

Psilopsida is a group simple in organization. It is characterised by:

- (a) root-less sporophytes,
- (b) dichotomously branched rhizome and aerial axes,
- (c) aerial axes are either naked (Gr. Psilos=bare) or have small spirally arranged appendages,
- (d) vascular cylinder is protostelic,
- (e) thick-walled sporangia either terminate branches or are borne laterally on them.

Psilopsida has been divided into two orders;

- (1) Psilophytales-Silurian to Devonian
- (2) Psilotales-No fossil record.

The former comprises fossil forms and the latter living forms.

In this account living forms are considered first.

PSILOTALES

Psilotales is an interesting group of plants, because its representatives are simple and similar in structural organisation to that of early land plants (Psilophytales). This group is related to early vascular plants in its ill-differentiated organs (Stewart & Rothwell, 1993). The group is, however, little understood. This is due to restricted distribution of its members and together they form an inconspicuous element of world flora.

The order comprises two genera, *Psilotum* and *Tmesipteris*. These genera are quite distinct from each other in foliar appendages, shoot architecture and synangia; sufficient for their placement in two separate families. However, in some details they intergrade. Some authors have suggested of two separate families, Psilotaceae and Tmesipteridaceae, for *Psilotum* and *Tmesipteris* respectively.

These genera also differ in their ecological range and behaviour. *Psilotum* has weedy tendencies; it is an effective colonizer of open situations such as recent roadside cuttings and volcanic scoria. Contrastingly *Tmesipteris* is characteristically an epiphyte of rain forest.

PSILOTUM

Two species of *Psilotum* recognized are, *P. nudum* and *P. flaccidum*

(*P. complanatum*). Of these *P. flaccidum* is a pendulous epiphyte, rare in distribution; restricted to Jamaica, Mexico, Hawaii and a few Pacific islands. On the other hand *P. nudum*, frequent in tropics and subtropics, is an erect slender shrubby plant of 20-25 cm height. It is generally found in the crevices of rocks, but rarely also occurs as an epiphyte. This species has been brought in cultivation in green houses, and is commonly known as 'whisk fern'. Horticultural value of *Psilotum* has waxed and waned. In Japan there are many variants and cultivars, so are also *Psilotum* Societies of enthusiasts.

Academic significance of *Psilotum* lies in its simple structure and plasticity. It is a phyletically reduced genus.

Morphology

The plant consists of a subterranean rhizome and dichotomously branched aerial axes (Fig. 2.1 A). The rhizome that anchors the plant is a cylindrical, prostrate and dichotomously branched mycorrhizic structure with numerous rhizoids. Apparently, there is an apical dominance; rhizome with intact apices form very few branches but in plants growing in sandy soil, due to apical injury, regeneration is quite common. The plants characteristically lack roots and instead the rhizoids, that are 1-3 cells long, serve for absorption. Mycorrhiza also assists in absorption. The fungus is considered to be intimately related to the physiology of plant. The tips of rhizoids in *P. nudum*, proliferate to form gemmae which on regeneration produce entire plants, and serve for vegetative propagation.

The subterranean axis is neither leafy nor capped (Gifford & Foster, 1989). In these respects as well as in its ill-organized apical meristem (Takiguchi, Imaichi & Kato, 1997) this axis is different from basic organs—stem and root—and seems to be an independent organ, representing a stage in evolution of plant organs.

Some branches of rhizome turn upwards and develop into aerial green branches of regular dichotomy. The rhizome and aerial branches are continuous. What induces some branches to turn upwards remains to be known; probably those nearer the surface and exposed to light turn upwards. The aerial branches are flattened in *P. flaccidum* and ridged in *P. nudum*; in that the lower portion is often pentagonal, and triangular towards distal dichotomy. On aerial branches, except the base, are present small awl-shaped leaf-like appendages (Fig. 2.1 A) which are without any vascular trace and stomata. Minute traces for these appendages do originate from stele in *P. flaccidum* but die out in cortex. An appendageless variant of *P. nudum* is on record (Rouffa, 1971).

