The characteristic features of the order are as follows: The gametophyte is differentiated into stem and leaves. The leaves are borne in a regular spiral succession along the stem. The apical cell is pyramid-like with three cutting faces. The stem usually bears three rows of leaves. Two rows of leaves are lateral and consisting of leaves of normal size. The third row of leaves consists of the under leaves which are commonly smaller than the lateral leaves. The archegonia are always restricted to the apices of the axis and its branches. The last formed archegonium is developed from the apical cell itself. With the result of this acrogynous formation of archegonia, the sporophytes remain always terminal in position. The antheridia are borne singly or in groups in the axils of leaves.

There are about 220 genera and 8500 species in this order. According to Evans (1938) this order consists of seventeen families. Here the genus *Porella* of family Porellaceae and *Frullania* of Frullaniaceae have been discussed in detail.

Family-Porellaceae

Characteristic features. The leaves are arranged in three rows on the stem. The ventral leaves are well developed and usually decurrent at the base. The dorsal leaves are incubuous. The postical lobe is distinct. The rhizoids are scarce and arise from the lower side of the stem in tufts generally near the base of underleaves (ventral leaves). The antheridia are solitary. The archegonia are borne in terminal cluster on small lateral branches. The archegonia remain surrounded by a large, inflated perianth. The spherical capsule dehisces by four valves which split only to half way down.

This family includes a single genus *Porella*. This has been discussed here in detail.

Genus PORELLA (MADOTHECA)

Occurrence and distribution. There are about 180 species in this genus. These species are mainly distributed in tropical regions, but many of

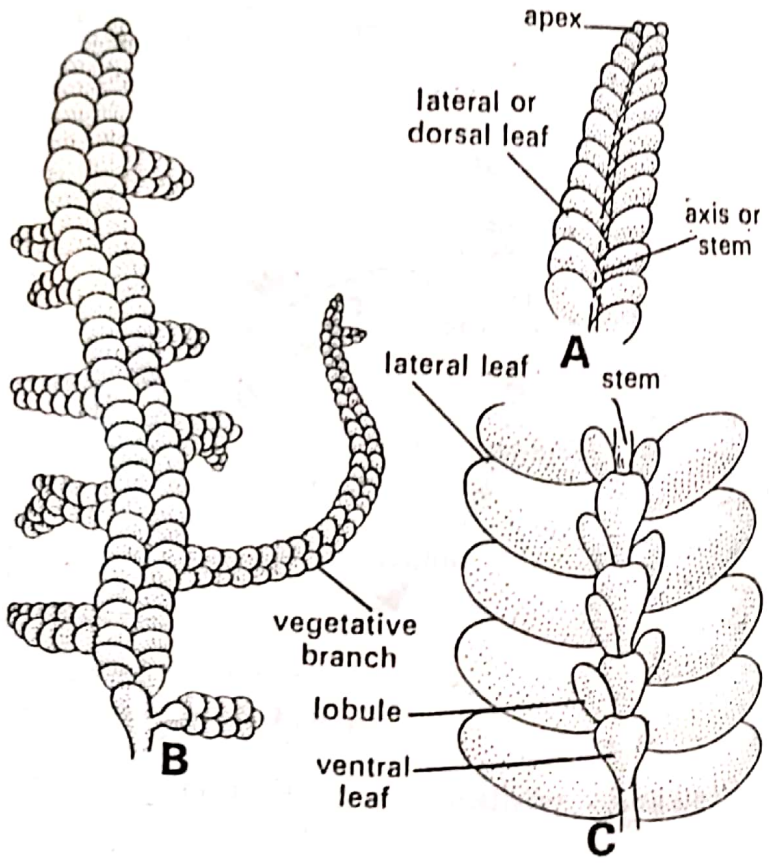

Fig. 5.1. *Porella* sp. Habit of plant . A, branch of a plant showing dorsal leaves, axis and apex; B, part of a plant with vegetative branch showing lateral or dorsal leaves; C, ventral view of a part of branch showing axis, lobules, ventral leaves and lateral (dorsal leaves).

them are also found in temperate zones. *Porella platyphylla* is most widely distributed species and is found in Europe, America, Asia and India. About 34 species have been reported from our country. Of these twenty one species have been reported from Himalayas by Kashyap, and a few from South India (Chopra, 1943). *Porella* usually grows in moist and shady places. It grows on rocks, stones, on the bark of tree, trunks and sometimes even on soil. Occasionally they are found so abundantly that they cover the entire substratum on which they grow.

