FUNARIA

A common moss, widely distributed in temperate as well as tropical regions of the world. One of the species *F. hygrometrica,* is cosmopolitan and best known. It is a terrestrial plant growing in close tufts and is one of the pioneers to colonise recently burnt forest land. It also occurs on moist rocks. In India this species is a common moss of hilly tracks and mountains. It is also found on moist soil of garden beds, and in crevices on walls of old abandoned buildings.

The plant body is a leafy gametophyte (Fig. 4.1A, B) about 1-3 cm high, consisting of an erect axis (stem) covered with small, simple and sessile leaves. The stem is branched, monopodially, a branch originates below a leaf. At the base of stem there are numerous branched rhizoids (Fig. 4.1A) which serve for anchorage and absorption.

A leaf (Fig. 4.1C) is ovate with a pointed apex, broad base and an entire margin. It is attached to stem by its broad base and the leaves are arranged in three rows, in spiral succession. Leaves are closely placed towards apical region of plant and are widely spaced in the basal region. The leaves at the base are not very regular in shape. A leaf is unistratose except at the middle where it forms a distinct midrib or costa. The marginal cells of leaf towards the apex tend to project, giving it a dentate appearance.

The rhizoids are branched and rebranched. The main strand arising from the stem is a relatively stout structure. It grows into the soil up to a distance of about 1 cm and helps to fix the plant. From the main strand arise lateral branches, of

