Funaria

as a stalk is taken over by a gametophyte-derived *pesedopodium.*

(j) The columella has the shape of a hemisphere.

(k) The capsule lacks peristome teeth.

(l) Cell walls of peat moss bind large amount of organic substance of colloidal nature. The cell walls function as ion exchanger which absorb calcium and magnecium ions and release hydrogen ions. Thus, they create and maintain a nutrient poor acidic environment (pH 3-4) that fosters their own growth, but is intolerable to all but a small variety of highly-specialised other plants.

FUNARIA

Systematic position

Phylum.	Bryophyta
Class.	Bryopsida
Sub-class.	Funariidae
Order.	Funariales
Family.	Funariaceae

Total number of species – About 117

Number of species found in India – About 18

Common Indian species – *Funaria hygrometrica, F. leptopoda.*

Distribution and Habitat – *Funaria* is a common terrestrial moss, grows both in tropical and temperate regions of the world. The plants prefer moist, shady places and grow in close tufts on damp alkaline soil, moist rocks, damp walls, burnt up lands and, rarely, on tree trunks.

THE PLANT BODY (THE ADULT GAMETOPHYTE)

External features

The erect gametophytic plant (Fig. 6.47A) is about an inch high with an erect leafy axis or stem attached to the substratum by rhizoids. The axis is radial, often branched axillary or extra-axillary. The axis is covered with spirally arranged leaves which are more crowded near the apex forming a rosette. Actually eight leaves are arranged in three complete spirals forming 3/8 phyllotaxy corresponding to the three cutting faces when young. The leaves are simple, sessile, ovate, with pointed apex, smoothed margin, attached to the stem by a broad base (Fig. 6.47B). The mature leaves have midribs but younger leaves are devoid of midribs.

The rhizoids are strong, much-branched multicellular (Fig. 6.48B). They are characterised by the presence of oblique septa. Young rhizoids are colourless but become brown or black when mature. The branches of rhizoids often produce chloroplasts when exposed to sunlight. They function as anchoring and absorbing organs.

Internal features

Stem : The transverse section of the mature stem shows three distinct regions viz., the outer **epidermis,** middle **cortex,** and the inner **central strand** (Fig. 6.47C).

Epidermis : It is the outermost layer of the stem. The epidermal cells contain chloroplasts and have no pores or stomata.

Cortex : It is a multilayered zone between the epidermis and the central cylinder and consists of large parenchymatous cells. The cells of the cortex contain chloroplasts when young but they are lost when the stem matures. All cortical

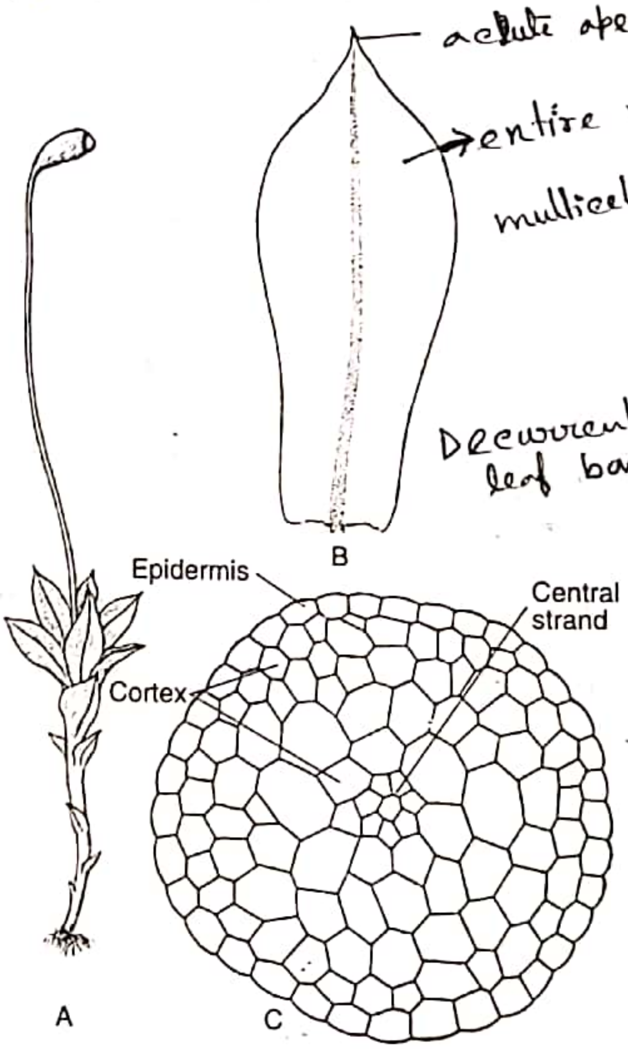


Fig. 6.47 : *Funaria hygrometrica* : A. Gametophyte plant with a mature sporophyte, B. A leaf, C. T.S. of gametophyte stem

cells of a young stem are alike, but as the stem matures the outer cells of the cortex become thick-walled and reddish-brown. The cortex also shows isolated patches of small cells in the peripheral region, representing the leaf traces. However, these traces have blind ends and do not join the central cylinder.

Central cylinder : It is composed of long, narrow, thin-walled colourless cells. These are dead cells and devoid of protoplasm, possibly help in the conduction of water and solutes.

Leaf : A transverse section of the leaf shows a well defined central midrib and the one-celled thick lamina (Fig. 6.48A). The midrib has a small strand of slightly thickened narrow cells, probably help in conduction. Lamina cells are elongated, thin-walled and rich in chloroplasts. The leaves are devoid of stomata or hairs.