THE GAMETOPHYTE

Structure. The plant body is large, greenish and leafy. It is 15cm. or sometimes even more long. The plants grow in compact flat greenish patches covering the substratum. The plant body of gametophyte is dorsiventral. It consists of a branched central axis bearing leaves. The branching in *Porella* is monopodial. The stem bears three rows of leaves. There are two rows

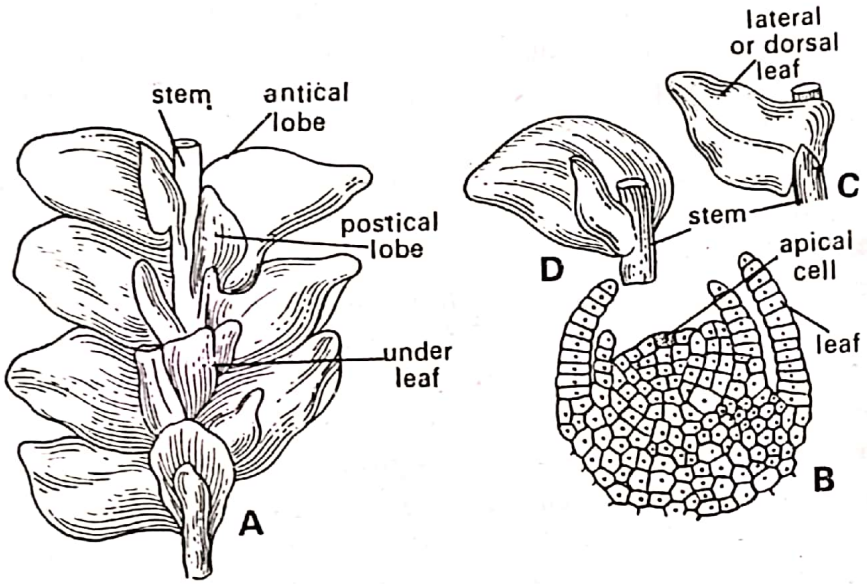

Fig. 5.2. *Porella* sp. Incubous leaves. A, incubous leaves seen from ventral side showing the under leaves and the antical and postical lobes of dorsal leaves; B, vertical section of shoot apex showing leaf and apical cell; C, lateral or dorsal leaf attached to the stem as seen from the above; D, lateral or dorsal leaf attached to the stem as seen from the ventral side.

of dorsal leaves and one row of ventral leaves. The dorsal leaves closely overlap each other and this way they cover the stem from above. The anterior edge of each leaf covers the posterior edge of the leaf next above it, when seen from above; such an overlapping arrangement of

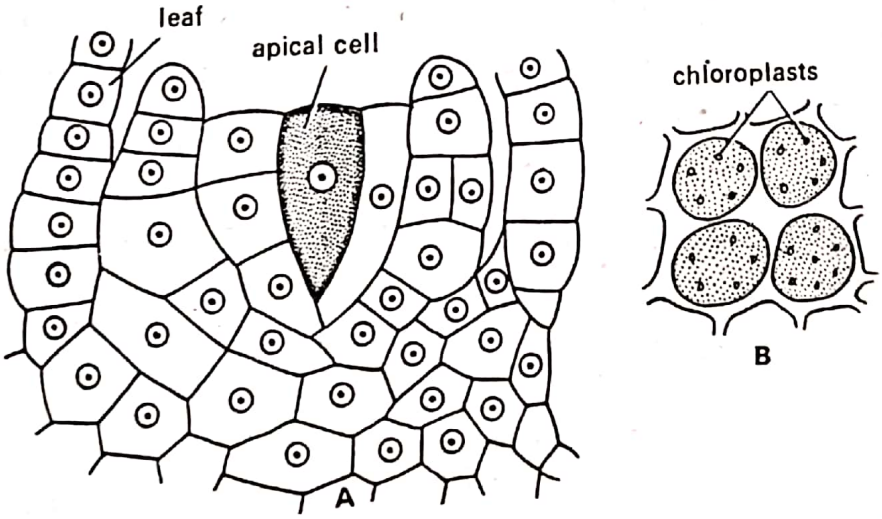

Fig. 5.3. *Porella* sp. A, median L.S. of the tip of leafy shoot, showing apical cell and developing leaves; B, cells of the stem. (A, after Campbell).

the leaves is known as incubous arrangement. Each dorsal leaf is bilobed and the lobes are unequal in size, of the two lobes the larger (antical) lobe is usually ovate and possesses a rounded apex. The much smaller postical lobe is known as **lobule;** it is narrow and acute at the apex; it appears like a separate leaf. The postical lobe (lobule) remains more or less parallel to the stem and frequently decurrent at the external base. The small leaves of the ventral row are designated as **amphigastria.** The amphigastria resemble the postical lobe (lobule) of the dorsal leaves but they are broader and frequently decurrent on both the sides at the base.

A larger number of rhizoids are found to be scattered on the lower side of the stem. The main function of the rhizoids is to anchor the plant to the substratum. The absorption of water takes place directly through the leaf and stem cells.

Anatomy. The young stem of *Porella* is very simple in its structure and shows little differentiation of tissues. The cell walls of cortical cells are thick; and the cell walls of medullary cells are thin. Comparatively the medullary cells are larger than those of cortical ceils.

The leaves are very simple in their internal structure. Each leaf consists of the thin plate of isodiametric polygonal cells. Each cell contains many chloroplasts. The midrib is lacking.

Apical growth. The plant increases in size by means of an apical cell. The apical growth is initiated by the activity of a tetrahedral pyramid like apical cell. This cell possesses three lateral cutting faces. This apical cell cuts off three sets of segments in regular spiral succession. The two sets are dorsal and lateral, and the third one is ventral. Each of these segments gives rise to a leaf and to a portion of the stem from which the leaf arises.

Reproduction. The reproduction takes place by vegetative and sexual methods. However, the asexual reproduction is the function of the sporogonium.

