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BBYCT - 131

BIODIVERSITY (MICROBES, ALGAE, FUNGI AND ARCHEGONIATES)

Block

4

BRYOPHYTES

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BLOCK 4 BRYOPHYTES

In the previous Blocks 2 and 3 you have studied the various aspects of the life of organisms called algae and fungi respectively. Although the algal forms are autotrophic and the fungi characteristically are heterotrophic. However, both of these groups of organisms have one very important characteristics in common : the absence of sterile covering in their sex-organs. All the multicellular, land plants possess sex-organs that have such sterile coverings. Bryophytes, possibly the first and successful migrant occupants of land habitat are very important groups of organisms from the view point of evolution. The ability of bryophytes to successfully complete their life cycle on land is attributed to the presence of multicellular, female sex-organ the archegonium and subsequent embryo-formation and matrotrophy. Bryophytes also produce motile male gametes which require a film of water for their motility and as a prerequisite to accomplish fertilization. Due to this reason bryophytes are regarded as amphibians of the plant kingdom.

You must have noticed the tiny plants growing on rocks, tree trunks, and on forest floors in hilly regions where these plants are found in abundance. They are also common in the form of green patches on the old walls of houses in moist and shady conditions, especially during rainy season.

In this block you will study bryophytes in detail. You will learn the changes that occurred in the morphological and reproductive structures as well as in the life cycle during this shift in habitat.

Besides being important from the evolutionary point of view bryophytes also play an important ecological role of being pioneers of vegetation. Recently, their potential has been realized as they are indicators of pollution, mineral deposits as well as accumulation of heavy metals. Besides this, they are also used in medicine and horticulture.

This Block comprises of four Units 12 to 15. In Unit 12, you will be introduced to the importance of multicellular sex organs, especially archegonium and their significance in evolution of land plants. Unit 13 provides you an insight to general structural, organizational and reproductive variations in bryophytes. You will also study the basis of classification of bryophytes. The life-cycles of a liverwort *Marchantia* and a moss *Funaria* is discussed in Unit 14. Unit 15 surveys the ecological and economic significance of bryophytes.

The titles of the four units of this block are :

Unit 12 : Introduction to Archegoniates

Unit 13 : Bryophytes : An Introduction

Unit 14 : Bryophytes : Type Studies

Unit 15 : Bryophytes : Ecology and Economic Importance

Objectives

The study of this block should enable you to :

- distinguish bryophytes from other groups of plants;
- list the characteristics of different groups of bryophytes;
- describe the general pattern of life cycle in bryophytes;
- discuss the adaptations acquired for the transition to land habitat;
- enumerate various uses of bryophytes; and
- comment on ecological significance of bryophytes.

UNIT 12

INTRODUCTION TO ARCHEGONIATES

Structure

12.1 INTRODUCTION

You have already learnt that R.H. Whittaker placed bryophytes, pteridophytes, gymnosperms and angiosperms, all together in the Kingdom Plantae. All of them are eukaryotic, autotrophic, multicellular and are primarily land plants. Among them, angiosperms (the flowering plants) are characterized by double fertilization and resultant endosperm development. Together with gymnosperms they are called seed plants (spermatophytes). However, the seeds of an angiosperm are enclosed within a fruit, while those of gymnosperms are naked and exposed. These seed plants together with pteridophytes constitute vascular plants due to the occurrence of vascular tissue - the xylem and phloem in their various organs. They also biosynthesise lignin and produce true roots, stems and leaves. The bryophytes though mostly terrestrial, are non-vascular and without true roots, stems and leaves. They possess root-like rhizoids and may have 'stem' (cauloid) and 'leaves' (phyllids).

Double Fertilization: plants with two fertilizations in their sexual reproductive cycle.

Syngamy: fusion of a male and a female gamete.

Triple fusion: fusion of a male gamete and two polar nuclei in the central cell of an embryo-sac.

An important characteristic reproductive feature that distinguishes these land plants from the earlier, more primitive and possible ancestral algal groups, is the presence of multi-cellular sex-organs with sterile coverings. You may recall, none of the thallophytes (algae and fungi taken together) form a sterile cover around their sex-organs, which often are unicellular. A very specialized female sex organ, the archegonium is present in bryophytes, pteridophytes and gymnosperms. Plant morphologists have credited the **archegonium** with

Archegonium:

Greek=''ápxn'' (beginning) + ''róoc'' (offspring) the origin and development of multicellular, diploid embryo and sporophyte in the land plants details of which you shall learn later in this unit. Thus, to a plant morphologist and an evolutionary biologist a specialized organ - the archegonium is of immense interest. So, is the group of plants that bear archegonia: bryophytes, pteridophytes and gymnosperms. Taken together, they are called archegoniates.

In this unit, you shall learn the unifying features of the group archegoniates. You shall also be exposed to the concept of alternation of generations and its possible role in the evolution and proliferation of land plants. You shall also learn the various, often specialized kinds of adaptations and modifications in structure, reproduction, and physiology in these primitive land plants. Such adaptations and modifications possibly made these and such plants suitable and fit for transition from the aquatic to land habitat.

Objectives

After studying this unit, you should be able to:

- identify the group of plants placed under archegoniates;
- list and describe salient features of archegoniates;
- describe the various structural, reproductive and physiological adaptations and modifications that have helped aquatic ancestors to establish on terrestrial habitats;
- define and discuss the concept of alternation of generations; and
- critically evaluate the theories regarding alternation of generations.

12.2 UNIFYING FEATURES OF ARCHEGONIATES

Recall the life-cycles of the algal forms you have learnt in the Unit 7 of Block 2. You will find that the sex-organs are unicellular in most of them. In fact, sterile cells are not present in the sex organs of any of the thallophyte. On the contrary, as already mentioned in the introduction of this unit, all the higher land plants possess sex-organs that are multicellular and are with sterile cover cells. Thus the question arises as to when, where and how the unicellular sex organs gave way to multicellularity and that too with some sterility. There are no specific answers to this question. Assumptions have been made and links suggested or looked for in the search for indisputable evidence for answer of this question. In this section you would study the form, significance, occurrence and the role that multicellular sex-organs with sterile coverings have played in the transition to land habit, their evolution and spread on land.

The Fig. 12.1 (a-d) represents the structural organisation of a male sex-organ, the *antheridium* (pl. antheridia) and a female sex-organ, the *archegonium* (pl. archegonia) in a liverwort, *Riccia*. There are numerous forms and variations among these organs in different forms of bryophyta, pteridophyta and gymnosperms.

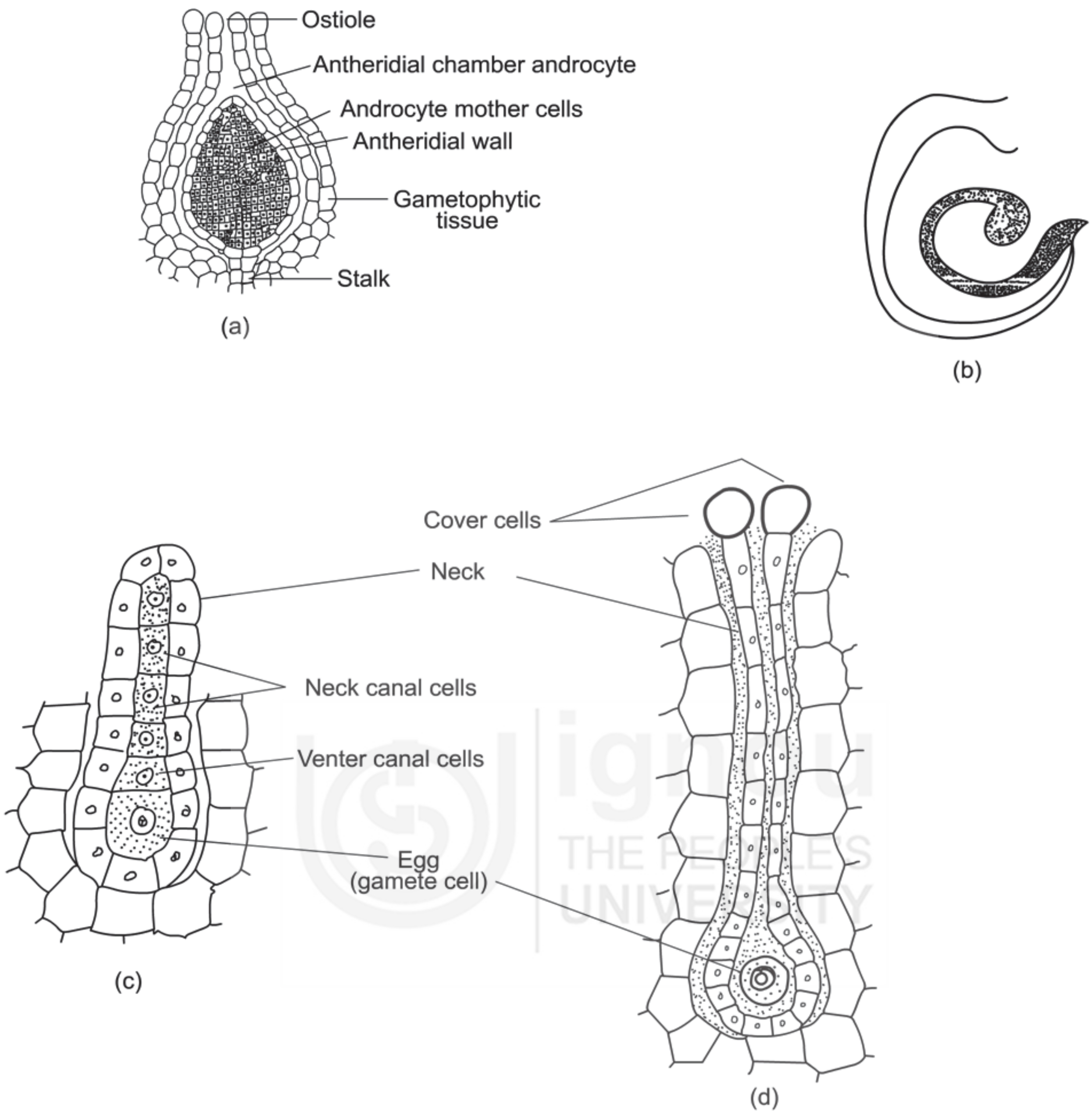

Fig.12.1 (a-d): Multicelluar sex organs in a liverwort, *Riccia.* a) An antheridium – a male sex organ; b) An antherozoid – a motile gamete; c) An archegonium – a female sex organ (young); and d) A mature archegonium ready for receiving the male gametes through an opening at the terminal end.
Source: (a) Vashishta,1994.

Antheridium: The antheridium as shown in Fig.12.1a is physically in contact with the thallus – gametophytic tissue. It possesses a multicelled, multilayered stalk and a globose head (the form may vary with species) that has a multicellular but unilayered antheridial wall. Within jacket are formed a very large number of androcytes or spermatids. Each spermatid at maturity gets metamorphosed into a single haploid biflagellated sperm cell, an antherozoid. Both the flagella are anteriorly inserted and are similar, whiplash type (Fig. 12.1b). All the cells of antheridium are haploid. Mitotic cell division precedes an androcyte formation.

Archegonium: See Fig. 12.1c and d. An archegonium is a flask-shaped organ. It consists of two parts: the basal swollen portion is called the venter and a long, slender neck. The venter is directly in physical contact with the thallus (gametophyte). In *Riccia* there is no distinct stalk. However, it may be present in many other bryophytes. There is a vertical row of cells, 4 in *Riccia*, the neck canal cells. A layer of sterile cells forms a protective jacket around the neck canal. The tip of the neck is made up of four specialized large cap/ cover/lid cells. The diameter of these cover cells is greater than the neck cells. The venter also has a jacket of sterile cells. The sterile cover jacket cells of neck and venter form a continuous cover. The cover of venter is called venter wall. It encloses a large venter/cavity. Within this venter cavity lie two cells. The larger, basal - egg cell and above it is a smaller venter canal cell. The venter canal cell, thus, has neck canal cells above it and an egg cell below it. All the cells of an archegonium are haploid. Mitotic cell divisions precede egg cell formation. The egg cell is a non-motile female gamete (Fig.12.1d). You may note that number of archegonia per gametophytic thallus and their position on the thallus and the size; number of stalk cells, neck cells and neck canal cells vary with species of an archegoniate. However, the function of the archegonium remains the same.

The algae and the angiosperms do not possess antheridia and archegonia. Gymnosperms form archegonia but no distinct antheridia. Thus, principal reproductive unit, the archegonium is the common characteristic of all the bryophytes, pteridophytes and gymnosperms. These three together are referred to as **archegoniates.** Associated with archegonium, there exist a number, of pre-, and post-fertilization events in the reproductive life of archegoniates. These events are referred here as unifying features of archegoniates. Some of them are listed and briefly described below.

1. Archegoniates are embryophytes

a) Recall the haplontic life cycle of, e.g., *Chlamydomonas* (cf. Sub-section 7.2.2 in Block 2). Soon after gametic fusion, syngamy, a diploid zygote is formed.

What happens to this diploid zygote? It divides immediately or after a dormant period by meiosis to form 4 haploid zoospores. A vast majority of algae except a few, e.g., *Ectocarpus, Sargassum, Polysiphonia* follow a similar pattern of the life cycle. Moreover, where do these events occur? Zygote is either formed independent of parental cells/gametangia, in free water or even if the zygote is formed within a female gametangium, the resultant progeny is released in surrounding aquatic medium, i.e., they do not get any protection, sustained nourishment from any of the parental cells/tissues (see Fig. 12.2). Archegoniates however, exhibit a major, regarded as a path breaking deviation. The zygote does not divide meiotically but undergoes mitosis and then sustained repeated mitotic cell divisions result in the formation of a multi-cellular diploid body of cells. This is regarded as an unifying feature of all archegoniates.

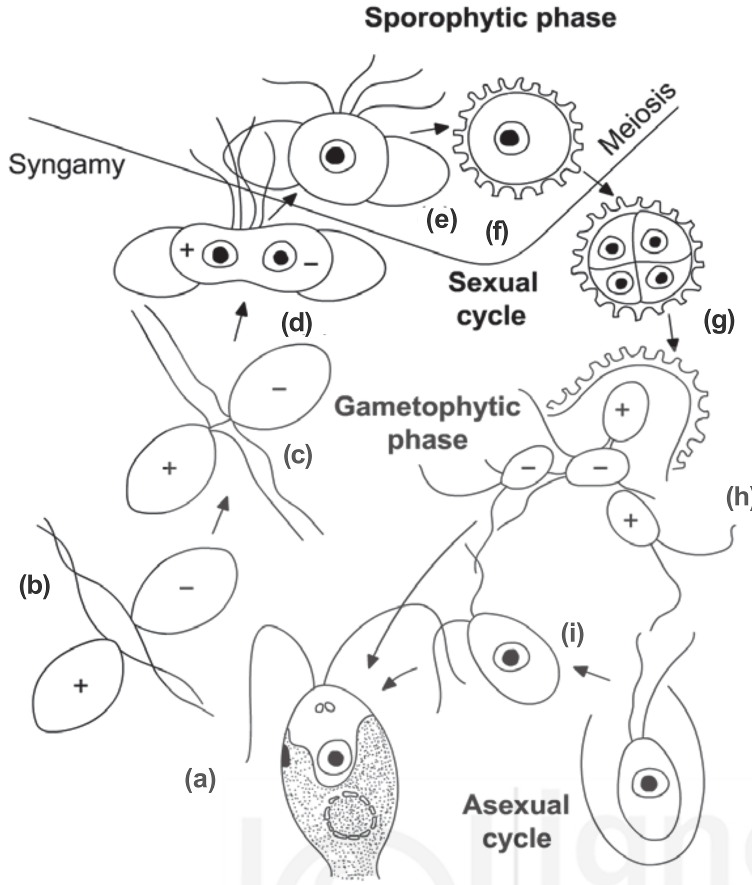

Fig. 12.2: Diagrammatic representation of sexual reproductive cycle in an isogamous *Chlamydomonas* sp. (a-i). a) Vegetative, haploid, gametophytic thallus; b) Two motile isogametes; c-d) Fusion of two opposite strains of gametes during fertilization; e) Syngamy; f) A diploid zygote (independent of maternal gametophytic thallus); g) Four haploid cells formed following meiosis in the zygote. The zygote cell represents the sporophytic phase in the life cycle; h-i) Four new gametophytic individuals. *Source*: (a-i) Graham et al., 2009.

b) In archegoniates, the initial events of syngamy, fertilization, zygote formation, followed by development of multicellular sporophyte happen within the confines of a venter of an archegonium. And this archegonium is still in physical contact of the gametophyte. Thus, in archegoniates early or all phases of sporophyte development takes place on the gametophyte.

c) The sporophytic tissue thus formed, initially or throughout remains achlorophyllous. At this stage, the sporophyte derives its nutrition from the maternal gametophytic tissue via the archegonium.

d) This initial phase in the life of a sporophyte is designated as **embryo.** Thus, all archegoniates produce a diploid multicelluar **embryo** within the confines of the archegonium/maternal gemetophytic body. Hence, they are also called **embryophytes,** the plants with embryos. Thallophytes do not form embryos.