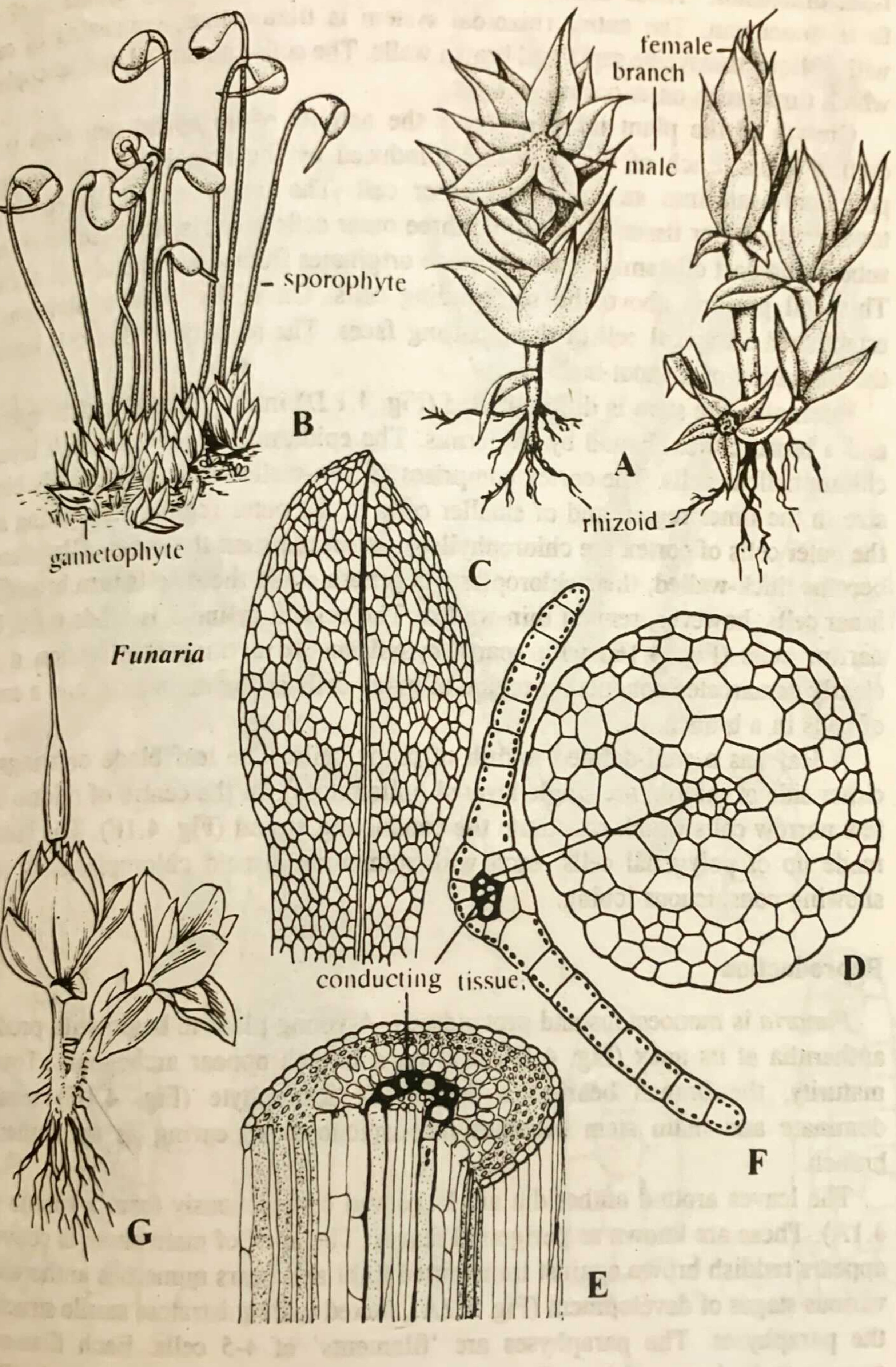

Fig. 4.1. *Funaria*, structure of gametophyte.
A, plant body, an antheridial (cup-shaped) and an archegonial head. B, a patch of *F. hygrometrica*, gametophytes bearing sporophytes. C, wholemount of a leaf, with a midrib. D, t.s. of young stem. E, 3-dimensional representation of stem showing stereid layer in cortex, a central cylinder of hydroids and leptoid-like cells around it. F, t.s. of a leaf. G, a plant with an antheridial and an archegonial branch bearing young sporophyte enclosed in a calyptra.

finer dimension. These branches in turn branch to form tertiary branches of yet finer dimension. The entire rhizoidal system is filamentous, consisting of cells with oblique transverse septa and brown walls. The cells contain oil and leucoplasts which turn green on exposure to light.

Growth of the plant takes place by the activity of an apical cell with three cutting faces. Each of the segments, produced by the apical cell, divides by a periclinal wall into an inner and outer cell. The three inner cells contribute towards the inner tissue of stem, the three outer cells give rise to three leaves and subtending part of stem. A lateral branch originates from a peripheral cell of stem. This cell projects above the surrounding cells. On it, by oblique divisions, is established an apical cell of three cutting faces. The activity of this cell leads to the formation of a shoot-bud.

Internally, the stem is differentiated (Fig. 4.1 D) into a narrow central cylinder and a broad cortex, bound by epidermis. The epidermis is one-cell-thick layer of chlorophyllous cells. The cortex comprises of thin-walled cells of relatively bigger size in the inner region and of smaller cells in the outer region. In a young stem the outer cells of cortex are chlorophyllous. In an old stem the outer cells of cortex become thick-walled, their chloroplasts degenerate and these cells turn brown; the inner cells, however, remain thin-walled. The central cylinder is made up of long narrow cells (Fig. 4.1E) with sparse cytoplasm. In a transverse section it is a clearly demarcated conducting region of many cells in the main axis, and a couple of cells in a branch.

A leaf has a well-defined midrib of many cells. The leaf blade or wings, on either side of midrib, are single layered (unistratose). In the centre of midrib are a few narrow cells which constitute the conducting strand (Fig. 4.1F). The blade is made up of polygonal cells, each with numerous discoid chloroplasts, at times showing conspicuous lobing.

Reproduction

Funaria is monoecious and protandrous. A young plant to begin with produces antheridia at its apex (Fig. 4.1A) and on a branch appear archegonia. Towards maturity, the branch bearing a developing sporophyte (Fig. 4.1G) tends to dominate and main stem becomes inconspicuous, appearing as an antheridial branch.