Vegetative reproduction. The species that grow in the humid and shady places reproduce by means of fragments. In *Porella rotundifolia* the vegetative reproduction takes place by means of discoid gemmae developed on the lower surface of the leaves; this view was propounded by Schiffner on the basis of the material collected from Brazil; but later on Degenkolbe (1938) did not find the gemmae in Schiffner's material and he concluded that these thin walled discoid bodies were blue green algae and not gemmae.

Sexual reproduction. *Porella* is dioecious. The male and female plants are easily recognizable. The male plants are smaller than the female ones. The antheridia and archegonia are borne on short side branches. The male branches arise at right angles from the main stem.

Development of antheridium. Each antheridium develops from a superficial dorsal cell which functions as an **antheridial initial.** The antheridial initial forms a papillate protrusion and divides by a transverse wall into a **basal cell** and an **outer cell.** The basal cell remains embedded within the tissue of the thallus whereas the outer cell protrudes out of the surface of the thallus. Thereafter the outer cell divides transversely forming a lower **primary stalk cell** and the upper **primary antheridial cell.** The primary stalk cell gives rise to the stalk of antheridium, while the primary antheridial cell divides longitudinally into daughter cells of equal size. By this time the dorsal cells of thallus that surround the antheridium divide

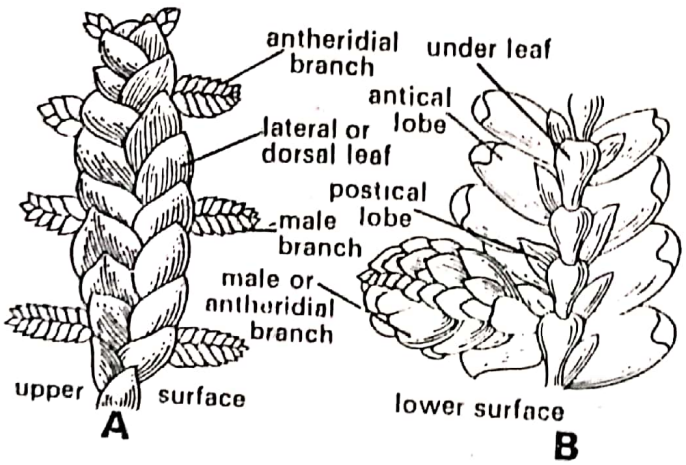

Fig. 5.4. ***Porella*** **sp.** Male plant. A, dorsal view of a part of male plant with antheridial (male) branches; B, ventral view of a part of a branch with male or antheridial branch.

again and again forming a ring-like involucre which opens on the dorsal surface of the thallus.

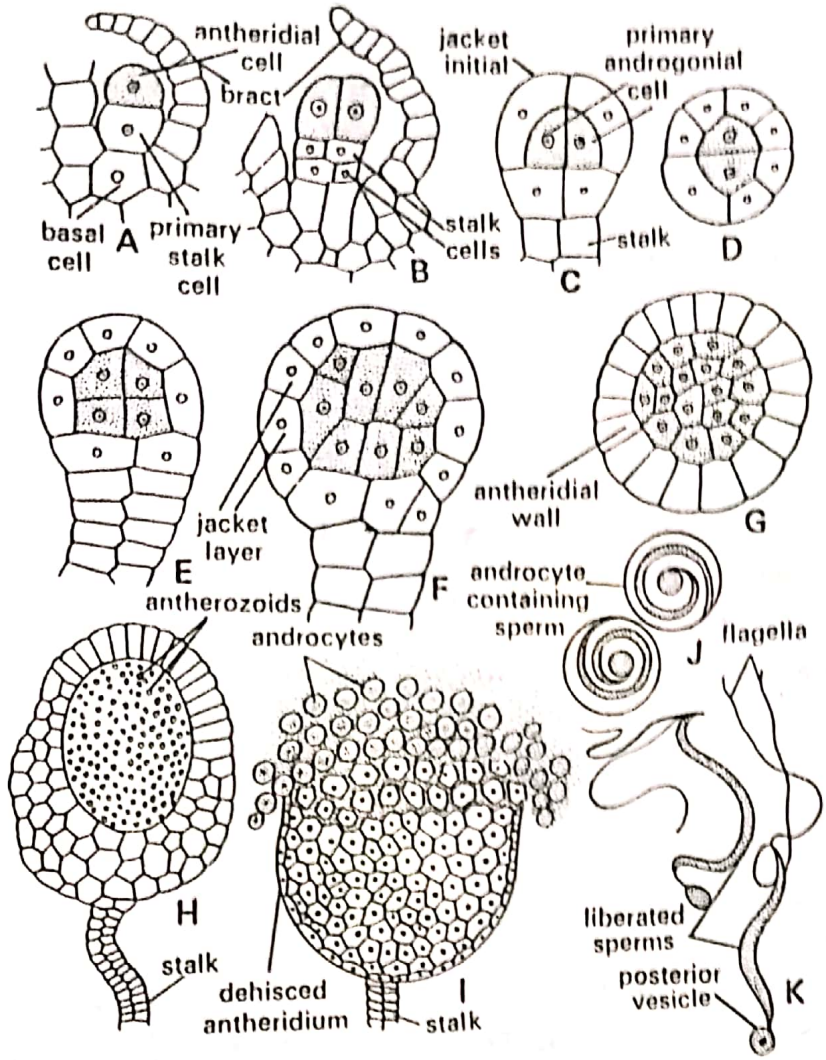

Fig. 5.5. *Porella* sp. Development of antheridium. A, antheridial initial and stalk cell; B-G, further successive stages in the development of antheridium; D and G, cross sections of developing antheridium at different stages; H, mature antheridium; I, dehisching antheridium; J, androcyte containing sperm; K, liberated biflagellate sperms.