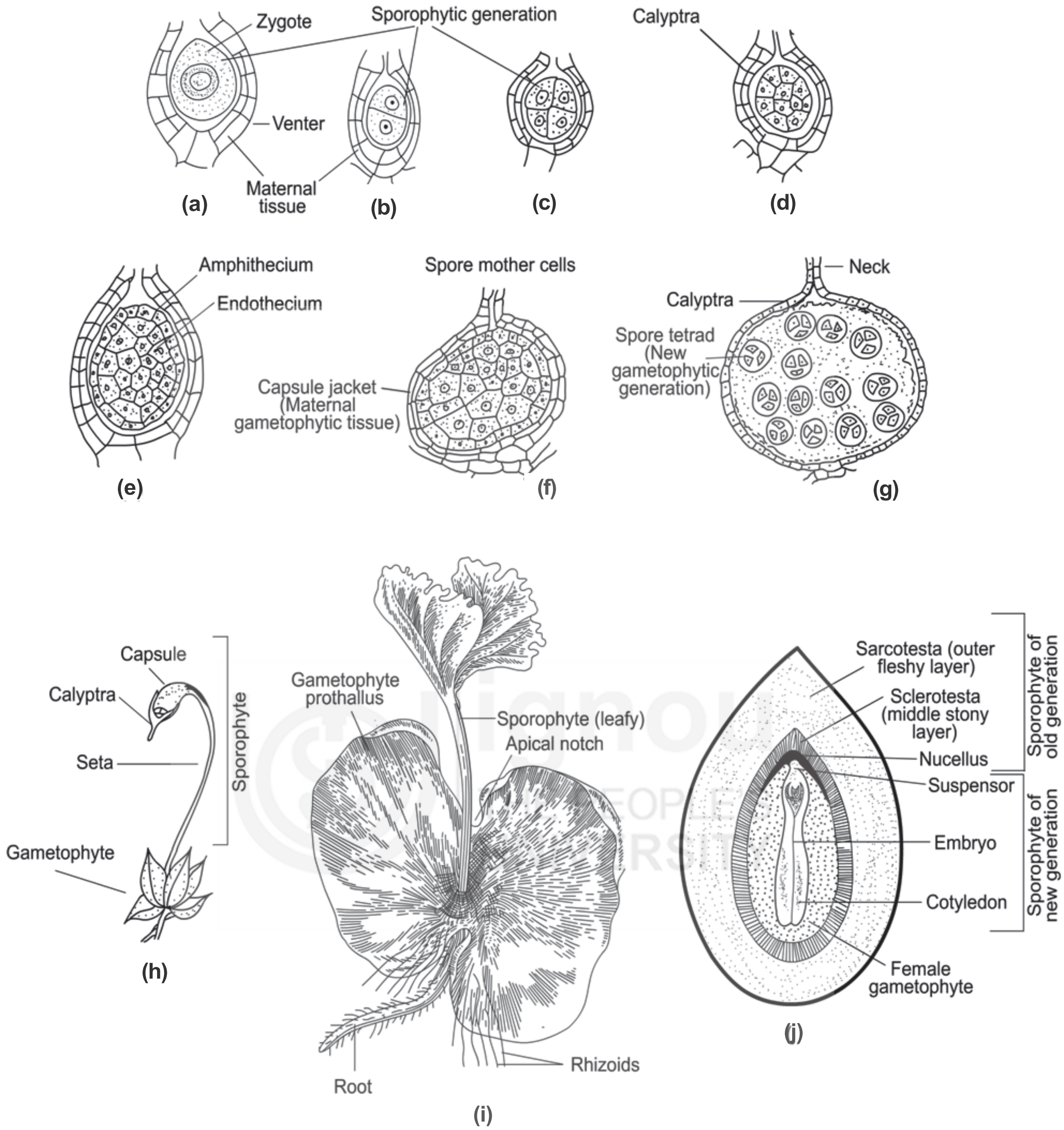

Fig. 12.3 (a-j): Matrotrophy in archegoniates. (a-g) Post-fertilization events in a liverwort, *Riccia* (diagrammatic). Venter, calyptra, and neck represent maternal gametophytic tissue. Zygote, multicellular sporophyte, capsule jacket, amphithecium, endothecium represent (2n) sporophytic generation. Spore tetrads in (g) are new gametophytic generation. Spores (n) are formed following meiosis in spore mother cells (2n). Diploid, sporophytic tissues are retained, anchored, nourished by mother gametophyte in an archegonium. (h) Diagrammatic representation of a sporophytic generation in a moss sporophyte (seta, calyptra, capsule on a leafy branch of gametophyte. The 2n foot of sporophyte is embedded in the maternal (n) tissue. Thus, the foot, seta, capsule of diploid sporophyte are in physical contact with the gametophyte. (i) Diploid sporophytic generation (leaf, root) in a fern are in physical contact with the gametophytic prothallus. (j) Diagrammatic representation of l.s. seed of *Cycas* – suspensor, embryo, cotyledons are the new sporophyte structures. They are formed protected and nourished by haploid gametophyte. All formed within 2n generation (ovule).
Source: (i,j) Bendre & Kumar, 2013.

2. **Archegoniates exhibit matrotrophy:** Since, these embryos derive their nutrition, from the maternal parent (archegonium-bearing gametophyte) this mode of nourishment, that is common to all the archegoniates, is known as matrotrophy (Fig. 12.3 a-j).

3. **Archegoniates produce large number of haploid spores.** As a consequence of development of a multicellular sporophyte, not only the number of diploid cells in the life of the organism increases manifold, the number of resultant meiotic cell divisions also increase. It results in production of large number of haploid spores (only four haploid spores are produced in a zygotic meiosis). The resultant fall-out is an increased number of haploid spores per zygote or by a single event of syngamy in archegoniates.

4. **A single syngamy produces many gametophytes:** Since, each spore develops into a gametophyte, a zygote in an archegoniate can produce large number of gametophytes.

5. **Male gametes travel to female gamete:** The male gametes produced within antheridium are always carried to the archegonium via aqueous medium (in bryophyta and pteridophyta) or through a pollen-tube, siphonogamy (in gymnosperm). In former, the male gametes are motile. In contrast, the egg-cell, in all archegoniates is stationary, static and non-motile. Fertilization, thus always is internal.

All the above-mentioned interesting events in the life of an archegoniate could occur just because a specialized female sex-organ, archegonium was formed. The development, of an archegonium is thus regarded as a milestone is the transition to land habitat (see next section).

Apart from the above salient unifying reproductive features there exist a few other ancestral features that are common to all archegoniates and flowering plants. Some of them are:

1) Differentiation of parenchyma cells with: primary cellulosic cell wall; prominent plasmodesmata; eukaryotic nucleus; true vacuole; pectin biosynthesis.

2) Photosynthetic pigments chlorophyll ‘a’ and ‘b’.

3) Starch, with glucose as monomer, as reserve storage photosynthetic product.

4) Grana in the chloroplast.

5) Dissolution of nuclear membrane during prometaphase stage of mitosis and reappearance of it at telophase.

6) Persistent spindle/phragmoplast formation during cytokinesis.

7) Occurrence of the enzyme glycolate oxidase in peroxisome. This enzyme is a scavenger of carbon that otherwise could be lost by excretion from a photosynthetic cell.

8) Occurrence of the enzyme copper/zinc superoxide dismutase that eliminates oxygen radicals from the cells.

9) Presence of mitochondrial group II introns except in liverworts.

10) A distinct heteromorphic mode of alternation of generations (see Section 12.4).

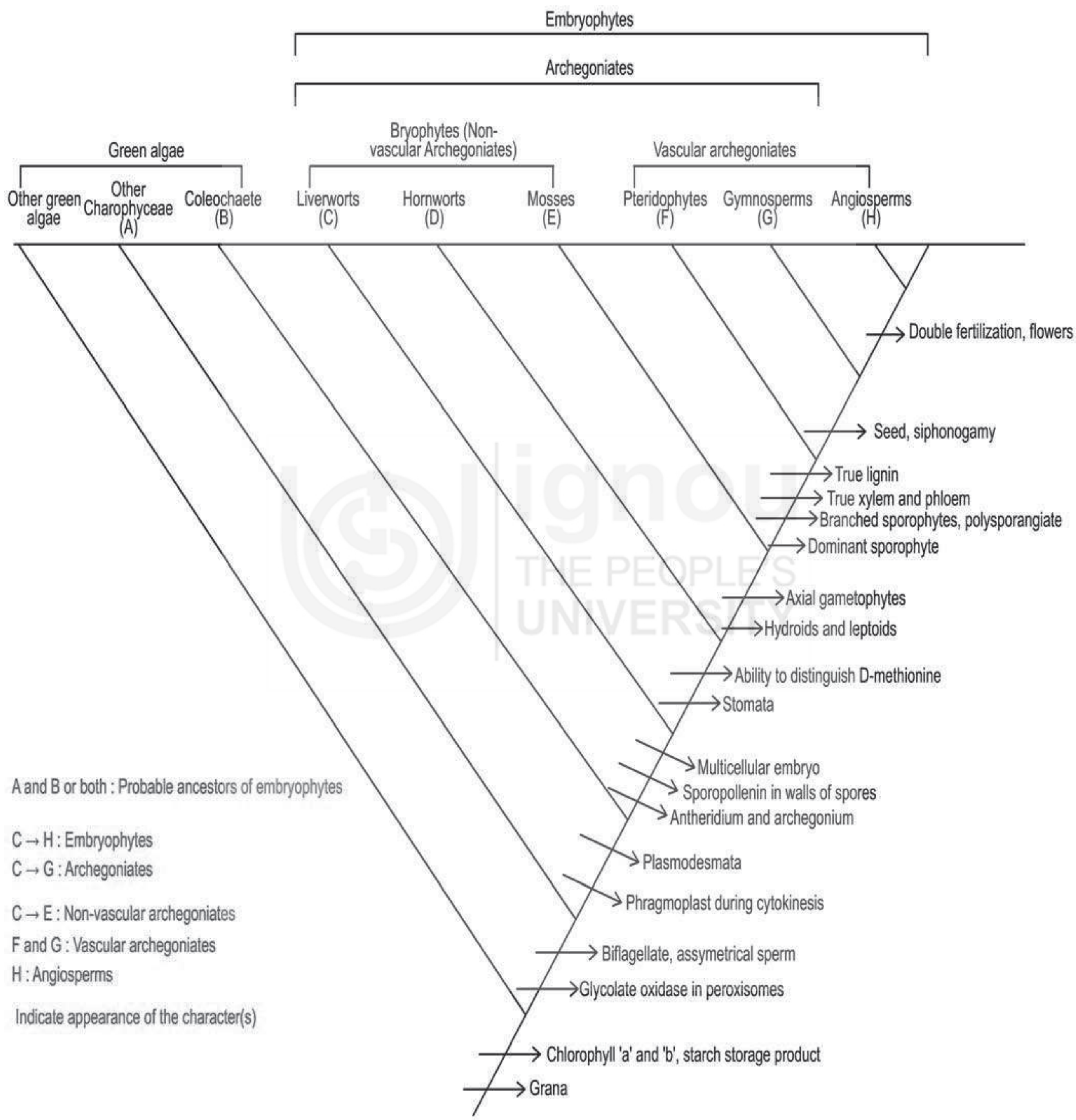

Fig. 12.4: A hypothetical cladogram exhibiting the affinities of archegoniates. Plant Groups: C – to – H are embryophytes. Plant Groups: C – to – G are archegoniates. Plant Groups : A or B or both are considered possible ancestors of archegoniates. *Source*: Raven et al., 2003.

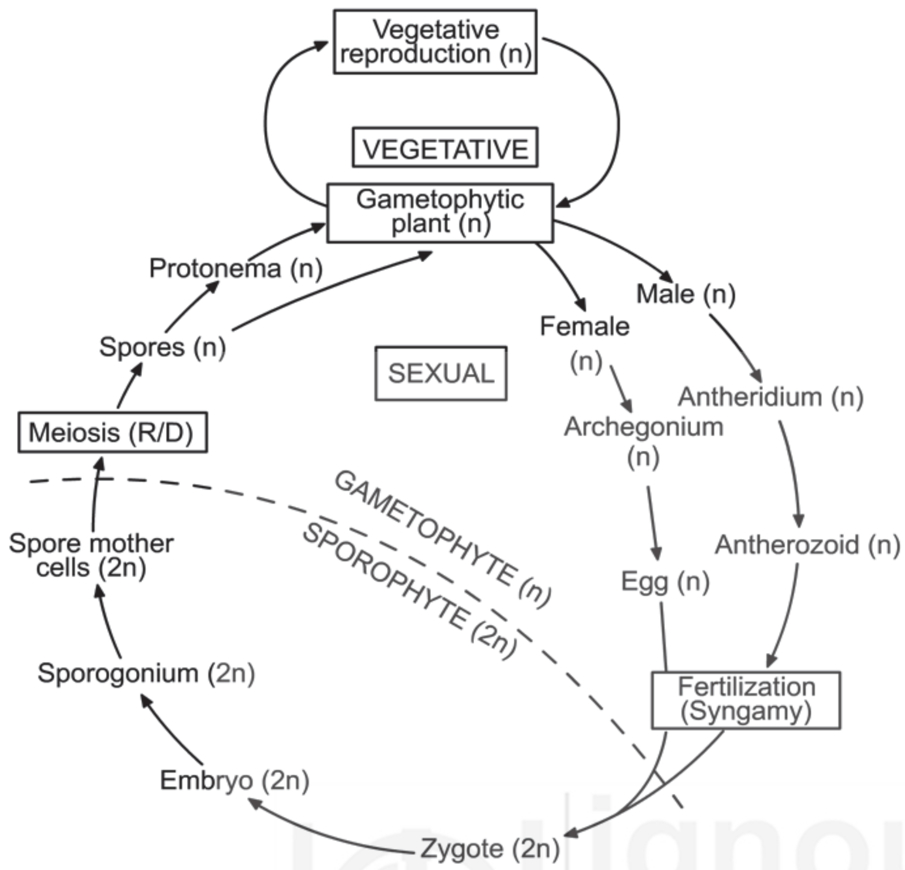

Fig. 12.5: A summarized life cycle of a homosporous archegoniate.

12.3 TRANSITION TO LAND HABIT

The transition of plants from aquatic environment to land is probably the most important and significant event in the history of our planet. How did it happen? Prior to this event, certain preconditions as mentioned below must have been set:

(1) environment had to change so as to suit the plants; and

(2) plants have to change so as to make use of changed environment.

12.3.1 Environmental Changes

What we know by certain that by ~430 mya (million years ago), i.e., by Silurian period plants were permanently adapted to land habitat - terrestrial and water-deficient.

For the plants to establish the presence of soil was necessary. Earlier bare surface did not possess biologically available humic elements such as N, P, Fe, and S. It is suggested that soils were enriched in P, Fe by weathering of rocks by early prokaryotes and eukaryotes, e.g., lichens. As you are aware that Cyanobacteria, non-photosynthetic bacteria, and eukaryotic algae are capable of weathering rocks releasing P and Fe. Chelating of Fe from rocks takes place by specific organic molecules, siderophore. These molecules are known to be secreted by prokaryotes and eukaryotes.

Simultaneously, the high level of CO_2 in the environment would have helped soil formation by any of the following three modes:

a) CO_2-enriched atmosphere favoured growth of photosynthetically active organisms. Decomposition of such microbes resulted in microbial mats, leading to release of inorganic nutrients in soil.

b) Increased precipitation caused acid rains thereby decomposing rocks. Physical disintegration of rocks occurred leading to soil formation.

c) Increased atmospheric CO_2 concentration promoted cast activity by burrowing organisms. They in turn increased water content of soil leading to increased chemical weathering and aiding the soil formation process.

In addition volcanic products enriched soils in S and N, directly or through rains. A lot of atmospheric Nitrogen that could be biologically usable could have been formed through lightening. It is estimated that lightening could indeed enrich soil with N in the range of 1 kg N per hectare per year.

Another environmental factor was temperature. Initially it was too high in range at above 40-45°C. By late Ordovician (450-440 mya), evidences suggest that the global climate became more variable, atmosphere became cooler and suitable for plant growth.

Now, with the abiotic parameters such as: soil, atmospheric CO_2 concentration, temperature, basic enrichment of soil/substratum with essential nutrients being met, the necessary structural and reproductive changes in aquatic plants must be made to help them establish, and flourish on the land.

This required both transfer from aquatic environment and then successful maintenance on land. Evidences from fossil record of middle Ordovician to early Silurian 470-730 mya suggest that such adaptations were actually made by the early plant life.

12.3.2 Adaptations by Plants

For proper adaptations, certain morphological changes in the life of plants were pre-requisite for land dwelling. These changes would be to meet the specific needs related to: anchor; photosynthesis, transport of nutrients and water, gaseous exchange, prevention of desiccation, ensured fertilisation, care of embryo, and search of new ecological niches. Let us now correlate the structures specific to such needs and those found in the archegoniates.

1) **Anchor:** The foremost need for any plant on land would be to anchor it at one place. Unicellular rhizoids in liverworts, hornworts and branched multicelluar rhizoids in mosses represent the early, primitive but equally effective mode for anchor to the substratum. These structures probably paved the way for more advanced root system in vascular archegoniates that could support the massive above ground sporophytes.

2) **Water and Mineral Uptake:** Ancestors of early archegoniates were aquatic and the plant body could get its water from the surroundings. Also, along with the water, the aquatic algae could get the required minerals. However, after being transferred to land, the plant would need constant source of water supply to replace the water lost by evaporation from its exposed surface. Bryophytes, in general, being very small in dimension had two fold advantages: their requirement of water would be marginal and being close to soil as well as thalli or axes growing in very close proximity they could get their water by surface tension. In addition, to compensate the water loss by evaporation from its exposed surface, the bryophytes generally completed their life cycle during the wet season, when the relative humidity in the atmosphere would be relatively high. The function of the rhizoids in bryophytes, therefore, is probably restricted to mineral uptake in addition to anchor. However, the roots of higher, vascular archegoniates have three principle roles: anchor; uptake of water, and dissolved minerals.

3) **Photosynthesis:** Most of the aquatic algal ancestor cells/filaments were involved in photosynthesis. On being migrated to land habitat the chlorophyllous, photosynthesing cells/tissue not only become specialized but strategically placed within the aerial organs to receive maximum solar radiations, e.g., upper photosynthetic chambers of *Marchantia*, 'leaves' (phyllids) of mosses, and mesophylls in leaves.

