusion product of two or more sporangia.

*Psilotum* stem demonstrates dichotomous branching, enations (no vascular tissue) and two of the three sporangia in a single synangium

The outer most layer of the aerial system is covered by an epidermis heavily cutinized and covered by a cuticle. Stomata are present mainly in areas between the longitudinal ribs and are without special subsidiary cells.

A broad cortex with three distinct zonation are found. Just beneath the epidermis the outer cortex with elongated, lobed parenchyma cells with internal spaces between the vertical rows are present. The cells contain starch grains.

The middle cortex composed of cylinder of vertically elongated and thick walled cells, with small intercellular air space. And few or no starch grain. The basal portion of the aerial stems this region is composed of lignified cells.

The inner cortex is composed of several layers of cells whose cell walls become thinner and less lignified with an increase in the number of starch grains per cell.
The boundary between cortex and vascular cylinder is marked by the endodermis with vertically elongated cells have distinct casparian strips on the radial and end walls.

![Diagram of plant structure](https://example.com/structure.png)

A single-layered parenchymatous pericycle is present just below the endodermal layer.

The vascular cylinder varies all along its length. The basal part is similar to rhizome, in having a protostele which is with or without stellar parenchyma and ill-defined pith. Higher up, the vascular cylinder is siphonostelic with sclerenchymatous pith. The xylem is sharply angled (stellate); pentarch to octarch in the main axis and triarch to diarch in distal region. The variation in number of projecting rays depends on species. It is a exarch condition that means the protoxylem is towards the periphery and metaxylem is inwards. Xylem is surrounded by phloem, which is consists of elongated tubular, thin walled cells lignified at their corner. A large pith in the central part made up of sclerenchymatous fibre with numerous simple pegs in their walls.
Transection of stem of *P.nudum* near base of the aerial branch

In the subterranean stem or rhizome the outer cortex consists of thin walled cells which are crowded with hyphae of an endophytic mycorrhizal fungus. The middle cortex consists of parenchymatous cells with abundant starch grains. The two or four layers of inner cortex lying next to the endodermis are usually dark brown in colour because of deposit of a substance known as phlobaphene which is formed from tannins by oxidation and condensation. The endodermis demarcates the stele from the cortex and the endodermal cells show casparian strips in the radial walls. The stele is protostelic, no clear distinction between proto and meta xylem. Surrounding the xylem phloem (elongated angular cells often lignified at corners) are present. Surrounding the phloem the one layer thick parenchymatous cell constitute the pericycle layer. The presence of secondary xylem is reported in *P. flaccidum*. 

*Psilotum* rhizome (cross-section)
Fig: *Psilotum spp.* (A) A portion of T.S of aerial shoot; (B) A portion of T.S of rhizome
APICAL GROWTH

The apical growth of both the rhizome and aerial shoots is by the activity of a single, large, wedge-shaped apical cell which is situated at the summit of the rhizome, or the aerial shoot. (Ford, 1904; Bierhorst, 1954; Marsden and Wetmore, 1954).

VEGETATIVE REPRODUCTION

(1) Gemmae on Sporophyte. *Psilotum nudum* multiplies rapidly by the gemmae or brood bodies which develop in large numbers over the surface of rhizome. They generally appear on the soft rhizoid covered portion in the vicinity of the growing point or in the axils between rhizome branches. These gemmae are small oval bodies, one cell in thickness (Fig. 5 A-E) and usually show a two-sided apical cell. The cells are filled with starch. The gemmae may germinate while still attached to the parent rhizome (Bierhorst, 1954), but usually they germinate when they fall on the proper substratum. On germination the gemma forms an elongated subterranean shoot composed of uniform parenchyma. These finally develop into typical rhizome with the differentiation of stele and cortex.

Gemmae on the Gametophyte. Gemmae are also borne on the surface of the prothallus (Holloway, 1939; Bierhorst, 1953). These gemmae are usually similar to those produced on the rhizome and there is nothing to distinguish between them (Fig. 5 F-H). Each arises as the result of proliferation of the terminal cell of a several-celled rhizoid-like structure. At maturity they are generally 8-12 cells in extent and are spheroidal to somewhat flattened. The gametophytic gemmae produce on germination a prothallus with a few scattered sex organs.

Besides the gemmae, vegetative buds of a very different manner of origin but of a similar function to that of gemmae, occur on the gametophytes. In contrast to the origin of gemmae the vegetative bud arises directly from a single or, from two surface cells which once subdivide and protrude (Holloway, 1939).

