18BZO14A-U2

CLASS: OOMYCETES
ORDER: PERSANOSPORALES
FAMILY: ALBIGINACEAE
GENUS: *ALBUGO CANDIDA*

Mycelium of Albugo:

It is well developed and consists of branched, aseptate, coenocytic hyphae. The hyphae live and ramify in the intercellular spaces of the susceptible host tissue. The hyphal wall contains cellulose and not chitin. The hyphal protoplasm is granular and vacuolate in the older parts.

It contains numerous nuclei, oil globules and glycogen. Electron micrographs reveal the presence of mitochondria, endoplasmic reticulum and ribosomes.

The cytoplasmic membrane which is closely appressed to the hyphal wall forms lomasomes. Septa remain suppressed in the actively growing hyphae but appear to separate reproductive structures and to seal off injured parts.

The fungus mycelium grows vigorously. The hyphae branch and ramify within the host attacking the tissues adjoining the point of infection. Sometimes both Albugo and Peronosporaoccur on the same host particularly Capsella bursapastoris. Albugo can, however, be distinguished from Peronospora by the smaller diameter of its hyphae and more numerous, vesicular haustoria (Fig. 6.50).

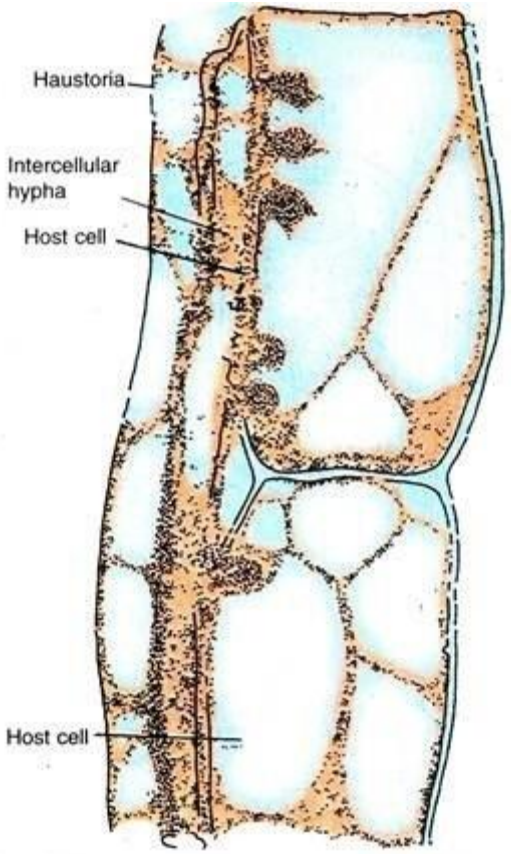

Fig. 6.50. *Albugo candida.* Section through the host stem showing a portion of the mycelium bearing haustoria. (Diagrammatic).

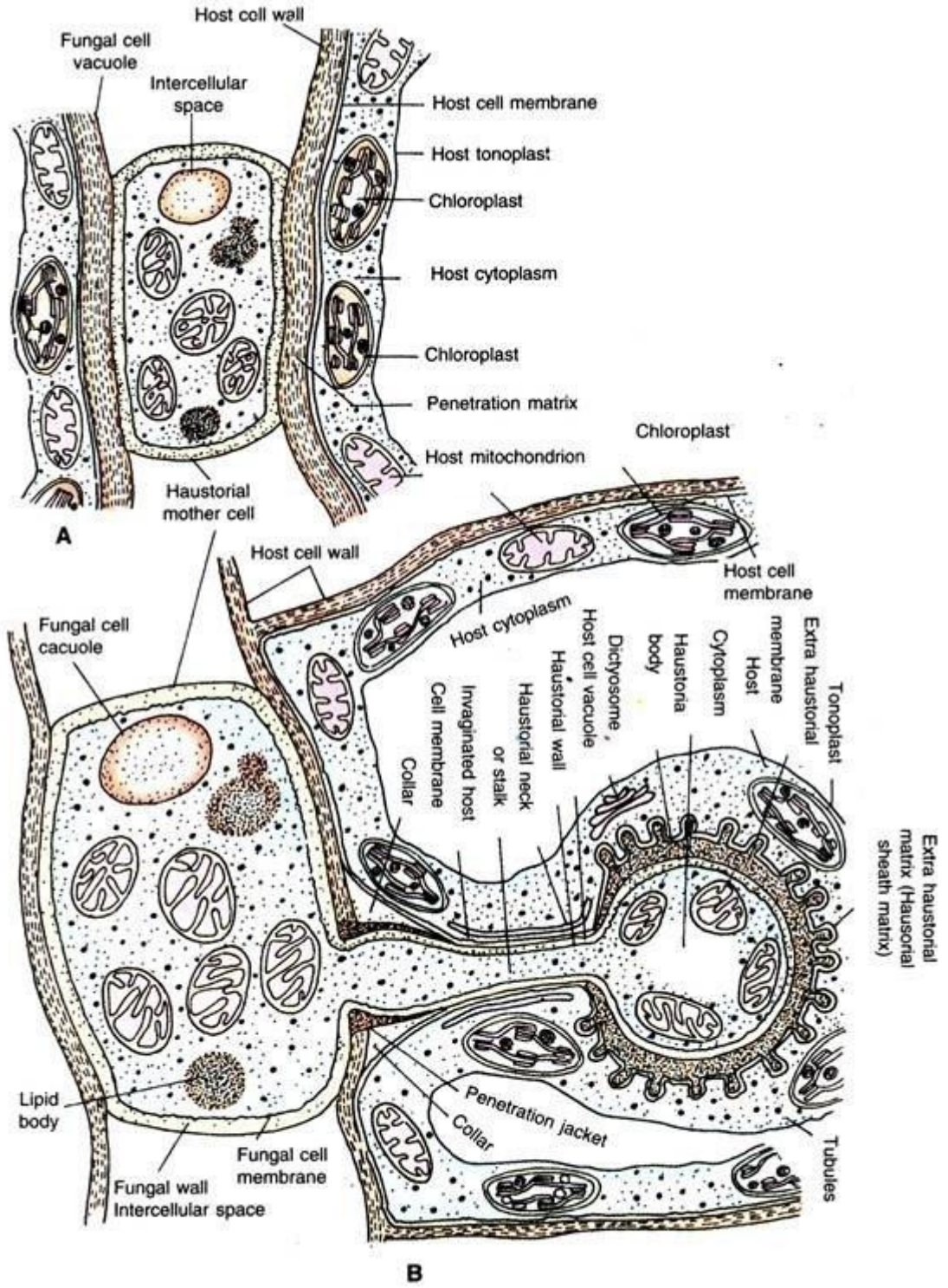

Fig. 6.51. (A-B). *Albugo candida*. Diagrammatic representation of ultrastructure of the haustorial apparatus in section passing through the host mesophyll cell (Based on Coffey)

The intercellular hyphae of this obligate parasite produce intracellular haustoria in the mesophyll cells of the host (Fig. 6.50). The haustorium arises as a lateral outgrowth at the site where the hyphal wall is tightly pressed against the mesophyll cell wall.

An electron- dense amorphous material known as the penetration matrix is usually deposited at the site of contact between the host and the hypha cell walls. It is described as the penetration site (Fig.
6.51).

The slightly crescent-shaped bulge of the haustorial mother cell known as haustorial initial perforates the host cell wall at the penetration site and protrudes into the lumen of the mesophyll cell to develop into a haustorium. It is bordered by the invaginated host plasma membrane.

With light microscope the haustorium is seen as a small, spherical structure consisting of two parts namely:

(i) The haustorial stalk or neck and

(ii) The terminal haustorial head or body.

The haustorial stalk passes through the penetration site to connect the haustorial body to the hyphal wall in the intercellular space between the mesophyll cell. Usually one or two, sometimes more, haustona are seen in the thin peripheral layer of the host cell cytoplasm adjacent to the chloroplasts.

Reproduction in Albugo:

Asexual Reproduction in Albugo:

When the mycelium has reached a certain stage of maturity it epidermis produces pads of hyphae at certain areas just below the epidermis. The tips of hyphae constituting the mat grow verticlly into short, upright, thick-walled, unbranched club-shaped hyphae.

These are the sporangiophores (=conidiophores). They are arranged in a closely packed palisade like layer forming a sorus between the epidermis and the mesophyll of the host leaf. Each sporangiophore appears constricted at its junction with the subtending hypha.

The lower two-third portion of sporangiophore is narrow, thick-walled, with a undulating surface whereas the upper one-third is broader, thin-walled with a smoother surface. According to Khan (1977), the sporangiophore wall towards its proximal end consists of two layers, the outer more electron-dense and thicker than the inner layer.

(a) Abstriction of sporangia:

In the lower fungi (Phycomycetes) Albugo is unique in that its lemon- shaped sporangia are produced in basipetal chains at the tips of clavate sporangiophores. Two different views have been put forth to explain their mode of development.

According to one view, the sporangial chains in Albugo are abstricted by percurrent proliferation. The second view advocates the blastic mode of development.

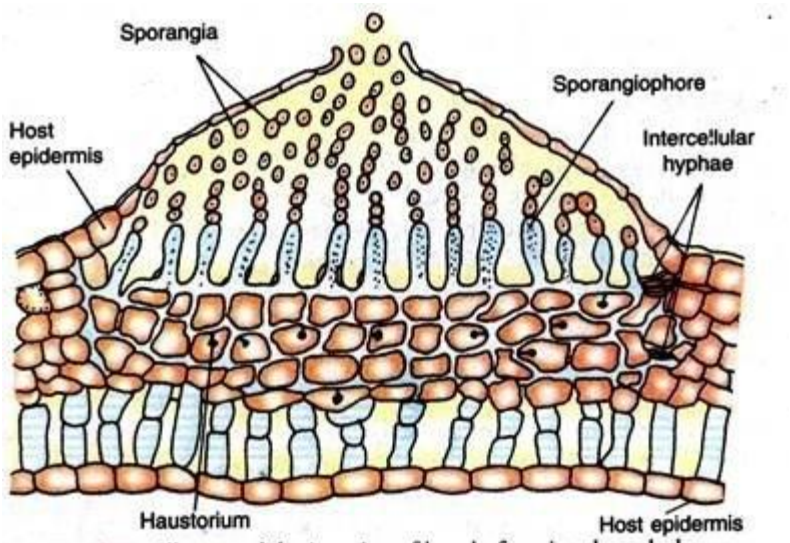

Fig. 6.52. *Albugo candida.* A section of host leaf passing through the sporangial sorus.

(i) Percurrent Proliferation (Fig. 6.53):

The sporangia in Albugo which are cut off in succession are arranged in a basipetal chain on the sporangiophore. According to Hughes (1971), they are produced by successive proliferations of the sporangiophore subtending a sporangium.

This mode of development of sporangia is termed per-current proliferation. Generally the sporangiophore increases in length as each successive sporangium is cut off from each successive proliferation at a higher level than the previous one. The first formed sporangium is a aleuriosporangium.

Reaching a certain size it is delimited from the sporangiophore by a basal septum. The latter eventually splits into two halves so that the subsequent proliferation of sporangiophore involves the exposed half septum. In Albugo each successive sporangium is capable of seceding from the sporangiophore or from the young sporangium.

The second sporangium is thus formed by proliferation of the sporangiophore with total involvement of the half of the fractured transverse septum exposed by the seceding first sporangium above it. Apart from this, septum is seen at the apex of the young sporangium.

The second sporangium is delimited in the same manner as the first. As the second sporangium increases in size it pushes the first upward without disjunction. The process is repeated resulting in a chain of sporangia. Probably the septum seen at the apex of each younger sporangium thickens on both sides to form a connective between the successive sporangia in the chain.

According to Hughes, besides increase in length of sporangiophores, this method of sporangium development is accompanied by marked lamination and thickening of the walls of the sporangiophores. The mature sporangiophores are thus longer, more thick-walled and show annellations.

Thakur (1977) corroborated findings of Hughes (1971) on formation of sporangia by percurrent proliferation in Albugo.

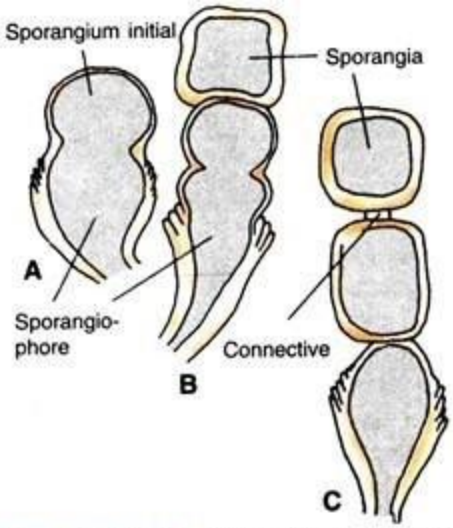

Fig. 6.53 (A-C). *Albugo ipomeae-pandurantae* showing stages in percurrent proliferation of sporangia (After Hughes)

(ii) Blastic mode of Sporangium development (Fig. 6.54):

According to Khan (1977) the sporangiophore has a fixed sporogenous locus at its apex. The sporangial initial arises as a bud from it (A). It contains about 4-6 nuclei and dense cytoplasm.

The two wall layers of the sporangium initial are continuous with those of the sporangiophore wall. Reaching a certain size, the initial is delimited by a basal septum near the sporogenous locus. It becomes the first sporangium and the oldest in the chain (B).

The septum is formed by the centripetal growth of the inner layer of the sporangiophore wall (C). A nearly complete septum has a narrow central canal and consists of three layers, upper and lower electron dense and the thick middle one of less electron density (D).

After the completion of the basal septum and conversion of the initial into a full-fledged sporangium, a new sporangium initial grows as a bud from the sporogenous locus (B). It pushes the newly-formed sporangium upward. Thus only one sporangium is formed at a time.

As the second sporangium initial grows to the normal size, it is also delimited by the formation of a basal septum as the first. The repetition of the process results in the

formation of a basipetal chain of sporangia. Soon after the formation of the first sporangium, the breakdown of its basal septum begains.

It is the middle layer which starts disintegrating from its periphery inwards whereas its upper layer fonns the wall of the upper sporangium and the lower layer completes that of the lower sporangium (E-F).

The fibrous product of dissolution of the middle layer is held in position by the pellicle which covers both the sporangia and the sporangiophore. It is seen as a connective or disjunctor between the successive sporangia in the chain. Khan (1977) did not notice any increase in length of the sporangiophore during sporangia formation nor did he observe any annellations on the sporangiophore surface.