Reproduction

Stout aerial branches bear large conspicuous sporangia (Fig. 2.1A). Each sporangium is a 3-lobed structure (Fig. 2.1 B,C). It is borne on a forked appendage. It has been described as (a) trilocular sporangium (b) trisporangiate structure, and (c) a synangium; a group of fused sporangia

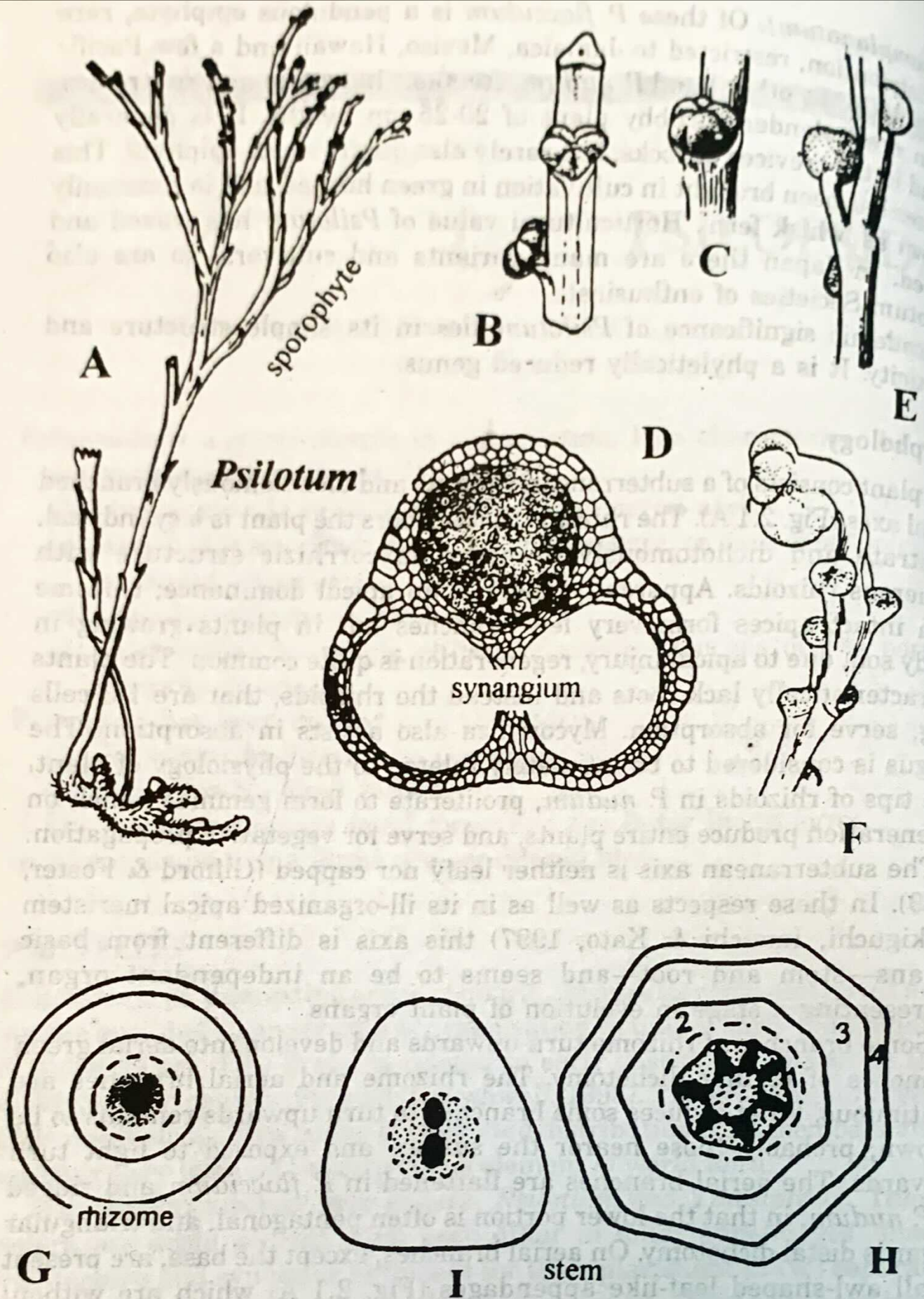


Fig. 2.1 *Psilotum*, morphology and anatomy of sporophyte.

A, *P. nudum*, morphology of plant. B-C, fertile regions enlarged to show sporangia. D, transection of a synangium. E, sporangia on short lateral branches (note, the absence of leaf-like structures). F, terminal and lateral sporangia. G,H,I, transection (diagrammatic) of rhizome, basal and distal region of aerial axis, respectively.

with distinct partition walls (Fig. 2.1.D). Rarely more than three sporangia are also seen.