SPORE-PRODUCING ORGANS

The trilocular fructifications are borne towards the distal end of the aerial shoots, but occasionally lower down. In any case fertile and sterile regions are not demarcated. Each fructification is situated in the axil of a minute bifid foliar appendage.
Reproduction by Spores

(Spores are produced in specialised bodies called the sporangia or synangia that appear on the aerial shoots (Fig. 3.1, A, B). The sporangia or the synangia are found at the distal ends of the aerial shoots and are spirally arranged.)

Sporangia

Structure. The sporangia in *Psilotum* are not terminal but appear as short-stalked trilobed structures (Fig. 3.1, B) associated with distinct bilobed foliar appendages. A section through the three lobed sporangium reveals that it is partitioned into three sporogenous regions (Fig. 3.6, E). The sporangial wall is made up of three or four layers of cells (Fig. 3.6, E). In some cases the wall is made up of even six layers (Bierhorst, 1971). At maturity the outer wall layer develops thickening material. Its cells become longer than broad except at the point of line of dehiscence (Fig. 3.6, G). A nonfunctional annulus is also discernible in the form of a patch of thick walled cells at one end of the line of dehiscence. It is positioned on the apex of the sporangia. The inner layers of the sporangial wall extend inwards to form septa of the trilocular sporangium (Fig. 3.6, E). Each of the three chambers contains a sporogenous tissue. Some of the cells of this tissue become spore mother cells (Fig. 3.6, E) whereas the rest disintegrate and serve as a nourishing fluid. The spore mother cells undergo meiosis and form tetrads of haploid spores.

The fertile sporangial apparatus of *Psilotum* is supplied by a single trace from the stele of the aerial shoot. It enters the base of the synangium without giving off any branches to the bilobed foliar appendages. Within the sporangial base it divides into three parts and later fades out.

Dehiscence. The sporangium dehisces along three apical lines (Fig. 3.7, A) passing through the median line (Fig. 3.6, G) of each sporangial lobe (iloculidal).
The trilocular fructifications are borne towards the distal end of the aerial shoots, but occasionally lower down. In any case fertile and sterile regions are not demarcated. Each fructification is situated in the axil of a minute bifid foliar appendage.

**Development of ‘Synangium’**. The development of the trilocular sporangia has been studied in detail by Bower. (Each sporogenous mass appears to be referable in origin to a single epidermal cell of the sporangiophore, but this has actually not
been proved, it being difficult to assign sharp limits to sporogenous masses. Development is apparently of the eusporangiate type. The first division of the primary cell is periclinal and separates the outer daughter cell, the jacket initial, and the inner daughter cell, the archesporial or primary sporogenous cell (Fig. 6 A). The jacket initial divides by repeated anticlinal and periclinal divisions to form a jacket layer four to five cells in thickness. The cells of the outermost layer take a deep prismatic form while the inner layers are shallow.

The archesporial cell also divides and redivides to form a large number of sporogenous cells (Fig. 6 D). The inner layers of the jacket as well as superficial portion of the sporogenous mass become disorganized but there is no clearly defined tapetum. As the sporangium develops, irregular groups of cells in the sporogenous tissue become filled with dense granular cytoplasm (Fig. 6 D). They subdivide and give rise to spore mother cells. The remaining sporogenous cells remain paler with more watery contents and ultimately form a plasmodial mass in which the spore mother cells and spores lie embedded (Fig. 6 F). The spore mother cells finally undergo the tetrad division to form the haploid spores.

Simultaneously with the formation of spores, the cell walls of the epidermal layer of the jacket begin to thicken except in a small vertical row, the future line of dehiscence of the mature sporangium. This row runs from the tip of each locule to its base.

**Structure of the Mature Synangium.** The fructification of *Psilotum* is usually externally trilobed and internally divided into three chambers. The wall consists of several layers of cells. A tapetum is lacking. Inside the wall there are numerous spores.

**Morphological nature of sporangium-bearing complex** is not clearly understood and has long been in dispute. The two chief alternative views in this connection are:

(i) It is a foliar structure (Solms-Laubach 1884), Velenovsky, Seward (1910), Bower (1908) and Schoute (1938). It has been suggested that the forked leaves are bifid sporophylls, each bearing a trilocular fructification (a single partitioned sporangium).

(ii) It is a short lateral shoot (Juranyi 1871), Strasburger and Goebel. According to this view the short fertile branch (axis) bears two sterile appendages (leaves) and terminates in a trilocular fructification (often individual locules being themselves regarded as sporangia which have become fused to form a synangium).