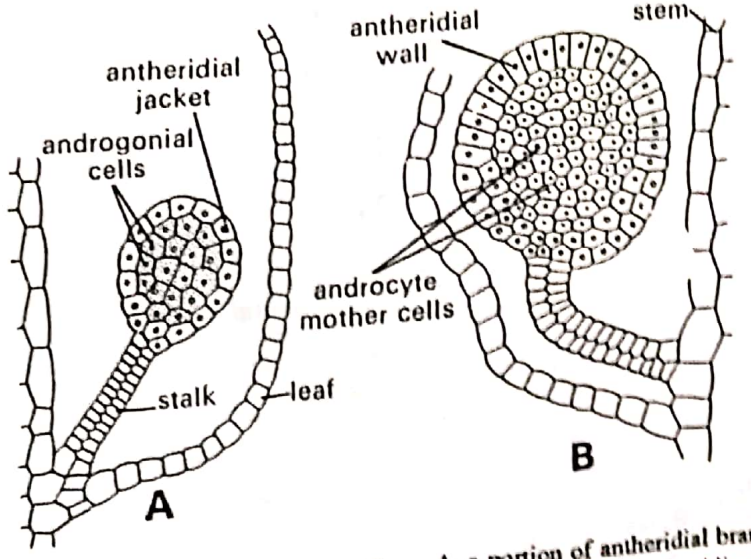

Fig. 5.6. *Porella* sp. Antheridium. A, a portion of antheridial branch showing young antheridium in the axil of leaf; B, a nearly mature antheridium in the axil of leaf.

Each of these two daughter cells developed from the primary antheridial cell divides by a periclinal wall into two unequal cells. This way, the outer jacket initials and two inner primary androgonial cells are formed.

The two primary androgonial cells divide again and again resulting in a large number of androgonial cells. The last cell generation of the cells is called the **androcyte mother cell.** Each androcyte mother cell divides diagonally forming two **androcytes.** Each androcyte

metamorphoses into an antherozoid. Simultaneously the jacket initials divide anticlinally again and again forming a single layered jacket around the antheridium.

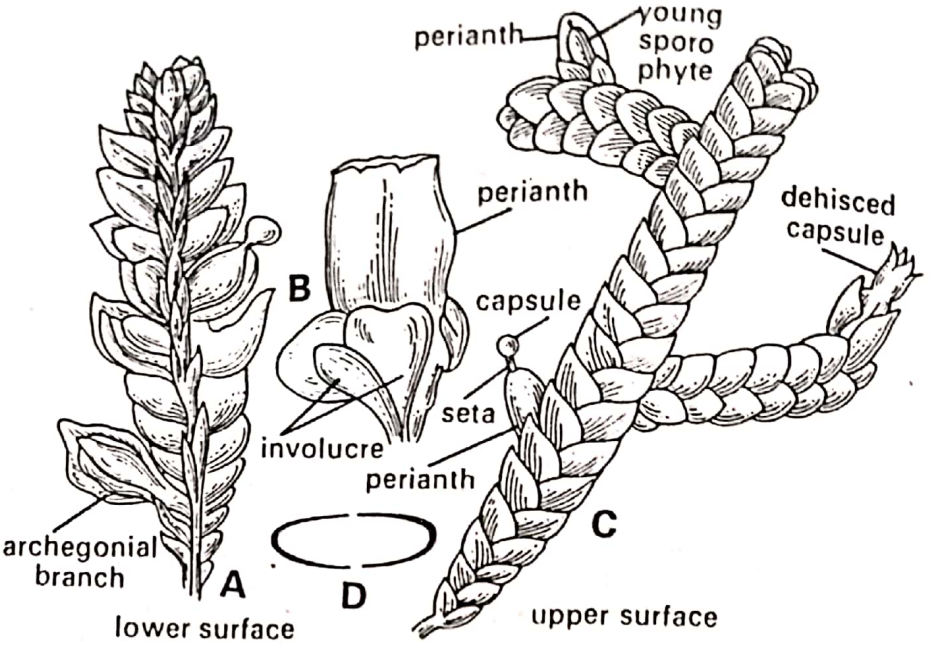

Fig. 5.7. *Porella* sp. Female plant. A, ventral view of a part of the female plant with archegonial branches; B, enlarged female branch; C, dorsal view of a part of plant with archegonial branches; D, plan of perianth.