The leaves around antheridia are large and conspicuously form a rosette (Fig. 4.1A). These are known as perigonial leaves. The apex of main shoot is convex, it appears reddish brown against transmitted light and bears numerous antheridia, in various stages of development (Fig. 4.2A), mixed with unistratose sterile structures; the paraphyses. The paraphyses are ‘filaments’ of 4-5 cells. Each filament is narrow at the base and its cells broaden towards distal region. The apical cell of a paraphysis is invariably globose. The enlarged apical cells of different paraphyses meet over the developing antheridia and provide them protection and moisture. The cells of paraphyses are ascribed to retain moisture and prevent undue drying of antheridia.

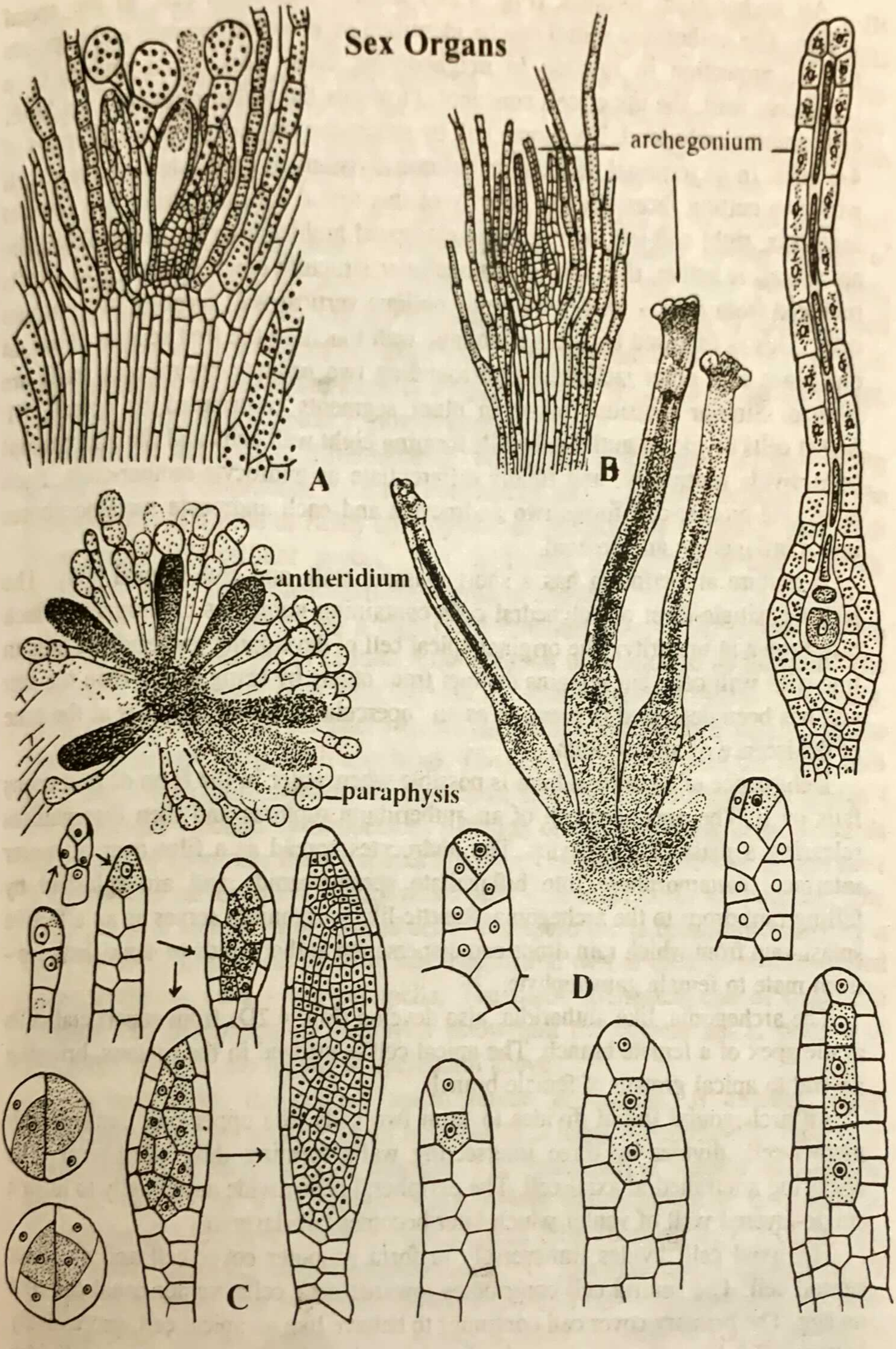

Fig. 4.2. *Funaria,* sex organs, structure and development.
A, l.s. of a male head and wholemount of male head on dissection and removal of leaves to show antheridia and paraphyses. B, l.s. of female head showing archegonia and paraphyses. C, stages in development, and a mature antheridium, D, stages in development of an archegonium, a mature archegonium and l.s. of an archegonium.

An antheridium initiates (Fig. 4.2C) from a superficial cell, at the apical region. The antheridial initial can be identified by its dense contents and papillate nature; projection in relation to neighbouring cells. This initial divides by a transverse wall, the upper cell contributes towards the antheridium and the lower cell remains embedded. The upper cell by successive divisions forms a filament of 4-5 cells. In its terminal cell, due to oblique divisions, is established an apical cell with two cutting faces. By the activity of this apical cell, in cutting two rows of segments, right and left, is formed an elongated multicellular structure. While the apical cell is active, the cells of multicellular structure down below - 3 to 4 cells removed from apex - start dividing by oblique vertical wall forming two unequal cells. This is followed by another oblique wall touching the first septum. Thus, at one place four outer jacket cells surrounding two primary androgonial cells are formed. Similar divisions occur in other segments contributed by apical cell. Jacket cells divide by anticlinal walls forming eight wall cells and the androgonial cells divide repeatedly, and finally differentiate as androcyte-mother-cells. Each androcyte-mother-cell forms two androcytes and each androcyte metamorphoses into a biflagellate antherozoid.