But a third view has also been suggested that it is an organ or a group of organs *sui generis*.

Moreover, it is an open question whether the trilocular fructification represents a single partitioned sporangium or three individual sporangia which have become united to form a synangium. The earliest developmental stages, however, seem to suggest that each locule arises separately from a single epidermal cell of the
sporangio- phore. Therefore it can be assumed that the structure is formed by a congenital union of three individual sporangia, i.e., it is a true synangium. Recently Bierhorst (1956) has shown that in *Psilotum* three separate archesporia originate behind the apical cell of the young spore-producing apparatus, and at maturity there is a separate vascular trace (quite reduced) corresponding to each of the three locules of the spore-producing apparatus. On the basis of these two observations Bierhorst suggests that each locule represents a separate sporangium. He interprets the fertile appendage as bearing a verticel of three sporangia fused to a central axis and a verticel of two sterile appendages. But other workers prefer to regard the partitions as representing sterile sporogenous tissue inside what they believe to be a single divided sporangium.

![Diagram](image)

**Fig. 7.17**: *Psilotum nudum*: A, T.S. of synangium; B, V.S. of fertile axis through a synangium

1. Each sporangium develops from a superficial cell of the sporangiophore. This cell divides **transversely** into an outer **jacket initial** and an inner **archesporial initial**.

2. The **jacket initial** divides to produce wall. This wall is **four to five cells thick**. The archesporial initial divides to produce a mass of **archesporial cells**. **Tapetum** is not produced in *Psilotum*.

3. In the mature sporangium some of the **archesporial cells** become **elongated**. They are filled with dense cytoplasmic contents. These cells act as **spore mother cells**. Each spore mother cell undergoes **meiosis** and produces four spores. The rest of the archesporial cells disintegrate to form protoplasmic mass or **tapetal fluid**. It nourishes the developing spores.

The **epidermal cells** of the sporangial wall become **thick walled**. But a single vertical line from the base of the sporangium to the apex remains thin walled. The mature sporangium **dehisces** along this line and the spores are liberated.
The gametophyte generation of *Psilotum* start with the spores. *Psilotum* is homo sporus. The spore tetrads may be tetrahedral or even isobilateral. The spore is opened by a narrow median slit. The spore has an outer thin and reticulate exine and inner intine. It is uninucleate and about 0.65-0.32 mm in size. The exine is spinulose. The spore is monolete.

(Psilotum sp. A, mature spore; B, optical section of spore; C, germinating spore first stage; D, next stage in the germination of spore; E, formation of the first cells of the prothallus; F-J, successive stages of the development of the prothallus.)

The color of the mature portions of the gametophyte varies from pale yellow to dark brown, or occasionally to nearly black. The meristematic apices are conspicuous by their nearly white color. There is no indication that a green color develops in the gametophytes upon exposure to light.

The branching patterns exhibited by the gametophytes are in general quite inconsistent. Apparent equal and unequal dichotomies, trichotomies and tetrachotomies are often present. Apices which resemble lateral buds are common. The angles between the branches vary greatly. The gametangia are usually relatively abundant and are distributed uniformly over the surface and length of the mature gametophytes.
In an occasional gametophyte, the antheridia almost completely cover the surface. Such a gametophyte is usually quite large and possesses few rhizoids. At the other extreme, there is an occasional gametophyte on which the antheridia are as much as 4 mm. apart. The archegonia are generally not as abundant as the antheridia. They are most conspicuous near the proximal limit of the meristematic apices, since they become dark in color before the surrounding surface cells.

Portions of gametophytes which are bilaterally symmetrical are relatively common. This condition is usually not extreme, but is expressed as merely an elliptical cross-section. Often when this condition exists, the gametangia and rhizoids are distributed along the two narrow sides.

(A prothallus. This subterranean, bisexual, independent gametophyte of *Psilotum nudum* bears antheridia and archegonia, the reproductive organs. [Drawing by L. Meszoly.]

The anatomical structure of the gametophyte *P. nudum* varies from 0.5-1.8 mm. The external features are the same for all size classes. The difference lies mainly in the presence or absence of a vascular strand. The surface cells of all of the gametophytes are living at maturity, contain fungal hyphae, and are hexagonal in face view. Their outer walls, radial walls, and also the inner corners of their walls are strongly cutinized, dark in color, and resistant to decay.