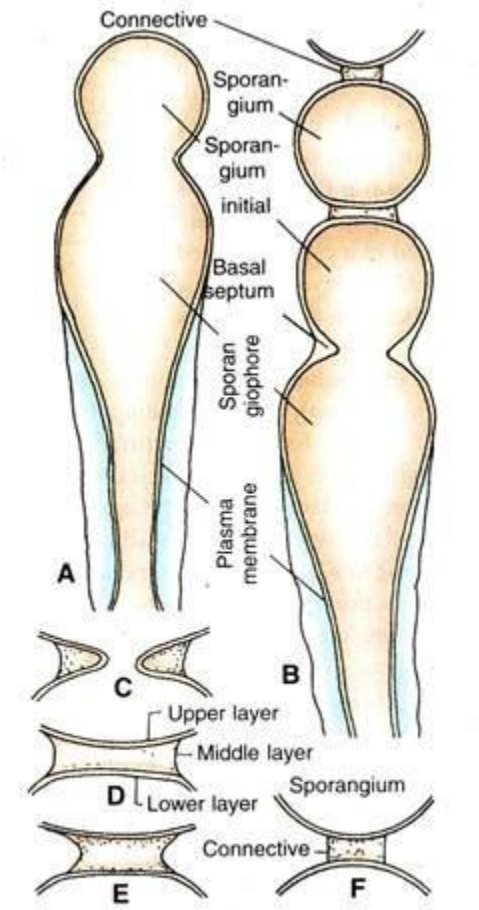

Fig. 6.54 (A-F). *Albugo candida* showing blastic mode of development of sporangia (After Khan)

Sporangia (Fig. 6.55 A, B):

They are small, hyaline, nearly spherical or lemon- shaped structures with a smooth or somewhat punctate surface.

The basipetal arrangement of sporangia in the chain (with the oldest at the top and the youngest at the base of the chain) serves two useful purposes:

(i) It permits ready dispersal of the oldest sporangia by air currents or rain water, and

(ii) It helps in the proper nourishment of the younger ones.

(i) Ultrastructure of sporangium (B):

According to Khan (1977), each newly formed sporangium is lemon-shaped and is about 19- 22 by 14-17 μ m in size. It bears remnants of the connectives or disjunctor pads at both the ends. The sporangium wall is differentiated into two distinct layers. The outer is more electron dense than the inner.

Within the sporangium wall is the highly convoluted plasma membrane enclosing the dense cytoplasm containing up to 4 nuclei. Besides, the cytoplasm contains endoplasmic reticulum, mitochondria, perinuclear, dictyosomes, ribosomes both free and attached to endoplasmic reticulum, vesicles of various kinds and lipid droplets.

Towards maturity the sporangial wall especially, its inner layer increases in thickness and the number of lipid droplets decrease as the sporangia matured. The oldest sporangia have none.

The endoplasmic reticulum becomes accumulated in the peripheral cytoplasm. Towards the end of sporangial maturation, the dictyosomes become quiescent, mitochondria decreased in number and also the amount of endoplasmic reticulum. The sporangial wall increased 3-fold the thickness.

(ii) Dispersal of sporangia:

The chains of sporangia lengthen and press on the epidermis above. This causes the leaf surface to bulge. The overlying epidermis eventually bursts over the growing sporangial sorus and exposes the white shining pustules consisting of masses of sporangia.

The pustules look like white blisters. The exposed sporangia are white. The distal ones by this time have matured. As the sporangia mature the connectives or gelatinous pads between them dry, shrink and finally disintegrate in moist air. The sporangia in the chain thus separate. They are then blown away in the air by wind or washed away by rain water.

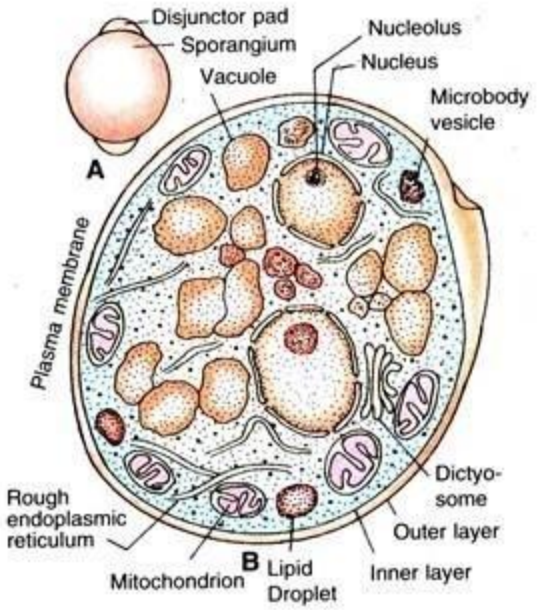

Fig. 6.55 (A, B). *Albugo candida*. A, Sporangium with remains of the disjunctor pads at both ends; B, ultrastructure of sporangium (Based on Khan).

Germination of sporangia (Fig. 6.56):

Landing on a suitable host the sporangia begin to germinate within two or three hours under suitable conditions.

At the time of germination they behave in either of the following two ways depending on temperature conditions:—

Indirect Germination (Fig. 6.56 B-E):

In the presence of moisture and low temperature, the sporangium functions as a zoosporangium (B). The optimum temperature for germination of sporangia is 10°C. It absorbs water and swells. A few vacuoles appear in its granular cytoplasm.

Later the vacuoles disappear and the multinucleate protoplast undergo division. It divides to form five or eight polyhedral uninucleate daugher protoplasts. Meanwhile an obtuse papilla forms on one side of the sporangium.

Each daughter protoplast shapes into a slightly concave-convex zoospore (E). It has a disc-like contractile vacuole on one side and is furnished with two flagella, one short and one long. The former is of tinsel type and the later whiplash. The flagella are attached laterally near the vacuole.

As the zoospores are differentiated, the papilla swells and opens. The zoospores still immobile, emerge usually one by one (Fig. 6.56 C). According to Vanterpool, the zoospores are, at first, released in a sessile vesicle formed by the swelling of the papilla. The vesicle soon vanishes.

Germination of zoospore and infection of host (Fig. 6.56 F-H):

Moisture on the surface of the host is essential for germination and infection. The released zoopores swim about in water for a while (E). Finally they settle down on the host, retract the flagella and round off.

Each secretes a wall around it (F). The encysted zoospore (cyst) then germinates. It puts out a germ tube (G) which gains entrance into the host thought a stoma (H). Once within the host tissue the germ tube grows and forms the mycelium

(ii) Direct Germination (Fig. 6.56 I-J):

At high temperature and under comparatively dry conditions the sporangium behaves like a conidium (I). It germinates directly to form a germ tube (J). The conidial method of germination of sporangia in Albugo is, however, not common.

The germ tube penetrates the host through a stoma or, through an injury in the epidermis. Within the host it develops into a mycelium. Re-infection of the host and infection of other healthy plants in the vicinity goes on by the production of sporangia throughout the growing season.

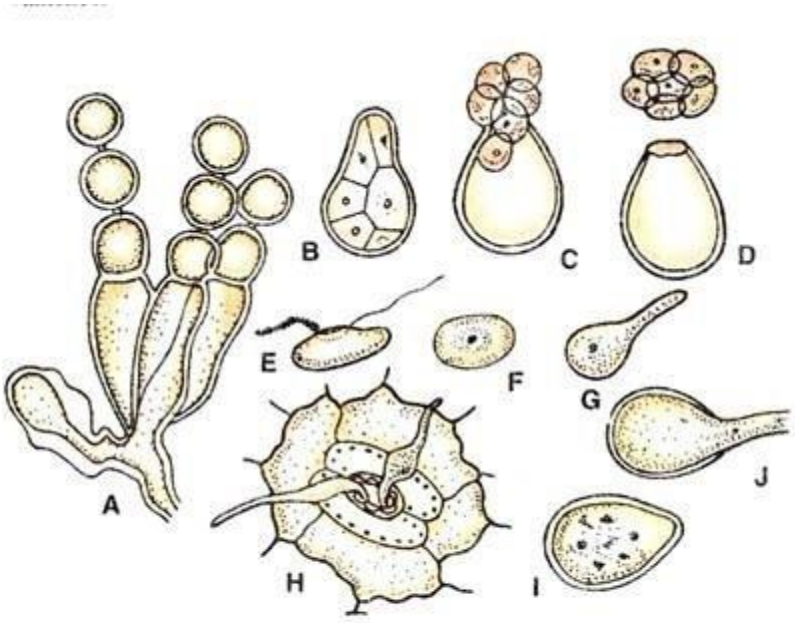

Fig. 6.56 (A-J). *Albugo candida*. A, cluster of sporangiophores bearing sporangia in chains; B-D, differentiation and liberation of zoospores; E, liberated zoospore; F, encysted zoospore; G, germination of cyst to form a germ tube; H, infection through a stoma; I-J, direct germination of sporangium. (After De Bary)

Sexual Reproduction in Albugo:

It is oogamous:

The male sex organ is called an antheridium and the female oogonium (A). They are developed near each other in the intercellular spaces of host tissues towards the end of the growing season. When the mycelium ages, some hyphae grow deep and lie buried in the intercellular spaces of the tissues of the stem, or petioles.

The sex organs arise on separate hyphae called the male and the female hyphae (A). The two soon establish contact. The antheridium comes in contact with the oogonium at the side. The development of sex organs within the host tissue is externally indicated by hypertrophy and distoration in shape in the particular organ.

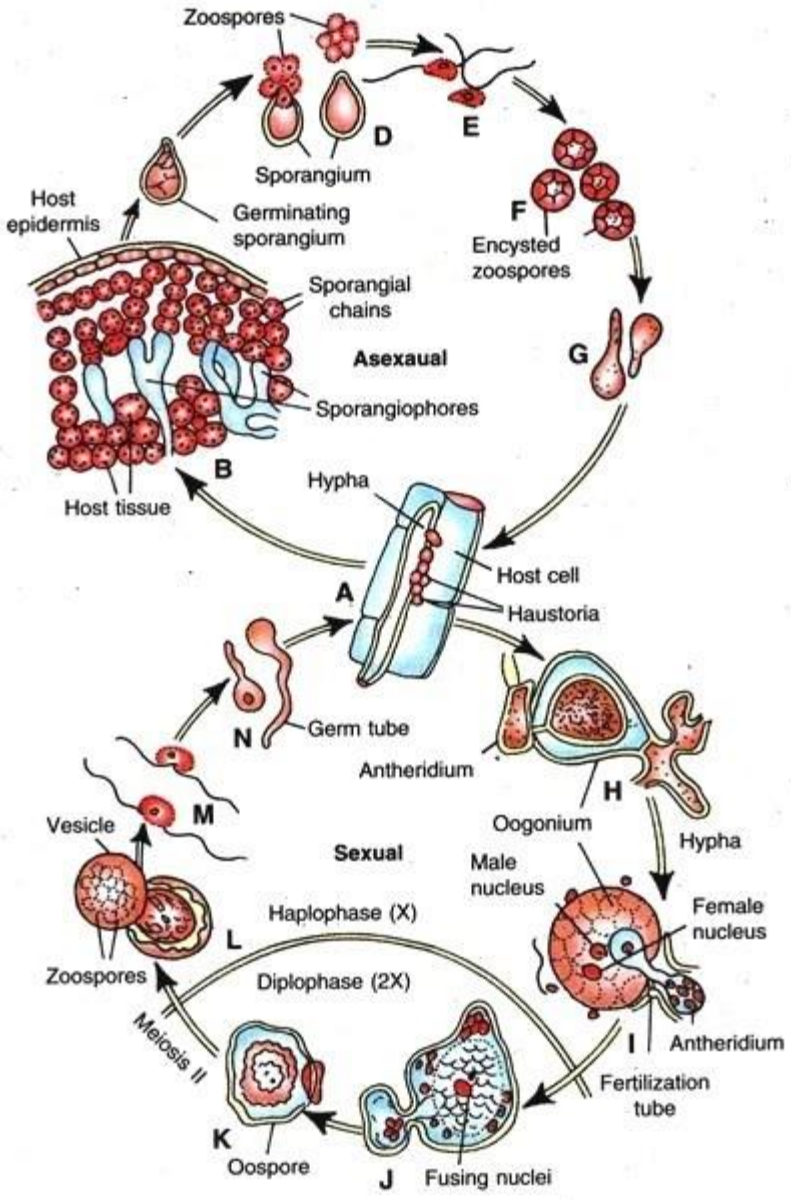

Fig. 6.61. Diagrammatic life cycle of *Albugo candida.*

(a) Oogonium:

It arises as a globular enlargement of the tip of the female hypha. Sometimes the oogonium is intercalary in position. The swelling is multinucleate(A) Across wall appears below this

inflation (B). It separates the terminal oogonium from the rest of the female hypha. The young ooglum has highly vacuolated contents.

The numerous nuclei and vacuoles are evenly distributed and the usual cell organelles are dispersed throughout the oogonium. The nuclei divided mitotically and increase in number as the oogonium advanced towards maturity. After the first Sc division the ooginial cystoplasm shows marked zonation (C).
It becomes differentia into two distinct regions with the rearrangement of the numerous nuclei and other cellular organellers. Most of the original cytoplasm of the oogonium forms the central,rounded dense ooplasm. It is multinucleate and contains only a few mitochondria,ribosomes and cisternae of ER. It is rich in lipid vesicles and reserve vesicles containing electron dense inclusions (reserve globules).

The ooplasm is surrounded by the peripheral cytoplasm constituting the periplasm. It is more vacuolate and spongy. The vacuoles are large. Besides, the periplasm is rich in nuclei, mitochondria endoplasmic reticulum and ribosomes. It has protoplasm of thinner consistency. Sometime after all the nuclei of ooplasm migrate into the periplasm (D) and become arranged in a ring.

Here they divide mitotically with the spindles lying in such a way that one pole of each that one pole mitosis one daughter nucleusthe ooplasm and the other in the periplasm (E). At the end of mitosis one daughter nucleus of each spindle goes to the ooplasm and the other to the periplasm (F). However, the ooplasm at maturity has a single centrally located nucleus (G).

There are two views with regard to this uninucleate condition of the mature ooplasm. According to one view, all the nuclei excepting one are extrude from the ooplasm and are deposited in the periplasm. The second view IS that in the later stages of development all the nuclei in the ooplasm excepting one degenerate and disappear. The uninucleate ooplasm functions as the female gamete or egg or oosphere (G).

(b) Antheridium:
It is an elongated club-shaped cell (A). It is multinucleate. The antheridium is developed at the end of a male hypha lying close to the oogonium. The end of the male hypha enlarges into club-shaped swelling.

The latter is then cut off by a cross wall from the rest of the male hypha (B). This terminal dub-shaped cell is called an antheridium. It contains several nuclei (usually 6-12), but only one is functional. The paragynous antheridium comes in direct contact with the oogonium at the side (C).

(c) Fertilisation:

At the point of contact of antheridium with the oogonium, the walls become very thin. A portion of the contents of the oogonium surrounded by a thin membrane grows into a papilla-like outgrowth (G).

This papilla-like oogonial bulging is called the receptive papilla It is functionless. The receptive papilla bulges (G) into the antheridium but soon disappears. This is followed by the formation of a slender tubular outgrowth from the antheridium.