In a collection from New Zealand, have been recorded free sporangia, two fused sporangia and a single sporangium (Bierhorst, 1971). Occasionally, sporangia terminate small lateral branches (Fig 2.1E). At times, the main axis also terminates into clusters of synangia (Fig. 2.1F) each with a variable number of sporangia (Bierhorst, 1971; Rouffa, 1971). Presence of terminal synangia on an appendageless *Psilotum* as well as typical appendaged *Psilotum* is a regular feature. These terminal synangia have been interpreted (Siegert, 1973) as crowded or fused lateral fertile appendages (sporophylls). In an extension of this concept, aerial axis of *Psilotum* is interpreted as phyletically reduced leafy shoot bearing sterile and fertile appendages (Kaplan, 1977). To what extent this reduction has taken place and in which direction it has proceeded remains an academic exercise.

Morphological Nature of Fertile Appendage

The morphological nature of fertile appendage has been controversial. It has been regarded either as a bifid sporophyll or a short lateral branch. Some investigators describe the synangium to be axillary in origin (Bower, 1935; Roth, 1963) whereas others describe the original primordium as fertile axis and the forked appendage as a lateral outgrowth on it (Bierhorst, 1956). However, the concept that the fertile axis -appendage as well as synangium- is a condensed branch system is favoured. This is substantiated by experimental evidence. Under long days (16hr at 200-300 ft.c.) the fertile axes of *P. nudum* elongated into definite branch-like structures (Rouffa, 1967). Rarely, such a situation is also encountered under natural conditions. On an appendageless *Psilotum*, from Japan, the synangia are borne (Rouffa, 1971) at the tips of branches.

Origin and Structure of Synangium

A synangium (Fig. 2.1D) on the outside of its loculi is bound by a single layer of large cells, followed by it are a few layers of smaller cells. The septum has elongate cells. Unlike foliar structures, the synangium is vascularized. A vascular bundle extends into a synangium and subdivides into three parts, corresponding to three sporangia (Bierhorst, 1971). Occasionally are seen multiple sporangium lobes in *P. nudum* which are not represented by individual vascular bundles (Rouffa, 1978).

The sporangium is eusporangiate in development. The primordium of a fertile appendage (Fig. 2.2A) is nearly of the same size as that of apex. It becomes two lobed. Immediately below the apex of an appendage differentiate three groups of sporangial initials which divide periclinally to form wall layers and sporogenous tissue. A part of the sporogenous tissue serves as nourishment to the sporocytes (Fig. 2.2B,C).

The numerous colourless kidney-shaped spores formed in tetrads, are all alike and disperse through slits in radial walls of the synangium. In