Reproduction

Funaria reproduces both vegetatively and sexually.

Vegetative reproduction

Vegetative propagation in *Funaria* is performed by the following methods :

(a) *Fragmentation of primary protonema* : The primary protonema is developed through the germination of the spore. Under certain circumstances, it breaks into several fragments. Each detached fragment bearing buds may grow into a new plant.

(b) *Secondary protonema* : The protonema developing from any part of the plant other than spores are called secondary protonema. Generally, they are formed on injured rhizoids, stems, leaves or reproductive structures. They bear buds that are capable of growing into a new plant (Fig. 6.48B).

(c) *Bulbil* : The bulbils are multicellular, brown, bud-like structures that develop on the rhizoidal branches. The bulbils are useful for propagation during unfavourable environmental conditions by detaching them from the parent plants.

(d) *Gemmae* : Gemmae (Fig. 6.48B) are multicellular green bodies formed from the terminal cells of the protonema. They remain dormant throughout the unfavourable condition. However, on return of favourable condition, a gemma detaches from the parent plant body and later germinates into a new plant.

(e) *Apospory* : Apospory is the condition in which the haploid (n) gametophyte is developed from the diploid (2n) sporophyte without the formation of spores. In case of *Funaria*, gametophytic protonema may develop from any unspecialised cells of the sporophyte. This protonema later, gives rise to gametophyte plant body. Though aposporously develop, gametophytes are normal in appearance, but are diploid (2n). Subsequently, the tetraploid sporophyte develops from the fusion of diploid gametes (2n) are sterile.

Sexual reproduction

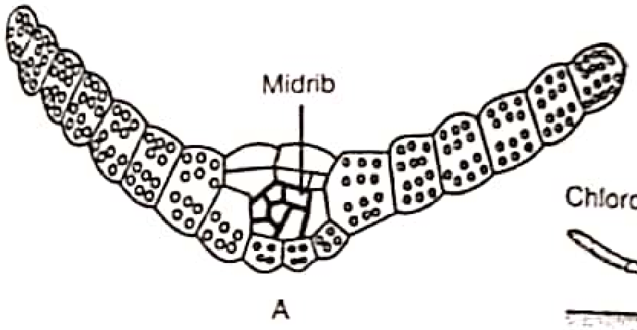
Funaria is autociously monoecious, because the male (antheridium) and female (archaegonium) reproductive structures develop on separate shoots of the same plant. Antheridia are borne on the main shoot of the plant. The female branch develops as a side shoot (Fig. 6.53), which grows more vigorously and becomes longer than the male branches.

Antheridium

The antheridia are borne in clusters at the apex of the main axis. A number of long multicellular hairs, called **paraphyses** are intermingled with the antheridia (Fig. 6.53). Both antheridia and paraphyses are surrounded by a number of bract-like leaves forming a rosette called the **perichaetium**. The paraphyses have swollen tips (capitate) and contain chloroplasts. Besides their photosynthetic function, paraphyses protect the young antheridia against desiccation. The paraphyses assist in the liberation of **antherozoids**.

Development of the antheridium

The antheridium develops from a superficial **antheridial initial** located at the tip of the male branch (Fig. 6.49A-G). It becomes papillose and projects above. It divides by a transverse wall to form an **outer cell** and a **basal cell**. The outer cell divides further by successive transverse divisions to form a linear filament of 2 to 4 cells. The terminal cell of the filament divides by two vertical intersecting walls to form a wedge-shaped apical cell with two cutting faces. It forms segments in two rows in alternate sequence. Each young seg-



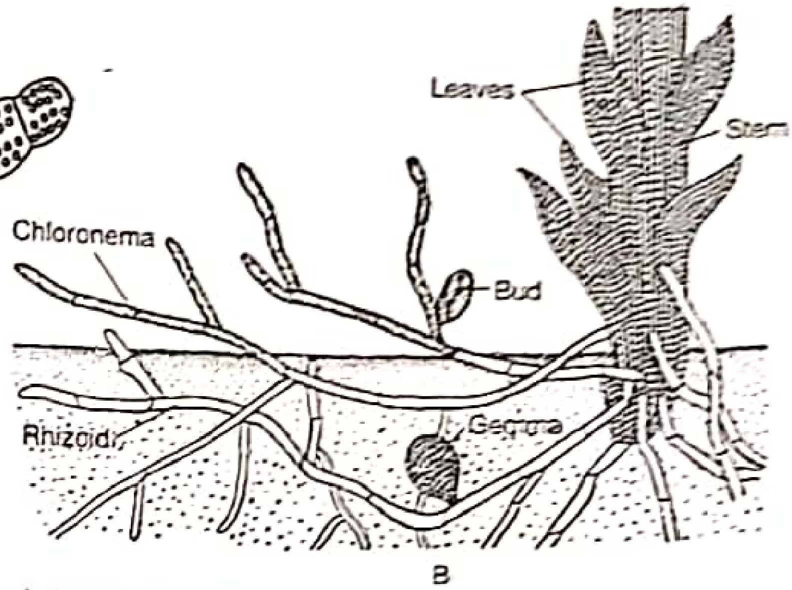


Fig. 6.48 : *Funaria hygrometrica* : A. T.S. of leaf, B. Gemma on gametophyte base.

ment of the upper 3 to 4 cells now divides by a vertically diagonal wall to form two unequal cells. The smaller peripheral cells are the first jacket initials. While, the larger sister cell, by a similar division, forms the outer second jacket initials and the inner primary androgonial cell.