It is the fertilisation tube (H). The fertilisation tube passes through the thin spot in the oogonial wall and enters the multinucleate periplasm. It then dips deep into the ooplasm. Prior to this a spherical and granular cytoplasmic body appears in the centre of the oosphere (H). It is known as the coenocentrum.
The single functional female nucleus is attracted towards it and becomes attached to a point near it.

The fertilisation tube finally reaches the coenocentrum and ruptures (I) at the tip to introduce a single male nucleus which fuses with the female nucleus. Thereafter the fertilisation tube collapes but persists and the coenocentrum vanishes. On removing or displacing the attached antheridium Tewan and Skoropad (1977) observed a clear hole surrounded by some fibrous material.

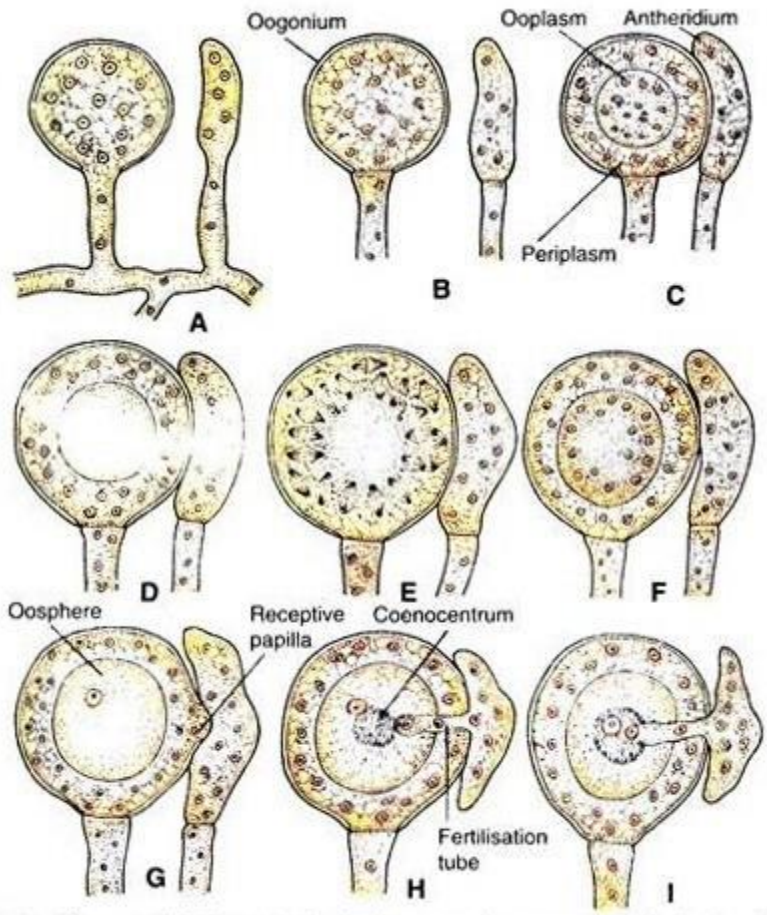

Fig. 6.57 (A-I). *Albugo candida*. Stages in the development of sex organs and fertilisation. Explanation in the text.

Oospore (Fig. 6.58 A-C):

Tewari and Skoropad (1977) investigated the fine structure and development of A. Candida oospores. According to them, the young oospore is delimited from the vacuolate periplasm by an electron-dense cell wall.

The single layered cell wall of the young oospore encloses dense cytoplasm containing a group of reserve vesicles, lipid vesicles and a few membranous organelles. It is surrounded by periplasm rich in vacuolate cytoplasm containing membranous organelles.

Further development of oospore if marked by the deposition of 4 layers, two on the outer and two on the inner side of the first (original) layer of the young oospore. The mature oospore thus has a thick highly differentiated 5-layered wall.

External to the oospore wall are the two addition protective investments formed by the persistent periplasm and the oogonial wall. The thick highly differentiated oospore wall together with the two surrounding additional layers contributes to the longevity of Albugo oospore. The authors suggest that periplasm plays an active part in deposition of oospore wall layers.

Within the fully developed oospore wall is the scanty cytoplasm surrounding a large central reserve globule. Some small bodies resembling the reserve globules in appearance and numerous lipid vesicles occupy most of the space between the oospore wall and the central reserve globule.

The highly differentiated thick, oospore wall together with the two additional layers constituted by the persistent perisperm and the oogonial wall provides protection and the numerous lipid vesicles in the oospore cytoplasm furnish energy for the long dormancy or overwintering by oospores in Albugo.

The outer layer of the oospore wall is comparatively thicker. It is warty or tuberculate. In other species it may have a network of ridges or other patterns.

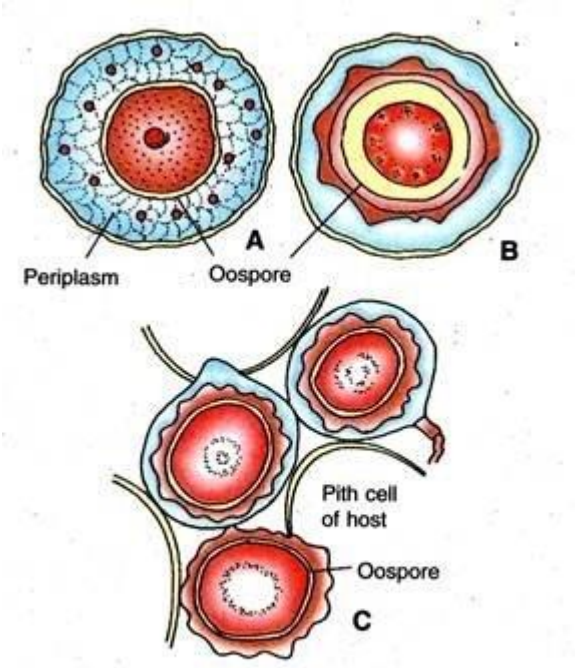

Fig. 6.58 (A-C). *Albugo candida.* Showing structure of oospore as seen under light microscope.

Location of meiosis:

The place of meiosis in Albugo is still under dispute. Stevens (1899) suggested that Albugo possesses diploid somatic nuclei which undergo meiosis in the gametangia (antheridia and oogonia). His interpretation was disputed by later workers. They held that Albugo and other Oomycetes, as a whole, are haploid. Oospore is the only diploid structure in the life cycle.

It undergoes zygotic meiosis. Walker (1969) observed that after fertilization when a thick wall is being developed around the oospore, its diploid nucleus divides repeatedly to form 32 nuclei. Probably the two earlier of these divisions constitute meiosis. In this 32 nucleate stage, the oospore enter the resting stage and tides over the period unfavourable for growth.

However, Sansome and Sansome (1974) have advanced evidence in support of gametangial meiosis and diploid life cycle in Albugo Candida. They hold that the first two divisions of nuclei which occur in the gametangia constitute meiosis. This view is gaining ground.

Germination of Oospore (Fig. 6.59):

On the onset of conditions favourable for growth, the oospore germinates. The central globule and the lipid droplets gradually disappear. The contents of the oospore assume uniform granular appearance.

The diploid nucleus undergoes repeated divisions to form many nuclei (about 100 or even more). A small amount of cytoplasm gathers around each daughter nucleus. Numerous uninucleate daughter protoplasts thus result. Each of these metamorhoses into a biflagellate zoosore.

The oospore then germinates to release the zoospores by either of the two following methods:— (i) The thick oospore wall cracks. A germ tube emerges through the split. It ends in a thin vesicle. From the oospore the zoospores pass into the vesicle. Soon the vesicle perishes to liberate the zoospores.

(ii) Through a crack in the oospore wall emerges a thin sessile' vesicle containing the zoospores (A).

The vesicle soon bursts to liberate the zoospores.

(iii) Verma and Petrie (1975) described direct germination of oospore without the intervention of zoospores. In this method after the disappearance of the central globule and the lipid dropletes the contents of oospore assume uniform granular apearance.

The thick oospore wall then cracks. The contents then emerge in the form of one or two simple or branched germ tubes. Direct penetration of the host by a germ tube has not been reported. Good germination occured at 10-20°C. They observed that 71 percent of the oospores collected from the field in August germinated within two weeks.

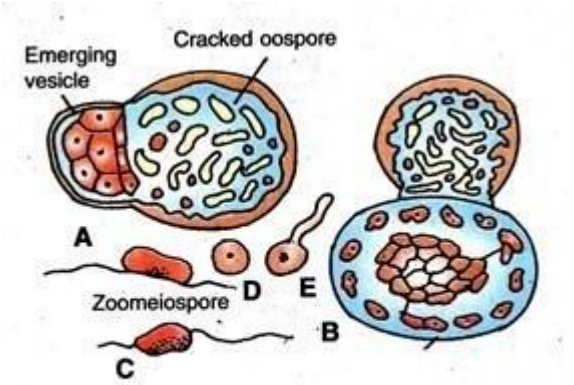

Fig. 6.59 (A-E). *Albugo candida.* A-B, Germination of Oospore; C, liberated zoospore; D-E, germination of zoospore. (After De Bary)

Structure of zoospore:

The liberated zoospore is a biflagellate, uninucleate structure which is reniform in shape. The two unequal flagella arise from a depression on the concave side. The shorter flagellum is of tinsel type and the longer one of whiplash type. The former is directed forward and the latter trails behind when the zoospore is in motion.

Germination of Zoospore (Fig. 6.59 D-E):

On coming in contact with a suitable host. The flagella are withdrawn. It then rounds off and secretes a wall around it (D). Soon the encysted zoospore (cyst) puts out a germ tube (E) which enters the host tissue through a stoma. Once within the host tissue the germ tube grows vigorously and forms a new mycelium.

Primary infection of host:

According to Verna et al. (1975), the zoospores produced in the germinating oospores serve as a primary inoculum for infection of the susceptible host. The emerging cotyledons are the infection sites.

After penetration the first haustorium originates near the tip of the young hypha. The latter then continues to grow leaving the haustorium as a side branch. The formation of the first functional haustorium is the critical step in primary infection. It indicates the establishment of a compatible functional host-parasite relationship.

From then onwards hyphal growth increases rapidly. The hyphae grow around the palisade mesophyll cells with haustoria penetrating the adjacent cells. The number of haustoria per cell varies from one to several. In the course of time a mycelial base is established inside the host tissue (cotyledons).

It produces masses of zoosporangia on the cotyledons which serve as secondary inoculum in initiating systemic infection. The parasite ultimately reaches the inflorescence region where it produces the oospores.

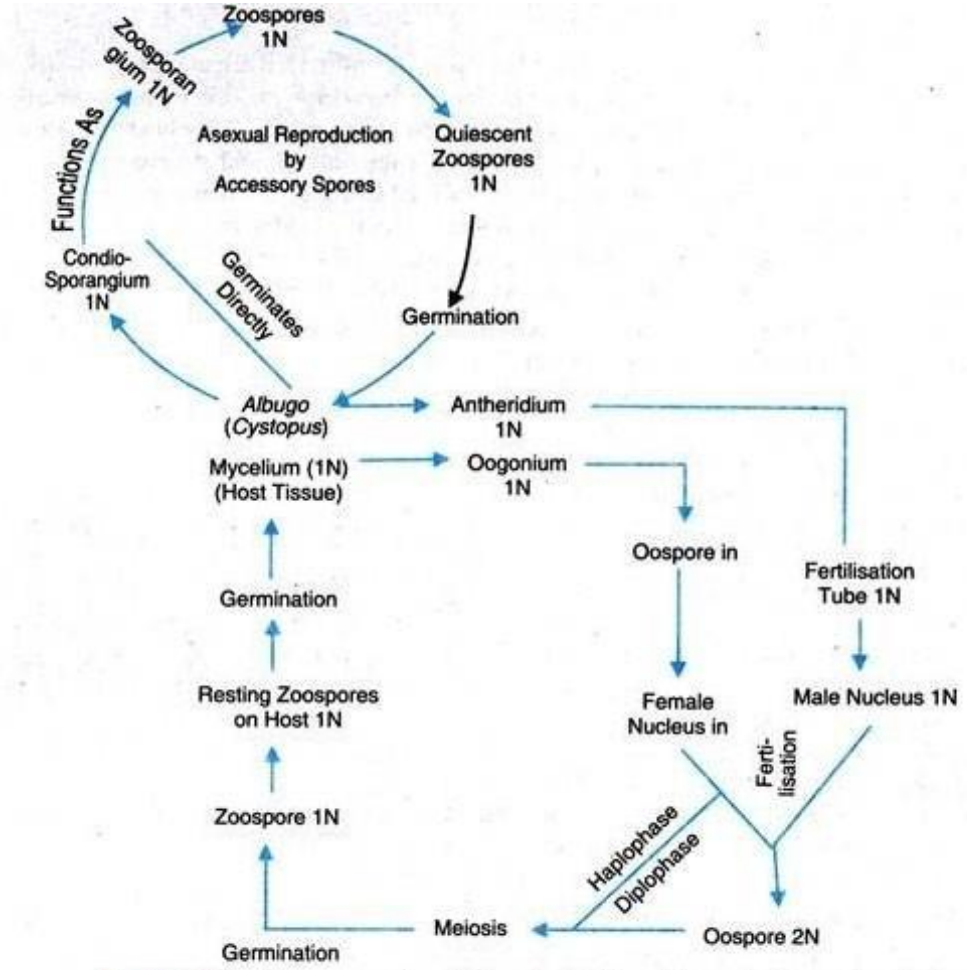

Fig. 6.60A. Graphic representation of life cycle of *Albugo (Cystopus)* with zygotic meiosis.

1. Cell Structure of Saccharomyces 2. Vegetative Body of Saccharomyces 3. Reproduction 4. Life Cycle Patterns.

Cell Structure of Saccharomyces:

The genus Saccharomyces (Gr. Saccharon, sugar; mykes, fungus) consists of about 41 species. 5. cerevisiae, commonly known as Brewer yeast or Backer's yeast is used widely in wine and baking industry.

It produces two types of enzymes: an extracellular invertase and an intracellular zymase. The invertase hydrolyses canesugar to dextrose or invert sugar and zymase breaks invert sugar into ethyl alcohol and carbon dioxide.