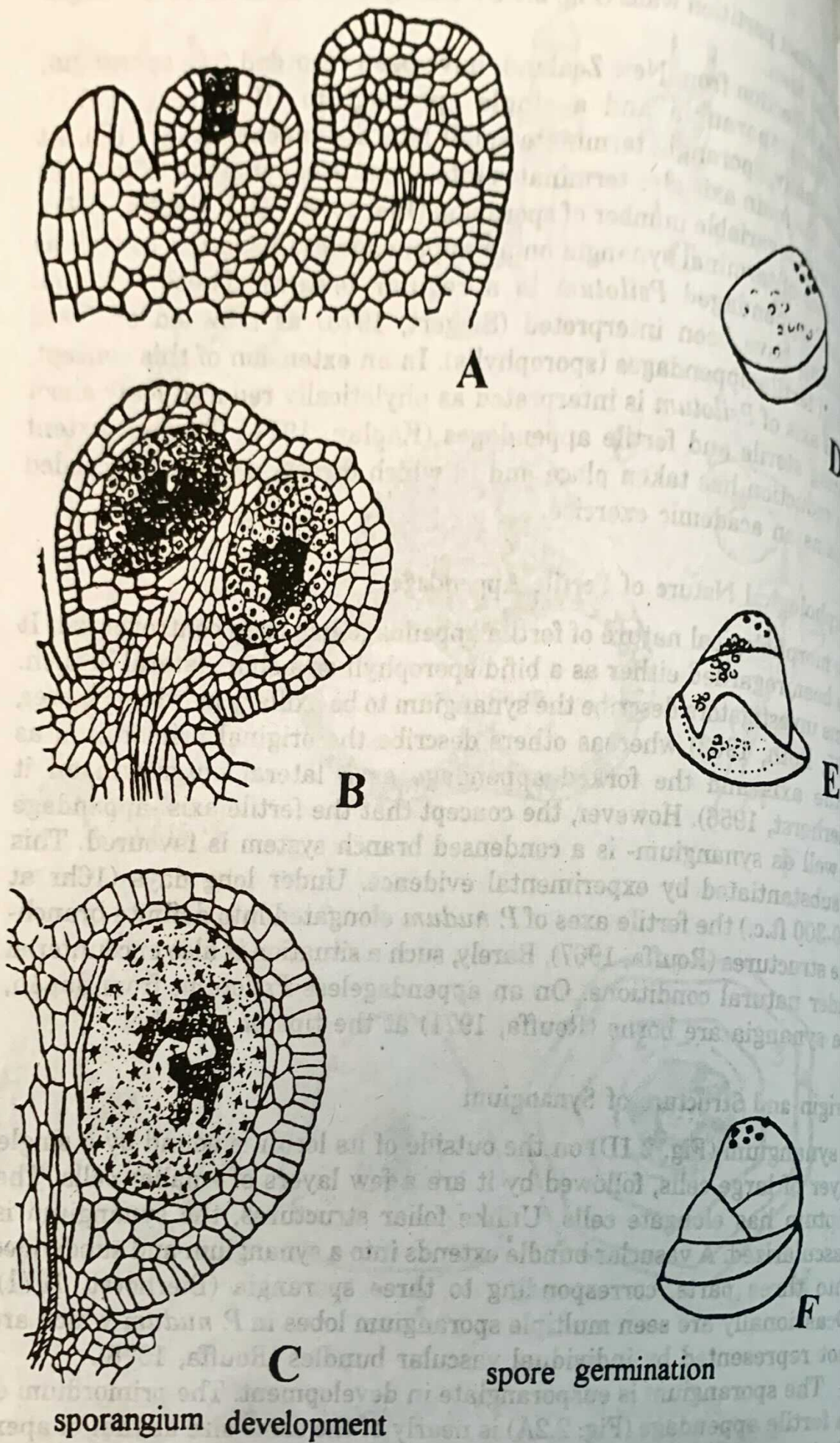


Fig. 2.2 *Psilotum*, origin and development of sporangium.
 A, *P. nudum*, vs of stem apex, showing sporangial initials on a hump, on the adaxial face of a bract. B-C, the same, at later stages of development. D-F, stages of spore germination.

subcellular features spore wall layers resemble more specifically with those of fern family Gleicheniaceae rather than lower pteridophytes (Lugardon, 1979).

Evolution of Synangium

About the evolution of a synangium it has been proposed (Eggert, 1974) that it might have evolved either by fusion of a group of individual sporangia, each borne on a separate axis, (as seen in Rhyniophytes and Trimerophytes of Devonian and Silurian), or by an evolutionary segregation of the sporogenous tissue of a single sporangium (as seen in Devonian genus *Horneophyton*). Anatomical and morphological data are supportive evidences showing that a synangium is derived from terminal subdivisions or bifurcations of the apical meristem (Rouffa, 1978). This is in favour of phyletic concept that synangium of Psilotaceae is basically terminal to an axis or axis homologue and it is probably evolved from terminal bifurcative branching.

Two phyletic models of synangium evolution are proposed (Rouffa, 1978) that can be used to explain this phenomenon and which should be tested by further evidence. According to first hypothesis, which is in essence based on telome concept, the synangium is derived from phyletic fusion of several ancestral terminal bifurcations each ending into an unlobed sporangium, supplied with a single vascular bundle. The second hypothesis derives the synangium from several massive and lobed sporangia.

Despite these explanations and supportive evidences from fossil record the evolution of *Psilotum* synangium remains to be answered convincingly. The main limitation is lack of substantive evidence.

Gametophyte

The spores germinate after four months and form gametophytes. During spore germination (Fig. 2.2 D-F) no rhizoid is formed and after a few divisions an apical cell is established which initiates the axial growth of the gametophyte.