The primary androgonial cell divides and redivides to form **androcyte mother cells.** Each androcyte mother cell divides to form two **androcytes.** The androcytes transform into biflagellate **antherozoids** or **sperms** (Fig. 6.49H). Antheridia in an antheridial head mature at the different times. Thus, antheridia of different developmental stages can be seen in a single antheridial head. The jacket initials only divide anticlinally to form a single-layered **antheridial jacket.**

Mature antheridium

A mature antheridium has a multicellular long stalk and a red or orange coloured club-shaped body (Fig. 6.49G & 6.53). The apical cell of the jacket forms a thick-walled, hyaline **operculum** or **cap** of the antheridium.

Dehiscence of the antheridium

The dehiscence of the mature antheridium only takes place in presence of water. The opercular cell absorbs dew or rain water and swells up. The pressure thus created ruptures the inner wall and eventually a pore is formed at the distal end of the antheridium. The androcytes spread out through the pore in the form of a viscous fluid due to the hygroscopic pressure developed within the antheridial cavity (Fig. 6.53).

Archegonium

The archegonia are borne in clusters at the apex of the archegonial branch (Fig. 6.53).

Development of the archegonium

A cell at the tip of the female shoot differentiates into the **archegonial initial.** It divides transversely to form a **upper cell** and a **lower cell** (Fig. 6.49I, J). The upper cell becomes the **archegonial mother cell** which divides by two intersecting oblique walls forming an **apical cell** with two cutting faces (Fig. 6.49K). The apical cell further divides by three intersecting oblique walls to form three **peripheral cells** surrounding a central **axial cell** (Fig. 6.49L). The peripheral cells divide anticlinally to form a single-layered **jacket** (Fig. 6.49M) which, by further divisions, becomes double-layered. The axial cell divides by a transverse wall to form an outer primary **cover cell** and an inner **central cell** (Fig. 6.49N, O). The central cell, by further transverse division gives rise to an outer **primary neck canal cell** and an inner **primary ventral cell.** Primary neck canal cell, by further transverse divisions, forms a row of **neck canal cells.** The primary ventral cell, by further transverse divisions, forms a **ventral canal cell** and an **egg** (Fig. 6.49P, Q).

The primary cover cell cuts off successively three lateral segments and a basal segment. The lateral segments form the **jacket** of the neck, while the fourth basal segment forms **neck canal cells.** Thus, the single-layered long neck of the archegonium of *Funaria* have double origin, one from primary cover cell and the other from central cell.

Mature archegonium

The mature archegonium consists of a long **stalk**, a basal swollen **venter** and an elongated **neck** (Fig. 6.49Q & 6.53). The twisted and tubular neck encloses 4 to 10 or more neck canal cells. The archegonial jacket is single-layered thick in the neck region, but it is double-layered in the region of the venter. The venter contains a ventral canal cell and an egg.

Fertilisation

During fertilisation, the ventral canal cell and the neck canal cells of the archegonium disintegrate forming a mucilaginous substance. This mucilaginous substance absorbs water accumulated as rain or dew water, then swells up and the resultant pressure breaks apart the terminal cover cell. Now sugar containing mucilaginous substances ooze out through the opening of the archegonial neck.

The liberated antherozoids are now attracted chemotactically towards the archegonia. A large numbers of antherozoids enter the neck, but only one of them fuses with the egg nucleus to form the diploid **zygote.**

THE SPOROPHYTE

The fertilised egg or zygote is the first cell of the sporophytic generation. The zygote swells up, increases in size and forms a wall around it prior to further divisions.