A mature antheridium has a short massive stalk and club-shaped body. The jacket is single-layer of polyhedral cells containing numerous chloroplasts which turn brown at maturity. The original apical cell of developing antheridium falls in line with wall cells but remains distinct from others by being larger than the rest and has been described to function as an "operculum" which detaches at the time of dehiscence of antheridium.

Dehiscence of an antheridium is possible when water in the form of rain drops falls on it. The opercular cell of an antheridium ruptures and then disorganises releasing a mass of androcytes. The androcytes spread as a film over air-water interface, metamorphose into biflagellate spermatozoids and are splashed by falling rain drops to the archegonia. Rosette-like perigonium serves as an effective splash-cup from which rain drops can disperse the antherozoids to some distance - from male to female gametophyte.

The archegonia, like antheridia, also develop (Fig. 4.2D) from superficial cells at the apex of a female branch. The apical cell is utilized in the process, bringing an end to apical growth of female branch.

An archegonial initial divides to form two cells, the upper one, archegonial-mother-cell, divides by three intersecting walls forming three peripheral cells enclosing a tetrahedral axial-cell. The peripheral cells divide anticlinally to form a single-layered wall of venter which later becomes two-layered.

The axial cell divides transversely to form an outer cover cell and an inner central cell. The central cell contributes towards neck cells, venter canal cell and an egg. The primary cover cell continues to behave like an apical cell, successively cutting off 3 lateral segments and a basal segment. Each lateral segment divides by a vertical wall so that six rows of cells form the neck of archegonium. Each basal cell adds to neck canal cell.

An archegonium is a flask-shaped structure (Fig. 4.2B) with a long narrow oblique neck of many neck canal cells, a dilated venter with a venter canal cell and an egg. The single-layered jacket of archegonium is of six rows of cells; at the venter it may become two-layered. In a mature archegonium, the neck canal cells and venter canal cell disintegrate forming a mucilaginous mass and terminal cells of neck gap apart leaving a mucilaginous passage for sperms to reach the egg. Entrance of antherozoids to an archegonium is a chemical-mediated response. Union of male and female nuclei is complete within 10 hrs. After fertilization zygote secretes a wall, enlarges and divides to give rise to an embryo.