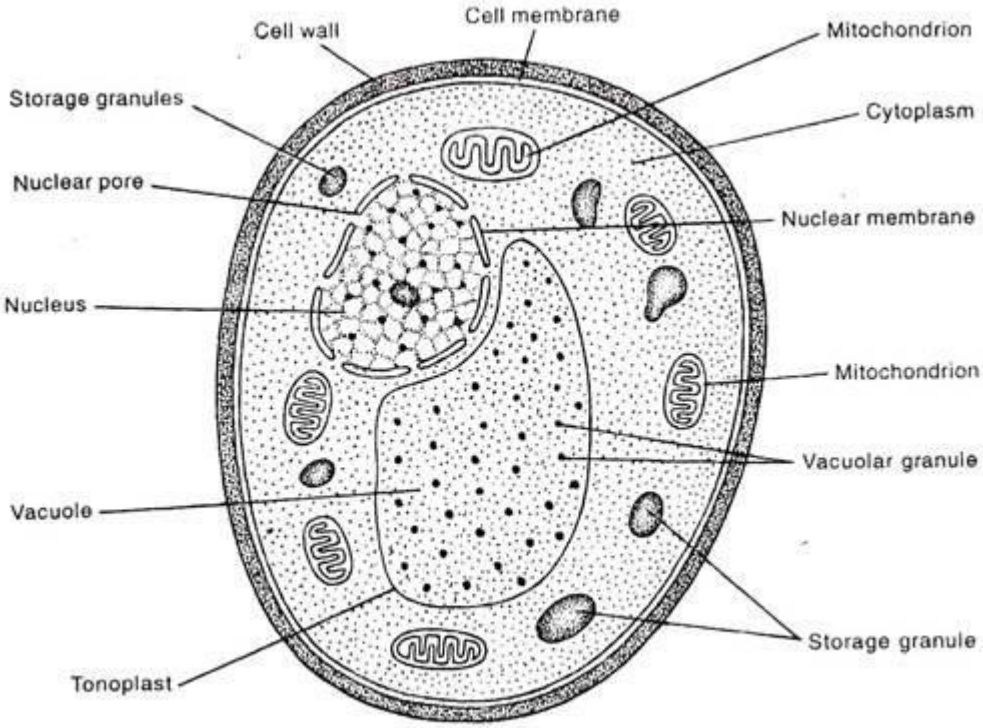

Fig. 4.34 : Cell structure of *Saccharomyces cerevisiae* under electron microscope

Vegetative Body of Saccharomyces:

The thalloid plant body is unicellular, but during rapid multiplication by budding the cells may remain attached in chain forming pseudo- mycelium (Fig. 4.38). The cells may be globose, elliptical, oval to even rectangular in shape and measure about 5-6 x 6-8 µm.

Electron microscopic studies (Fig. 4.34, 4.35) and chemical analysis of Saccharomyces cerevisiae show that the cells are surrounded by a distinct cell wall with three layers. The outermost layer mainly consists of protein-mannan and some chitin; the middle layer mainly of glucan and the innermost layer consists of proteinglucan.

Some phosphate and lipids are also present, while cellulose is absent in the cell wall. Inner to the cell watl is the cell membrane (plasmalemma), i.e., an usual unit membrane having series of shallow, elongated pits or invaginations (Fig. 4.35).

In the centre, the cell having a large central vacuole, limited by a single membrane, the tonoplast, which contains a watery substance, granules of polymetaphosphate and lipid.

The cytoplasm is granular and contains organelles like nucleus, mitochondria, golgi apparatus, endoplasmic reticulum, ribosome and other substances like glycogen bodies, volutin granules, oil globules etc.

Some hydro- lytic enzymes like proteases, esterases, ribonuclease etc., are also present in the cytoplasm. The nucleus having outer perforated double unit membrane remains by the side of the vacuole. The nucleus is bipartite in nature having major Feulgen positive and a smaller Feulgen negative regions (Moor and Muhlethaler, 1963).

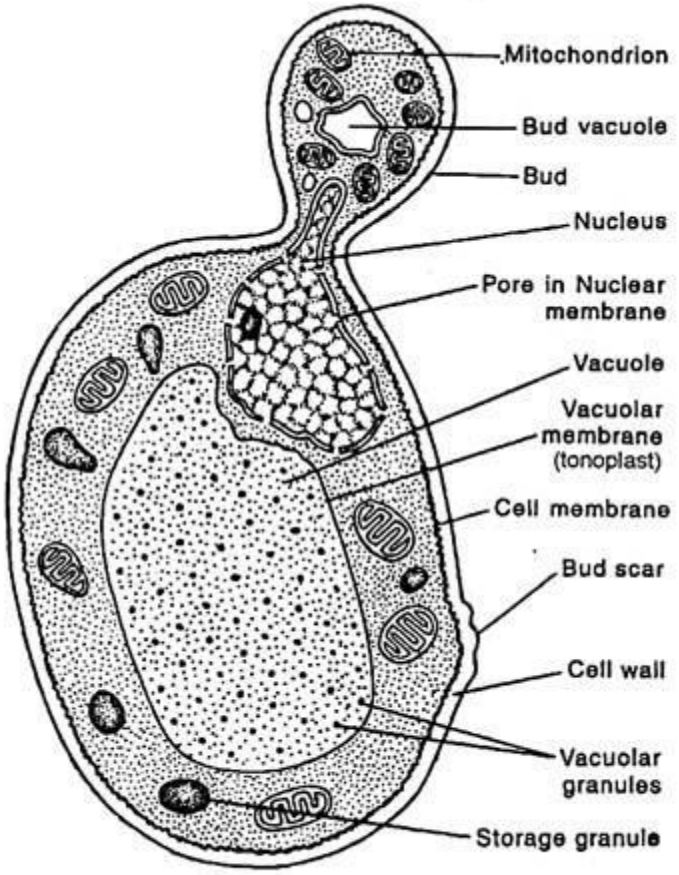

Fig. 4.35 : Structure of a budding cell of *Saccharomyces cerevisiae* under Electron microscope

Reproduction in Saccharomyces:

Saccharomyces reproduces by vegetative, asexual and sexual means.

A. Vegetative Reproduction:

Vegetative reproduction takes place by fission and budding.

(a) Fission:

It takes place during favourable condition. In this process, single vegetative cell forms two daughter cells of equal size (Fig. 4.36). During fission, a constriction

appears in the middle of the cell and simultaneously nucleus undergoes mitotic division.

Both the steps progress simultaneously. After nuclear migration, one at each side, partition wall forms almost in the half way of the mother cell and, as such, two daughter cells are formed.

(b) Budding:

Budding also takes place during favourable condition. The protoplasm of vegetative cell swells up at one side in the form of a bud (Fig. 4.37). The nucleus undergoes mitotic division. Out of two nuclei formed by mitosis, one goes to the bud and other one remains in the mother. Bud enlarges and eventually cuts off from the mother by partition wall.

The size of the bud is always smaller than the mother cell. After maturation, these bud separate from the mother and leave a convex scar on the surface, called bud scar. Similar scar with concave surface remains on the wall of the bud, called birth scar.

Sometimes due to rapid division, large number of buds develop without being detached from one another and persist in the form of branched or unbranched chain, called pseudo- mycelium (Fig. 4.38). Finally the cells get detached and grow individually.

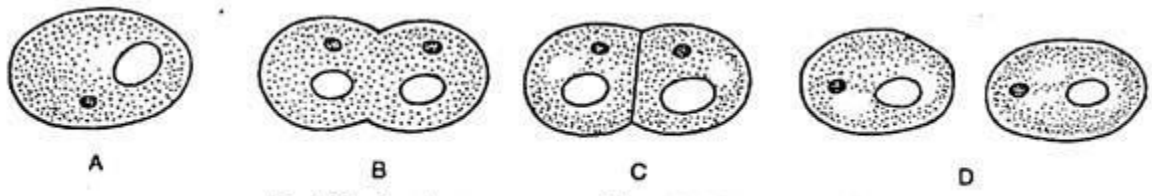

Fig. 4.36 : *Saccharomyces cerevisiae* : A-D. Stages of fission

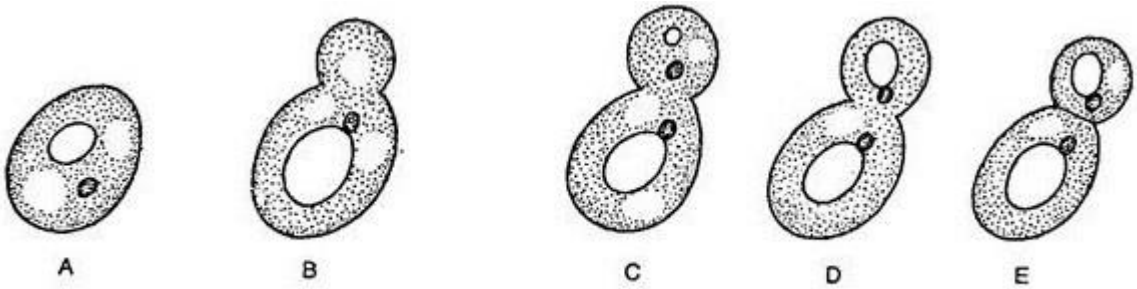

Fig. 4.37 : *Saccharomyces cerevisiae* : A-D. Stages of budding

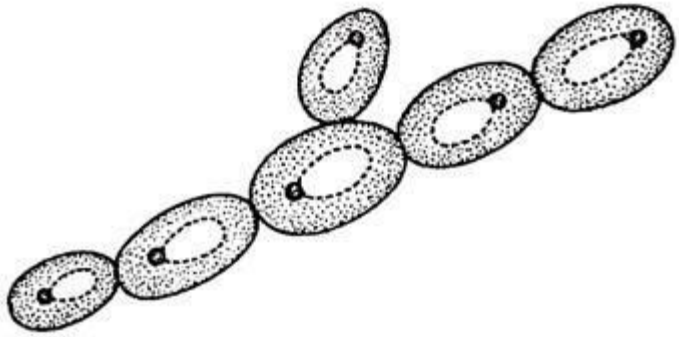

Fig. 4.38 : Pseudomycelium of *S. cerevisiae*

B. Asexual Reproduction:

It takes place during unfavourable condition by the formation of thick walled spore, called endospore (Fig. 4.39). During this process nucleus divides mitotically and forms four nuclei.

The protoplast divides into four units, each with one nucleus and forms four endospores.

During favourable condition, endospore germinates by budding and buds grow individually.

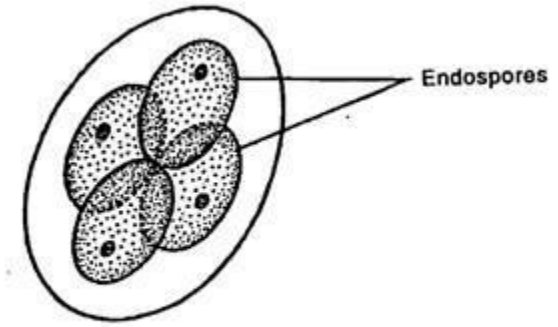

Fig. 4.39 : *Schizosaccharomyces pombe* : Endospores (four) in a cell

C. Sexual Reproduction:

Sexual reproduction takes place during unfavourable condition. In this process, two vegetative cells or ascospores behave as gametangia (Fig. 4.40). Two such cells come very close and develop beak-like outgrowth towards each other. Both the outgrowths come in contact and the intervening walls between them dissolve.

The nuclei of both the gametangia come to the fused outgrowth (conjugation tube) and they fuse therein to form a diploid zygote. The zygote behaves as an ascus. The diploid nucleus of zygote undergoes meiotic division forming 4 or 8 (with additional mitosis) ascospores. The ascospores are liberated by breaking the ascus wall and behave as somatic cell.

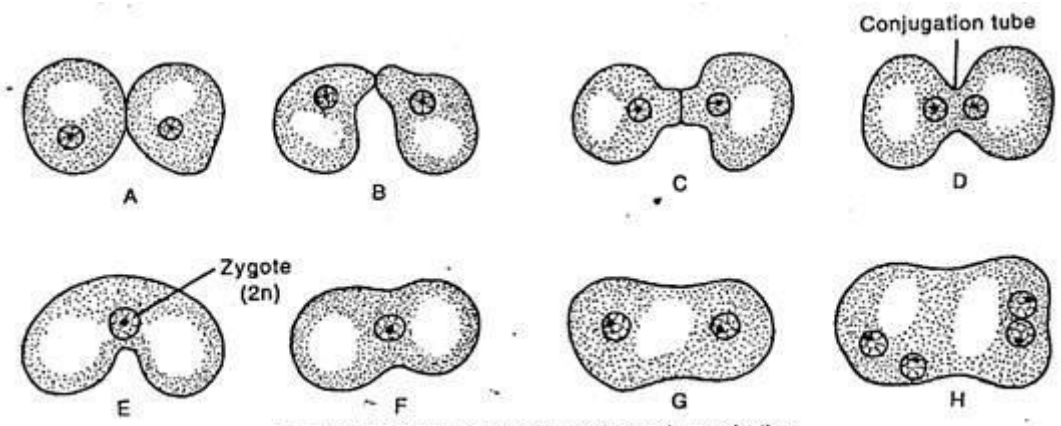

Fig. 4.40 : Different stages (A-H) of sexual reproduction

Life Cycle Patterns of Saccharomyces:

Three patterns of life cycle are found in yeast:

Haplobiontic, diplobiontic and haplodiplobiontic (Fig. 4.41):

1. Haplobiontic Type:

This type of life cycle is characterised by more elaborate haploid phase than the diploid phase, found in Schizosaccharomyces octosporus (Fig. 4.41 A). The diploid phase is restricted only in the zygote. The vegetative cells are haploid and behave as gametangia.

Two such gametangia fuse together and form a diploid cell. The diploid cell behaves as an ascus whose nucleus divides first meiotically, then mitotically; results in the formation of eight ascospores. After maturation, the ascospores liberate by bursting the ascus wall. The ascospores then behave as vegetative cell and continue multiplication through budding.