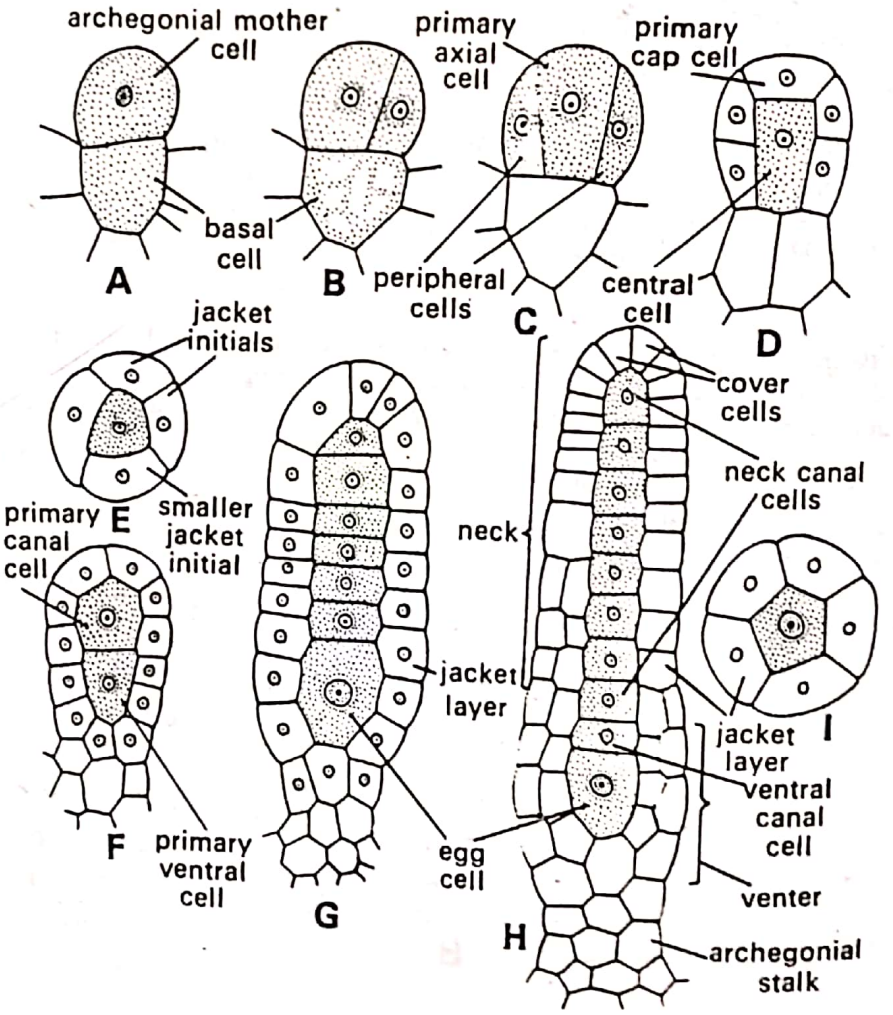

Fig. 5.8. *Porella* sp. Development of archegonium. A, archegonial mother cell; B-F, further successive stages in the development of archegonium; G, young archegonium; H, nearly mature archegonium; I, transverse section of archegonium.

Structure of mature antheridium. A mature antheridium of *Porella* possesses a long stalk and globular body. The stalk is composed of two rows of cells. The body of antheridium remains surrounded by a single-layered jacket in its upper part while 2 to 3 layered jacket in its basal part. The androcytes are found within the jacket. Each androcyte metamorphoses into a biciliate antherozoid.

The mature antheridium dehisces in a very characteristic manner. The upper part of the antheridial jacket is thinner than that of the basal part. On access of water the upper part of antheridium bursts open by a number of irregular lobes which curl back strongly. The whole mass of androcytes is escaped out into the water that causes the rupture. Thereafter the antherozoids liberate from the androcytes and swim to the water with the help of their cilia.

The archegonial branch. The archegonia are produced on the lateral branches of plants other than antheridial branches. These branches are much less distinct than the antheridial branches. The archegonia remain situated at the apex of the archegonial branch. There are four or five leaves on each archegonial branch. The apical cell of an archegonial branch cuts off two or three segments in the same manner as in the vegetative branch; these segments develop leaves. Thereafter each segment cut off by an apical cell divides into an inner (basal) and outer (distal) cell. The distal cell acts as the mother cell of the archegonium. The first formed few archegonia arise in acropetal order and ultimately the apical cell of the branch also acts as an archegonial initial and this way the further growth of archegonial branch is checked.

Development of archegonium. The development of archegonium is in a manner characteristic of the Jungermanniales as described in *Pellia* on page 60.

Structure of mature archegonium. The mature archegonium possesses a neck which is composed of five vertical rows of cells. The neck contains within it 6 to 8 neck canal cells. The wall of venter is two-layered. It encloses the small oosphere (egg) and a ventral canal cell.

Fertilization. On the access of water the mature archegonium opens at its tip and the cover cells separated from each other. The antherozoids from the antheridia of male plants are carried to the archegonia of the female plants through the agency of water. To facilitate this process the male and female plants grow in close vicinity in the dense patches closely covering the substratum. The antherozoid reaches the egg and fertilization takes place. This process results in the formation of zygote (oospore).