The sporophyte (Fig. 4.1B) is differentiated into three parts - foot, seta and capsule. A foot is dagger-like conical structure embedded in the tissues of gametophyte, it serves for anchorage and absorption of nutrients. Seta is long, slender, wiry structure bearing the capsule. The capsule in turn is differentiated (Fig. 4.3A) into three regions (a) apophysis - the sterile basal portion of capsule, it is in continuity with seta, (b) theca or body of capsule, which is the fertile region, and (c) operculum, the apical region of capsule.

Apophysis shows tissue differentiation (Fig. 4.3B). In the centre is a conducting strand which is continuous with the conducting strand of seta. Surrounding the central tissue is a zone of richly chlorophyllous, transversely elongated cells with conspicuous intercellular spaces. The epidermis of apophysis has stomata. Apophysis is the main photosynthetic region of capsule.

Body or theca of capsule is a highly differentiated (Fig. 4.3A) region and can serve as a good example of cellular differentiation in relation to its function. The outermost 2-3 layers of cells form the wall of capsule. Inside a distinct epidermis, there are two layers of compact parenchyma which become one layered in the lower region and merge with apophysis. The cells contiguous with the inner wall layer are richly chlorophyllous, the innermost layer of cells has large air spaces - the trabeculae - bound by filamentous partition of chlorophyllous cells. Towards the region of apophysis the air spaces are more conspicuous. Following this zone is a region of narrow non-chlorophyllous cells - the outer cover of spore sac. The spore sac is a zone of sporogenous cells. The spore sac is bound internally by a layer of cells, inner cover of spore sac. The central part of theca is of thin-walled parenchymatous cells - the columella. The basal attenuated end of columella extends into the region of apophysis below and the conical apical portion of columella merges into region of operculum above.

The operculum, the conical apical region of capsule, is another highly differentiated region serving as an example of cellular differentiation as well as organogenesis in relation to its function. The operculum is marked off from the body of capsule by a constriction. Just below the constriction is a circular diaphragm of 2 to 3 layers of radially elongated cells, forming the rim of capsule. Immediately above the rim is annulus (Fig. 4.3A), five to six super-imposed layers of epidermal cells. The two lowest layers of annulus cells are elongated and thin-walled, other cells are thick-walled. Attached below the edge of rim is the region of peristome - two rings of 16 peristome teeth. The outer ring of 16 peristome teeth are very conspicuous by their red colour and thick transverse thickening bands; sixteen teeth of the inner ring (Fig. 4.4A) are delicate and colourless, their bases are covered by outer peristome.

An appreciation of this highly differentiated structure - the capsule - is possible in a follow up of its developmental details, starting with zygote.