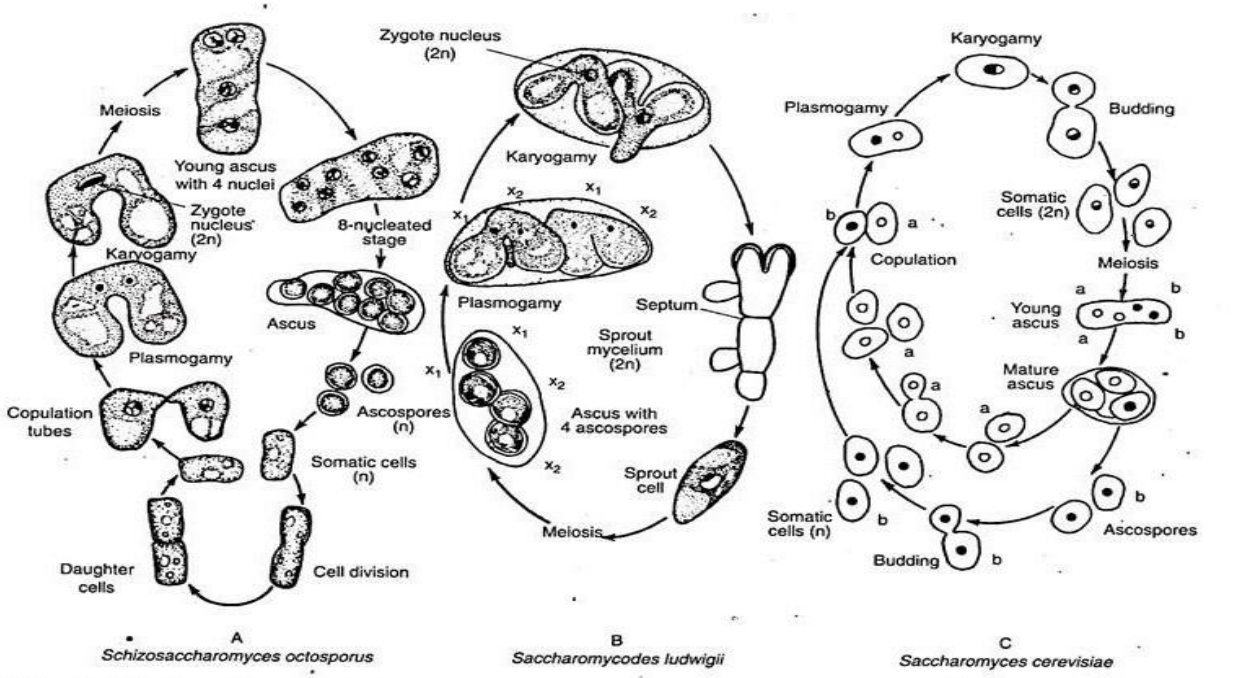

Fig. 4.41: Life cycles of three types of yeasts : A. Haplobiontic (*Schizosaccharomyces octosporus*). B. Diplobiontic (*Saccharomycodes ludwigii*), C. Haplo-diplobiontic (*Saccharomyces cerevisiae*).

2. Diplobiontic Type:

This type of life cycle is characterised by more elaborate diploid phase than the haploid phase, found in Saccharomycodes ludwigii (Fig. 4.41 B). The haploid phase is restricted only in ascospore, with short duration. The ascospores behave as gametangia and, without liberating from ascus, they unite in pair. The paired gametangia after fusion produce diploid zygote.

The zygote then germinates by producing germ tube which comes out through the ascus wall. The germ tube becomes multicellular from which diploid sprouts develop by budding. After detachment from the mother, the diploid sprouts function as asci and produce four ascospores by reduction division.

3. Haplo-Diplobiontic Type:

This type of life cycle is represented by haploid and diploid phases, of more or less equal duration, found in Saccharomyces cerevisiae (Fig. 4.41 C). The haploid cells of opposite mating type normally multiply by budding. Two such cells of opposite mating behave as gametangia and undergo fusion. The fused gametangia develop a diploid zygote.

The diploid zygote like the haploid cells undergoes budding and forms many diploid cells. With the scarcity of food, the diploid cell behaves as an ascus and by

reduction division it forms four haploid ascospores. After liberating from the mother wall, the ascospores undergo budding and form many haploid somatic cells.

Economic Importance Of Fungi

Fungi are one of the most important microorganisms carrying out essential functions which may not be visible but are crucial in accelerating biological processes. These eukaryotic entities are closely related to the fauna and distantly related to the flora with respect to their characteristics and classification. A few features that set fungi apart from other microbes are :

- Fungi are osmotrophic – can absorb food
- Possess a characteristic hypha at their tips which carry out food exploration
- They possess nucleic cells containing chromosomes
- They are heterotrophs, cannot synthesize their own food.
- Reproduce through spore formation(Mushrooms)

Although we usually think of fungi as food perishing agents, they are economically very beneficial. Fungi are extensively used across industries in various forms and stages of processes.

Fungi are an important organism in human life. They play an important role in medicine by yielding antibiotics, in agriculture by maintaining soil fertility, are consumed as food, and forms the basis of many industries. Let us have a look at some of the fields where fungi are really important.

Importance in Human Life

Fungi are very important to humans at many levels. They are an important part of the nutrient cycle in the ecosystem. They also act as pesticides.

Biological Insecticides

Fungi are animal pathogens. Thus they help in controlling the population of pests. These fungi do not infect plants and animals. They attack specifically to some insects. The fungus *Beauveria bassiana* is a pesticide that is being tested to control the spread of emerald ash borer.

Reusing

These microbes along with bacteria bring about recycling of matter by decomposing dead matter of plants and excreta of animals in the soil, hence the reuse enriches the soil to make it fertile. The absence of activities of fungi can have an adverse effect on this on-going process by continuous assembly and piling of debris.

Importance in Medicine

- Metabolites of fungi are of great commercial importance.
- Antibiotics are the substances produced by fungi, useful for the treatment of diseases caused by pathogens. Antibiotics produced by actinomycetes and moulds inhibits the growth of other microbes.
- Apart from curing diseases, antibiotics are also used fed to animals for speedy growth and to improve meat quality. Antibiotics are used to preserve freshly produced meat for longer durations.
- Penicillin is a widely used antibiotic, lethal for the survival of microbes. The reason it is extensively used is since it has no effect on human cells but kills gram-positive bacteria.
- Streptomycin, another antibiotic is of great medicinal value. It is more powerful than Penicillin as it destroys gram-negative entities.
- Yield-soluble antibiotics are used to check the growth of yeasts and bacteria and in treating plant diseases.
- Administration of Griseofulvin results in the absorption by keratinized tissues and are used to treat fungal skin diseases(ringworms).
- Ergot is used in the medicine and the vet industry. It is also used to control bleeding post-child-birth.
- LSD – Lysergic acid, is a derivative of ergot and is used in the field of psychiatry.
- Consuming fungi called Clavatia prevents cancer of the stomach.

Importance in Agriculture

The fungi plant dynamic is essential in productivity of crops. Fungal activity in farmlands contributes to the growth of plants by about 70%.

Fungi are important in the process of humus formation as it brings about the degeneration of the plant and animal matter.

They are successively used in biological control of pests. Plant pests are used as insecticides to control activities of insects. For example – *Empausa sepulchralis*, *Cordyceps melonhae*. Use of fungal pesticides can reduce environmental hazards by a great extent.

Fungi are also used in agricultural research. Some species of fungi are used in the detection of certain elements such as Copper and Arsenic in soil and in the production of enzymes. For instance, biological and genetic research on fungi named Neurospora led to the One Gene One Enzyme hypothesis.

The fungi live in a symbiotic relationship with the plant roots known as mycorrhiza. These are essential to enhance the productivity of farmland. 80-90% of trees could not survive without the fungal partner in the root system.

Importance in Food industry

Some fungi are used in food processing while some are directly consumed. For example – Mushrooms, which are rich in proteins and minerals and low in fat.

Fungi constitute the basis in the baking and brewing industry. They bring about fermentation of sugar by an enzyme called zymase producing alcohol which is used to make wine.

Carbon dioxide- a byproduct in the process, is used as dry ice and also in the baking industry to make the dough (rising and lightening of dough).

Saccharomyces cerevisiae is an important ingredient in bread, a staple food of humans for several years. It is also known as the baker's yeast.

Life Cycle of Marchantia (With Diagram) | Hepaticopsida

The gametophytic phase, reproduction and sporophytic phase in the life cycle of marchantia.

Gametophytic Phase of Marchantia:

External Features of Gametophyte:

The plant body is gametophytic, thalloid, flat, prostrate, plagiotropic, 2-10 cm. long and dichotomously branched (Fig. 1 A).

Dorsal surface:

Dorsal surface is dark green. It has a conspicuous midrib and a number of polygonal areas called areolae. The midrib is marked on the dorsal surface by a shallow groove and on the ventral surface by a low ridge. Each polygonal area represents the underlying air chamber.

The boundaries of these areas represent the walls that separate each air chamber from the next. Each air chamber has a central pore. The midrib ends in a depression at the apical region forming an apical notch in which growing point is situated (Fig. 28 B).

Dorsal surface also bears the vegetative and sexual reproductive structures. The vegetative reproductive structures are gemma cup and develop along the midrib. These are crescent shaped with spiny or fimbriate margins and are about one eighth of a inch in diameter (Fig. I A, 15).

Sexual reproductive structures are borne on special Stalked structures called gametophores or gametangiophores. The gametophores bearing archegonia are

called archegoniophores and that bearing antheridia are called antheridiophores (Fig. 1 A, B).

Ventral surface:

The ventral surface of the thallus bears scales and rhizoids along the midrib. Scales are violet coloured, multicellular, one cell thick and arranged in 2-4 rows (Fig. 1 C). Scales are of two types:

(i) Simple or

ligulate (ii)

Appendiculate

.

Appendiculate (Fig- 1 C, D) scales form the inner row of the scales close with midrib. Ligulate scales form the outer or marginal row and are smaller than the appendiculate scales (Fig. 1 C, E).

Rhizoids are unicellular, branched and develop as prolongation of the lower epidermal cells. They are of two types: (i) Smooth-walled rhizoids, (ii) Tuberculate rhizoids.

In smooth-walled rhizoids both the inner and outer wall layers are fully stretched while in tuberculate rhizoids appear like circular dots in surface view (Fig. 1 F). The inner wall layer modifies into peg like in growth which projects into the cell lumen (Fig. 1 H). The main functions of the rhizoids are to anchor the thallus on the substratum and to absorb water and mineral nutrients from the soil.

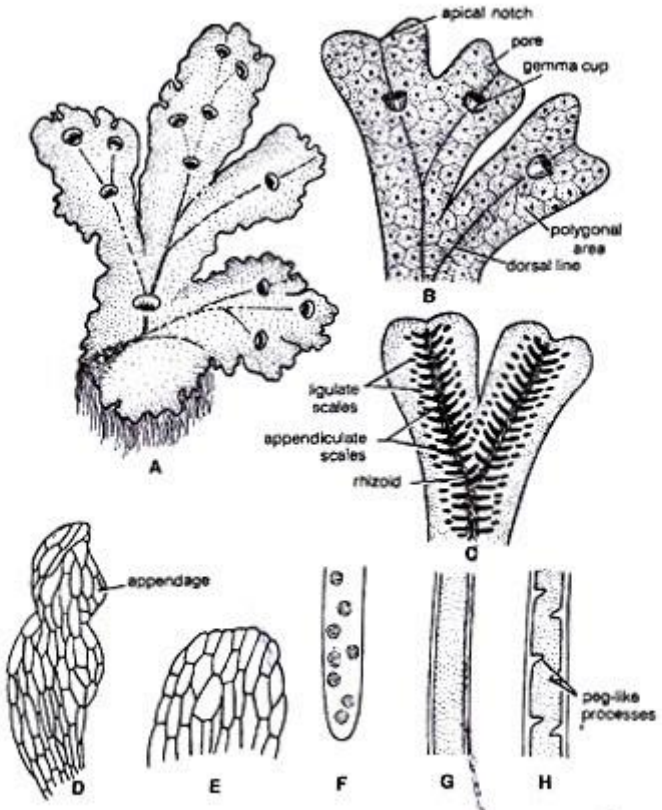

Fig. 1. (A–H). *Marchantia*. Thallus structure (A) Vegetative thallus, (B) Dorsal surface, (C) Ventral surface, (D) Appendiculate scale, (E) Ligulate scale, (F) Tuberculated rhizoid (surface view), (G) Smooth-walled rhizoid, (H) Tuberculated rhizoid showing internal view.

Anatomy of the Gametophyte:

A vertical cross section of the thallus can be differentiated photosynthetic zone and lower storage zone (Fig. 2 A, B, E).

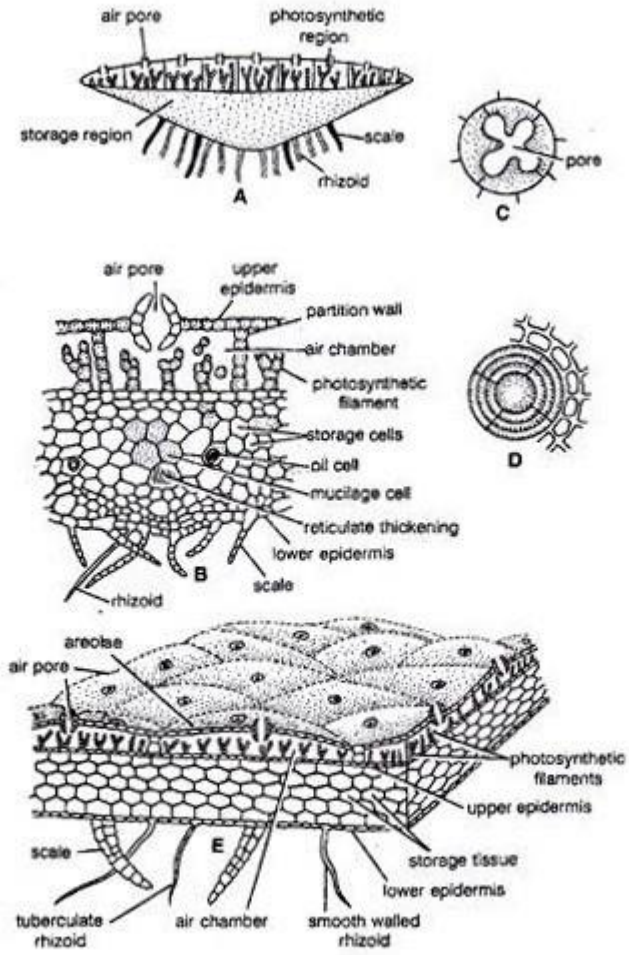

Fig. 2. (A-E). *Marchantia.* Internal structure of the thallus. (A) Vertical Transverse Section (V.T.S.) of thallus (diagrammatic), (B) V.T.S. of thallus (a part cellular), (C) Air pore as seen in the ventral view, (D). Air pore as seen in the dorsal view, (E). V.T.S. of thallus in three dimensional view.

Upper Photosynthetic zone:

The outermost layer is upper epidermis. Its cells are thin walled square, compactly arranged and contain few chloroplasts. Its continuity is broken by the presence of many barrel shaped air pores. Each pore is surrounded by four to eight superimposed tiers of concentric rings.
(Fig. 2 B) with three to four cells in each tier (Fig. 2 D).

Air pores are compound in nature. The lower tier consists of four cells which project in the pore and the opening of the pore looks star like in the surface view (Fig. 2 C). The walls of the air pore lie half below and half above the upper epidermis (Fig. 2 B).

Just below the upper epidermis photosynthetic chambers are present in a horizontal layer (Fig. 2 B). Each air pore opens inside the air chamber and helps in exchange of gases during photosynthesis.

These are chambers develop schizogenously (Vocalized separation of cells to form a cavity) and are separated from each other by single layered partition walls. The partition walls are two to four cells in height. Cells contain chloroplast. Many simple or branched photosynthetic filaments arise from the base of the air chambers (Fig. 2 B).

Storage zone:
It lies below the air chambers. It is more thickened in the centre and gradually tapers towards the margins. It consists of several lasers of compactly arranged, thin walled parenchymatous isodiametric cells. Intercellular spaces are absent.