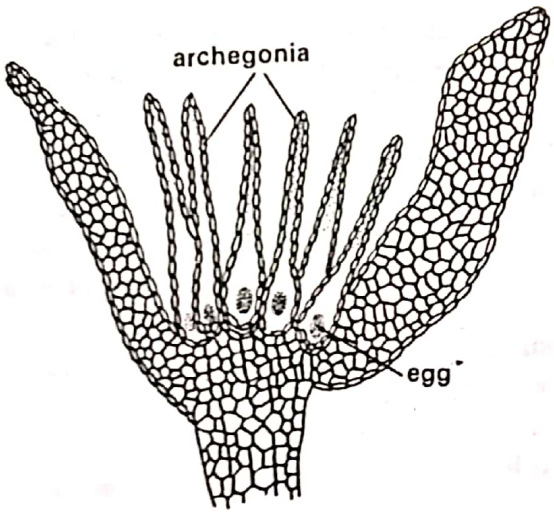

Fig. 5.9. ***Porella*** **sp. Female sex organs. A female branch with cluster of mature archegonia with eggs.**

THE SPOROPHYTE

Development of sporogonium. The zygote secrets a wall and increases in size. It divides by a transverse wall into two halves. The upper cell is called **epibasal cell** and lower cell the **hypobasal cell.** Thereafter the epibasal cell again divides by a transverse wall resulting into two cells. At this stage the young embryo is composed of three cells. The hypo-basal cell does not divide anymore and develops into a **haustorium** or **suspensor.** The whole sporogonium develops from the two cells formed by the transverse division of cell. Subsequently the vertical and trans-

verse divisions take place in these two cells. These divisions are in irregular sequence and, therefore, the limits of the primary segments are less distinct. It is also difficult to demarcate between seta and capsule and the number of segments which make the capsule cannot be known with certainty. Campbell reports that in the terminal segments of the embryo the first periclinal

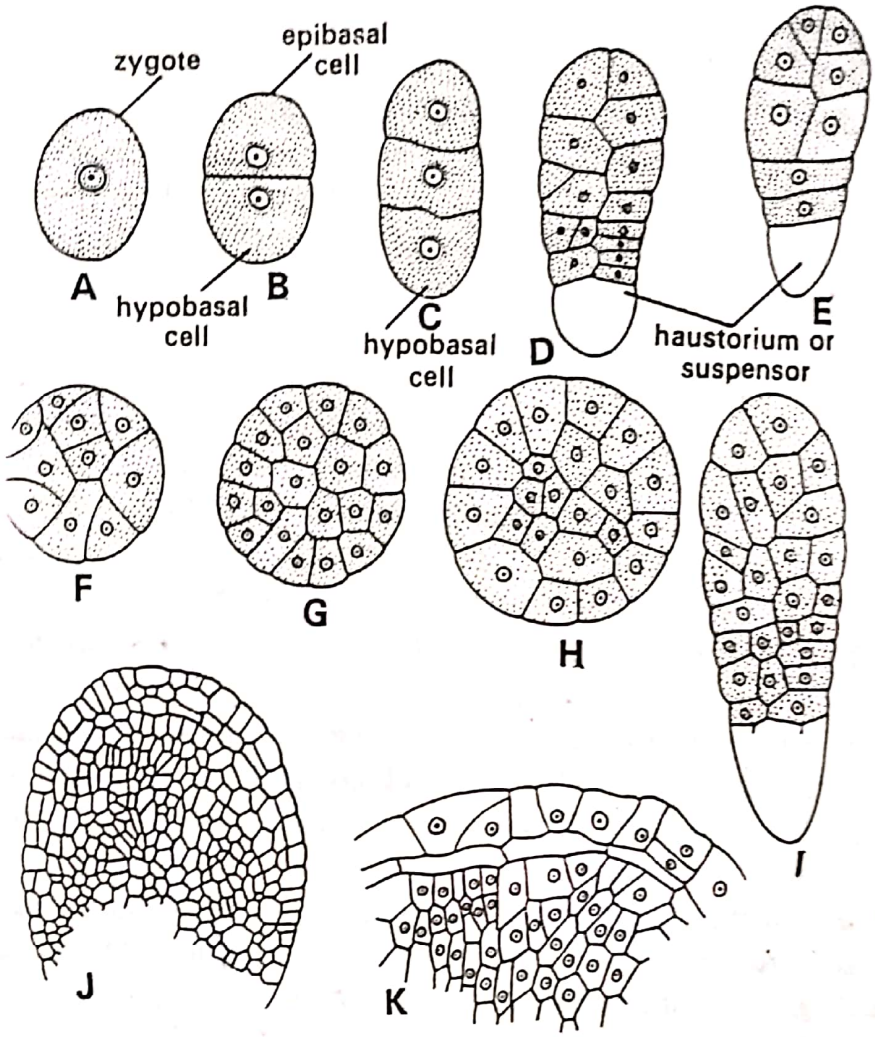

Fig. 5.10. *Porella* sp. Development of sporophyte. A, zygote; B, transversely divided zygote with epibasal and hypobasal cells; C-I, further successive stages in the development of sporophyte; F-H, cross sections at different stages; I, embryo with a mass of undifferentiated cells; J-K, further advanced stages of development of embryo (sporophyte)

walls appear at different distances from the surface and therefore, the first periclinal divisions do not determine differentiation of the archesporium and the jacket layer of the capsule. At a later stage these regions are well defined. Now the sporogenous cells are arranged in more or less marked rows radiating out from the base of capsule. Some of the sporogenous cells do not divide further and grow in a regular sequence in all directions forming the young spore mother cells. The remaining sporogenous cells may divide further and form the elongated young elaters. The spore mother cells and the elater cells remain intermingled. They are not arranged in a definite or regular order.