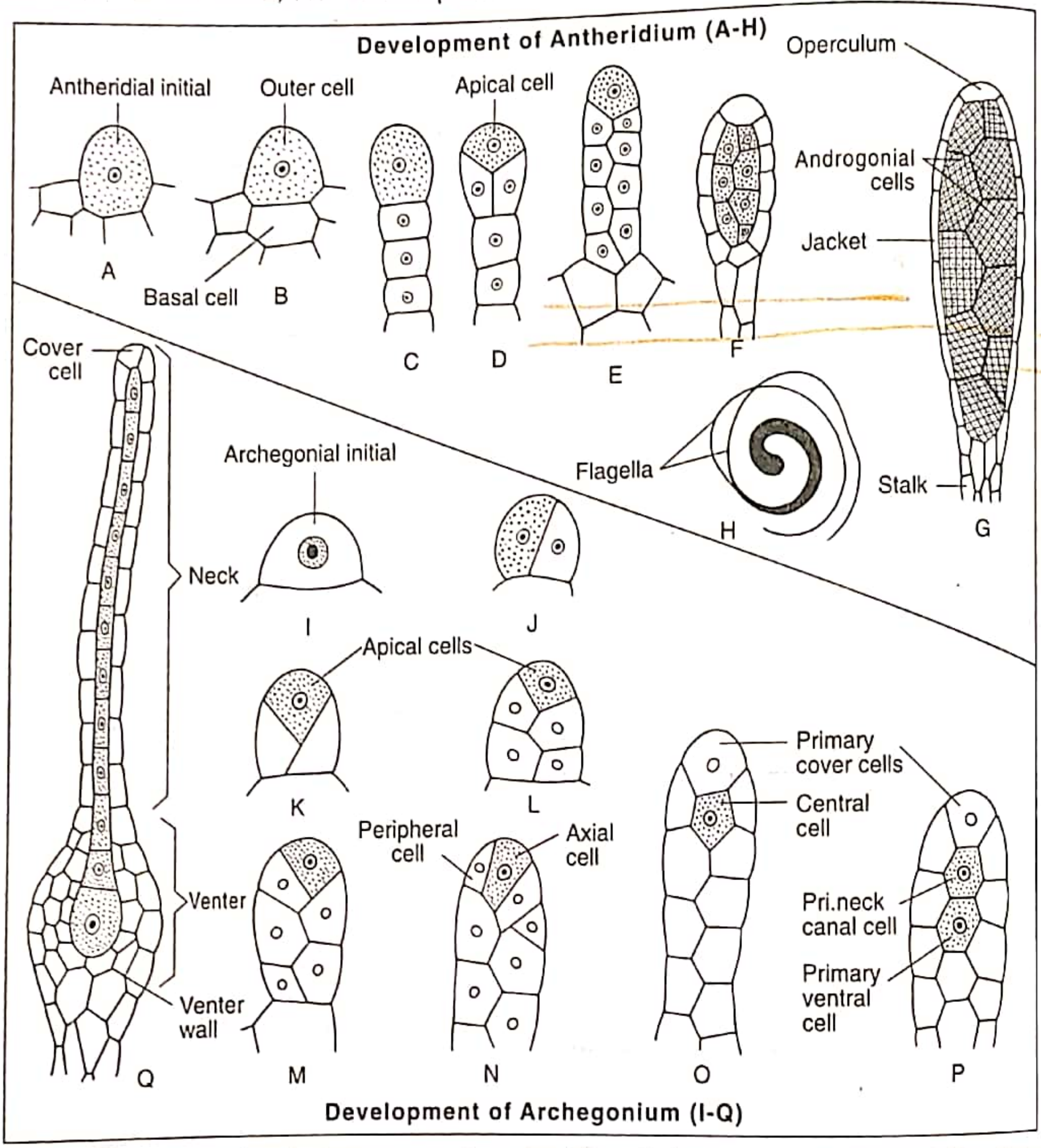


Fig. 6.49 : *Funaria hygrometrica* : A-G. Development of antheridium, H. A sperm, I-P. Development of archegonium, Q. A mature archegonium

Development of the sporophyte

The zygote divides transversely to form an upper **epibasal cell** and a lower **hypobasal cell.** Both the hypobasal and epibasal cells divide repeatedly to form an young embryo with two growing points at the two opposite ends, each representing an **apical cell** with two cutting faces. The archegonial wall enlarges and forms calyptra which covers the capsule till maturity. A long slender sporophyte is then differentiated. The capsule differentiates at a later stage where the amphithecium surrounds the endothecium. The multilayered jacket of the capsule is formed from the amphithecium, while the outer layers of endothecium forms the archesporium and axial layer produces the columella. The epibasal cell gives rise to the capsule and the upper part of the seta, while the hypobasal cell forms the lower part of the seta and the foot.

Structure of the mature sporophyte

The mature sporophyte of *Funaria* is differentiated into a **foot**, a long **seta** and a pear-shaped **capsule** at the tip.

Foot : It is a poorly developed conical structure embedded in the apex of archegonial branch.

Seta : Seta is long, green in colour when young, but becomes reddish brown at maturity. T.S. of seta shows a single-layered epidermis, a central conducting strand of thin-walled cells surrounded by a cortex made up of comparatively thick-walled cells (Fig. 6.50A). Seta helps in conduction of nutrients and water from gametophyte to capsule.

Capsule : The mature capsule is pear shaped, asymmetrical (Fig. 6.50B, C). Internally, it is divided into three distinct parts viz., the sterile basal region, **the apophysis**, the central fertile region, **the theca** and **the apical-region**.

Apophysis

The lowermost part of the capsule is the apophysis or the neck that connects it with the seta below. The axis of the apophysis shows in the lower part a central strand of thin-walled elongated cells connected with the similar tissue of the seta. Loosely arranged chlorophyllous cells are bounded by a rather thick-walled epidermis which is interrupted by the stomata (Fig. 6.50C).

The presence of chlorophyllous tissue in the apophysis makes the sporophyte carry out photosynthesis. Therefore, the sporophyte of *Funaria* is not fully dependent on the gametophyte for nutrition.

The theca or fertile zone

The central zone of the capsule situated in between the apophysis and the operculum is called the **theca**. It is a slightly bent cylindrical structure, fertile in nature and has four distinct regions — (a) capsule wall, (b) spore-sacs (c) air chamber and (d) columella.

(a) Capsule wall

The capsule wall is many-layered. The single-layered outermost wall forms the epidermis which is followed by a 2-3 layered parenchymatous hypodermis (Fig. 6.50C). The inner 2-3 layers of parenchymatous cells are chlorophyllous, which constitute the photosynthetic tissue of the capsule.

(b) Spore sacs

The columella is surrounded by two elongated spore-sacs (Fig. 6.50C). The spore-sac has a inner wall of one layer of small cells and an outer wall of 3 to 4 layers of such cells. The spore sacs are formed from the single layered archesporium. Archesporium first develops 6-8 layers of sporogenous cells. The sporogenous layer becomes a spore-sac by the production of spores from spore mother cells through meiotic divisions.

(c) Air chamber

The outer wall of the spore-sac is followed by a big cylindrical air chamber. It is traversed by strings of filaments of elongated green cells, known as **trabeculae** which bridges the air space between the outer wall of the spore-sac and the innermost layer of the capsule wall (Fig. 6.50C).