4) **Transport:** Transition to land habitat required three strategies: need to transport water to all the aerial parts of the plant (hundreds of meters in some gymnosperms); transport of minerals to these cells, tissues, organs and transport of photosynthetic products to all non-photosynthesing parts of plant including roots. Initially, in certain bryophytes, the elementary, simple tissues hydroids and leptoids can be observed performing these functions. Specialized xylem and phloem tissues are characteristic of vascular archegoniates. These tissues are present both in root and shoot systems. Xylem transporting water and minerals and food being transported via phloem.

5) **Control of Evaporation and Gaseous Exchange:** As the aerial parts of the plant grow away from the soil (source of water), its surface gets exposed to the atmosphere. Additionally, with increased expanse of the leafy shoots, the exposed surface area increases manifold. The increased photosynthetic abilities thus get compromised with evaporation and transpiration of water from the exposed surface.

To maintain balance between uptake and loss of water, the surface cell layers of the organs (including thalli and leafy axes of mosses) plants developed epidermal layers without any spaces between neighbouring cells. In addition outer wall layers of epidermis were deposited with a layer of cuticle. The cuticle is impervious to water.

Cuticle is deposited on exposed wall of epidermis, and is made up of lipids + hydrocarbon polymers impregnated with wax.

Presence of cuticle has its own disadvantages. The ultimate, exposed regions of the aerial parts of the plants are also photosynthetic and require CO_2 from the atmosphere. Thus, plants developed stoma (pl. stomata) within epidermal layers. Through stomata the organ could diffuse in CO_2 from the atmosphere. However, with stomatal apertures open for intake of CO_2, water vapours would diffuse out through it. It could create water-imbalance for the plant. This probably was circumvented by the ability of stomata to open and close through some internal/external stimuli. The 'stoma' like structures are first reported from certain aerial sporophytes of hornworts and mosses. However, they remain open throughout. Hence, they are only good for gaseous exchange but not for regulating water loss. Can you imagine why bryophytes are uncommon in dry, hot places and seasons?

6) **Matrotrophy:** In Section 12.2 (Figure 12.3) you have learnt that zygote once formed in an archegonium is retained at the site of its formation. Not only that it divides by mitosis and further mitotic cell divisions result in the development an embryo. Such 'embryos' in all the archegoniates are achlorophyllous. Thus, they need a constant supply of food and water. How do they get it? From where do they derive it? Herein, lies perhaps the most dynamic modification, made by plants that transferred to land habitat, to protect and nourish the young embryo (may be entire sporophyte as in the liverworts). The photosynthetic products of the gametophyte/stored food in the gametophyte (as in gymnosperms) is transferred to the 'embryo' via venter of archegonium. It has been established that the cells at the interface of gametophytic tissue of archegonium and the peripheral cells of sporophyte possess 'transfer cell' characteristics. Thus, in archegoniates, the whole embryo is nourished by the "mother cells" of the gametophyte. It is perhaps parasitic on it. This phenomenon is called matrotrophy. Morphologists, are of the view that matrotrophy is the most important event in transition to land by the plants.

Transfer cell are specialized parenchyma cells that have increased surface area due to infolding of the plasma membrane. They help to transport nutrients.

Endosperm: The young embryo in angiosperms is not fed by gametophyte but by a specialized tissue: endosperm is a product of triple fusion during double fertilization.

In the most evolved vascular plant group, the angiosperms, the role of matrotrophy is taken over by a specialized, post fertilization product, the endosperm.

7) **Siphonogamy:** In primitive aquatic algal ancestors the male gametes (often female gametes too) are flagellated, and motile. They move towards female gamete to ensure fertilization. As the transition to land occur, the non-motile female gamete the egg cell is restricted to the base of an archegonium. The antheridia release a large number of motile male gametes, the antherozoid/spermatozoids. These spermatozoids swim in water and are carried to the tip of the archegonium. Fertilization is ensured within the archegonium. In order to ensure fertilization the output of antherozoids need to be substantial as the chances of it travelling to a prospective archegonium depends on the availability of a film of water at a given appropriate time and place. However, in gymnosperms the male gametophytes are small non-motile reproductive units, called pollen grains. They are carried by

wind to the ovules that bear female gamete, the egg cell. On landing on the ovules, the pollen grains develop tube-like outgrowth which carries and deposits male gametes near the egg cell for fertilization (you shall learn more about it in Unit 20). Such a mode of transfer of male gamete to the female gamete is called siphonogamy. Thus, this mode of fertilization is independent of external water medium and helps the plant to diversity itself on the land territory far and wide with no dependence on the aqueous surrounding.

(8) **Sterility of Sporophyte:** By delaying the meiosis and through repeated mitotic divisions a multicellular embryo is produced in archegoniates. More the number of cells in sporophyte, wider is the ability to diversify. The differentiation of tissues, viz., epidermis; stoma; chlorophyllous cells; hydroids and leptoids; foot, seta, capsule or even different organs, viz., roots, stem, leaves, sporophyll, and rhizome.

Another advantage of multicellular embryo/sporophyte is the possibility of a large number of cells being designated as spore mother cells. Each of these cells in turn undergoes meiosis to produce four haploid cells, called spores. This ensures that a single zygote can produce a very large number of haploid spores (contrast a *Chlamydomonas*, where a zygote produces 4 haploid spores only). More spores ensure wider spread; ability to search newer niches into more interior of land mass, eventually better colonization of land habitat.

Interestingly, to ensure that the tiny, one-celled non-chlorophyllous spore, with its limited food supply to survive the journey through unknown territory, it was essential to protect it from desiccation, intense heat and solar radiation. Transition to land habit possibly has been successful because of the ability of a spore to get deposited with a very specialized, and hardy chemical sporopollenin. This substance is known to survive harshest physical and chemical adverse effects. Many spores and pollen grains of fossils are preserved, may be because they had sporopollenin on their exterior wall.

Sporopollenin: Oxidatively polymerized carotenoid biopolymer deposited on the outer surface of spores.

SAQ 1

In the following statements choose the alternative correct word given in the parentheses.

i) Multicellular sex organs with sterile cover is characteristic of (archegoniates/all green organisms).

ii) In archegoniates both the gametic cells are (similar/dissimilar).

iii) (Cuticle/Stomata) help land plants in gaseous exchange.

iv) (Matrotrophy/Vasculature) is always associated with archegoniates.

v) (Mitosis/Meiosis) in zygote helps in the formation of multicellular sporophyte.

SAQ 2

In the following statements fill in the blanks spaces with appropriate words:

i) Young sporophytes derive food from the maternal tissue through the specialized cells called .... cells.

ii) Delay in .... helps sporophyte to produce a large number of haploid spores.

iii) .... are vascular embryophytes but they do not produce archegonia.

iv) The enzyme glycolate oxidase in the peroxisomes are ....of carbon.

v) The deposition of ....helps to prevent desiccation of dispersed spores in land plants.

12.4 ALTERNATION OF GENERATIONS

German poet and botanist A.V. Chamisso (1819) introduced the term "*alternatio generationum"* while studying the life cycle of a barrel-shaped planktonic tunicate – a salp. Danish scientist J.S. Streenstreep (1842) suggested a Danish term, "*Vexlende Generationsrcekker*" for the same phenomenon. It was translated into German as "*generationweschsel*" in 1845. In english literature the commonly used term is alternation of generations. Initially it was used to describe the sexual and asexual forms in animals. However, now this term is exclusively associated with the life cycles of plants, especially referring to the alternations of gametophytes and sporophytes in the life of a plant.

W. Hofmeister (1862) wrote: '*that mosses and ferns 'exhibit' remarkable instances of a regular alternation of two generations very different in their organization. The first generation that forms the spore is destined to produce the different sexual organs. The object of second generation is to form numerous free reproductive cells - the spores by the germination of which the first generation is reproduced'.*

The investigations of Hofmeister were in 'pre-cytological' era. The chromosomes were discovered later in 1880's. He was unaware, therefore, with the term chromosome. In 1894, a Polish botanist Edward Strasburger reported that the asexual generation of a fern had twice the chromosome number of a sexual generation. C.E. Overton (1893) had earlier reported that pollen mother cells possessed reduced chromosome numbers relative to archesposial cells.

Thus, by the end of 19th century, it was firmly established that in a life cycle of plant there is alternation of generations associated with alternation of chromosome numbers (ploidy).

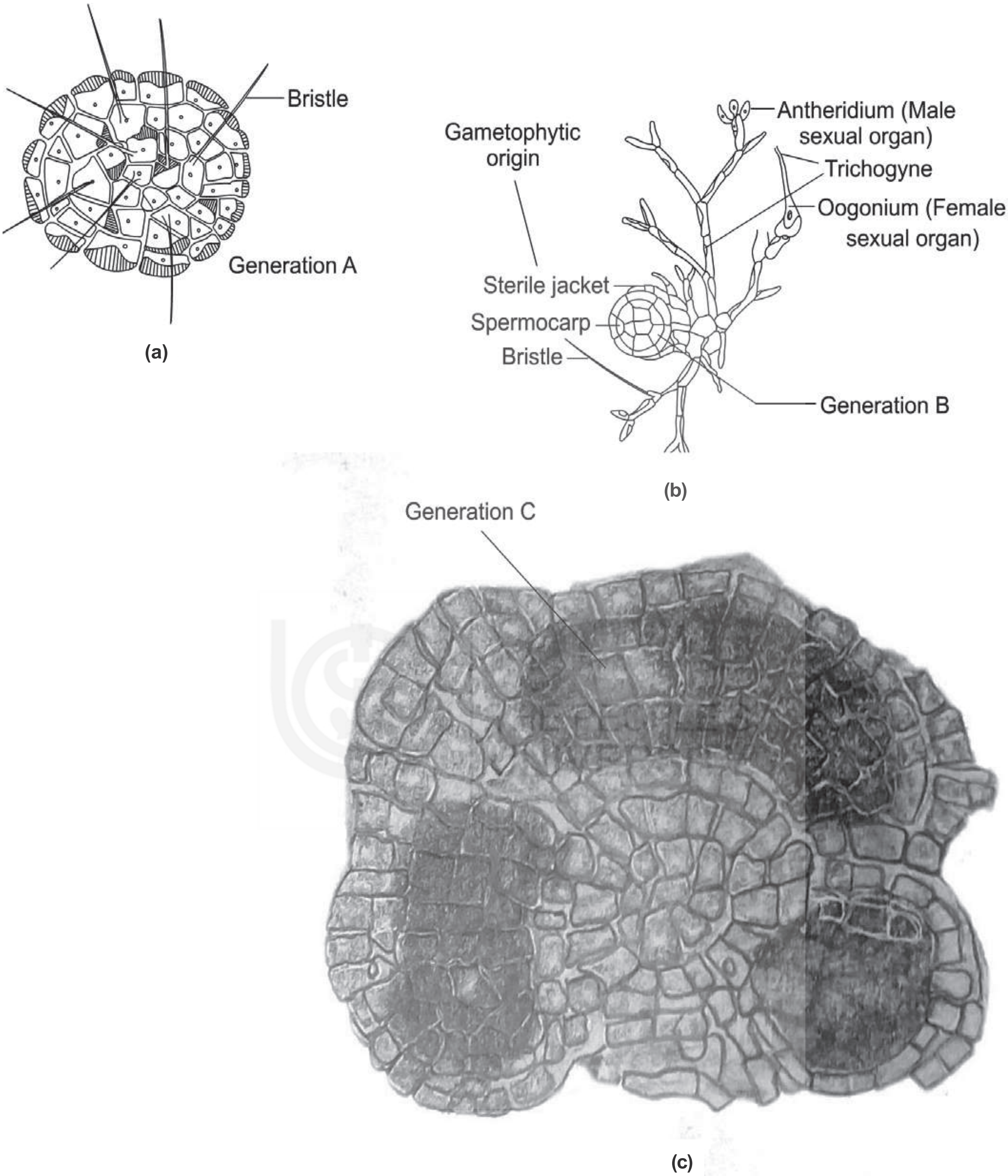

Fig. 12.6 (a-c): ***Coleochaete*, an alga : a) Generation A: a multicellular gemetophytic thallus; b) Generation B: a thallus with sex-organs antheridium and oogonium; c) Generation C: following fertilization zygote retained on gametophyte; (B); zygote divides by meiosis to form gametophyte of new generation, still retained, nourished and protected by sterile cells of maternal origin. The reproductive product 'spermocarp/fruit' on maternal gametophyte.**

***Source*: (a,b) Kumar, 2007; and (c) Graham et al., 2009.**

You shall be learning the details later in this block as well as in Blocks 5 and 6 about alternation of generations in heterosporous archegoniates. Some important, salient features are summarized as follows:

- The life cycle of a sexually reproducing organism involves an alternation of gametophytic and a sporophytic generation.
- These two generations could be homomorphic or heteromorphic.
- In homomorphic alternation of generations, e.g., *Polysiphonia, Ulva* (refer Section 6.3.4 of Block 2), both the generations are morphologically alike.
- In heteromorphic alternation of generations, there is distinct variation in size and form between the two generations (e.g., all archegoniates).
- Gemetophytic generation produces gametes (haploid). It is also called sexual or gametic generation. All the cells are haploid (n).
- Sporophytic generation is also called asexual, sporic or neutral generation. All the cells of this generation are diploid (2n).
- Some cells in the sporophytic generation, called spore-mother cells (2n) undergo meiosis (reduction division) to produce haploid (n) spores.
- All the spores could be alike (homosporous); or could be small (microspores) or large (megaspores) and thus heterosporous.
- Haploid spores germinate to produce gametophytic generation. Heterospores produces micro- and mega gametophytes respectively.
- Gemetophytic generation produces sex-organs/gametangia, to produce haploid gametes.
- In archegoniates, the male sex-organ is antheridium which produces male gametes, flagellated antherozoid/spermatozoid (bryophytes and pteridophytes) or non-motile male gametes (gymnosperm). The female sex-organ, archegonium bears large, non-motile, static female gamete the egg cell (refer Section 12.2).
- Fusion of two gametes (iso- or hetero-) results in formation of a diploid cell, the zygote. This act is called syngamy.
- Zygote undergoes mitotic cell division. Further repeated mitotic cell divisions form a multicellular sporophyte representing a sporophytic generation.
- The cycle is repeated.
- The two events that help/control the alternation of two generations are meiosis and syngamy.

Also, the two generations are categorized as:

- sexual vs asexual
- haploid vs diploid
- gametophytic vs sporophytic

Origin of Generations

One of the most fascinating as well as fiercely debated topic concerning the origin of land plants is the origin of generations in plants. Of the two generations the gametophytic vs. sporophytic, the question arises: which one is primary and which one is derived? Did both the generations arose separately or spontaneously. The answer to the above questions shall also throw light on the ancestor or ancestors of land plants. Let us introduce ourselves to this enigmatic as well as debatable topic.

12.4.1 Origin of Gametophytic Generation

It is almost well agreed that the plant life originated in the water. The foremost life could have been eukaryotic, unicellular, free-living, and autotrophic. This cell in itself was an organism. It had the capacity to produce spore(s) and then gametes. This ability to produce gametes led to the origin of sexuality in plants. The primitive early gametes were similar, isogametes or anisogametes. An important milestone must have been the origin of oogamy where one of the two gametes was non-motile, static and larger in dimension. With the evolution of multicellularity in the gametophytic generation, the gamete producing ability was restricted to only specific cell(s) the gametangium (pl. gametangia). It established the onset of the concept of division of labour (refer the life histories of *Chlamydomonas,* and *Oedogonium* from Block 2, Algae of this course).

12.4.2 Origin of Sporophytic Generation

There is unanimity among the scientists that the gametophytic generation was first to be evolved. In such an assumption the diploid zygote, in a haplontic type of life cycle represents the single-celled sporophytic generation. Such a condition is quite prevalent in a large number of aquatic algal forms. What then debatable is the origin of multicellularity of sporophytic generation. It also raises a question: when did this condition arise? Also, was the origin and prevalence of multicellularity of sporophyte accompanied by a reduction of gametophytic phase in the life of an organism?

You may recall from your School Biology Text Book, the haplobiontic and diplobiontic type of life cycles in plants.

Two prominent theories are prevalent. These are : Homologous Theory vs Antithetic Theory.

A) Homologous Theory: Homologous theory also referred to as Transformation or Modification Theory is advocated by N. Pringsheim (1876) and strongly supported by Scott (1895), Long (1909).

It envisages that sporophytic generation is not a new structure but simply a modification of existing gametophytic generation under certain developmental condition(s). They refer to the sporophytic generation as neutral generation, whose primary role is to produce a large number of spores, e.g., as exemplified in the life cycles of isomorphic alternation of generations in certain algae, e.g., *Ulva* (a green alga) and *Dictyota* (a brown alga).

Long suggested that both the generations are homologous and that spore and fertilized egg had the same developmental potential but produced different plant-bodies because they developed under different environmental influences.

The theory also envisages simultaneous and successful migration of both of these generations to the land habitat.

B) Antithetic Theory: L. Celakovsky (1874) and F.O. Bower (1890) are the strong proponents of Antithetic Theory of sporophyte origin. This theory is commonly referred to as Interpolation Theory or Intercalation Theory.

In contrast to Homologous Theory, this theory envisages that sporophyte is a new, progressively a vegetative structure. It is interpolated (inserted) in the haplobiontic kind of life cycle during transition of plants from aquatic to land habitat.

Proponents of this theory suggest that sporophyte originated as a new component of life cycle from an alga which lacked a sporophyte. How could it have happened? Let us elaborate a model of hypothesis (see Box 12.1).

Land plants originated from an alga which was haploid, multicelluar and had haplobiontic life cycle. This multicellular gametophyte could have been added by interpolation of a multicelluar neutral sporophyte just by delaying the meiosis in zygote and by retaining zygote and its products on the gametophyte.

This sporophyte would be initially parasitic on the gametophyte. They regard the genus *Coleochaete,* a Charophycean alga as an ideal ancestral aquatic alga.

Box 12.1: Life cycle of *Coleochaete*.

Celakovsky believed that *Coleochaete* exhibited both Antithetic and Homologous alternation. It possesses three kinds of generations: A, B and C.