Prior to meiosis the spore mother cells become four lobed. The nucleus of spore mother cell divides meiotically and one daughter nucleus is being transferred to each lobe. Finally the lobes are being separated by cell wall which are laid simultaneously between them. A tetrad of haploid spores is formed. It remains surrounded by a common sheath. Later on the sheath breaks and the ripe spores are separated.

The seta is short. It merges gradually into the base of the capsule. It projects a little beyond the surrounding protective sheath. In *Porella*, the **calyptra, perianth** and **involucre** make this

protective sheath. The calyptra is several-layered thick. The perianth is developed by the coalescence of two distal bracts just below the cluster of archegonia. The involucre is formed by

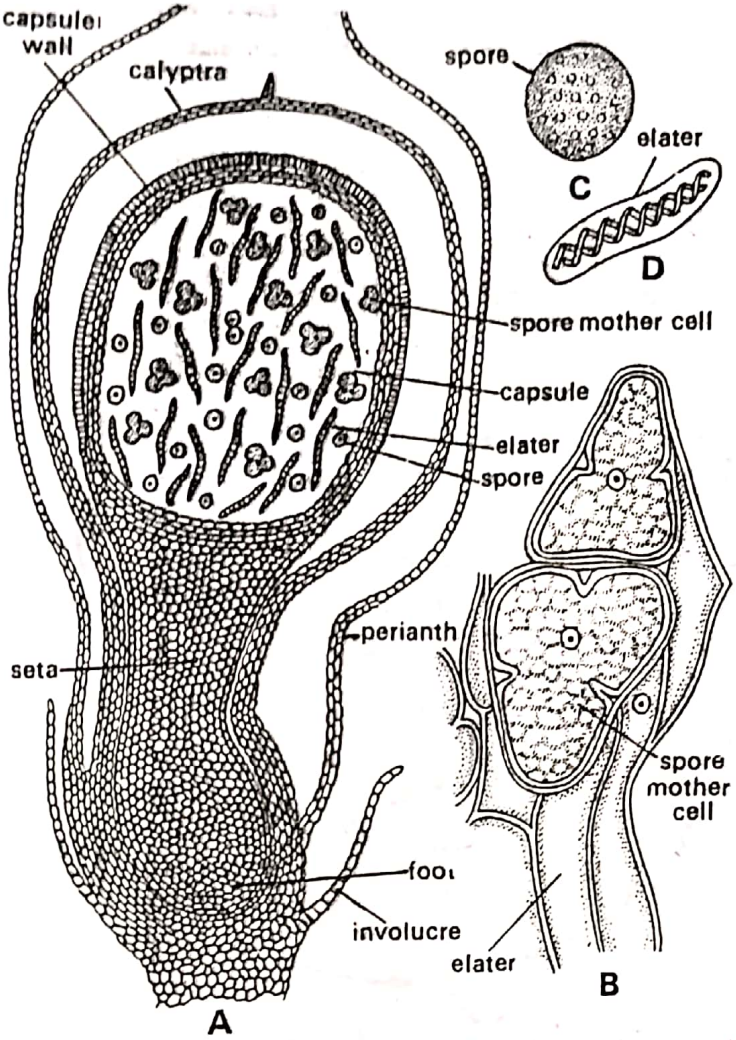

Fig. 5.11. *Porella* sp. Sporophyte. A, longitudinal section of nearly mature sporogonium showing foot, seta and capsule; B, enlarged lobed spore mother cells and elater cells within sporogonium; C, single mature spore; D, single elater showing double spiral band.

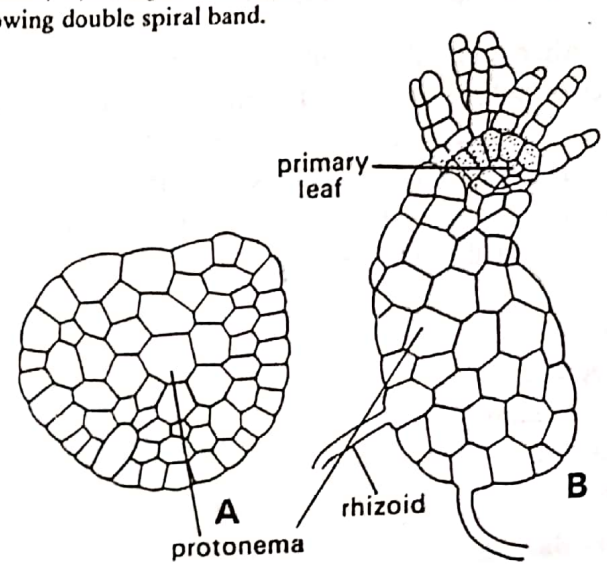

Fig. 5.12. *Porella* sp. A, discoid protonema; B, the sporeling-primary leaves and rhizoids develop on disc-like protonema.

the enlarged bracts which surround the base of the perianth. The foot is inconspicuous and is simply a somewhat enlarged portion of the seta.