(d) Columella

It is the central, axial part of the fertile zone, comprising of thin-walled, colourless, compact, parenchymatous cells, constricted at the base just above the apophysis (Fig. 6.50C). The distal part of the columella is cone-shaped which projects into the concavity of the operculum. The columella serves the purpose of conduction of water and nutrients to the growing sporophyte.

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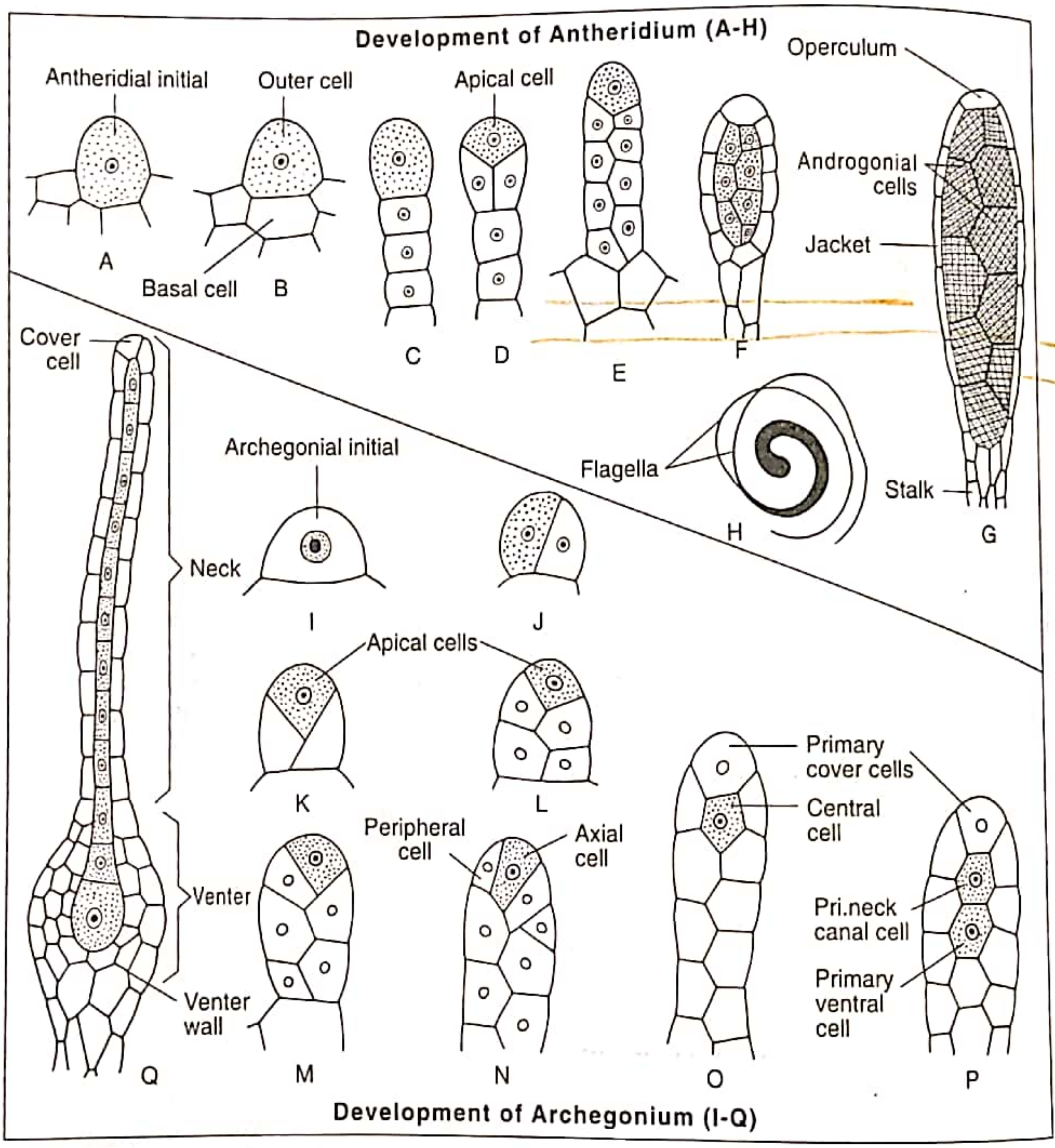

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Acrocarpic – female branch is present in the apex of main axis.
Pleurocarpic – just below the apex.