- Generation A was represented by vegetative asexual bionts that produced zoospores;
- Generation B reproduces by sexual means that produce oospores.
- Generation C (a rudimentary antithetic generation) develops from fertilized oospore.
- Asexual A generation and sexual generation B are homologous.
- Generation C (the "fruit"/spermocarp) is Antithetic to generation A and B.

Inferences:

- Asexual generations of mosses and vascular cryptogams were similar to generation C of *Coleochaete*. And therefore, antithetic to the sexual generation (gametophyte).
- In land plants generations A and B have combined to become shoot.
- Protonema in a moss is equivalent to generation A; leafy shoot to generation B and parasitic sporophyte as interpolated generation C.

It is now believed that embryophytes were derived from within the Charophycean green algae. And the closest extant relatives of embryophytes possess a multicellular haploid body but lack a multicellular diploid body. Therefore, the sporophyte has been interpolated into basically haploid life cycle. This assumption supports antithetic theory rather than homologous theory of alternation of generations.

Recent molecular analysis also strongly suggests Charophycean link to the origin of higher land plants see (Fig. 12.7).

However, debate continues whether:

- the sporophyte originated from a dispersed zygote, or
- the sporophyte originated from a zygote that was retained on a maternal gametophyte.

Contemplating the Sections 12.2, 12.3 and 12.4 all together of this unit, you shall be in position to integrate the concepts of archegonium; oogamy; retention of zygote; delayed meiosis; embryo development; matrotrophy; life cycle patterns; alternation of generations and migration to land.

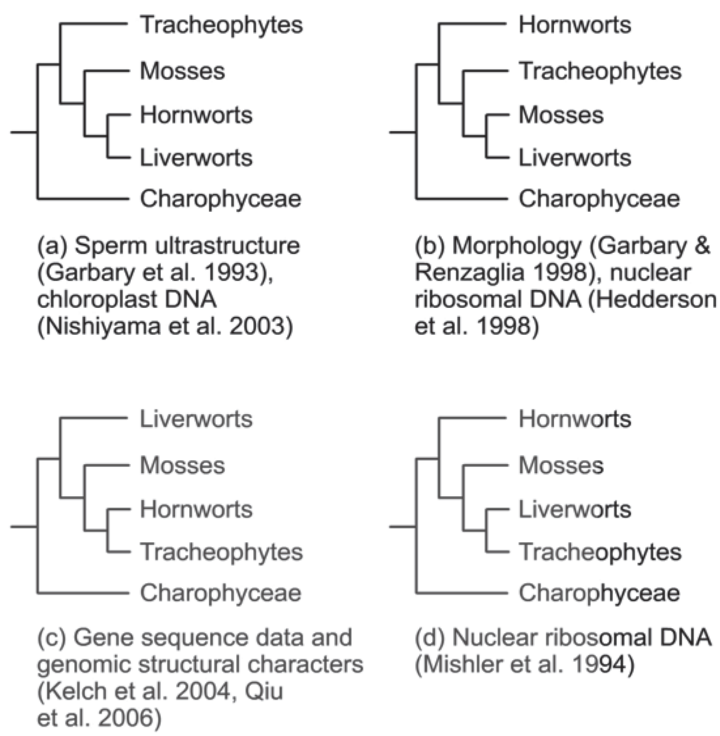

Fig. 12.7 : Summary of alternative phylogenetic relationships among extant lineages of land plants based on molecular analysis.
***Source*: Vanderpoorten & Goffinet, 2010.**

SAQ 3

In the following statements fill in the blank spaces with the appropriate words.

i) The alga .... (*Ulva/Coleochaete*) is regarded as the ancestor of land plants according to Antithetic Theory of alternation of generations.

ii) The concept of alternation of generations seeks to explain the origin of a .... (sporophyte/gametophyte).

iii) Delay in .... (mitosis/meiosis) results in the development of a multicellular sporophyte after fertilization.

SAQ 4

Match the name of the scientists given in Column I with the discoveries/theories mentioned in the Column II.

	Column I		Column II
a)	W. Hofmeister	i)	Alternation of ploidy during alternation of generations
b)	F.O. Bower	ii)	Homologous Theory
c)	E. Strasburger	iii)	Alternation of generations in mosses
d)	N. Pringsheim	iv)	Antithetic Theory

12.5 SUMMARY

Let us summarise what has been learnt so far:

- The group of plants possessing the female sex-organ the archegonium are collectively called archegoniates. Bryophytes, pteridophytes and gymnosperms are archegoniates.
- All archegoniates basically are multicelluar, autotrophic, terrestrial plants. Their sex-organs are multicellular and with sterile covering. The female gamete cell is a non-motile egg cell and is placed within the venter of the archegonium. The male gamete could be motile antherozoid/ spermatozoid (in bryophytes and pteridophytes) or non-motile sperm cells (in gymnosperms).
- Aqueous medium is necessary for the transfer of male gametes to the female gamete in bryophytes and pteridophytes. Pollen-tubes help carry male gametes for fertilization in gymnosperms.
- Some salient unifying characteristics of archegoniates are: embryo development, matrotrophy, and production of large number of haploid spores.
- Transfer of aquatic plants to the terrestrial habitat required: availability of suitable environment conditions and innovative changes in the life of an organism to survive in terrestrial environment.
- Some of the important innovations involved are: development of anchoring system; ability to take up water and minerals from soil substratum; specialized regions/parts of exposed areas of plant to do photosynthesis; differentiation of tissues for transportation of water, mineral and food to various parts; prevention of water loss to environment and controlled gaseous exchange; matrotrophy; siphonogamy; sterility of sporophyte and division of labour by sporophytic tissues.
- Heteromorphic alternation in archegoniates. The sexual gamete - producing, gametic generation alternates with spore-producing sporic or neutral generation. Syngamy and meiosis are key to these events.
- The two theories that make attempt to explain the alternation of generations are: Homologous/Transformational/Modification Theory and Antithetic/Interpolation/Intercalation Theory. Former theory considers a diplobiontic green alga as ancestor to land plant while the Antithetic Theory envisages *Coleochaete*-like Charophycean alga as an ancestor to origin of sporophytic generation.

12.6 TERMINAL QUESTIONS

1. Explain briefly:

   (a) Homologous Theory of alternation of generations.

   (b) Matrotrophy.

2. Write brief definitions for the following terms:

   (a) Archegoniates

   (b) Siphonogamy

   (c) Alternation of generations

3. Write a note on Antithetic Theory of alternation of generations.

4. Enumerate the unifying characteristics of archegoniates.

5. Discuss the adaptive strategies developed by aqueous plants during the phase(s) of transfer to land habitat.

12.8 ANSWERS

Self-Assessment Questions

1) i) archegoniates, ii) dissimilar, iii) Stomata, iv) Matrotrophy, v) Mitosis.

2) i) transfer, ii) meiosis, iii) Angiosperms/Flowering plants, iv) scavengers, v) sporopollenin.

3) i) *Coleochaete* ii) sporophyte iii) meiosis.

4) a) iii)

   b) (iv)

   c) (i)

   d) (ii)

Terminal Questions

1. a) Refer to Subsection 12.4.1

   b) Refer to Section 12.2, Subsection 12.3.2

2. a) Refer to Section 12.1

   b) Refer to Subsection 12.3.2

   c) Refer to Section 12.4

3. Refer to Subsection 12.4.2

4. Refer to Section 12.2

5. Refer to Subsection 12.3.2

12.8 GLOSSARY

Antheridium : A multicellular, male sex organ characteristic of bryophytes and pteridophytes. It possesses a sterile covering, jacket layer, over large number of male gametes, the motile antherozoids.

Archegoniates : Plant bearing female sex-organ archegonium, e.g., bryophytes, pteriodophytes and gymnosperms.

Archegonium : A multicellular, female sex organ characteristic of bryophytes, pteridophytes and gymnosperms. It possesses stalk, venter neck cells, neck canal cells, venter canal cells (all of them sterile) and a large, non-motile, female gamete, the egg.

Alternation of generations : Alternation of a gamete-producing gamotophytic phase and a spore-producing sporophytic phase in the sexual life cycle of a plant.

Embryo : A multicelluar, sporophytic, structure produced from a fertilized egg, the zygote (2n). It develops within the venter of an archegonium.

Embryophytes : All vascular plants are characterized by the formation of an embryo post syngamy.

Gametophytic generation : Gamete producing phase in the sexual life of a plant. Also called sexual phase.

Siphonogamy : Mode of transfer of male gametes to the egg cell in the female reproductive organs via a tube like structure formed by the pollen grain.

Sporophytic generation : Spore-producing phase in the life of a plant. Also called neutral or sporic phase.

Syngamy : Fusion of two haploid gametes to produce a diploid cell, the zygote.

12.9 FURTHER READING

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UNIT 13

BRYOPHYTES : AN INTRODUCTION

Structure

13.1 INTRODUCTION

Bryophytes are most abundant in moist, temperate and tropical areas along the edges of streams and wetlands. Some of them even inhabit deserts or on dry exposed rocks. Mosses are found to be dominant vegetation on rocky slopes above the timber-line in mountains. Bryophytes can withstand severe cold of Antarctic continents. A few of them are aquatic or even grow on rocks that are splashed by oceanic waves. None of them, however, are truly marine.

Bryophytes represent the most primitive land plants. They exhibit a sharply defined heteromorphic alternation of generations. Asexual sporophytic phase is associated with the sexual phase of gametophyte. The gametophytes are nutritionally independent and dominant of the two phases. Bryophytes require and are dependent on external water as medium for transfer of male gametes.

Majority views suggest that bryophytes arose from algae and probably from some green algae. The probable ancestry is suggestive of their origin from some of green algae viz. member(s) of family Chaetophoraceae, Cladophoraceae, and Ulvaceae. However, there are dismal fossil records to substantiate such arguments.

Recall Section 12.3 of the preceding unit which provides us valuable insights into strategies adopted by plants to invade, establish and flourish on land habitats. Understanding the biology of bryophytes is pivotal to unravel those epic and historic events of the past.

In this unit you shall learn the general characteristics of bryophytes in general and of liverworts and mosses in particular. You shall also study the adaptations that possibly made bryophytes successful pioneers of land habitat. Also, you will learn the criteria chosen for classifying bryophytes into various taxonomic ranks. You are advised to study Unit 12 of this block and Units 5, 6, 7, 8 and 10 pertaining to Algae for better understanding of text of this unit.

Objectives

After studying this unit, you should be able to:

- describe the general characteristics of bryophytes;
- give reasons why algae are considered to be ancestors of bryophytes;
- describe the adaptations acquired by bryophytes during transfer to land habitat from the aquatic environment;
- provide distinguishing characteristics to segregate the plants designated as bryophytes into: liverworts, hornworts and mosses; and
- provide a review of systems of classification of bryophytes along with the chosen criteria.

13.2 GENERAL CHARACTERISTICS

The Division Bryophyta includes the simplest and the most primitive members of land plants that lack roots, and do not have a vascular system. There are some mosses that have a primitive system of tubes that conduct water and food. The water-conducting tubes are called **hydroids.** They have elongated, thick, dead cells and contain polyphenolic compounds. But they are not lignified like tracheids and vessels that are characteristic of vascular plants. The food-conducting tubes are called **leptoids,** and they are connected through plasmodesmata.

A single plant is very small, hardly a few cm in size. It seldom grows in to a large plant because of lack of supporting tissues. Thousands of tiny moss plants often grow together and give a thick, green carpet-like appearance. Asexual reproduction in bryophytes can be achieved in three ways: (1) by growth and branching, followed by death and decay of older parts; (2) by the separation of whole organs and the regeneration of new plants from them, and (3) by means of specialized units of propagation termed gemmae. The first mode is very widespread, e.g., in most thalloid liverworts. The separation of whole organs can be the most effective means of spreading a plant. It is very common among mosses. The gemmae is a fairly common mode of asexual mode of reproduction in many liverworts. The structure, size, place of origin of gemmae could be very variable among different genera. You are advised to refer Sub-section 14.3.3 in the Unit 14 of this block for a representative example.

Bryophytes show two distinct and well defined phases of life cycle, sexual and asexual, which follow each other. The **gametophyte** is haploid and produces gametes. Sexual reproduction in bryophytes is oogamous. The biflagellate motile male gametes, the antherozoids, travel to the non-motile female gamete the egg enclosed in an archegonium through the medium of water. Although the bryophytes are land plants, the dependence on water to complete the sexual life cycle is considered reminiscent of their aquatic ancestry. The diploid zygote, the product of fertilization, is formed within an archegonium (physically in contact with the gametophyte) and is nourished by maternal tissue. This phenomenon is termed **matrotrophy** (food derived from mother). Recall Section 12.2 of previous Unit in this block for the significance of matrotrophy in evolution of plants. The **sporophyte** is diploid and produces haploid spores. The haploid generation alternates with diploid generation. Both the gametophyte and sporophyte may be several centimeters in length but the gametophyte is the dominant generation.

The gametophyte may be thalloid, leafy thalloid or has an axis differentiated into stem-like and leaf-like structures which lack xylem and phloem. You may refer Section 14.2 of next unit of this block for the range of organization in bryophytes. You may note that these leaf-like structures are part of gametophyte, whereas in vascular plants the leaves strictly develop on sporophyte. The adaxial surface of some thalli in liverworts, for example in *Marchantia* are especially modified to reduce water loss to the atmosphere. This adaxial surface also possesses specialized pores to increase CO_2 permeability. The gametophyte is green, photosynthetic and nutritionally independent, and anchors to the soil by unicellular or multicellular filaments called **rhizoids**. Rhizoids appear like roots but unlike roots they lack vascular tissues and are much simpler in structure. Rhizoids mainly help as anchor. The intake of minerals and water is mostly and directly from the surface of gametophyte.

In the following account you will learn about the general pattern of sexual reproduction that is more or less uniform in this group of plants.

While learning about reproduction in algae, you noticed that in primitive forms the sexual reproduction was isogamous. During evolution, other forms of sexual reproduction such as anisogamy and oogamy evolved.

During migration from water to land, the need of protecting the gametes arose. So possibly the sex organs developed a layer of sterile cells forming a jacket around gametes. You have learnt that in bryophytes the male and female reproductive organs are known as antheridia and archegonia, respectively. An antheridium consists of a single layer of protective sterile cells enclosing the mass of antherozoid mother cells or androcytes (Fig.13.1), each of which gives rise to a single, biflagellated motile antherozoid. The position and shape of antheridia varies in different species. The archegonium is so characteristic of bryophytes, pteridophytes and gymnosperms, that these three groups are collectively known as the **Archegoniates** (refer Section12.2 of preceding unit in this block). The archegonium is a multicellular, more or less flask-shaped structure. Its swollen basal portion is known as venter, and the upper

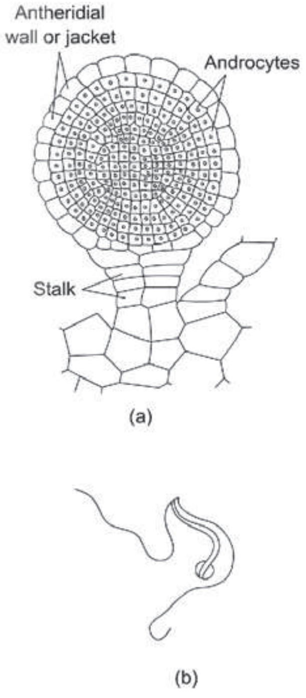

Fig. 13.1 : (a) An antheridium; (b) An antherozoid in a bryophyte.
***Source*: Vashishta, 1994.**

elongated portion as the neck. It consists of an axial row of cells surrounded by a sterile jacket. The axial row of cells can be distinguished into **neck canal cells** (which are variable in number according to the species), **a ventral canal cell** (venter canal cell) and a single large basal cell the egg or **oosphere** (Fig. 13.2). The archegonium provides nourishment and protection to the egg and after fertilization to the developing embryo. The nutrient transfer from gametophyte to sporophyte takes place across cell walls through extensive labrynth of highly branched cell wall. This increases the surface area of plasmalemma, across which nutrients are transferred. This tissue can be considered analogous to placenta of animal kingdom.

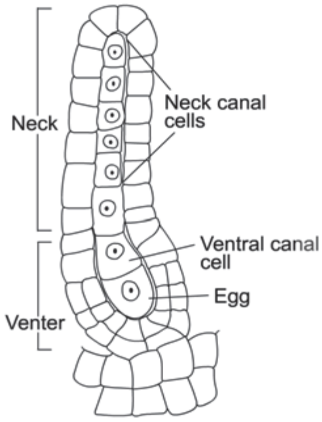

Fig. 13.2 : An archegonium in a bryophyte. ***Source*: Vashishta, 1994.**

In bryophytes since the male gametes are ciliated they require water to swim in order to reach up to the neck of an archegonium and also for their passage through the neck canal to the venter. A single antherozoid fertilizes the egg and the zygote is formed. The zygote begins to grow at once, and divide by mitosis. Further repeated mitotic divisions leads to the development of multicellular embryo. You may note that there is no resting phase for the embryo as in higher plants. You may recall that in higher plants the embryo may remain dormant till the onset of favourable conditions for germination of seed.

The embryo is not liberated and is retained within the archegonium. After fertilization the basal portion of wall of archegonium enlarges, becomes multilayered, and forms a protective envelop around the developing embryo. The embryo eventually grows into a sporophyte. This protective envelop is known as **calyptra**. The development of sporophyte is very limited. The embryogeny is soon followed by spore formation. The **sporophyte** or **sporogonium** is simple structure. Unlike other land plants, it is not differentiated into stem, leaves and roots. Generally, it is distinguishable into a **foot, seta** and a terminal spore producing **capsule** or sporangium. In certain species, seta is absent and more rarely also the foot. The spore mother cells develop inside the capsule and they represent the last stage of sporophytic generation. Spore mother cells divide by meiosis to form tetrads of haploid spores which usually separate before their discharge from the capsule. In bryophytes the sporophyte has no connection with the soil and it is wholly dependent on the gametophyte for its nutrients. In some of the bryophytes the sporophyte may possess chloroplasts, and are partly autotrophic.