The cells of this zone contain starch. Some cells contain a single large oil body or filled with mucilage. The cells of the midrib region possess reticulate thickenings. The lower most cell layer of the zone forms the lower epidermis. Some cells of the middle layer of lower epidermis extend to form both types of scales and rhizoids (Fig. 2 B).

Reproduction in Marchantia:
Marchantia reproduces by vegetative and sexual methods.
(i) Vegetative Reproduction:
In Marchantia it is quite common and takes place by the following methods:
1. By Gemmae:
Gemmae are produced in the gemma cups which are found on the dorsal surface of the thallus (Fig. 3 A). Gemma cups are crescent shaped, 3 m.m. in diameter with smooth, spiny or fimbriate margins (Fig. 3 B).

V. S. passing through the gemma cup shows that it is well differentiated into two regions:
Upper photosynthetic region and inner storage region (Fig. 3 D).

The structure of both the zones is similar to that of the thallus. Mature gemmae are found to be attached at the base of the gemma cup by a single celled stalk.

Intermingled with gemmae are many mucilage hairs. Each gemma is autotrophic, multicellular, bilaterally symmetrical, thick in the centre and thin at the apex. It consists parenchymatous cells, oil cells and rhizoidal cells. It is notched on two sides in which lies the growing point (Fig. 3 C).

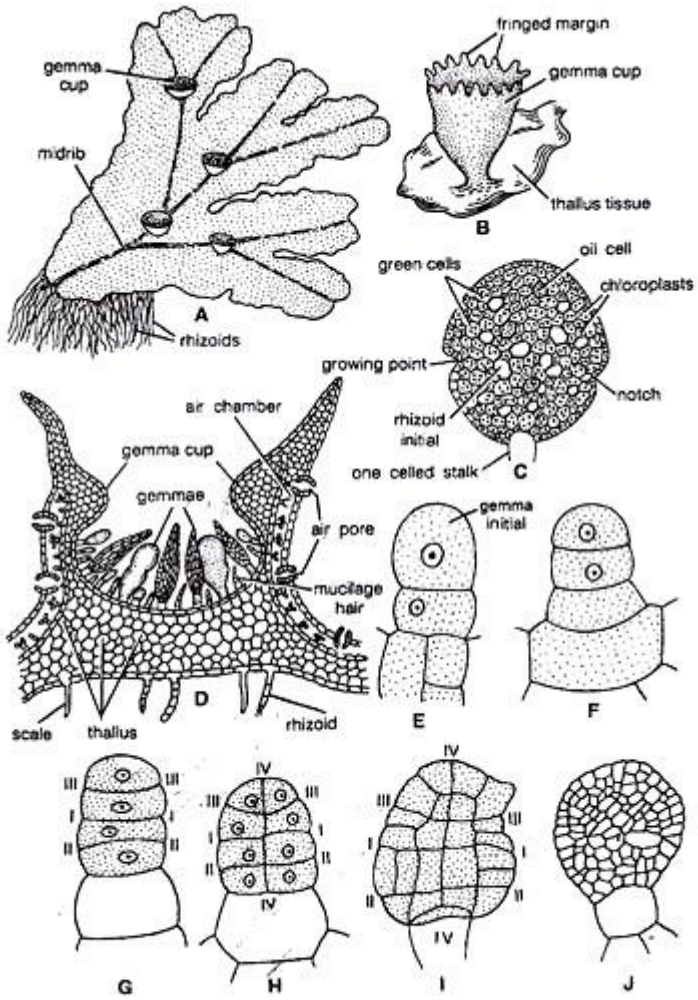

Fig. 3. (A-J). *Marchantia*. Gemma cup. (A) Thallus showing gemma cup on the dorsal surface. (B) A gemma cup, (C) Gemma, (D) Gemma cup in a vertical section, (E-J). Different stages in the development of Gemma.

All cells of the gemma contain chloroplast except rhizoidal cells and oil cells. Rhizoidal cells are colourless and large in size. Oil cells are present just within the margins and contain oil bodies instead of chloroplast.

Dissemination of Gemmae:

Mucilage hairs secrete mucilage on absorption of water. It swells up and presses the gemmae to get detached from the stalk in the gemma cup. They may also be detached from the stalk due to the pressure exerted by the growth of the young gemmae. The gemmae are dispersed over long distances by water currents.

Germination of Gemmae:

After falling on a suitable substratum gemmae germinate. The surface which comes in contact with the soil becomes ventral surface.

The rhizoidai cells develop into rhizoids. Meanwhile, the growing points in which lies the two lateral notches form thalli in opposite directions. Thus, from a single

gemmae two thalli are formed. Gemmae which develop on the male thalli form the male plants and those on the female thalli form the female plant.

Development of Gemma:

The gemma develops from a single superficial cell. It develops on the floor of a gemma cup. It is papillate and called gemma initial (Fig. 3 E). It divides by a transverse division to form lower stalk cell and upper cell (Fig. 3 F). The lower cell forms the single celled stalk.

The upper cell further divides by transverse division to form two cells. Both cells undergo by similar divisions to form four cells (Fig. 3 G). These cells divide by vertical and horizontal division to form a plate like structure with two marginal notches. It is called gemma (Fig. 3 H-J).

2. Death and decay of the older portion of the thallus or fragmentation:

The thallus is dichotomously branched. The basal part of the thallus rots and disintegrates due to ageing. When this process reaches up to the place of dichotomy, the lobes of the thallus get separated. The detached lobes or fragments develop into independent thalli by apical growth (Fig. 4 A-C).

3. By adventitious branches:

The adventitious branches develop from any part of the thallus or the ventral surface of the thallus or rarely from the stalk and disc of the archegoniophore in species like M. palmata (Kashyap, 1919). On being detached, these branches develop into new thalli (Fig. 4 D).

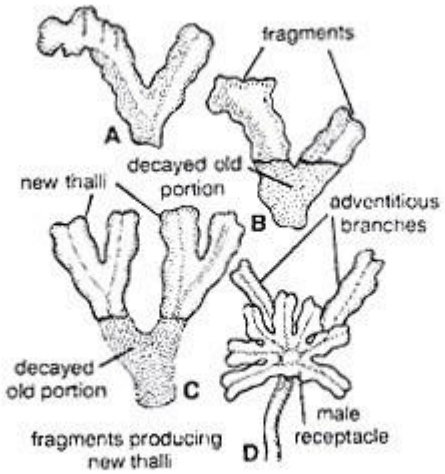

Fig. 4. (A-D). *Marchantia*. Vegetative reproduction. (A-C). Fragmentation, (D) Adventitious branches arising between the lobes from the lower surface of the male disc.

(ii) Sexual Reproduction:

Sexual reproduction in Marchantia is oogamous. All species are dioecious. Male reproductive bodies are known as antheridia and female as archegonia. Antheridia and archegonia are produced an special, erect modified lateral branches of thallus called antheridiophore and archegoniophore arpocephalum) respectively (Fig. 5 A, B).

Further growth of the thallus is checked because growing point of the thallus is utilised in the formation of these branches. In some thalli of M. palmatci and L. polymorpha abnormal receptacle bearing both anheridia and archegonia have also been reported, such bisexual receptacles are called as androgynous receptacles.

Internal structure of Antheridiophore or Archcgoniophore:

Its transverse section shows that can be differentiated into two sides: ventral side and dorsal side. Ventral side has two longitudinal tows with scales and rhizoids. These grooves, run longitudinally through the entire length of the stalk. Dorsal side shows an internal differentiation of air chambers. (Fig. 5 C).

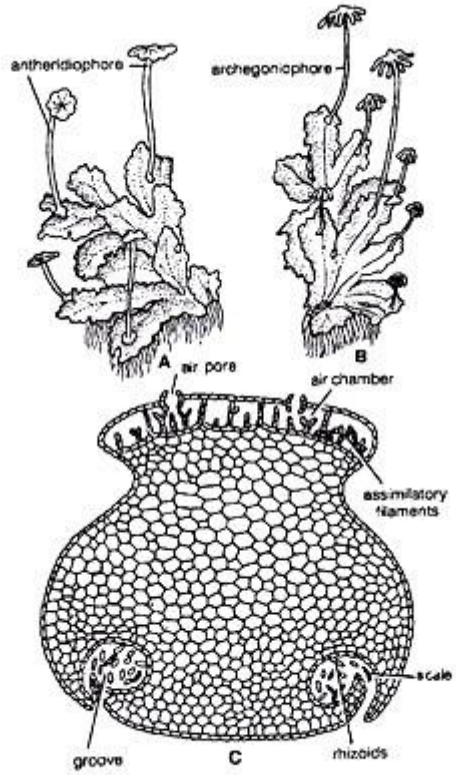

Fig. 5. (A-C). *Marchantia*. Gametophores. (A) Thallus bearing antheridiophores, (B) Female thallus bearing archegoniophores, (C) Transverse section of gametophore.

Antheridiophore:

It consists of 1-3 centimetre long stalk and a lobed disc at the apex (Fig. 32). The disc is usually eight lobed but in M. geminata it is four lobed. The lobed disc is a result of created dichotomies.

L.S. through disc of Antheridiophore:

The disc consists of air chambers alternating with heridial cavities. Air chambers are more or less triangular and open on upper surface by n pore Called ostiole. Antheridia arise in acropetal succession i.e., the older near the center and youngest at the margins. (fig. 6 A).

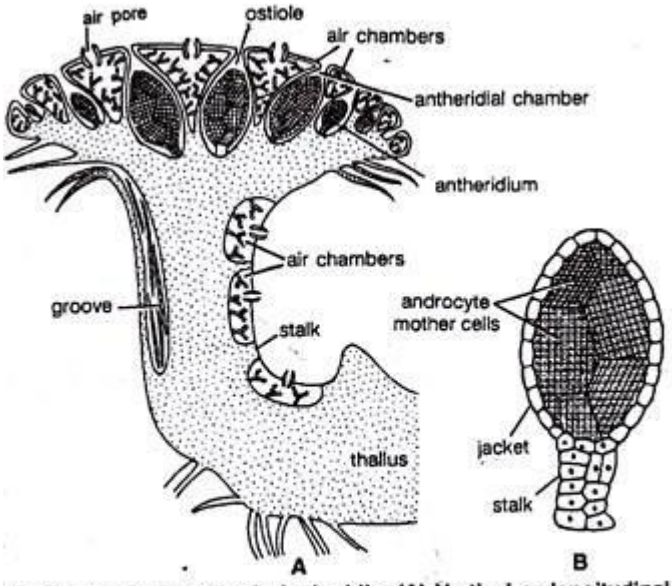

Fig. 6. (A-B). *Marchantia* Antheridia. (A) Vertical or longitudinal section passing through disc of antheridiophore, (B) a mature antheridium antheridium.

Mature Antheridium:

A mature antheridium is globular in shape and can be differentiated into two parts stalk and body. Stalk is short multicellular and attaches the body to the base of the antheridial chamber. A single layered sterile jacket encloses the mass of androcyte mother cells which metamorphosis into antherozoids (Fig. 6 B, 7 G). The antherozoid is a minute rod like biflagellate structure (Fig. 8 H).

Development of Antheridium:

The development of the antheridium starts by a single superficial cell which is situated on the dorsal surface of the disc, 2-3 cells behind the growing point. This cell is called antheridial initial (Fig. 7 A). The antheridial initial increases in size and divides by a transverse division to form an outer upper cell and a lower basal cell (Fig. 7 B).

Basal cell remains embedded in the tissue of the thallus, undergoes a little further development and forms the embedded portion Of the antheridial stalk. Outer cell divides to form a filament of four cells. Upper two cells of the four celled filament are known as primary antheridial cells and lower two cells are known as primary stalk cells (Fig. 7 C).

Primary stalk cells from the stalk of the antheridium. Primary antheridial cells divide by two successive vertical divisions at right angle to each other to form two tiers of four cells each
(Fig. 7 D). A periclinal division is laid down in both the tiers of four cells and there is formation of eight outer sterile jacket initials and eight inner primary androgonial cells (Fig. 7 E).

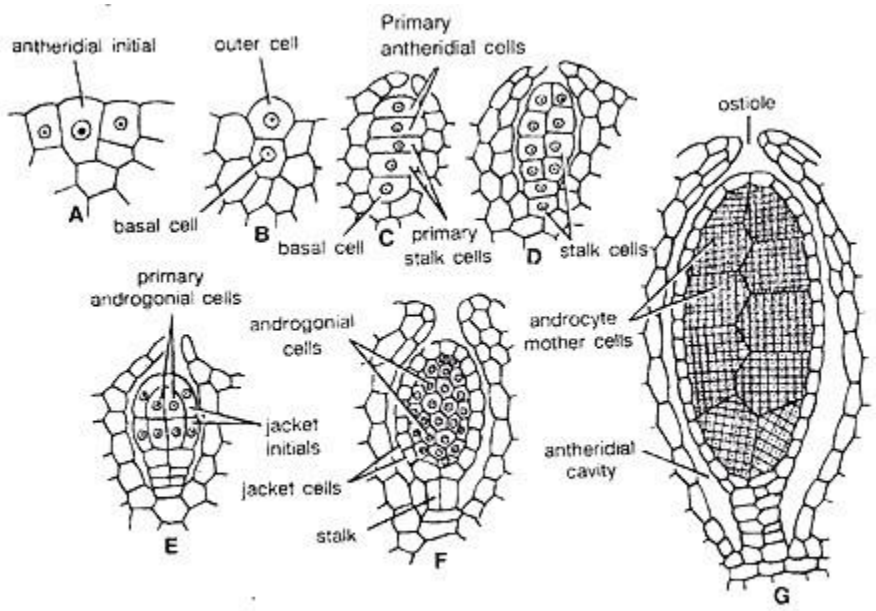

Fig. 7. (A-H). *Marchantia*. Development of antheridium (A-F). Successive stages in the development of antheridium, (G). A mature antheridium.

Jacket initials divide by several anticlinal divisions to form a single layer of sterile antheridial jacket. Primary androgonial cells divide by several repeated transverse and vertical divisions resulting in the formation of large number of small androgonial cells (Fig. 7 F).

The last generation of the androgonial cells is known as androcyte mother cells (Fig. 7 G). Each androcyte mother cells divides by a diagonal mitotic division to form two triangular cells called androcytes. Each androcyte cell metamorphosis into an antheozoid (Fig. 8 A-G).