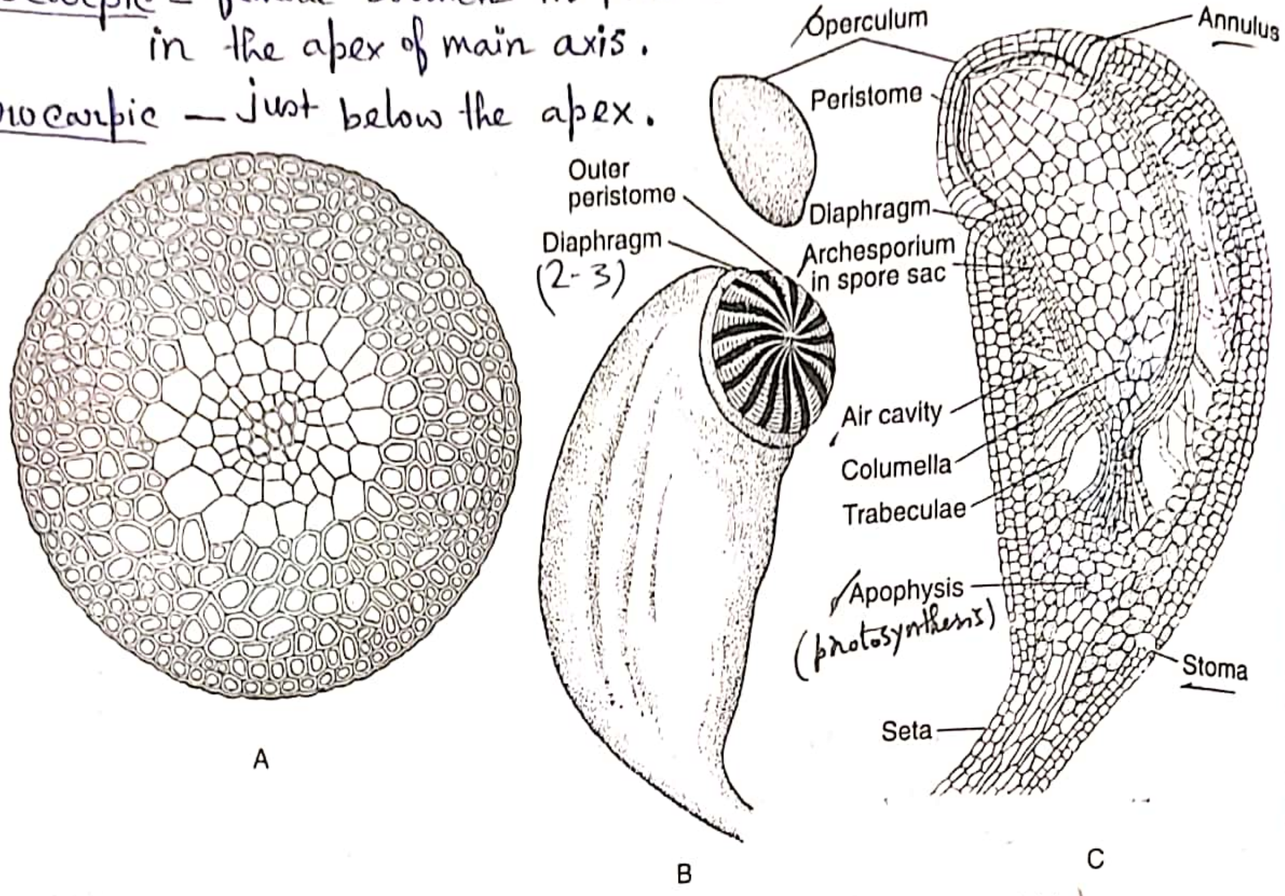

Fig. 6.50 : *Funaria hygrometrica* : A. T.S. of seta, B. Mature capsule with operculum removed (shown on side), C. L.S. of capsule

The apical region

The apical region of the capsule is a complicated structure. This joins the capsule proper through a notch (Fig. 6.50B, C). An **annular rim** (or **diaphragm**) of 2-3 layers of radially elongated small cells is present at this notch. The diaphragm demarcates the upper limit of the theca proper.

The **operculum** is an obliquely placed, dome-shaped lid that closes the mouth of the capsule (Fig. 6.50B). It is composed of 2 to 3 layers of thin-walled parenchymatous cells (Fig. 6.50C). The lower part of the operculum forms a ring of slightly large conspicuous cells, the **annulus.** The operculum keeps the **peristome teeth** covered, while the annulus helps in the dehiscence of the capsule.

The peristome teeth lies just below the operculum and are attached beneath the edge of the diaphragm. It consists of two rings of long triangular teeth, one within the other (Fig. 6.51A, B). The teeth are not cellular in nature and are made up of cuticle.

Each ring of peristome possesses 16 teeth. The outer teeth (**exostome**) are larger, thicker, brown in colour and ornamented with transverse thickening bands. The inner peristome teeth (**endostome**) are small, delicate and of a pale colour. The whole structure is called **peristome** which is **epicranoid** in nature, because the outer peristome teeth are superposed on the inner ring. The tapering distal ends of the outer peristome teeth are joined to a centrally placed disc of tissue (Fig. 6.50B & 6.51A).

Dehiscence of the capsule and the dispersal of spores

At maturity, the operculum begins to dry up due to the non-availability of water supply to the capsule. Consequently, the thin-walled cells of the operculum, including the annulus which hold the operculum in place, shrink and shrivel. Ultimately, the annulus breaks and the loosened operculum is thrown away leaving the peristome teeth exposed (Fig. 6.50B).

The peristome teeth are twisted spirally appearing like an iris diaphragm (Fig. 6.50B).