For details you will learn the life cycles of a liverwort (*Marchantia*) and a moss (*Funaria*) in the next unit. Bryophytes may also harbour symbionts such as blue-green algae and mycorrhiza as additional adaptation. These microbes help provide the host additional nutrients.

Now let us sum up the distinguishing features of bryophytes.

1. They lack vascular system. In some mosses a primitive conducting system is present that transports food and water.

2. They exhibit heteromorphic alternation of generations.

3. The gametophyte is dominant and independent generation and the sporophyte remains attached to it. They exhibit matrotrophy.
4. They are dependent on water for transfer of male gametes for fertilization.
5. The sex-organs, the male antheridium and the female archegonium are multicellular but with sterile cover of cells.
6. The sporophyte is completely or substantially dependent on the gametophyte for food and water.
7. They are homosporous.
8. In mosses, a prominent haploid multicellular protonema develops from a spore. The gametophores(s) arise from the protonema.
9. They exhibit widespread asexual mode of reproduction – death and decay of older region, separation of whole organ, and through the formation of gemma(e).
10. The rhizoids, unicellular or multicellular, are principally the structures of anchor to the substratum rather for absorption of minerals and water.

SAQ 1

a) Which of the following statements regarding bryophytes are true?

   i) Bryophytes show oogamous type of reproduction.

   ii) Ascogonium is the female reproductive organ.

   iii) Antheridium is the male reproductive organ.

   iv) Bryophytes do not require water for fertilization.

   v) Sporophyte in a bryophyte is differentiated into stem, leaves and roots.

   vi) The male gametes are biflagellate.

   vii) The embryo is autotrophic.

   viii) Some bryophytes are heterosporous.

   ix) Alternation of generations is heteromorphic.

   x) Some green alga(e) is/are probable ancestor(s) of bryophytes.

b) Choose the correct alternative words given in the parentheses in the following statements.

   i) The dominant phase in life cycle is (gametophyte/sporophyte).

   ii) (Roots/Rhizoids) anchor the plant to the substratum.

   iii) The protonema is (haploid/diploid).

   iv) None of the bryophytes are truly (marine/epiphytic).

13.3 ADAPTATIONS TO LAND HABIT

You have learnt that most algae are aquatic. Some algae have also adapted to terrestrial mode of living. What about bryophytes? They are principally land plants. Their adaptation to land is not absolute because their male gametes are still motile and have to swim through a film of water to fertilize the eggs. Hence, in this aspect they are similar to amphibians of the animal kingdom.

Some bryophytes such as *Fontinalis antipyretica* (watermoss), *Fissidens viridulus*, *Palustriella commutata*, *Cratoneuron filicinum* are aquatic. Some of them show high preference for clear, turbulent, fast-flowing water with specific phosphate and ammonium as requirements.

In Unit 12 you have learnt that some scientists believe that land plants might have originated from certain fresh water green algal ancestors that are related to some extant groups such as members of Charales and Coleochaetales. Although there are no fossil records available to substantiate this belief, bryophytes share the following structural and biochemical characteristics with algae that support this view.

i) The chloroplasts of bryophytes have chlorophylls and carotenoid pigments similar to that of green algae.

ii) The food reserves of both the groups consist mainly of amylase and amylopectin. They produce motile spermatozoids.

iii) The flagella are of the whiplash type, i.e., they are naked structures; lateral appendages do not occur.

iv) Their cell wall contains pectin and cellulose.

v) The glycolytic pathway is quite similar in the two groups.

So, there are strong reasons to believe that green algae served as ancestors of bryophytes.

The move from water to land offers an organism some distinct competitive advantages as well as challenges. What could be the advantages of the terrestrial habitat over the aquatic? Some of the advantages are as follow:

i) greater availability of sunlight for photosynthesis,

ii) increased level of carbon dioxide, and

iii) decreased vulnerability to predation.

Some of the challenges, however, could be as follows:

1. Plants on land are exposed to direct sunlight and air, hence there is danger of drying out or desiccation because of evaporation. Gametes and zygotes are also susceptible to desiccation.
2. The aquatic plants are supported by the buoyancy of water, but on land, plants need some anchor to fix to the ground and also require support to stand erect.
3. Absorption of minerals and water, and their transportation to the parts which are not in contact with soil. In other words, land plants need supply lines for the distribution of water and nutrients.

4. Effective dispersal of spores at right time and at right place for the survival of progeny.

The adaptations of land plants in general are: epidermis with cuticle; stomata; vascular system; lignified thickenings which provide support; sporopollenin - a decay and chemical resistant biopolymer; gametes protected by sterile layer of cells, and the nourishment of embryo by the maternal tissues. Almost all of these adaptations are associated with transfer of plants to the land habitat (refer Section 12.3 of preceding unit).

13.4 CLASSIFICATION

You have already learnt that all the eukaryotic, multicellular, autotrophic and basically terrestrial organisms were placed in the Kingdom Plantae by R.H.Whittaker (1969). In the previous Unit 12 of this block, you have also learnt the salient unifying characteristics of archegoniates, which also included the plants, popularly known as bryophytes. In Section 13.2 above you were also introduced to the general characteristics of this group. However, these morphologically simple, evolution-wise significant and ecologically important plants have long challenged taxonomists. A fairly acceptable classification which will be at once reasonably natural and clearly workable has not been easy to meet. We shall attempt to summarize in this sub-section some landmark contributions in the field of classification of bryophytes - still an evolving field of science.

Robert Braun (1864) used the term ‘Bryophyta’ for the group that comprised algae, fungi, lichens and mosses. Later, algae, fungi and lichens were separated from this group and collectively comprised “thallophyta”. An independent rank, **Bryophyta** was first proposed by Schimper (1879) to include liverworts and mosses. Later Eichler (1883) recognized two sub-groups, the classes, **Hepaticae** and **Musci** in the Bryophyta. Engler (1892) subdivided each of these classes into three orders as follows.

Division Bryophyta

Class Hepaticae

- Order 1 **Marchantiales**
- Order 2 **Jungermanniales**
- Order 3 **Anthocerotales**

Class Musci

- Order 1 **Bryales**
- Order 2 **Andreales**
- Order 3 **Sphagnales**

The above classification as proposed by Engler is still followed by many bryologists.

A large number of bryologists, however, were of the view that order Anthocerotales should not be placed within the class Hepaticae. M.A. Howe (1899) raised the order Anthocerotales to the status of class, **Anthocerotes.** Hence, he suggested that Division Bryophyta be divided into 3 classes, such as :

Bryologist : The scientist who specializes in the study of bryophytes.

1. Class : **Hepaticae**
2. Class : **Anthocerotes**
3. Class : **Musci**

Many eminent scientists such as D.H. Campbell (1918, 1940), G.M. Smith (1938, 1955), A.L. Takhtajan (1953) supported the division of Bryophyta into 3 classes. However, G.M. Smith, A.L. Takhtajan, C.W. Wardlaw (1955) and R.M. Schuster (1958) preferred the term **Anthocerotae** for the class Anthocerotes (Howe, 1899). The consensus view, thus, emerged that the Division Bryophyta be divided into 3 classes as follows:

Division **Bryophyta**

1. Class **Hepaticae** 2. Class **Anthocerotae** 3. Class **Musci**

Rothmaler (1951) suggested that the taxon **Hepaticae**, **Anthocerotae** and **Musci** be renamed as **Hepaticopsida**, **Anthoceropsida** and **Bryopsida.** Thus, the Division Bryophyta be divided into 3 classes.

1. Class : **Hapaticopsida**
2. Class : **Anthoceropsida**
3. Class : **Bryopsida**

Rothmaler's suggestion have also been recognized by International Code of Botanical Nomenclature (ICBN). J. Proskauer (1957) suggested the name **Anthocerotopsida** for the class, **Anthoceropsida**. We are following this nomenclature in this course.

Division : Bryophyta

1. Class : **Hepaticopsida** (liverworts)
2. Class : **Anthocerotopsida** (hornworts)
3. Class : **Bryopsida** (mosses)

The salient characteristics of these classes and a few common representative genera are listed in Table 13.1.

In many texts, the three classes Hepaticopsida, Anthocerotopsida and Bryopsida have been elevated to the rank of phylum (division): Hepatophyta; Anthocerophyta and Bryophyta (H.C. Bold 1956-57). In these units, we shall follow the nomenclature as suggested by ICBN and modified by Proskauer (1957).

Table 13.1 : Salient characteristics of the three classes of Division Bryophyta.

Class : Hepaticopsida (Hepaticae)

1. Gametophyte is usually dosiventral, either thallose or leafy. When leafy, leaves are without midrib.
2. Internally gametophyte is either simple or differentiated, but the photosynthetic cells always contain numerous chloroplasts without pyrenoids.
3. Rhizoids are unicellular and unbranched.
4. Sex organs develop from dorsal superficial cells of the thallus.
5. Sporophyte may be simple; or differentiated into foot and capsule; or into foot, seta and capsule.
6. Archesporium develops from the endothecium of an embryo.
7. Elaters are generally present.

Examples : *Riccia*, *Marchantia*, *Pellia, Sphaerocarpos*, *Calobryum*, *Haplomitrium*, *Riccardia*.

Class : Anthocerotopsida (Anthocerotae)

1. Like Hepaticopsida the plant body is dorsiventral but shows no internal differentiation.
2. Each cell of the thallus usually has a single chloroplast with a conspicuous central pyrenoid.
3. Rhizoids are smooth walled, scales are absent.
4. Sex organs are hypodermal in origin and are embedded in the gametophyte.
5. Sporophyte consists of bulbous foot, a meristematic region and a long cylindrical capsule.
6. Sporophyte shows continuous growth due to the presence of intercalary meristem.
7. Archesporium develops usually from amphithecium.
8. Pseudoelaters are present.

Examples : *Anthoceros*, *Notothylas*

Class : Bryopsida (Musci)

1. Gametophyte is differentiated into stem-like axis and leaf-like lateral appendages.
2. Rhizoids are branched, multicellular with oblique cross walls.
3. Gametophyte has two stages of development – first protonemal stage represented by multicellular branched, filamentous protonema, which is followed by next stage represented by erect leafy gametophores produced on the protonema.
4. Sex organs are situated at the apex of erect gametophores.
5. Sporophyte is generally differentiated into foot, seta and capsule. Capsule wall consists of many layers with functional or non-functional stomata. Archesporium develops from endothecium or amphithecium.
6. Peristome is present for dispersal of spores.

Examples : *Funaria*, *Bryum*, *Physcomitrium*, *Polytrichum*, *Pogonatum*, *Sphagnum*, *Andreaea*.

Classification of Hepaticopsida (Liverworts)

There are about 330 genera and more than 8000 species of liverworts that belong to class Hepaticopsida.

Engler (1892) subdivided the class Hepaticae into 3 orders : Marchantiales, Anthocerotales and Jungermanniales. After Howe's upgrading the status of order Anthocerotales to that of class Anthocerotopsida, only two orders were left in the class Hepaticopsida. F. Cavers (1910) added an order Sphaerocarpales. In 1936 D.H. Campbell added one more order, namely Calobryales and later Engler's Jungermanniales was split into two orders – Metzgeriales and Jungermanniales. S. Hattori and H. Inoue (1958), and S. Hattori and M. Mizutani (1958) added a new order Takakiales to this class. Thus, a more or less consensus view is to split class Hepaticopsida into six orders namely:

1. Marchantiales (chambered-hepatics), e.g., *Marchantia*
2. Sphaerocarpales (bottle-hepatics), e.g., *Sphaerocarpos*
3. Metzgeriales (multiform-thallose hepatics), e.g., *Pellia*
4. Jungermanniales (scale-moss hepatics), e.g., *Jungermannia*
5. Takakiales (see Box. 13.1), e.g., *Takakia*
6. Caloboryales (moss-like hepatics), e.g., *Calobryum*.

See Fig. 13.3 for morphology of some representative genera.

Some bryologist add Monocleales (Giant-thallose hepatics) to this list. Genus *Monoclea* represents this order

Box 13.1 : *Enigmatic Takakia*

S. Hattori and H. Inoue (1958) and S. Hattori and M. Mizutani (1958) described the morphology of a new liverwort discovered from Japan and Western North America respectively. This new plant was named *Takakia lepidozioides*. It has many features so different from the other known liverworts that they proposed a new order Takakiales with one family Takakiaceae. Some of the key characteristics of this new order are: gametophytes with stem with a group of linear, cylindrical "phyllids" (usually 2 or 3 together); rhizomatous; large archegonia borne terminaly in groups; no rhizoids; exogenous and intercalary mode of branching and 3-sided apical cell.

Sporophytes have been discovered by Smith and Davidson (1993). The sporophytic features such as: lack of elaters; presence of feeble columella; a calyptra that ruptures as the distal portions are elevated on the capsule; persistent seta are moss-like (Fig. 13.4).

The peculiar 'mix' of criteria makes it both as a liverwort or a moss. There is a suggestion that it could be elevated to an independent status of a class 'Takakiopsida' with similarities to Calobryales (liverwort) and Andreales (moss). This led Smith and Davidson (1993), on the basis of similarities of sex organs and schistocarpous capsule shared by *Takakia* and *Andraeobryum* transferred *Takakia* to mosses.

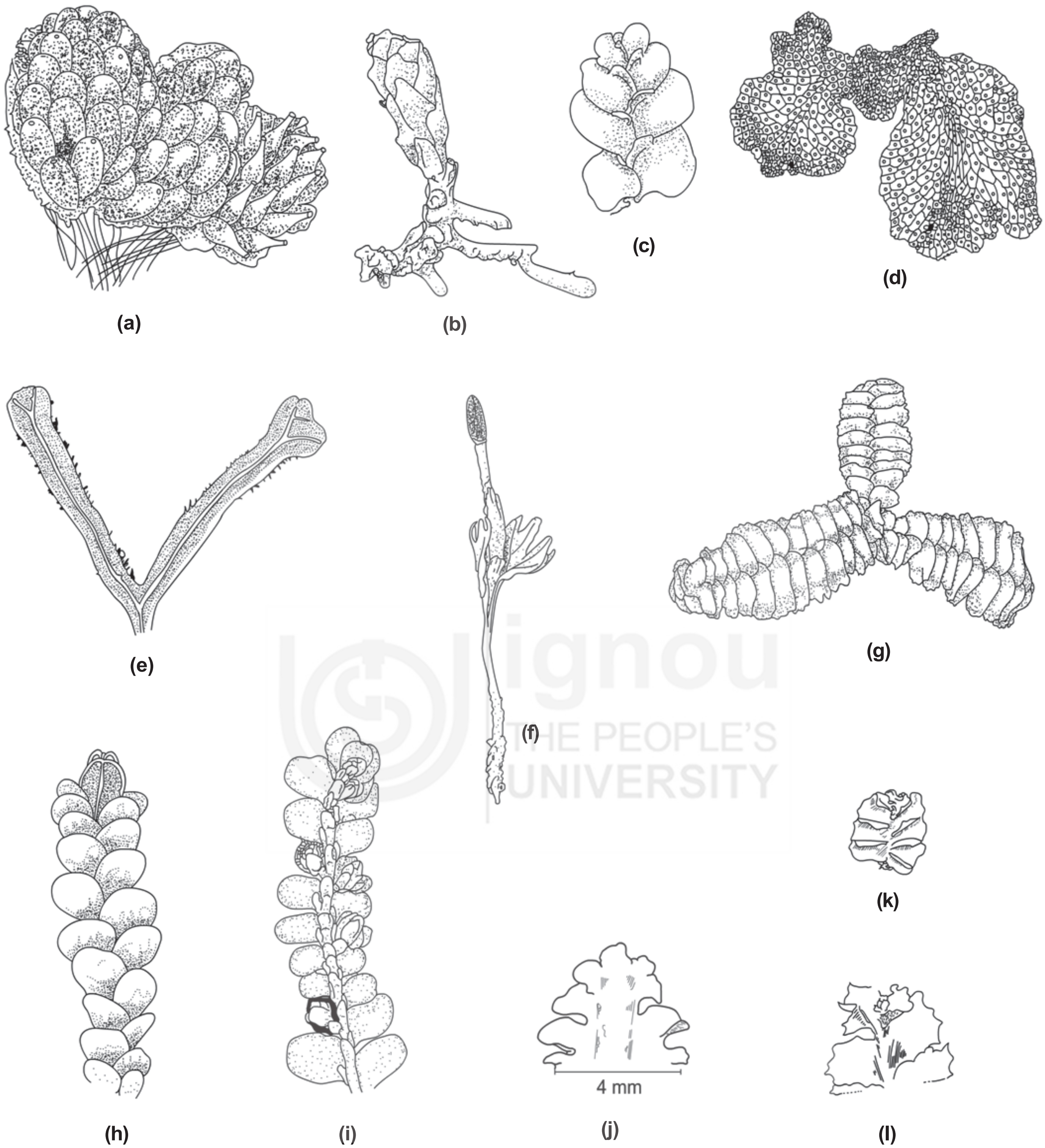

Fig. 13.3 : Morphology of some representative liverworts (Hepaticopsida) : a) *Sphaerocarpos*; b) *Haplomitrium*; c) *Treubia*; d) *Conocephalum*; e) *Metzeria*; f) *Jenssenia*; g) *Bazzania*; h) *Lejeunea*; i) *Porella*; j) *Blasia*; k) *Petalophyllum*; l) *Fossombronia*. *Source*: (a) Rashid, 2010; (b-l) Vanderpoorten & Goffinet, 2010.

Classification of Anthocerotopsida

This class has only one order Anthocerotales and 5 genera *Anthoceros*; *Phaeoceros*; *Notothylas*; *Megaceros*; and *Dendroceros* and the total number of species are more than 300. See Fig. 13.5 for morphology of some representative genera.