The gametophytes are irregularly branched cylindrical structures covered with rhizoids (Fig. 2.3 A). They closely resemble pieces of rhizome and remain either underneath the humus in soil or in organic accumulation on tree trunks and are, therefore, difficult to trace. Each gametophyte is a simple parenchymatous structure with a prominent apical cell. It lacks differentiation and quite early in its development comes to have mycorrhizic association. The gametophytes are non-green saprophytic structures, supported by fungal association. The fungus enters through rhizoids and invades all the cells except the apical meristem. The hyphae are a good source of lipids which are, used as energy source by the gametophyte. The entire gametophytic surface, including rhizoids, has a cuticular covering. The gametophytes of tetraploid *P. nudum* are known to have a central vascular cylinder. Occasionally, it is a complete

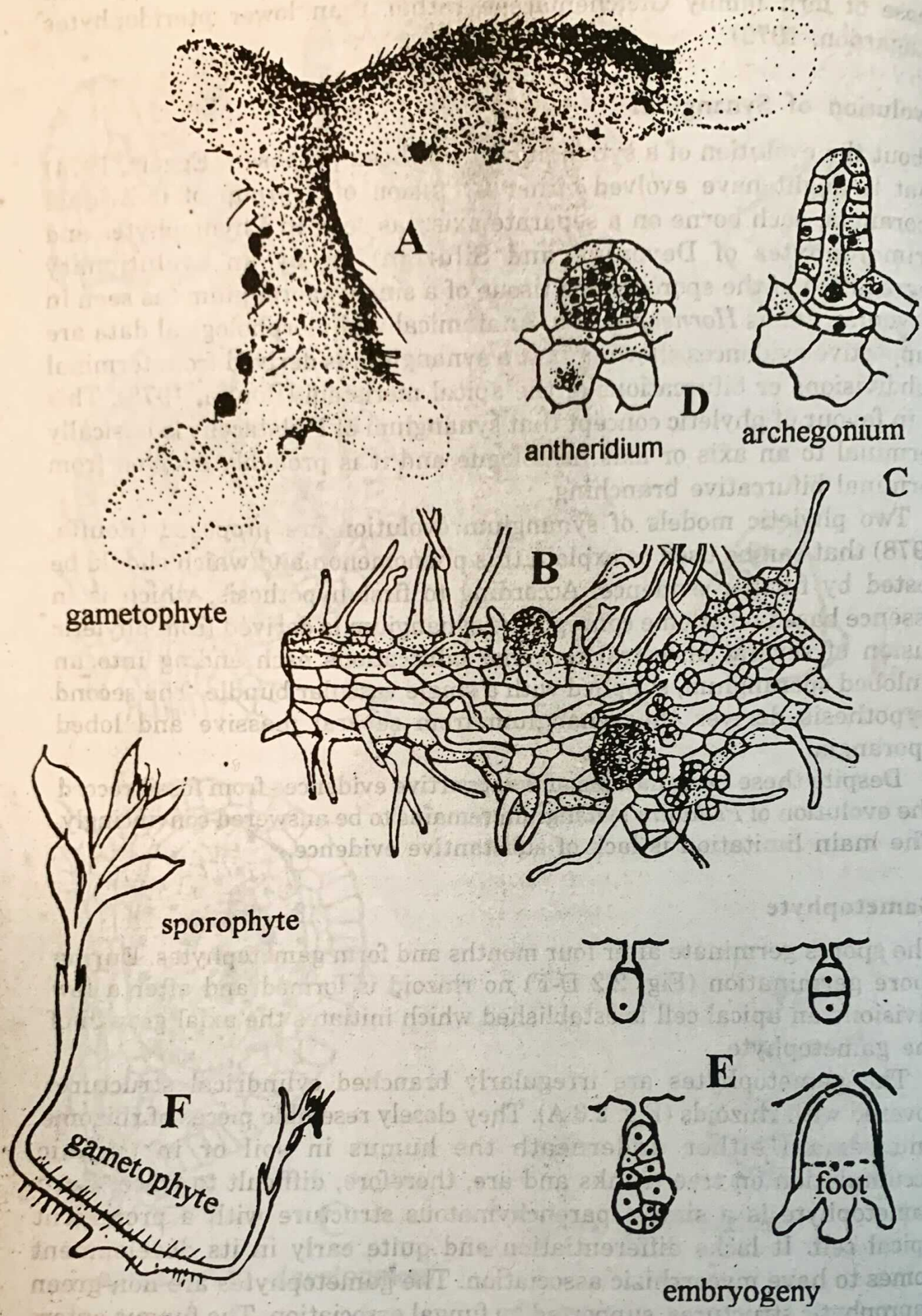


Fig. 2.3 *Psilotum* and *Tmesipteris*, gametophyte and embryony. A,B, gametophytes of *Psilotum* and *Tmesipteris*. C,D, mature archegonium and antheridium. E, stages of embryony. F, young sporophyte with both ends of gametophyte producing sporophytes.