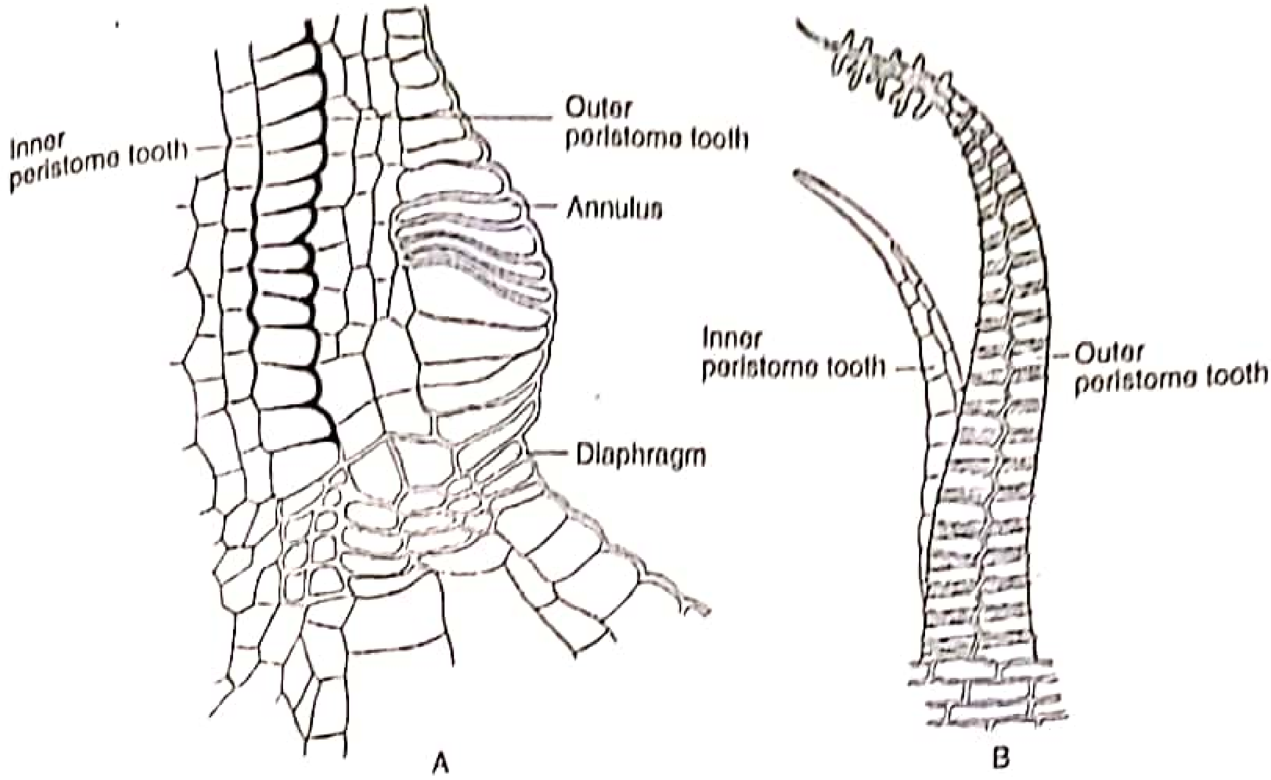

Fig. 6.51 : *Funaria hygrometrica* : A. L.S. of capsule at diaphragm-annulus region (after Sachs), B. Diplolepideous epicranoid peristome teeth (an inner and an outer peristome teeth shown)

The outer peristome teeth are hygroscopic which show inward or outward movements according to the presence or absence of moisture in the environment. During dry atmosphere, the outer peristome teeth bend outwards with jerky movements. The slits between the inner peristome teeth widens due to the outward movements of the outer peristome teeth, thus allowing the spores to escape through these slits. In high humidity, the hygroscopic teeth of the outer peristome absorb water and bend inwards and close the slits. This prevents the escape of spores in wet weather.

The young sporophyte is covered by **calyptra** that develops from the old archegonial venter wall. It protects the capsule from drying and sheds prior to its dehiscence.

The New Gametophyte

The haploid **spore** is the first cell of the gametophytic generation. It is small, spherical, measuring 12-20 μm in diameter. The spore wall is differentiated into an outer thick, brown coloured **exine** (**exosporium**) and an inner thin, colourless **intine** (**endosporium**) (Fig. 6.52A).

Under favourable environmental conditions the spore germinates. The exine is ruptured and the intine protrudes out as a germ tube (Fig. 6.52B, C). The germ tube elongates, becomes septate and produces a filamentous **protonema** (Fig. 6.52D, E). The protonema branches freely and forms two types of branches viz., **chloronemal branches** and **rhizoidal branches** (Fig. 6.52F). or Caulonema

The chloronemal branches possess conspicuous chloroplasts in their cells and become green in colour which are either erect or very close to the substratum that form the partition walls at right angles to the lateral walls. The rhizoidal branches develop below the substratum, brown in colour and the partition walls are oblique to the lateral wall. The rhizoidal filaments are primarily meant for anchoring the protonema in the substratum.

The chloronemal branches develop many minute buds (Fig. 6.52F) and each bud grows into an erect leafy gametophore. They become independent shortly after the death of the protonema. A dense growth of the plants are observed because of this property. An young gametophyte comprises of leafy stem, rhizoids and protonema.

Fig. 6.53 depicts the diagrammatic representation of the life cycle of *Funaria hygrometrica*.