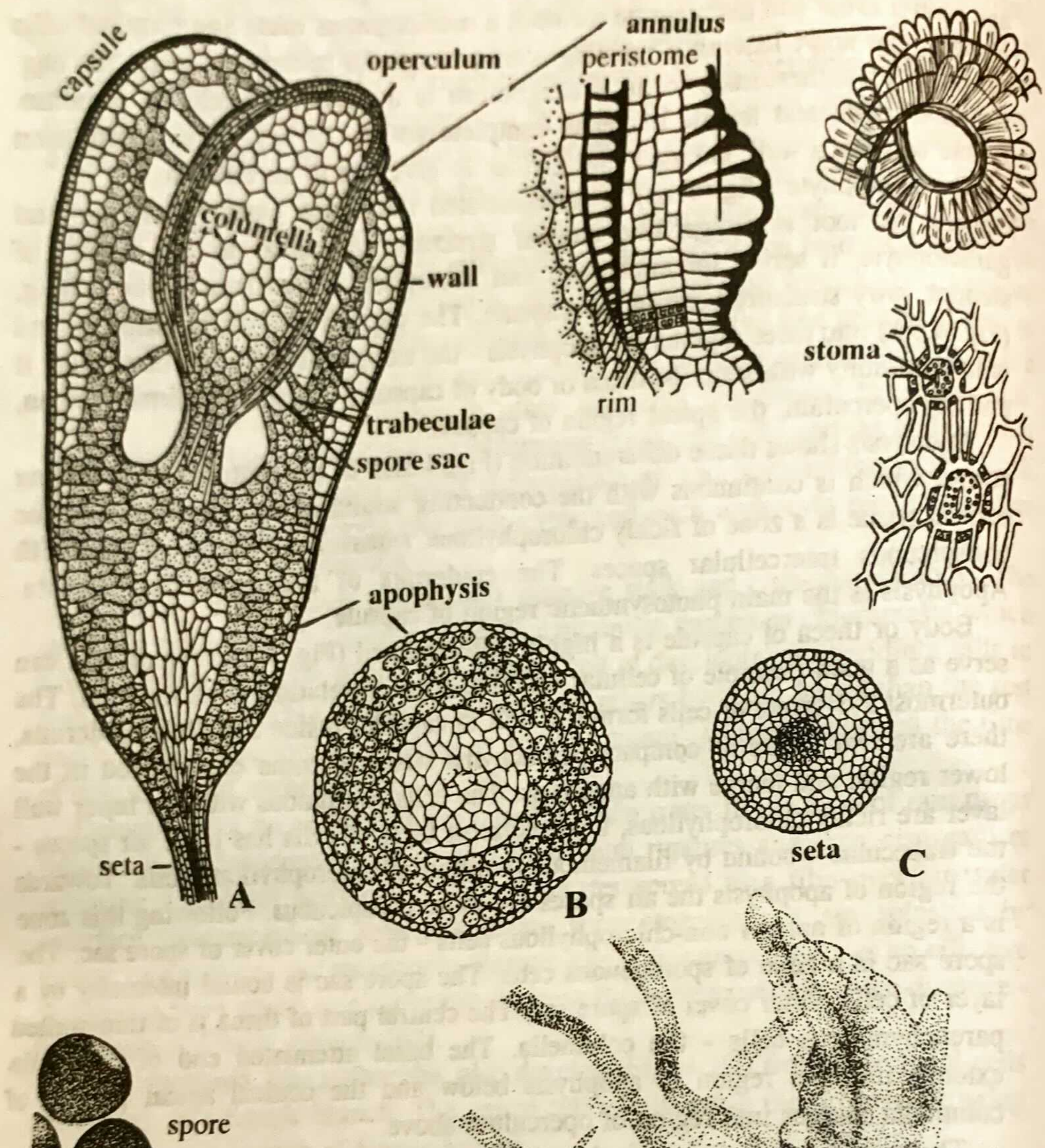

Fig. 4.3. *Funaria,* capsule and spore.
A, l.s. of capsule, cells of annulus and apophysis with stoma B, t.s. at the region of apophysis. C, t.s. of seta. D. germination of spores. E, shoot-bud on protonema.

First division of zygote is transverse (Fig. 4.7C). The epibasal cell by its two successive diagonal divisions differentiates an apical cell with two cutting faces. Similarly the hypobasal cell differentiates an apical cell. In this way the embryo at an early stage acquires polarity and the entire sporophyte is derived by the activity of these two growing points.

A young embryo (Fig. 4.7C) is long and slender. Its lower end penetrates the stalk of archegonium and tissue below it; the apex of gametophyte. During early embryogeny the venter of archegonium divides and redivides to become several cell-thick to form a calyptra which encloses the developing sporophyte (Fig. 4.1G). However more rapid growth and elongation of embryonic sporophyte results in rupture of calyptra and its severed upper portion remains as a cap on the sporophyte apex, up to the maturity of the capsule.

The divisions of lower apical cell contribute to the foot of sporophyte and lower portion of seta. The upper apical cell cuts off many segments right and left; the divisions in these segments ultimately give rise to capsule and major portion of seta.