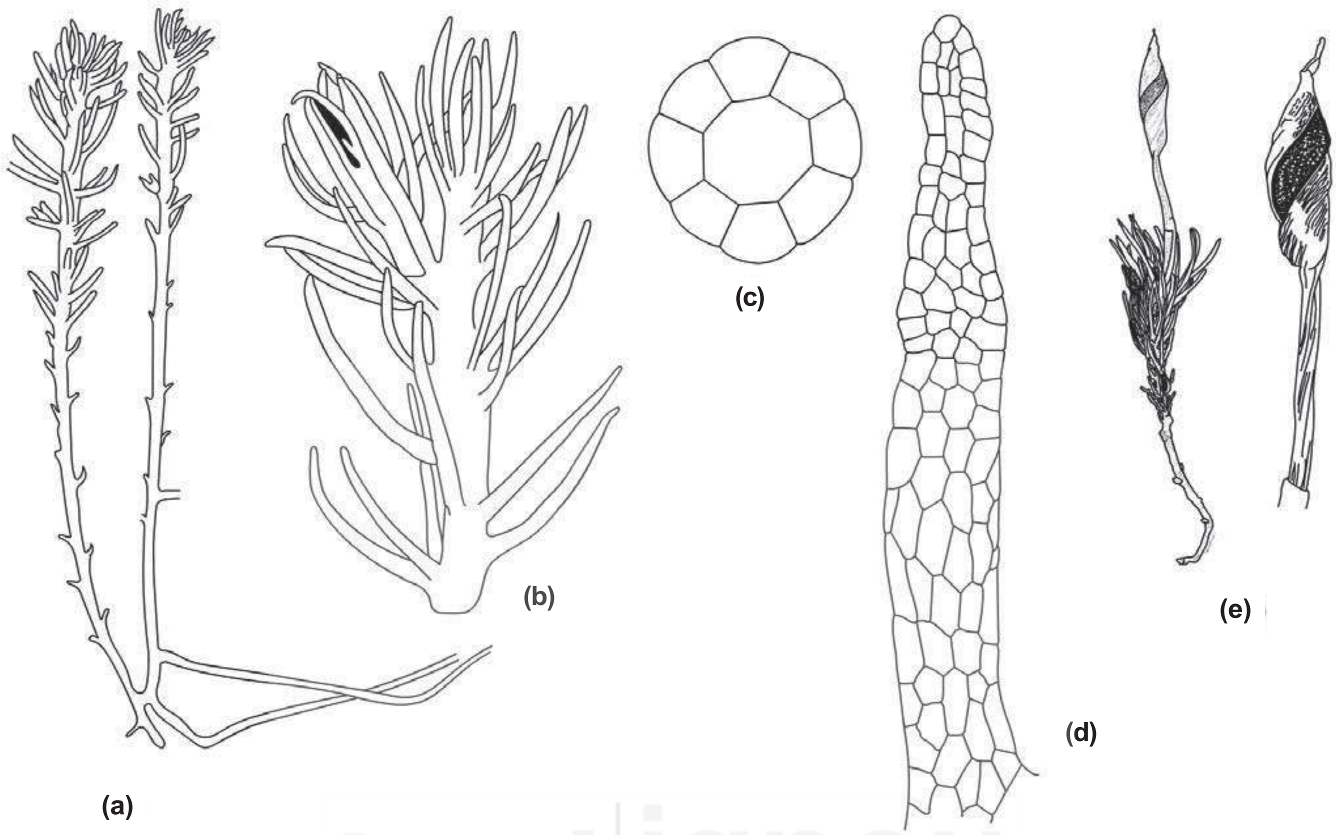

Fig. 13.4 (a-e) : **Morphology of *Takakia*. a) Plant with rhizomatous and erect leafy axis; b) A leafy axis (enlarged); c) A leaf in cross-section; d) A stalked-archegonium; e) *Takakia ceratophylla*, capsule dehisces along a spiral line.**
***Source*: (a-d) Rashid, 2010, (e) Vanderpoorten & Goffinet, 2010.**

Classification of Bryopsida

More than 700 genera and about 15000 speices comprise the class Bryopsida. Smith divided the class into 3 sub-classes : Sphagnobrya; Andreaeobrya and Eubrya. Bower (1935), Campbell (1940) and others divided the class Bryopsida into 3 orders: Sphagnales; Andreaeales and Bryales. However, the much prevalent and accepted classification of Bryopsida (Musci) is the one given by Reimers in Engler's *Syllabus der Pflazenfamilien* (1954). He segregates the class Musci (Bryopsida) as follows:

Class: Musci
Sub-Class: Sphagnidae
1 Order: Sphagnales (1 family) Representative genus - *Sphagnum*

Sub-class: Andreaeidae
1 Order: Andreaeales (1 family) Representative genus - *Andreaea*

Sub-Class: Bryidae
12 Orders

1.	Archidiales	(1 family)	:	*Archidium*
2.	Dicranales	(7 familes)	:	*Dicranella*
3.	Fissidentales	(1 family)	:	*Fissidens*
4.	Pottiales	(3 families)	:	*Pottia*

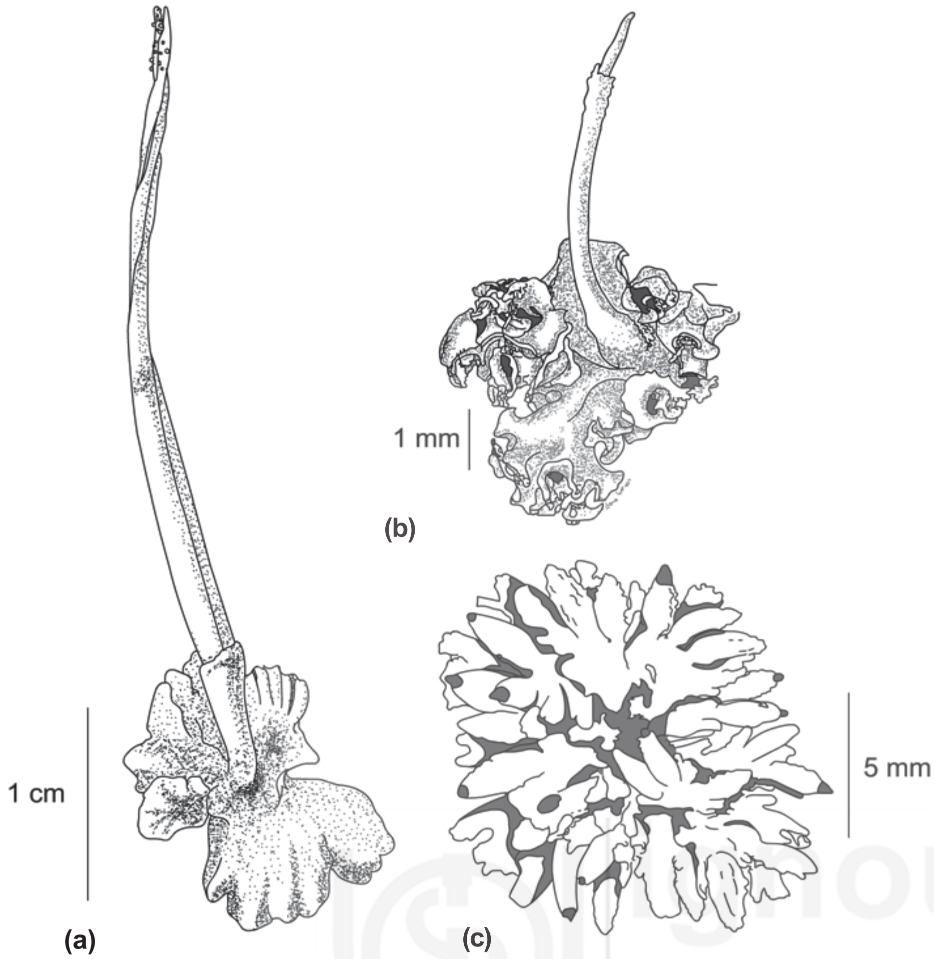

Fig. 13.5 (a-c): Morphology of some representative hornworts:
a) *Phaeoceros*; b) *Dendroceros*; and c) *Notothylas*.
***Source*: (a-c) Vanderpoorten & Goffinet, 2010.**

5.	Grimmiales	(1 family)	:	*Grimmia*
6.	Funariales	(6 families)	:	*Funaria*
7.	Schistostegales	(1 family)	:	*Schistochila*
8.	Tetraphidales	(1 family)	:	*Tetraphis*
9.	Eubryales	(16 families)	:	*Bryum*
10.	Isobryales	(23 families)	:	*Barbella*, *Isobryum*
11.	Hookeriales	(6 families)	:	*Hookeria*
12.	Hypnobryales	(12 families)	:	*Mnium*

Sub-Class : Buxbaumiidae
1 order : Buxbaumiales (2 families) : *Buxbaumia*

Sub-Class : Polytrichidae

Orders : 1. Polytrichales (1 family) : *Polytrichum*
2. Dawsoniales (1 family) : *Dawsonia*

The differences are minor between most modern systems of classification of mosses, if any, they are limited to rank and terminology. Rarely, with position or even the existence of a given order. This does not mean that there is an unanimity on the probable course of evolution in the Musci. Generally, seven evolutionary lines among music are recognized. They are :

Fig. 13.6 (a-j) : Morphology of some representative mosses (Bryopsida). a) *Sphagnum*; b) *Andreaea*; c) *Buxbaumia*; d) *Gymnostomiella*; e) *Plagiothecium*; f) *Climacium*; g) *Polytrichum*; h) *Tetraphis*; i) *Funaria*; j) *Andreaeobryum*.
***Source*: (a-j) Vanderpoorten & Goffinet, 2010.**

(k)

1.	Brylaes	(Joint toothed mosses)
2.	Archidiales	(Large-spored mosses)
3.	Tetraphidales	(Four-toothed mosses)
4.	Polytrichales	(Hair-cup mosses)
5.	Buxbaumiales	(Bug mosses)
6.	Sphagnales	(Bog/peat mosses)
7.	Andraeales	(lantern mosses)

SAQ 2

a) Match the classes of bryophytes mentioned in the column I with the characters mentioned in Column II.

Column I	Column II
i) Archesporium is amphithecial in origin	a) Hepaticopsida
ii) Peristome helps in spore dispersal	b) Anthocerotopsida
iii) Elaters are generally present	c) Bryopsida

b) In the following statements regarding classification of Bryophytes fill in the blank spaces with appropriate word(s).

i) Rhizoids are branched, multicellular with oblique walls in class ....

ii) Presence of pyrenoid within chloroplast is characteristic of class ....

iii) Sex organs develop from dorsal superficial cells in the class ....

iv) Order Jungermanniales belongs to class ....

v) Eichler recognized two sub-groups of bryophytes, namely ....and ....

vi) The genus *Dendroceros* belongs to class ....

13.5 SUMMARY

- Bryophytes represent the most primitive land plants. They exhibit sharply defined heteromorphic alternation of generations. The asexual, sporophyte is always attached to sexual phase of gametophyte.
- Gametophytes are nutritionally independent and dominant of the two generations. They are non-vascular, lack roots, stem, and leaves. They could be thalloid, leafy or erect with leaf-like appendages. Such 'leaves' do

not possess mid-rib. When erect, the stem-like axis may possess water-conducting tubes, 'hydroids' rich in polyphenolic compounds but devoid of lignin. Food-translocating tubes 'leptoids' may also be present.

- Gametophytes anchor to substratum through unicellular/multicellular, branched or unbranched rhizoids.

- Asexual reproduction is through death and decay of older parts; separation of whole organs, or through specialized units of propagation, the gemmae.

- Sex-organs are multicellular and with sterile covering of cells of the jacket. Biflagellate, male gametes, the antherozoids are formed in antheridium, the male sex-organ. The female gamete, egg cell, is present in the specialized, urn-shaped structure, the archegonium. Sexual reproduction is oogamous. The antherozoids travel to female gamete through water-medium.

- The zygote divides mitotically and produces multicellular, wholly or partially dependent on gametophyte for anchor, food and protection. It exhibits matrotrophy.

- Sporophyte may be differentiated into foot, seta and capsule. Specialized structures such as elators, pseudoelators, and peristome-teeth may be formed to facilitate the dispersal of spores. Bryophytes are homosporous.

- Migration to land provides the plant greater availability of sunlight for photosynthesis; greater CO_2 availability and decreased vulnerability to predation.

- Epidermis, cuticle, 'stomata', conducting strands, rhizoids, large number of spores for dispersal to newer areas, are some of the adaptations to the habitat.

- Most acceptable system of classification divides bryophytes into : classes Hepaticopsida (liverworts); Anthocerotopsida (hornworts), and Bryopsida (mosses).

- Liverworts could be thalloid, dorsiventral, dichotomously or unevenly branched, leafy and partly erect with unicellular unbranched rhizoids. Sex organs are exogenous.

- Hornworts are lobed, with single chloroplast per cell. Chloroplast possesses a pyrenoid. They possess endogenous sex organs and a meristematic zone in the sporophyte.

- Upright axis, the 'stem' and the appendages, the 'leaves', multicellular, branched rhizoids, apical sex-organs are characteristic features of mosses.

- Foot, seta and capsule are characteristic features of the sporophytes of mosses. A protonemal phase precedes the gametophore development from a spore in mosses.

13.6 TERMINAL QUESTIONS

1. Discuss the challenges that bryophytes could have faced when they adapted to terrestrial habitat.
2. Enumerate the structural and biochemical characteristics that provide strong reasons to believe that green algae could have been the ancestors of bryophytes.
3. Briefly describe the distinguishing features of bryophytes.
4. Provide arguments to suggest that bryophytes are the most primitive land plants.
5. Compare the characteristics of liverworts, hornworts and mosses in the form of a table.

13.7 ANSWERS

Self-Assessment Questions

1. a) i) True vi) True
   ii) False vii) False
   iii) True viii) False
   iv) False ix) True
   v) False x) True

   b) i) gametophyte
   ii) Rhizoids
   iii) haploid
   iv) marine

2. a) i) (b)
   ii) (c)
   iii) (a)

   b) i) Bryopsida
   ii) Anthocerotopsida
   iii) Hepaticopsida
   iv) Hepaticopsida
   v) Hepaticae and Musci
   vi) Anthocerotopsida

Terminal Questions

1. Refer Section 13.3
2. Refer Section 13.3
3. Refer Section 13.2
4. Refer Section 13.1
5. Refer Section 13.4, Table 13.1

13.8 GLOSSARY

Amphithecium : Outer tissue of young sporophyte which in sporangial region gives rise to capsule wall of bryophytes and in *Sphagnum*, *Andreaea* and *Anthoceros* also the sporogenous tissue.

Calyptra : Membranous structure derived at least in part from the modification of archegonium, following fertilization; protects developing embryo.

Capsule : Spherical/elongate structure enclosing the spore-producing tissue.

Columella : Axial sterile tissue in capsule of mosses and hornworts.

Elater : Single elongated cell in sporogonium of liverworts and hence endothecial in origin, with spiral, hygroscopic thickenings, help in dispersal of spores.

Endothecium : Inner tissue of young sporophyte (interior to amphithecium) that gives rise to sporogenous tissue in all bryophytes except *Sphagnum*, *Andreaea* and *Anthoceros*.

Hydroid : Differentiated, highly elongated cells with thick non-perforated walls; occur in stem and some times also in leaf costa of some mosses; help in transport of minerals.

Leptoid : Specialized cells in the central strand of stem, costa of leaf and seta of some mosses; involved in conduction of photosynthetic products.

Protonema : First multicellular, filamentous stage following germination of a spore or an asexual propagule.

Pseudoelators : Uni-/multicellular filamentous structure, produced within sporogonium of *Anthoceros*.

Pyrenoid : Differentiated region of a chloroplast where starch is biosynthesized. Present in chloroplasts of *Anthoceros*.

Rhizoid : Filamentous anchoring organs of bryophytes; uni-/multicellular, could be branched.

Seta : Stalk of sporophyte terminated by the sporogonium in liverworts and mosses.

Spore : Haploid cell produced by reduction division of spore mother cell.

Zygote : First stage of diploid phase in the life of an organism; resulting from the fusion of two gametes. In bryophytes, produced in the venter of an archegonium. Always divide by mitosis in bryophytes.

13.9 FURTHER READING

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UNIT 14

BRYOPHYTES: TYPE STUDIES

Structure

14.1 INTRODUCTION

In the previous unit you have learnt the general characteristics and classification of a group of plants, the bryophytes. If you may recall, some of the striking characteristics of this earliest group of land plants are: heteromorphic alternation of generations; dominant and photosynthetic gamete-producing haploid, gametophytic generation; multicellular sex-organs, the female archegonia and the male antheridia; sex-organs possess sterile cover of cells; haploid egg cell and diploid zygote are retained within the archegonium that is physically and physiologically in contact with the rest of the gametophyte; totally dependent sporophytic generation on the gametophyte for anchor and totally or partially dependent for water, minerals and nourishment (exhibits matrotrophy); certain cells/tissues are modified to help absorb, transport water, mineral and foods, typical vasculature is absent; as adaptations to prevent water-loss, the aerial portions of the plants develop cuticle, and epidermis (sometimes with pores).

You have also been introduced to the classification of bryophytes as liverworts, hornworts and mosses. In this unit, you shall study the range of organization in bryophytes as well as morphological, anatomical and reproductive characteristics of a liverwort - *Marcharita*, and a moss - *Funaria*.

Objectives

After studying this unit, you should be able to:

- ❖ describe the range of organization in the gametophytic plant body of bryophytes;
- ❖ describe the morphology and anatomy of the gametophytes of *Marchanita* and *Funaria*;
- ❖ study the structures of sex organs, antheridia and archegonia and associated gametophytic cells/tissues in *Marchantia* and *Funaria;*
- ❖ study the structure of sporophytes in *Marchantia* and *Funaria*;
- ❖ describe the structure of a gemma cup, a gemma in *Marchantia* and protonema in *Funaria*.