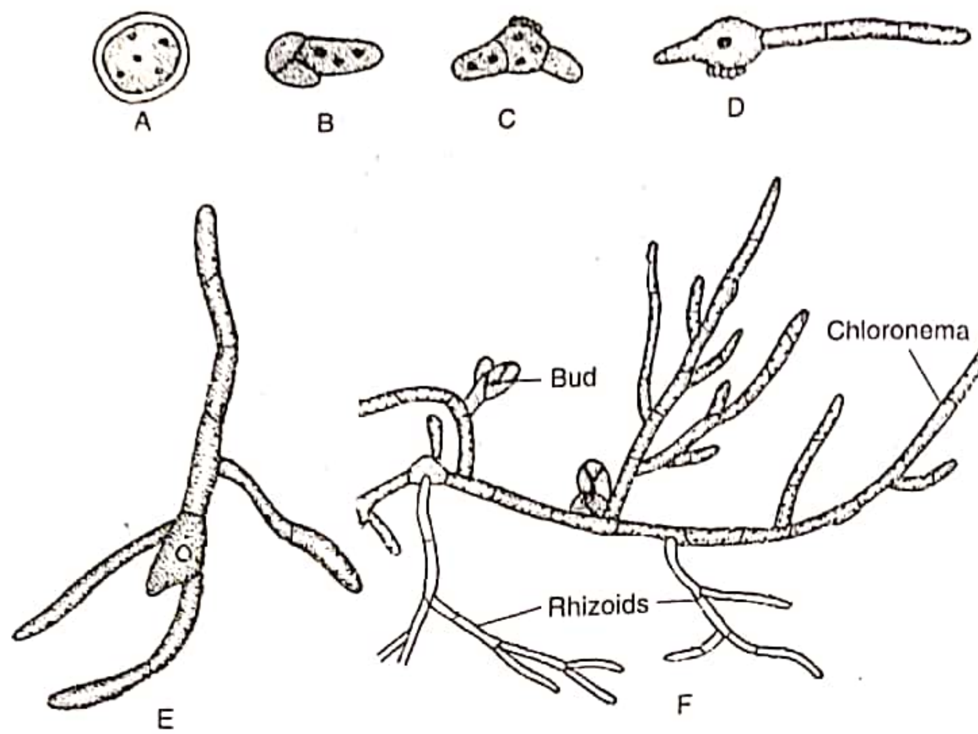

Fig. 6.52 : *Funaria* : A. Spore, B-F. Germination of the spore and development of the Protonema

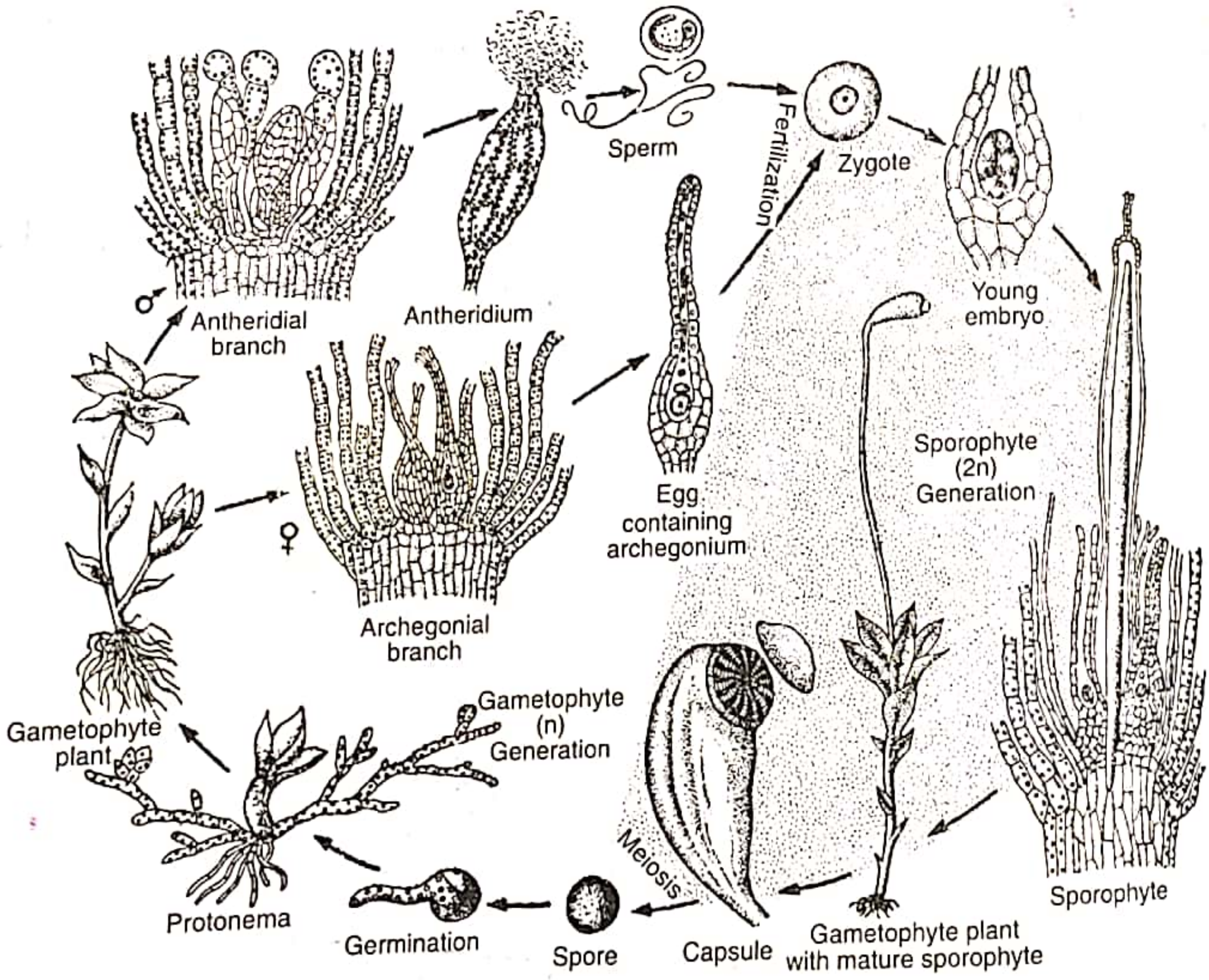

Fig. 6.53 : The life cycle of *Funaria hygrometrica*