stele with 1-3 tracheids surrounded by phloem and endodermis or is represented merely by a few elongate thick-walled cells. There is no vascular tissue in gametophytes of diploid races. A diploid strain ($n=52$ to 54) occurs in Ceylon (Manton, 1950) and Fiji and New Caledonia (Bierhorst, 1968). Other populations (Tryon & Tryon, 1982) from different parts of world are tetraploid ($n = 104$) and octoploid ($n = 210$).

Sex organs, antheridia and archegonia, occur in large numbers all over the gametophyte (Fig. 2.3 A,B). The archegonium (Fig. 2.3 A-C) is embedded in gametophyte at its venter, the neck is projecting. The antheridium is large superficial structure (Fig. 2.3 A,B,C) with one-cell-thick jacket of variable cells and encloses numerous spirally coiled multiflagellate antherozoids.

First division of zygote is transverse (Fig. 2.3 E), forming outer epibasal cell and inner hypobasal cell. The latter divides repeatedly to form a lobed "foot" (Fig. 2.3 F) and from the former is derived the rhizome. This embryogenic pattern in which shoot-forming apical cell is directed outwards is described as 'exoscopic' and is characteristic of liverworts and mosses and is quite uncommon in pteridophytes. Also during embryogeny is formation of calyptra-like outgrowth due to proliferation of gametophytic tissue from which the sporophyte has to emerge.

Anatomy

Growth of rhizome and aerial branches takes place by divisions of a single apical cell. During dichotomy it divides equally, forming two apical cells which result in two meristems.

Internal structure of rhizome varies with its diameter. Slender rhizome (about 1 mm in diameter) is a simple parenchymatous structure. An increase in diameter is accompanied with cellular differentiation. To begin with, in the centre can be seen elongate cells. Larger rhizome has a well-developed central vascular cylinder (Fig. 2.1 G) which is a typical protostele, (central core of xylem surrounded by phloem). The xylem lacks differentiation into protoxylem and metaxylem. Structure of stele also varies with diameter of rhizome. Smaller rhizome has a compact vascular cylinder but in larger rhizome the xylem mass is dissected to various degrees by differentiation of parenchyma. Cortical cells of rhizome are infested with fungus. In addition to its avascular to vascular nature which depends on its thickness, in the rhizome can be seen longitudinal interruptions of stele.

In aerial axis also, the vascular cylinder varies all along its length. The basal part is similar to rhizome, in having a protostele which is with or without stelar 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 (Fig. 2.1 H) and triarch to diarch in distal region (Fig 2.1 I). Protoxylem points are at the ends of stellate xylem (exarch) and poorly developed phloem surrounds xylem. Light microscope has failed to provide detailed information (Esau,

1969) about structure and development of phloem as compared to electron microscope (Perry & Evert, 1975). Young sieve elements are characterized by distinctive plastids, presence of refractive spherules and dense cytoplasm. With increasing age the sieve-element wall undergoes a marked increase in thickness. At maturity, the plasmalemma-lined sieve elements have a parietal network of ER, plastids, mitochondria and remnants of nuclei. P-protein and callose are lacking at all stages of development. Enclosing the phloem are several layers of pericycle cells and an endodermis with casparian strips in radial walls.

In cortex 3 or 4 zones (Fig.2.1 H) can be identified. The innermost zone is marked with its brown cell contents (phlobaphene, an oxidation condensation product of tannin). It is followed by a parenchymatous zone, without intercellular spaces, and the third zone is sclerenchymatous. The last cortical zone comprises vertically elongated cells which are full of chloroplasts. Small intercellular spaces in this region connect to the outer atmosphere through stomata in the cutinized epidermis. The stomata are slightly sunken, confined to furrows and are with small substomatal chambers. The stomata are without special subsidiary cells (Pant & Mehra, 1963). It is comparable to situation in gymnosperms. As the plants lack leaves this cortical zone is assimilatory in function.

Internally an appendage consists of photosynthetic parenchyma cells. There is no vascular bundle in the appendage of *P. nudum* but in *P. complanatum* a leaf trace ends at the base of foliar structure.