The ground parenchyma is continuous across the axis of the smaller gametophytes which lack a vascular strand. It forms a cortex in the larger, vascularized gametophytes. This tissue is composed of thin-walled, living, mycorrhizal, parenchymatous cells, the wall of which are often cutinized and slightly thickened in the corners. They are generally 5- or 6-sided in transverse section and 6-sided in longitudinal section. They are frequently slightly elongate, up to five times as long as wide, along the
long axis of the gametophyte. Starch grains are frequently present in these cells, with a greater number in the cells near the surface. In the younger (recently matured) portions of the gametophyte of *P. nudum*, the ground parenchyma and surface cells possess a very small amount of cytoplasm, are largely vacuolate, and possess a single, small, but conspicuously staining nucleus. The nuclei are often larger in the near-surface layers. In older portions of gametophytes, many of the ground parenchyma and surface cells have somewhat decomposed contents and are occasionally multinucleate; in which case, there are generally one relatively large nucleus and several smaller nuclei.

**DEVELOPMENT OF ARCHEGONIUM**

Each archegonium develops from a single superficial cell. It divides transversely into an upper **primary cover cell** and a lower **central cell**. The primary cover cell divides to produce a group of **four neck initials**. These neck initial divides to produce **neck**. The **central cell divides** transversely into a primary neck canal cell and a **primary ventral cell**. Primary ventral cell functions as an egg directly.

![Diagram of archegonium development](image-url)

*Fig. 7.20: Psilotum nudum: A-E. Stages in the development of archegonium, F. A mature archegonium*
Development of antheridium:

Each antheridium develops from a single superficial cell. It divides into an outer jacket initial and an inner primary androgonial cell. The jacket initial divides to produce a single layered wall. The primary androgonial cell divides to produce a mass of androcytes or antherozoid mother cells. Each androcyte gives rise to a single, coiled and multiflagellate antherozoid. The antheridial wall ruptures to release the antherozoid.

Gametophytes are monoecious, i.e., they are homothallic. Both the sex organs, i.e., antheridia and archegonia are borne on the same gametophytic plant body.

1. Antheridia:- Antheridia begin to develop on the gametophyte earlier than the archegonia. Each antheridium is a projected spherical body, covered by a single layer of jacket cells. Within the jacket layer, lies numerous sperm mother cells, which metamorphose into numerous spiral, multiflagellate sperms, i.e., antherozoids.

2. Archegonia:- The archegonia are shrunken with short projecting neck, which breaks away at maturity. The neck consists of 4-5 cells long, and consists of 2 neck canal cells. The venter consists of one ventral canal cell and an egg cell.
(Psilotum nudum prothallus cross section. Mature antheridia release spirally coiled, undulipodiated, sperm (n) that swim to mature archegonia. Each archegonium contains an egg (n), which is fertilized by a sperm)

Examination of the prothallus reveals two types of external sex organs. The male sex organs, called antheridia, are microscopic bumps ringed with a layer of surface cells. A few cells away, on the same gametophyte (prothallus), are smaller female sex organs, archegonia. Each archegonium is composed of several ranks of cells with an opening that forms between them when the middle layer breaks down. The bisexual prothallus produces several archegonia, each with a mitotically produced egg at the base of the opening, as well as antheridia. Curled sperm with many undulipodia form inside the antheridia by mitosis. Sperm fertilize eggs within the archegonia. Because the sperm that are released into the soil must swim, moisture must be present for fertilization to occur. The resulting zygote develops into the multicellular diploid sporophyte embryo characteristic of all plants. At first, the young sporophyte is nourished through a foot anchored in the gametophyte. Later, the sporophyte takes up an independent, photosynthetic life aboveground.
Fertilization:

The neck canal cells of mature archegonium disintegrate. It produces a pore through which antherozoids enter the archegonium. Only one antherozoid fuses with the oosphere to produce oospore.

Development of Sporophyte:

1. The oospore divides transversely into an upper and a lower cell.

2. The lower cell by further divisions produces a foot. Foot buried into the tissue of the prothallus. It absorbs nourishment for the developing embryo.

3. The upper cell divides to produce a mass of cells. Its one or two peripheral cells act as apical cells. The apical cell divides and increases the size of embryo. The gametophytic tissue completely surrounds the young embryo like calyptra in early stages. But later, it comes out of the calyptra. Some of its surface cells produce rhizoids. Other cells are infested with the mycorrhizal fungi and the embryo becomes independent. The embryo by further growth becomes the rhizome. Rhizome develops aerial dichotomous branches.
Life Cycle of *Psilotum nudum*