A transverse section of embryo apex at an early stage shows four quadrately arranged cells (Fig. 4.4B). It is followed by vertical divisions of each of four cells, resulting into an octant. As seen in a transverse section in each quadrant one daughter cell is almost triangular and other is almost rectangular. Periclinal divisions of four rectangular cells result in differentiation of a quadrant of endothecial cells encircled by eight amphithecial cells. Subsequent divisions are in very regular sequence. The amphithecium divides periclinally to form two concentric layers, eight cells in perimeter, the inner of which is referred as first ring. The cells outer to first ring divide by anticlinal walls to form 16 cells, which undergo periclinal division. The inner of two rings thus produced is referred as second ring. Like this third, fourth and fifth rings are formed.

The four cells of endothecium also divide in a sequence similar to that of amphithecium. Thus an outer layer of four endothecial cells surround four endothecial cells. The four endothecial cells divide, by vertical intersecting walls, forming 16 cells which differentiate into central region of capsule, the columella. The eight peripheral endothecial cells divide, first by radial wall and then by anticlinal walls, to form two layers of cells. The inner layer forms the inner wall of spore sac. The outer layer forms sporogenous tissue, all cells of which differentiate into spore-mother-cells. Each spore-mother-cell undergoes meiosis to form a spore tetrad.

In the capsule of *Funaria* tissue differentiation in fertile portion and opercular regions is different; development of these two regions will be taken up separately.

In the fertile region, tissues external to sporogenous region are amphithecial in origin. The tissue maturation from first to fifth rings, derived from amphithecium, is as follows :

The three-layered outer wall of spore sac develops from first ring. The chlorophyllous cells and air spaces develop from the second ring. The chlorophyllous cells adjacent to earlier ones arise from the third ring. Non-chlorophyllous cells of capsule wall develop from fourth ring and epidermis of capsule is derived from fifth ring.

The tissues of apophysis develop in a manner similar to that of capsule. The endothecium contributes to cells in continuity with columella above and cells of seta below. The amphithecium contributes to chlorophyllous spongy tissue and the epidermis.

As for differentiation in the regions of operculum and peristome the central cells of operculum are derived from endothecial cells. The amphithecium, of 5 rings of cells, differentiates into wall of operculum and peristome in the following manner :

First two rings contribute to the peristome. The first ring becomes 32 cells in perimeter and constitutes the inner peristomial layer. Cells in the two layers are oriented in such a way that one outer peristomial cell lies external to two inner peristomial cells. The second ring remains 16 cells in perimeter and constitutes the outer peristomial layer. The teeth are composed of thickened portions of cell wall. Third, fourth and fifth rings give rise to operculum. The third and fourth rings jointly develop into a thin-walled tissue, 3-cell-thick, of operculum. Cells of fifth ring mature into epidermis of operculum. Epidermal cells at the base of operculum enlarge radially to form an annulus, the lowermost cells of which remain thin-walled at maturity. Other cells of epidermis become thick-walled.

During final maturity of capsule there is loss of water. Dehiscence of capsule is due to dehydration and consequent stress on different tissues. The delicate cells of annulus act as a weak point. The operculum is separated from the body of capsule exposing the peristome teeth (Fig. 4.4A). Shedding of operculum is due to drying and shrivelling of : (a) thin-walled opercular cells below the epidermis, (b) thin-walled cells at the base of annulus, and (c) upward hygroscopic movement of peristome teeth. The peristome covers the spore sac. However, on exposure and drying the outer teeth bend backwards with a jerk exposing the spore sac. Along with these, the twisting and untwisting of seta influenced by humidity and wind bring about dispersal of spores.

A spore readily germinates (Fig. 4.3D) to form one or two germ tubes. These germ tubes elongate to produce a branched filamentous protonema. To begin with the protonema consists of highly chlorophyllous short cells with transverse septa. This stage of protonema is described as chloronema. The chloronema matures into caulonema, the shoot-producing protonema. The caulonema comprises of erect filaments (similar to chloronema) and prostrate filaments with elongated cells, oblique septa and brown contents. From the cells of prostrate filaments develop an initial, either for a branch or a bud (gametophyte). The branch initial divides transversely to produce a branch but a bud-initial divides by oblique partition walls to differentiate an apical cell with 3-cutting faces which give rise to stem and leaves (Fig. 4.3E). Rhizoids develop from the base of a bud.