14.2 RANGE OF ORGANISATION

In the previous unit, Section 13.2, you have learnt the general characteristics of bryophytes. You may recall that of the two phases that alternate in the life of a bryophyte, the haploid, gamete producing gametophytic phase is independent and dominant of the two generations. The structure and organization of a gametophyte in bryophytes is most diverse in plant kingdom. Though the structure of sporophytes too plays an important role in taxonomy and classification of bryophytes, we shall restrict ourselves to study the range of organization in gametophytes in this sub-section. On the basis of organizational morphology of the gametophytes, the bryophytes can be segregated into three sub-groups: *thalloid liverworts*; *leafy liverworts,* and *mosses* (Fig. 14.1 a-j).

14.2.1 Thalloid Liverworts

About 50 genera and thousands of species comprising almost 15 per cent of all liverworts are thalloid.

Four distinct forms of thalloid liverworts can be indentified. The characteristics of them are described below.

A) The dorsiventral thallus is very small and delicate, but with a distinct apical cell. They posses simple rhizoids arising out of a central cushion from the ventral surface. The sex organs are protected by involucres. The genus *Sphaerocarpos* and members of order Sphaerocarpales are representatives of this kind.

B) The dorsiventral thallus is deep green and transluscent. Though not with much internal differentiation, yet chlorophyllous cells are restricted to layers nearer the dorsal and ventral superficial cells. The parenchymatous tissue is without any air spaces. The rhizoids, restricted to the ventral surface are uniform and simple. The sex-organs are derived from the apical cell along the mid-rib on dorsal surface. They are uniform, simple and without any involucres around them. Generally antheridia

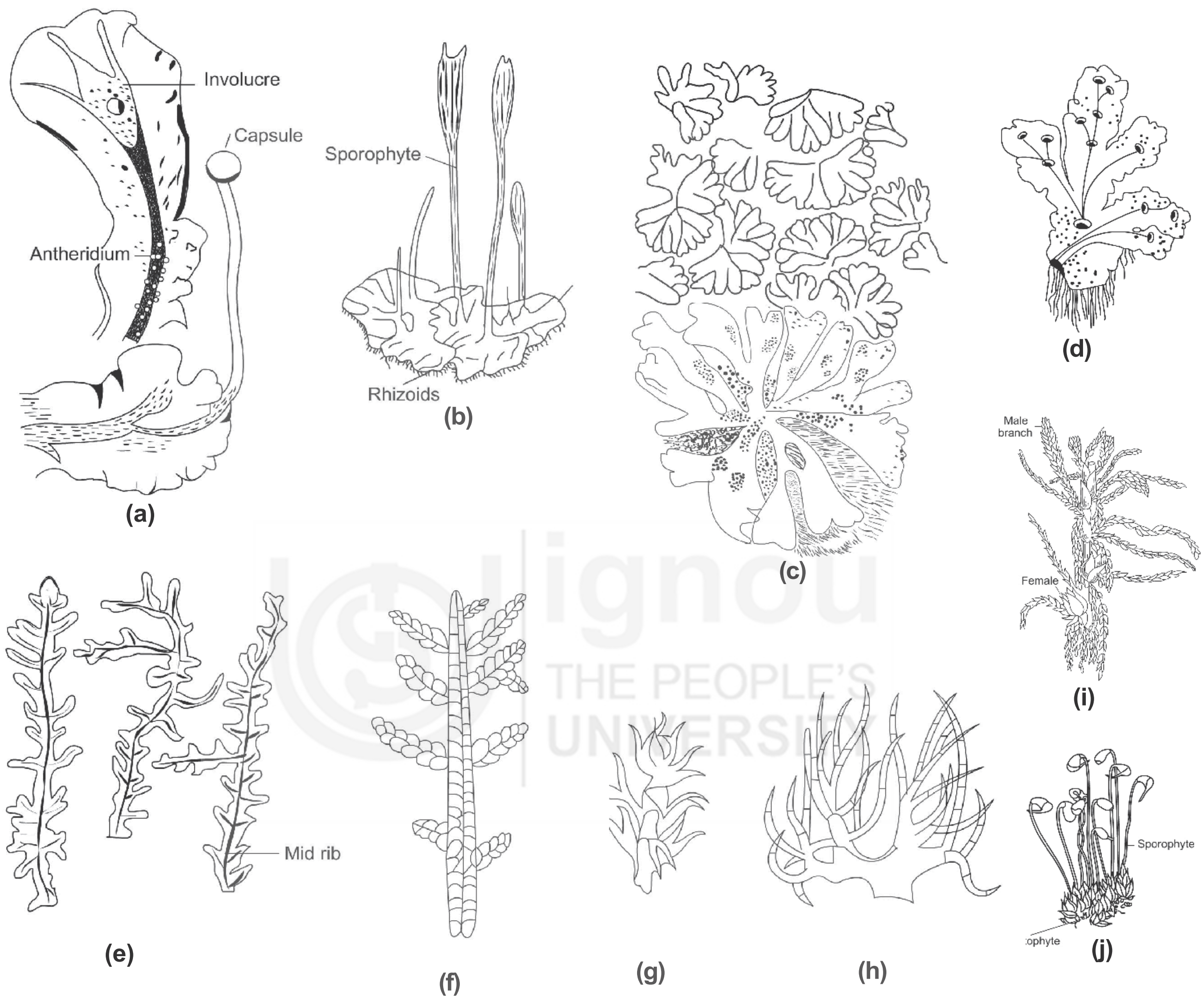

Fig. 14.1 (a - j): Some representative gametophytes of bryophytes. (a - e) Thalloid liverworts; (f - h) Leafy liverworts; (i - j) Mosses: a) *Pellia*; b) *Anthoceros*; c) *Riccia*; d) *Marchantia*; e) *Metzeria*; f) *Porella*; g) *Herberta*; h) *Trichocolea*; i) *Sphangum*; j) *Funaria*. *Source*: (a, c, d, f, i, j) Rashid, 2010; (b) Vashishta, 1994; (e) Santra et al., 1993; (g, h) Watson, 1967.

develop earlier than archegonia in a thallus. The members of order Metzeriales, characterized by the genus *Pellia* exhibit this organization.

C) The dorsiventral thalli are irregularly shaped, grow in rosettes and are of wavy outline. The surface could be crimped. Every lobe of the thallus possesses an apical cell, the starting point of a new thallus growth. Thalli are typically dark green and without gloss. Most of the thalli are with extensive internal cavities on the ventral surface and harbour atmospheric nitrogen fixing, Cyanobacteria, e.g., *Nostoc*. The smooth, simple rhizoids are present on the ventral surface. Only one chloroplast with a pyrenoid per cell is present in the parenchymatous cells. Members of order *Anthocerotales, e.g.*, *Anthoceros* and *Notothylas* possess this kind of thallus. The sex organs in thalli are embedded in the thallus and are endogenous in origin.

D) The dorsiventral thallus is thick, dichotomously branched, and with prominent apical notch with apical initials. The thallus internally is sharply divided into upper photosynthetic zone and lower storage zone. The dorsal surface possesses epidermis and numerous areolae, demarcating air-chambers. Each of them open with a barrel-shaped pore. Numerous chlorophyllous filaments arise from the base of such air-chambers. The ventral surface has a very prominent thick mid-rib. Along mid-rib arise numerous multicellular, dark scales and two kinds of rhizoids: simple and tuberculate. This kind of thallus organization in genera *Marchantia*, *Preissia*, *Conocephalum* along with other members of order Marchantiales, probably represent the climax of thallus evolution in Liverworts.

14.2.2 Leafy Liverworts

About 280 genera and more than 7000 species comprising almost 85 per cent of liverworts are leafy liverworts. They resemble mosses at first glance. They grow by an apical cell which resemble an inverted pyramid. The apical cell has 3-cutting faces and a base. This cell contributes to the axis, ‘stem’ and the laterals, the ‘leaves’. The arrangement of ‘leaves’ is 3-ranked (very rarely arranged radially). All the ‘leaves’ are alike in size. Majority of ‘leaves are 2-lobed and each of the lobe with a growing point established very early in life. Such growth leads to a bi-lobed/cleft ‘leaves’ at maturity. Of the 3 rows of leaves two rows are placed laterally. The third row of ‘leaves’ lying along the mid-ventral line are called under leaves or amphigastria. Amphigastria are smaller in size than the lateral ‘leaves’. These ‘leaves’ could be 3-4 lobed and with 3 to 4 finger-like projections.

The shoot is horizontal and plagiotropic. The rhizoids are produced in large numbers from the side of shoot that is close to the substratum. In species where shoots are erect, rhizoids are sparsely present. Rhizoids are colourless, brownish when old, or occasionally purple and multicellular.

Branching of shoot is very complex and varied. Shoots of this kind exhibit a great deal of variation in gametophytic morphology. Members of order Jungermanniales are typical leafy liverworts. Some prominent genera are: *Herberta*, *Lepidozia* and *Trichocolea*.

14.2.3 Mosses

In mosses a branched filamentous or plate-like protonemal phase precedes upright, erect gametophores with prominent 'leaves'.

The leafy shoot exhibits a great diversity of gross form. The majority of mosses grow by means of a tetrahedral apical cell in the form of an inverted pyramid with 3-cutting faces. The arrangement of 'leaves' on the 'stem' is generally 3-ranked. However, due to growth torsions and consequent displacement, this precise 3-ranked arrangement is disturbed. Branches, if present, arise just below the 'leaves' rather than in their axils.

The 'stem' and the 'leaves' are referred to as cauloid and phylloids respectively. The gametophores may exhibit vertical growth of several centimeres, bearing laterals only in the form of a subterminal crown of branches – providing a 'miniature tree' appearance, the dendroid habit, e.g., in *Clamacium dendroides*. The cauloid cells may bear prominent conducting strands.

In many instances, the leaves surrounding reproductive organs are a little different from vegetative leaves. These are called perichaetial leaves.

The rhizoids are branched, multicellular and non-chlorophyllous.

The genera, *Funaria*, *Bryum*, *Polytrichum*, *Sphagnum*, *Andreaea* exhibit this type of body organization.

SAQ 1

Choose the correct alternatives from the one mentioned in the parantheses:

i) *Sphaerocaros* is an example of (thalloid/leafy) liverwort.

ii) Dorsiventral dichotomous, thalloid gametophytes are observed in (*Anthoceros*/*Marchantia*).

iii) Cyanobacteria, colonies are associated with the thalli of (*Pellia*/*Anthoceros*).

iv) Protonemal phase is characteristically present in a (thalloid liverwort/ moss).

SAQ 2

Which of the following statements are true?

i) *Sphaerocarpos* thallus is highly differentiated.

ii) Rosette habit is characteristic of *Pellia* gametophytes.

iii) Amphigastria are characteristically present in Jungermanniales.

iv) Habit of *Polytrichum* gametophyte is thalloid.

14.3 *Marchantia*

The family Marchantiaceae, to which *Marchantia* belongs, includes about 23 genera the approximately 200 species. The special features of this family is that in all the genera the gametophyte bears archegonia on vertical stalked receptacles called archegoniophore (carpocephala). In *Marchantia* antheridia are also produced in stalked receptacles known as antheridiophores. The type-genus *Marchantia* with about 65 species of which *Marchantia polymorpha* is the most widely distributed. *Marchantia* usually grows in cool moist places along with mosses and in areas of burnt grounds. The thalli are deep green.

Marchantia

Division – Bryophyta

Class – Hepaticopsida

Order – Marchantiales

Family – Marchantiaceae

14.3.1 Morphology

Its gametophyte is a flat, prostrate, dorsiventral and dichotomously branched thallus (Fig. 14.2 a). There is a prominent midrib which is marked on the dorsal surface by a shallow groove and on the ventral surface by a low ridge covered with rhizoids (Fig. 14.2 b). Along the midrib there are a number of cup-like structures with frilled margins. These are called gemma cups (Fig. 14.2 a, c) which contain numerous vegetative reproductives bodies called gemmae (sing. gemma). In mature thalli the antheridiophores and the archegoniophores, which bear antheridia and archegonia (Fig. 14.2 d and e) respectively, are present at the growing apices of certain branches. *Marchantia* is dioecius. The apex of each branch is notched and a growing point is situated in it. On the dorsal surface of thallus marked hexagonal areas are visible to the naked eye (Fig. 14.2 c). If we examine with a hand lens we can see a pore at the centre of each hexagon.

The thallus of *Marchantia* is anchored to the surface by rhizoids which are smooth walled as well as of tuberculate type (Fig. 14.2 f and g). Scales are also present on the ventral surface and they are arranged on both sides of the midrib (Fig. 14.2 b, h). The detailed structure of a scale is shown in Fig. 14.2 h.

14.3.2 Anatomy

The internal structure of the thallus is shown in Fig. 14.3 a and b. When examined under the compound microscope, you will note a high degree of internal differentiation of tissues. The thallus is divided into two distinct zones :

a) The upper photosynthetic zone corresponding to the dorsal surface, and

b) The lower storage zone corresponding to the ventral surface.

The upper zone is covered by a single layer of thin walled cells which form the upper epidermis. These cells contain a few chloroplasts. The layer is

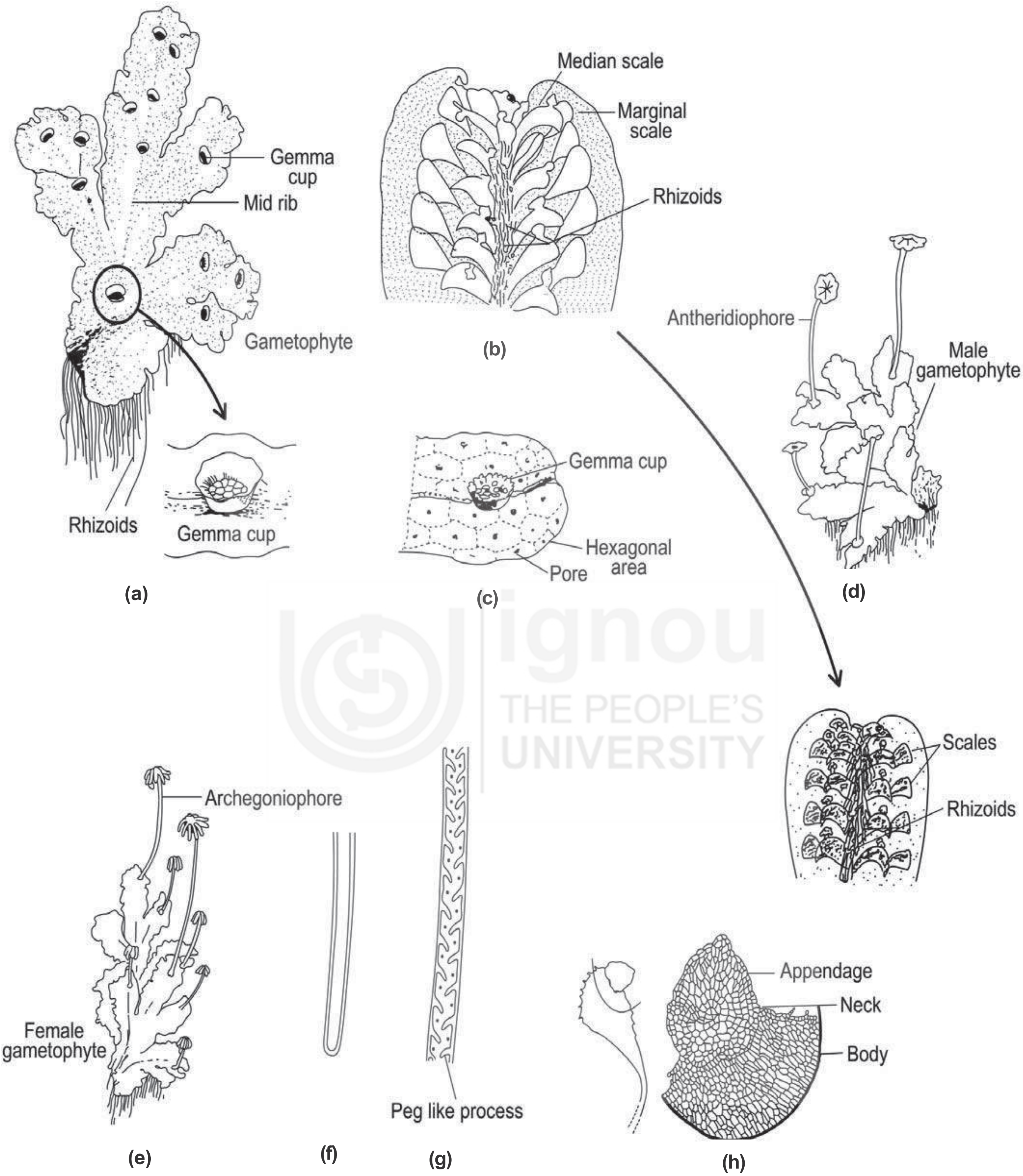

Fig. 14.2 (a-h): **Morphology of *Marchantia polymorpha*: a) Vegetative thallus (dorsal surface) with gemma cups; b) Ventral surface of the vegetative thallus; c) A portion of 'a' enlarged. Note the hexagonal markings with a pore in the centre of each on the surface of the thallus; d) Thallus with antheridiophores; e) Thallus with archegoniophores; f) Smooth walled rhizoids; g) Tuberculate rhizoids; and h) An appendaged scale enlarged.**
***Source*: (a, b, d, e, h) Rashid, 2010; and (g) Vashishta, 1994.**