Structure of mature sporogonium. The sporogonium consists of an inconspicuous foot, short seta and a globular capsule. The jacket of capsule is two to four-layered thick. The capsule contains within it short elaters and the spores.

Dehiscence of the capsule. On the maturity of the spores the seta elongates, and with the result, the protective sheath consisting of calyptra, perianth and involucre, ruptures. The capsule then ruptures by four valves releasing the spores outside. The hygroscopic

movements of the elaters help in thrusting away the spores to some distance.

The spore and its germination. The spores are .03 to .05 mm in diameter. The spo wall consists of two layers, the exospore and the endospore. The exospore is either smooth echinulate.

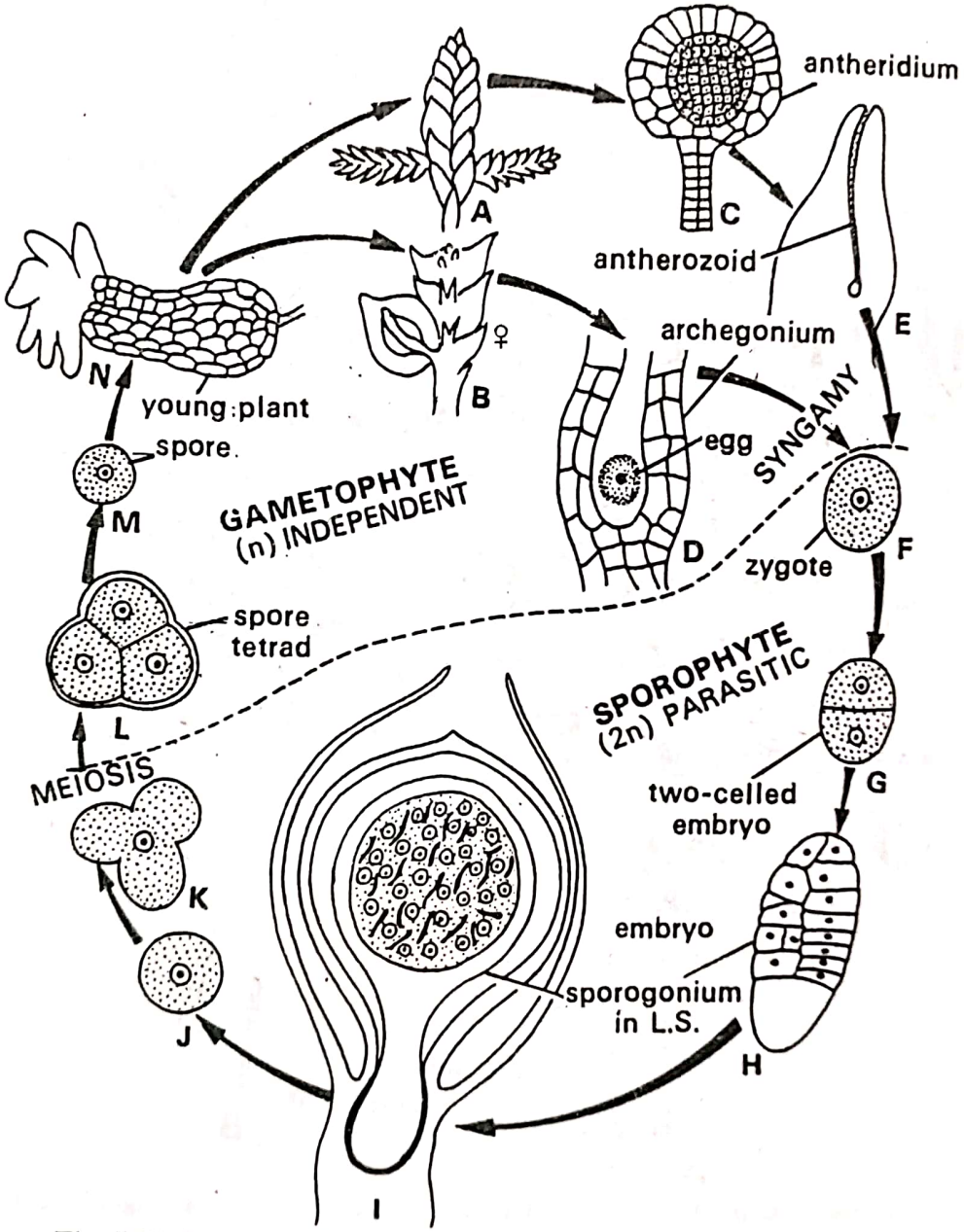

Fig. 5.13. *Porella* sp. Diagrammatic life-cycle (modified after Parihar).

The spores begin to germinate immediately after their liberation from the capsule. The spores of *Porella* divide by precocious divisions even before the capsule bursts and, therefore, the spores appear to be multicellular. The development proceeds within the exospore. The exospore does not rupture and the germ tube is not formed. By means of the division of the protoplast the endospore expands. The repeated division of the protoplast produces a mass of cells, the **protonema.** One or more rhizoids may be developed on this protonema. Thereafter an apical cell is formed at the edge of the protonema.

Systematic position