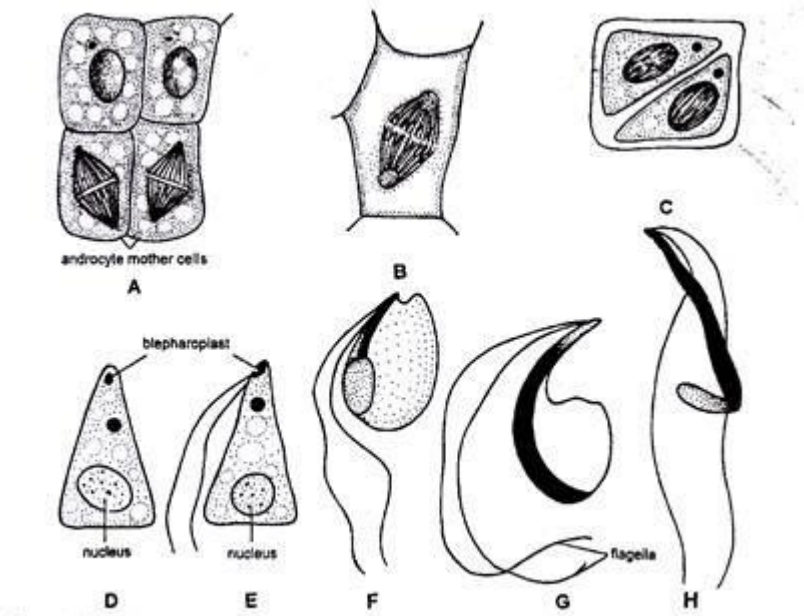

Fig. 8. (A-H). *Marchantia.* Spermatogenesis. (A-C) Formation of androcytes, (D-G). Stages in Spermatogenesis, (H). A single antherozoid.

Spermatogenesis:

The process of metamorphosis of androcyte mother cells into antherozoids is called spermatogenesis.

It is completed in two phases:

(1) Development of blepharoplast.

(2) Elongation of androcyte nucleus.

1. Development of Blepharoplasty:

In the young triangular androcyte (Fig. 8 D) blepharoplast appears as a dense granule in one of the acute angles. It elongates to some extent and puts its whole body in close contact with the inner contour of androcyte. From the elongated blepharoplast emerge the flagella.

2 Elongation of Androcyte nucleus:

With the elongation of blepharoplast, the nucleus also elongates. The spline apparatus acts as a cytoskeleton for the elongation of nucleus. Spline apparatus is a multilayered structure which comprises tubules (Fig. 8 E-H).

Archegoniophore or Carpocephalum:

It arises at the apical notch and consists of a stalk and terminal disc. It is slightly longer than the antheridiophore. It may be five to seven cm. long. The young apex of the archegoniophore divides by three successive dichotomies to form eight lobed rosette like disc.

Each lobe of the disc contains a growing point. The archegonia begin to develop in each lobe in acropetal succession, i.e., the oldest archegonium near the centre and the young archegonium near the apex of the disc. (Fig. 10 A). Thus, eight groups of archegonia develop on the upper surface of the disc. There are twelve to fourteen archegonia in a single row in each lobe of the disc.

Development:

The development of the archegonium starts on the dorsal surface of the young receptacle in acropetal succession. A single superficial cell which acts as archegonial initial enlarges and divides by transverse division to form a basal cell or primary stalk cell and an outer cell or primary archegonial cell (Fig. 9 A, B).

The primary stalk cell undergoes irregular divisions and forms the stalk of the archegonium.

The primary archegonial cell divides by three successive intercalary walls or periclinal vertical walls resulting in the formation of three peripheral initials and a fourth median cells, the primary axial cell (Fig. 9 C, D).

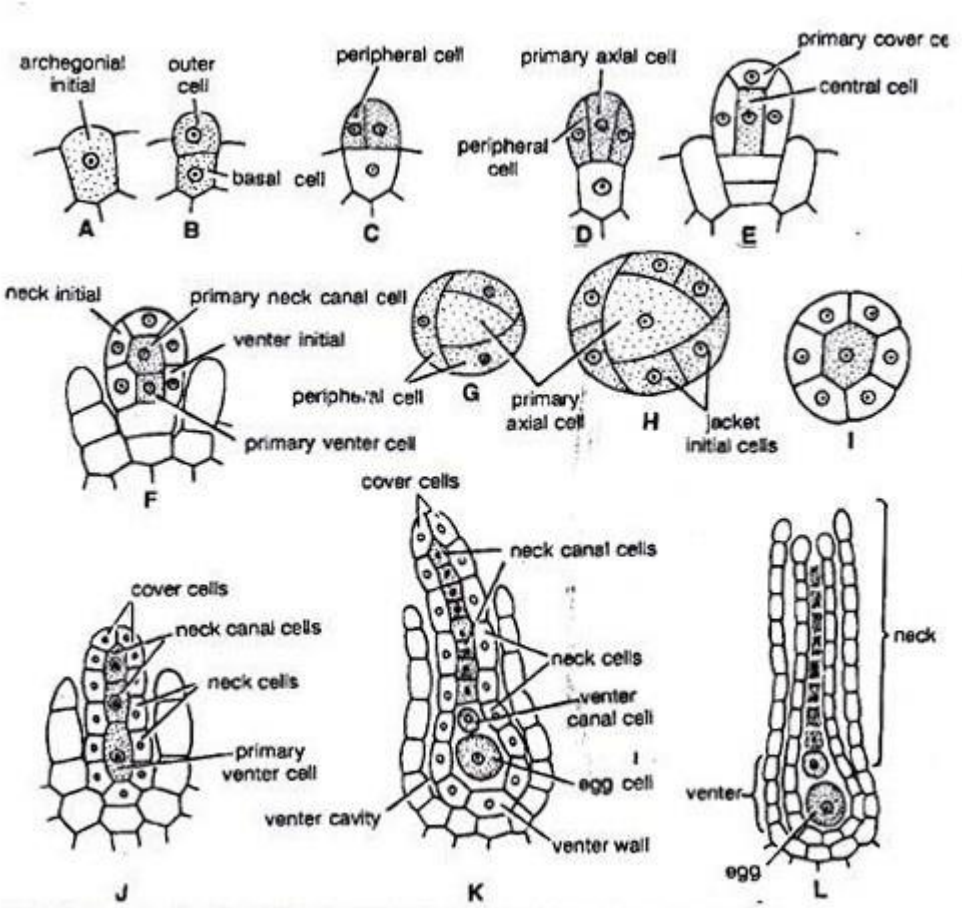

Fig. 9. (A-L) *Marchantia*. Development of archegonium. (A-K) successive stages in the development of archegonium. (L) A mature archegonium.

Each of the three peripheral initials divide by an anticlinal vertical division forming two cells (Fig. 9 G, H) In this way primary axial cell gets surrounded by six cells. These are called jacket initials (Fig. 9 H, I). Six jacket initials divide transversely into upper neck initials and lower venter initials (Fig. 9 F). Neck initial tier divides by repeated transverse divisions, to form a tube like neck.

Diversity of Algae, Lichens & Bryophytes:
Neck of the archegonium consists of six vertical rows. (Fig. 9 I). Each row consists six to nine cells Venter initials tier also divides by rapid transverse divisions to form a single wall layer of swollen venter (Fig 9 K). Simultaneously, the primary axial cell divides transversely and unequally to form upper small primary cover cell and lower large central cell (Fig. 9 E).

The central cell divides into primary neck canal cell and a lower venter cell. Primary neck canal cells divides by a series of transverse divisions to form a row of about eight thin walled neck canal cells (Fig. 9 J, K).

Primary venter cell divides only once and forms a small upper venter canal cell and a lower large egg or ovum (Fig. 9 K). The primary cover cell divide by two vertical divisions at right angle to one another to form four cover cells which form the mouth of the archegonium.

Mature Archegonium:
A mature archegonium is a flask shaped structure. It remains attached to the archegonial disc by a short stalk. It consists upper elongated slender neck and basal globular portion called venter. The neck consists of six vertical rows enclosing eight neck canal cells and large egg.
Four cover cells are present at the top of the neck. (Fig. 9 L).

Fertilization in Marchantia:
Marchantia is dioecious. Fertilization takes place when male and female thalli grow near each other. Water is essential for fertilization. The neck of the archegonium is directed upwards on the dorsal surface of the disc of the archegoniophore (Fig. 9 A).

In the mature archegonium the venter canal cell and neck canal cells disintegrate and form a mucilaginous mass. It absorbs water, swells up and comes out of the archegonial mouth by pushing the cover cells apart. This mucilaginous mass consists of chemical substances.

The antherozoids are splashed by rain drops. They may fall on the nearby female receptacle or swim the whole way by female receptacle. It is only possible if both the male and female receptacles are surrounded by water.

Many antherozoids enter the archegonial neck by chemotactic response and reach up to egg. This mechanism of fertilization is called splash cup mechanism. One of the antherozoids penetrates the egg and fertilization is effected. The fusion of both male and female nuclei results in the formation of diploid zygote or oospore. Fertilization ends the gametophytic phase.

Sporophytic Phase:

Post Fertilization Changes:

After Fertilization the following changes occur simultaneously:

1. Stalk of the archegoniophore elongates.

2. Remarkable over-growth takes place in the central part of the disc. As a result of this growth the marginal region of the disc bearing archegonia is pushed downward and inward. The archegonia are now hanging towards the lower side with their neck pointing downwards (Fig. 10 B-D).

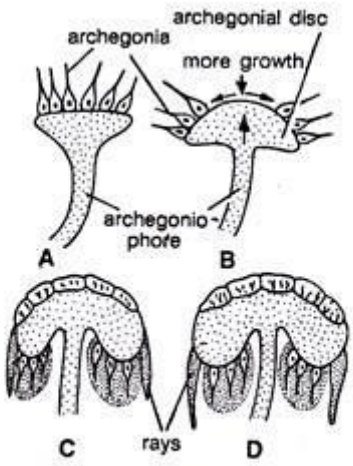

Fig. 10. (A-D). *Marchantia.* (A) Position of the archegonia before fertilization, (B-D). Inversion of the archegonia after fertilization.

3. Wall of the venter divides to form two to three layered calyptra.

4. A ring of cells at the base of venter divides and re-divides to form a one cell thick collar around archegonium called perigynium (Pseudoperianth).

5. A one celled thick, fringed sheath develops on both sides of the archegonial row. It is called perichaetium or involucre. Thus, the developing sporophyte is surrounded by three protective layers of gametophytic origin i.e., calyptra,

perigynium and perichaetium (Fig. 11). The main function of these layers is to provide protection, against drought, to young sporophyte.

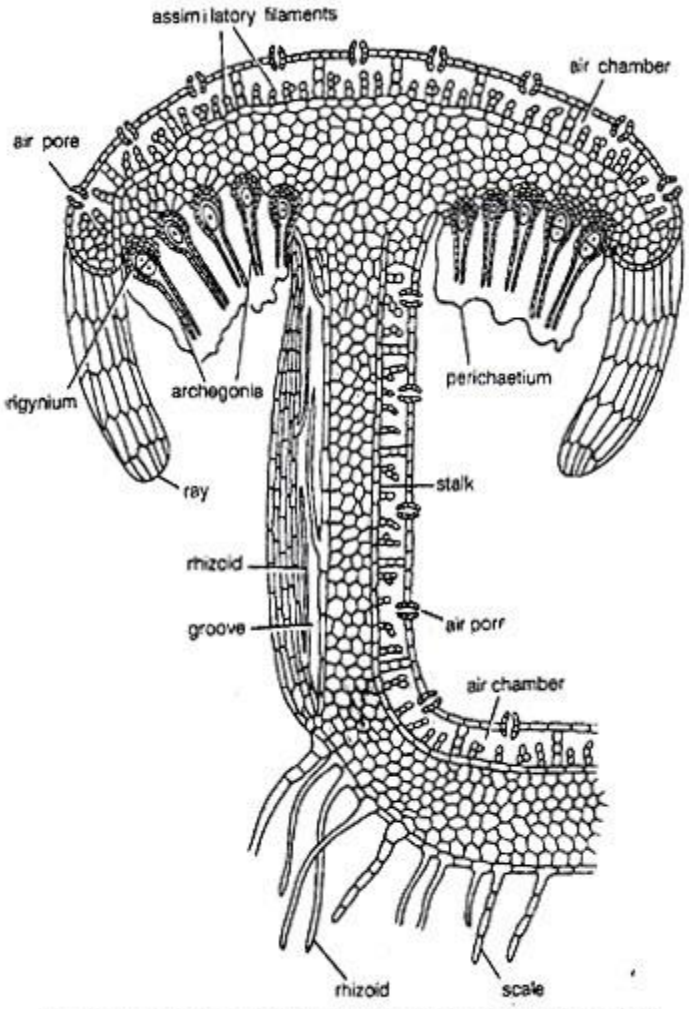

Fig. 11. *Marchantia.* Vertical longitudinal section (V.L.S.) of archegoniophore showing protective layers and rays. (After fertilization)

6. Between the groups of archegonia, long, cylindrical processes develop from the periphery of disc. These are called rays. They radiate outward, curve downwards and give the disc a stellate form. In M. polymorpha these are nine in number.

7. Zygote develops into sporogonium.

Development of Sporogonium:

After fertilization the diploid zygote or oospore enlarges and it completely fills the cavity of the archegonium. It first divides by transverse division (at right angle to the archegonium axis) to form an outer epibasal cell and inner hypo basal cell (Fig. 12 A, B).

The second division is at right angle to the first and results in the formation of four cells. This represents the quadrant stage (Fig. 12 C). The epibasal cell forms the capsule and hypo basal cells form the foot and seta.

Since the capsule is developed from the epibasal cell and forms the apex of the sporogonium, the type of embryogeny is known as exoscopic. The next division is also vertical and it results in formation of eight celled stage or octant stage.

Now the divisions are irregular and globular embryo is formed (Fig. 12 D). The lower cells divide to form a massive and bulbous foot. The cells of the seta divide in one plane to form vertical rows of cells.

In upper region of capsule (when the young sporogonium is about a dozen or more cells in circumference) periclinal division occurs and it differentiates it into outer single layered amphithecium and multilayered endothecium (Fig. 12 E, F).

The cells of the endothecium divide only by anticlinal divisions to form a single layered sterile jacket or capsule wall. The endothecium forms the archesporium. Its cells divide and re-divide to form a mass of sporogenous cells (sporocytes). Half of the sporogenous cells become narrow and elongate to form the elater mother cells. (Fig. 12 G, I).

In M. polymorpha sporogenous cells divide by five successive divisions to form thirty-two spore mother cells while in M. domingensis sporogenous cells divide only by three to four divisions to form eight or sixteen spore mother cells. The elater mother cells elongate considerably to form long, slender diploid cells called elaters.

Elaters are pointed at both the ends and have two spiral bands or thickenings on the surface of the wall. These are hygroscopic in nature and help in dispersal of spores (Fig. 12 K). The spore mother cell is diploid and divides meiotically to form four haploid spores which remain arranged tetrahedrally for quite some time (Fig. 12 J). The spores later become free and remain enclosed by the capsule wall along elaters. (Fig. 12 H).

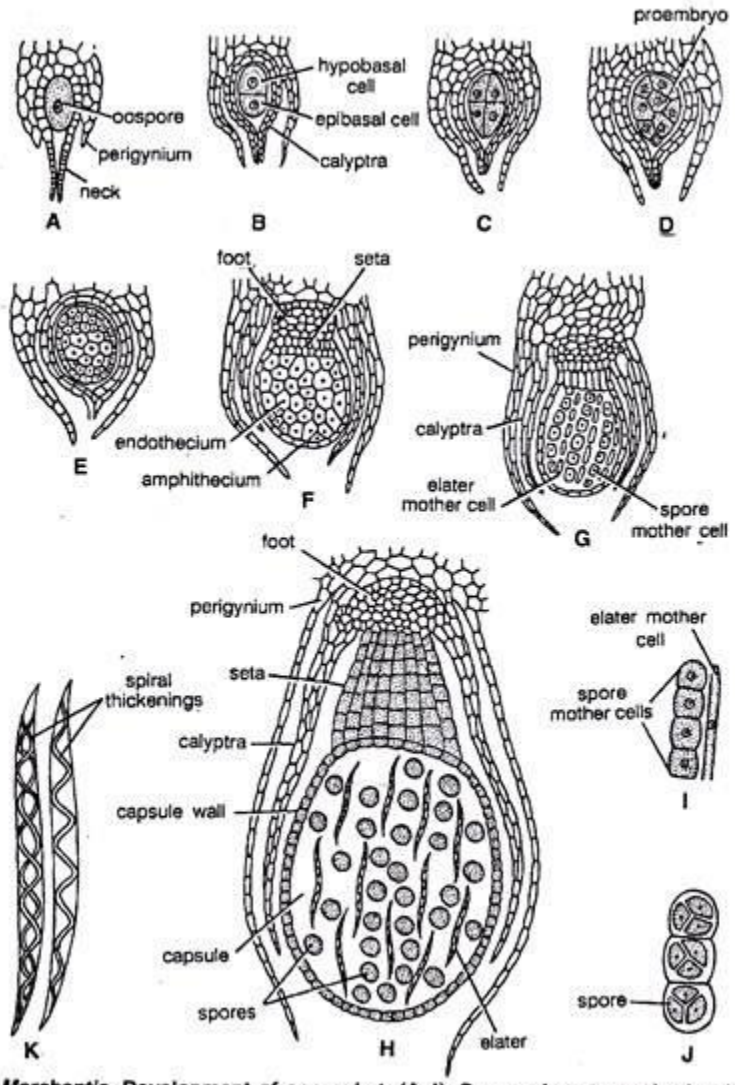

Fig. 12. (A-J). *Marchantia*. Development of sporophyt. (A-J). Successive stages in the development of sporoginium, (H). L.S. of mature sporogonium, (J) Spores tetred, (K) Two elaters.

The quadrant type of development of sporogonium is quite common in many species of Marchantia (e.g., M. polymorpha) but in a few species zygote divides by two transverse divisions to form the 3-celled filamentous embryo. In it the hypo basal cell forms the foot, the middle seta and the epibasal cell develops into capsule. However, it is the rare type of embryo development in M. chenopoda.

Mature Sporogonium:

A mature sporogonium can be differentiated into three parts, viz., the foot, seta and capsule (Fig. 13 H). Foot. It is bulbous and multicellular. It is composed of parenchymatous cells. It acts as anchoring and absorbing organ. It absorbs the food from the adjoining gametophytic cells for the developing sporophyte.

Seta:

It connects the foot and the capsule. At maturity, due to many transverse divisions it elongates and pushes the capsule through three protective layers viz., calyptra, perigynium and perichaetium.

Capsule:

It is oval in shape and has a single layered wall which encloses spores and elaters. It has been estimated that as many as 3, 00,000 spores may be produced in single sporogonium and there are 128 spores in relation to one elater.

Dispersal of Spores:

As the sporogonium matures, seta elongates rapidly and pushes the capsule in the air through the protective layers (Fig. 13 A). The ripe capsule wall dehisces from apex to middle by four to six irregular teeth or valves. The annular thickening in the cells of the capsule wall causes the valves to roll backward exposing the spores and elaters.

The elaters are hygroscopic in nature. In dry weather they lose water and become twisted. When the atmosphere is wet, they become untwisted and cause the jerking action. Due to this the spore mass loosens and spores are carried out by air currents (Fig. 13 B, C).

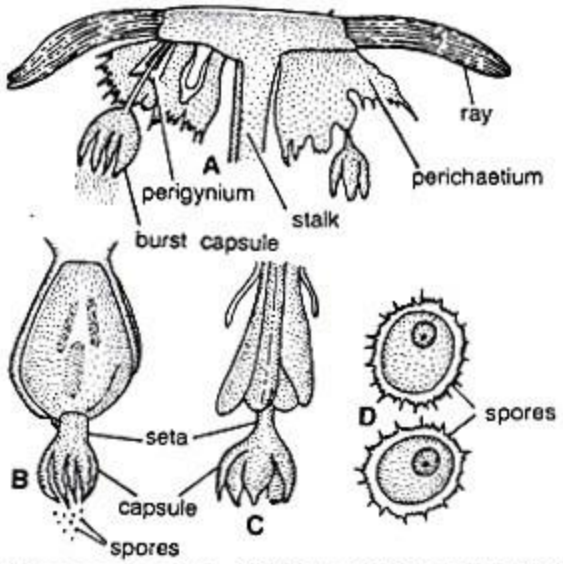

Fig. 13. (A-D). *Marchantia*. Dehiscence of capsule. (A) V.LS. of archegoniophore after the formation of capsule, (B, C). Dehiscence of capsule, (D) Spores.

Structure of Spore:

Spores are very small (0.012 to 0.30 mm in diameter). They are haploid, uninucleate, globose and surrounded by only two wall layers. The outer well layer is thick, smooth or reticulate and is known as exospore or exine. The inner wall

layer is thin and is called endospore or intine. In M. torsana and M. caneiloba they are tetrahedrally arranged.

Germination of Spores and Development of Gametophyte:

Under favourable conditions, the spores germinate immediately. In first year the spore viability is approximately 100%. Before germination it divides by transverse division to form two unequal cells (Fig. 14 A, B). The lower cell is small in size.

It is relatively poor in cell contents, achlorophyllous and extends to form germ-rhizoid (Fig. 14 C). The large cell is chlorophyllous and undergoes divisions to form a six to eight cell germ-filament or protonema (Fig. 14 D). At this stage the contents of the cells migrate at the apex.

The apex is cut off from the rest of the sporeling by a division. It behaves as apical cell. It is wedge-shaped with two cutting faces. The apical cell cuts off five to seven cells alternately to the left and right. These cells by repeated divisions form a plate like structure (Fig. 14 F).

According to O' Hanlon's (1976) a marginal row of cells appears in the apical region in this plate. By the activity of these marginal cells, the expansion of the plate takes place into thallus, a characteristic of Marchantia.

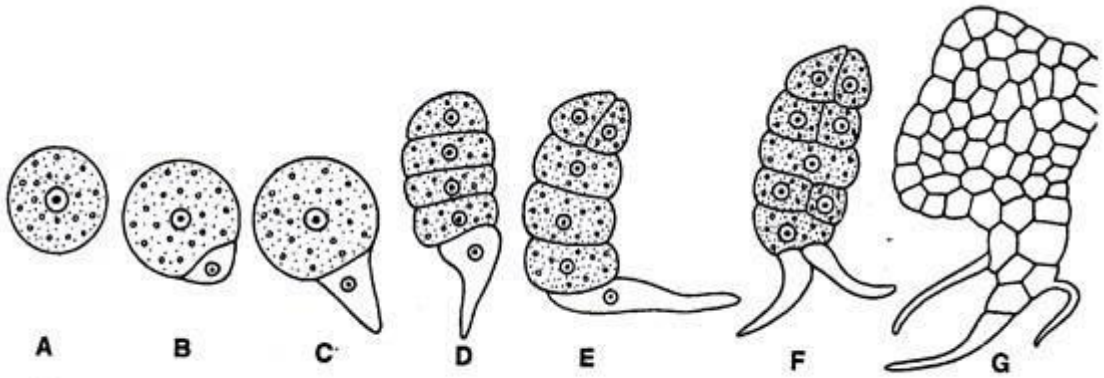

Fig. 14. (A-G). *Marchantia*. Successive stages in the germination of spore and development of sporophyte.

Marchantia is dioecious, 50% of the spores develop into male thalli and 50% develop into female thalli (Fig. 15).

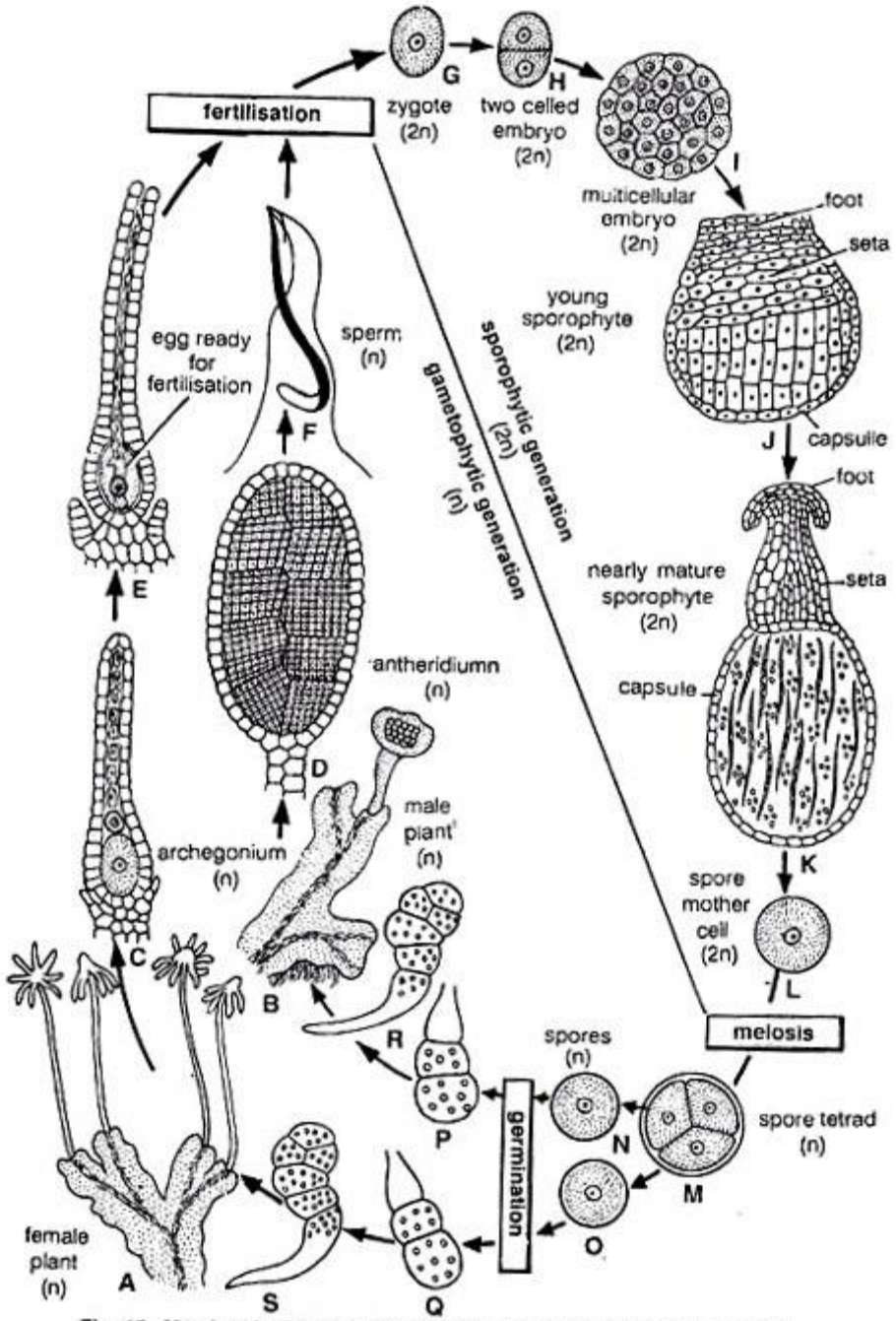

Fig. 15. *Marchantia*. Diagrammatic representation of the sexual life cycle.

Alternation of Generation in Marchantia:

The life cycle of Marchantia shows regular alternation of two morphologically distinct phases. One of the generations is Haplophase and the other is diplophase.

(i) Haplophase or Gametophytic Phase:

In Marchantia this phase is dominant and produces the sex organs. Sex organs produce gametes to form a diploid zygote.

(ii) Diploid Phase or Sporophytic Phase:

Zygote develops into sporophyte. In Marchantia sporophyte is represented by foot, seta and capsule. The sporophyte produces the spores in the capsule. The spores on germination produce the gametophyte.

So, in Marchantia two morphologically distinct phases (Haplophase and Diplophase) constitute the life cycle. The life cycle of this type which is characterised by alternation of generations and sporogenic meiosis is known as heteromorphic and diplohaplontic (Fig. 16).

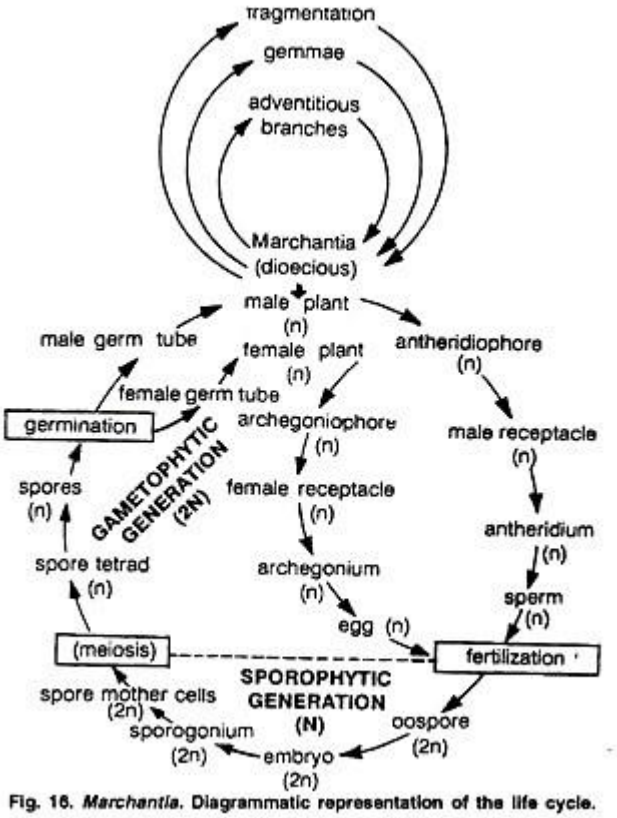

Fig. 16. *Marchantia*. Diagrammatic representation of the life cycle.