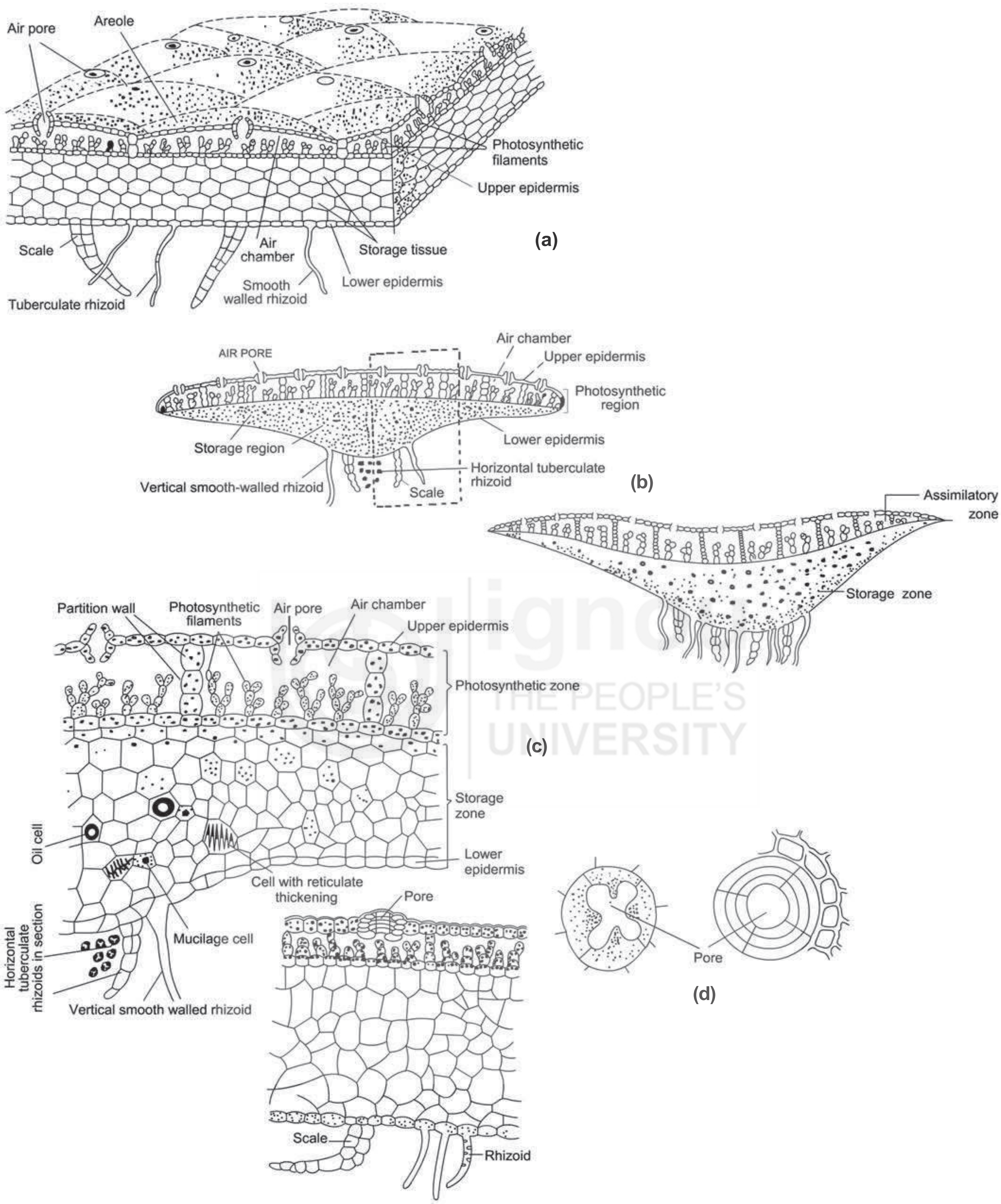

Fig. 14.3 (a-d): Internal structure of *Marchantia*: a) A part of thallus in three-dimensional view; b) Vertical transverse section of a thallus (diagrammatic); c) The marked portion in 'b' enlarged to show the detailed structure of the thallus. Note the air pore; d) An air pore seen from below (left-hand figure), it is surrounded by papillose cells, air pore as seen from top (right hand figure).
***Source*: (a-d) Vashishta, 1994.**

interrupted by many barrel shaped pores (Fig. 14.3 a-c). Below the upper epidermis there are a number of air chambers in a single horizontal layer.

These air chambers are separated from one another by single layered partitions. The visible hexagonal markings seen on the dorsal surface are actually the outlines of these air chambers. Within each air chambers there are usually simple or branched photosynthetic filaments which arise from the base of the chamber (Fig. 14.3 a,b).

The ventral side of gametophyte is achlorophyllous, parenchymatous and several celled in thickness (Fig. 14.3 b). A few cells of this region contain a large oil body. Some cells are filled with mucilage. The lowermost layer form a well defined lower epidermis. Two or more transverse rows of multicellular scales arise from it. The scales protect the ventral surface and the growing regions. The smooth-walled and tuberculate rhizoids arise from the ventral surface between the scales.

14.3.3 Reproduction

In this section you will learn about the reproduction in *Marchantia*. As you know it also belongs to Class Hepaticopsida. Like other thalloid liverworts *Marchantia* also reproduces by vegetative as well as sexual methods. In the following account you will learn about both the methods in detail.

Vegetative Methods

In *Marchantia* the progressive death and decay of the thallus near the dichotomy causes separation of the branches, and each branch independently forms a new thallus. In some species of *Marchantia* adventitious branches arise from the ventral surface of thallus. They also arise though rarely from the archegoniophores. These branches get detached from the parent tissue and form new thalli.

The most common method of vegetative reproduction in *Marchantia* is by characteristic asexual bodies known as gemmae (sing. gemma) (see Fig. 14.4 a-e). The gemmae are produced in large numbers in gemma cups which are present on the dorsal surface of the thallus and have colourless, fringed margins (Fig. 14.4 a).

The gemmae arise from epidermal cells on the floor of gemma cups (Fig. 14.4 b, c). An epidermal cell becomes papillate and functions as gemma initial.

At maturity each gemma is a multicellular, biconvex, bilaterally symmetrical, disc-like structure which is vertically inserted in the gemma cup with one-celled hyaline stalk (Fig. 14.4 c). Each gemma has two growing points, one in each of the two lateral shallow notches (Fig. 14.4 b, e). Most of the cells of the gemma contain chloroplasts (Fig. 14.4 d, e), but the marginal cells contain oil bodies instead of chloroplasts. Many colourless densely protoplasmic cells are present on both flattened faces and they are slightly larger than neighbouring cells. These cells are known as rhizoidal cells as they form rhizoids on germination (Fig. 14.4 d, e). Some club-shaped hairs present on the floor of the gemma cup secrete mucilage. This mucilage swells on absorbing water

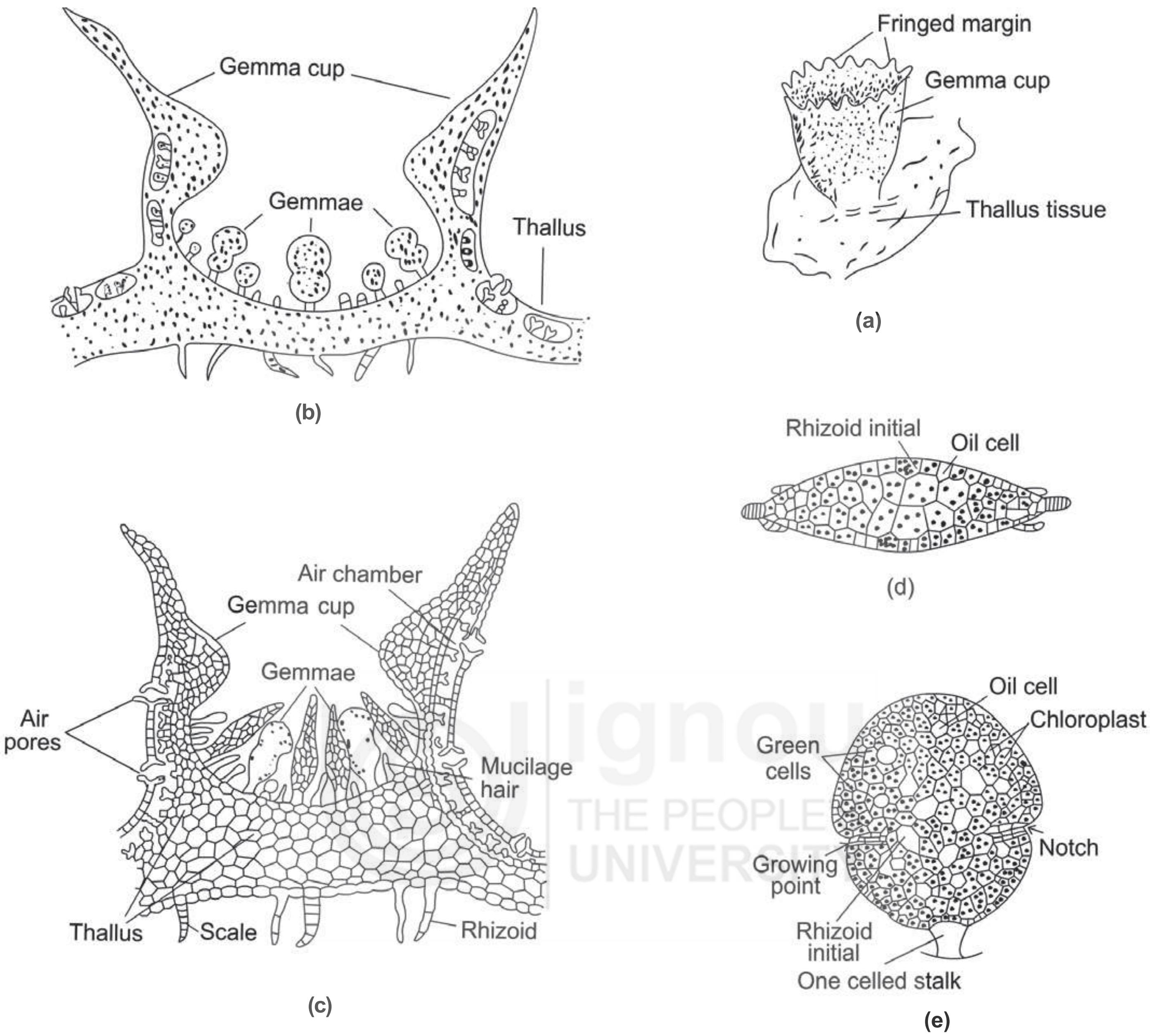

Fig. 14.4 (a-e): Vegetative reproduction in *Marchantia* : a) A gemma cup in side view with a portion of thallus showing many gemmae; b) Outline diagram of vertical section (v.s.) of a gemma cup showing many gemmae; c) V.S. thallus through a gemma showing cellular details; d) Transverse section (t.s.) of a gemma; e) Detailed structure of a gemma.
***Source*: (a, c-e) Vashishta, 1994.**

and causes the gemmae to break away easily from their stalks. The detached gemmae are finally washed away by rain drops. Gemmae are also detached by the pressure exerted by the growth of new gemmae.

When a gemma falls on the soil and conditions are favourable for its germination, the rhizoidal cells in contact with soil form rhizoids. The apical cells in the two marginal notches become active simultaneously and form two young thalli growing in opposite directions. After sometime, the central part of the gemma disintergrates, resulting in the separation of two new thalli. They produce more rhizoids from the lower surface and grow into adult thalli.

Sexual Reproduction

In *Marchantia* antheridia and archegonia are borne on special erect, branches of the thallus called antheridiophores and archegoniophores, respectively (Fig. 14.2 d and e). As *Marchantia* is dioecious the antheridiophores and archegoniophores are borne on separate thalli. These erect sexual branches are continuation of the thallus and grow vertically upwards through the notches at the end of the prostrate branch.

An antheridiophore consists of a stalk with an eight-lobed disc at its apex (Fig. 14.2 d). In fact, it represents a much modified branch system in which each lobe is comparable to the apex of a branch. This disc is formed as a result of repeated localized forkings of the young antheridial branch. A transverse section of antheridiophore shows the dorsiventral symmetry, typical of the thallus (Fig. 14.5 a). The side corresponding to the ventral surface of the thallus usually has two deep furrows containing rhizoids and scales. The middle of the terminal disc has anatomy similar to that of the thallus, with an upper epidermis interrupted by barrel-shaped pores that open into air chambers containing branched chlorophyllous filaments. In addition to the air chambers, there are many flask-shaped cavities which also have openings on the upper surfaces. Antheridia are produced inside these cavities. Each growing point of the disc produces a number of antheridia in acropetalous manner (Fig. 14.5 b). The development of antheridia is shown in Fig. 14.6 a.

A mature antheridium consists of a short stalk and a globular body. The jacket of the body is formed by a single layer of thin-walled cells and it encloses a large number of androcytes (Figs. 14.5 c and 14.6 a viii).

When water enters into the slightly concave disc of antheridiophore it moves through the narrow canal into the antheridial cavity. Now, some cells of the upper portion of jacket of the antheridium disintegrate. The androcytes come out from the dehisced antheridium (Fig. 14.6 c) and form biflagellated antherozoids (Fig. 14.6 b), its development is diagrammatically depicted in Fig. 14.6 b. An antheridium at the time of dehiscence is shown in Fig. 14.6 c.

The position of archegoniophores on the thallus is similar to that of antheridiophores. An archegoniophore also consists of stalk and lobed disc (Fig. 14.2 e). The stalk has two longitudinal furrows running along the length as seen in transverse section (Fig. 14.7 a). Internal structure of the disc is similar to that of the thallus.

Like antheridia the archegonia are produced in acropetal succession from cells cut off by apical cells on the dorsal face of each lobe. Depending on the species eight or more groups of archegonia develop on the upper surface of the disc corresponding to growing points of the disc (Fig. 14.7 b). Initially, when the stalk of the archegoniophore is very short, the archegonial necks are directed upwards and fertilization occurs at this stage (Fig. 14.7 b). After fertilization, the stalk of archegoniophore elongates and the central part of the disc shows considerable growth due to which the marginal apical region of the disc alongwith the groups of archegonia is pushed over to the lower surface of the disc. Finally, the growing apices become incurved, and lie close to the stalk of archegoniophore (Fig. 14.7 b iv). Now the archegonial necks are

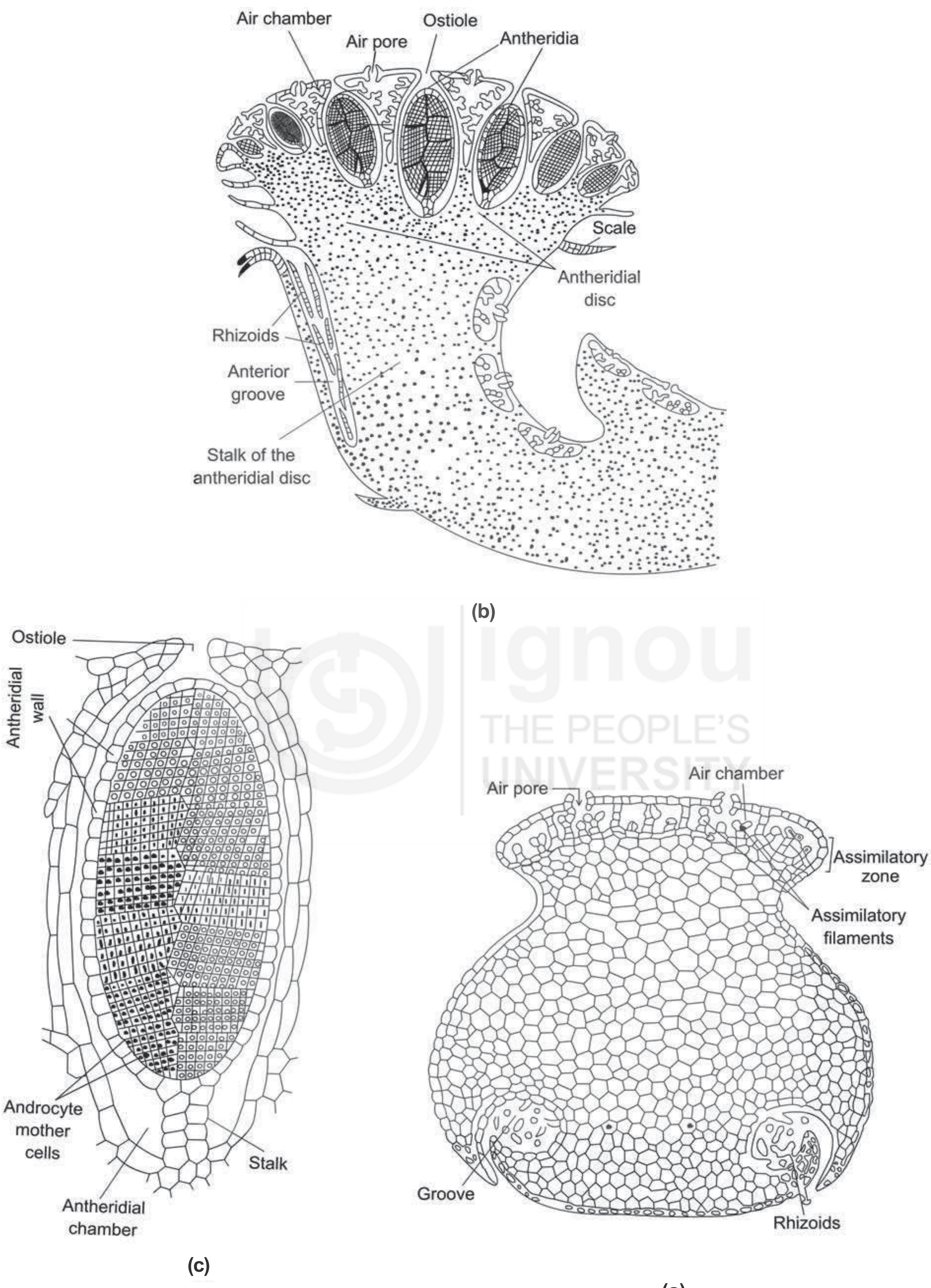

Fig. 14.5 (a-c) : *Marchantia* : a) T.S. antheridiophore stalk; b) Longitudinal section through a developing antheridiophore; c) A portion of 'b' enlarged showing a mature antheridium in the antheridial chamber.
***Source*: (a - c) Vashishta, 1994.**

(a)

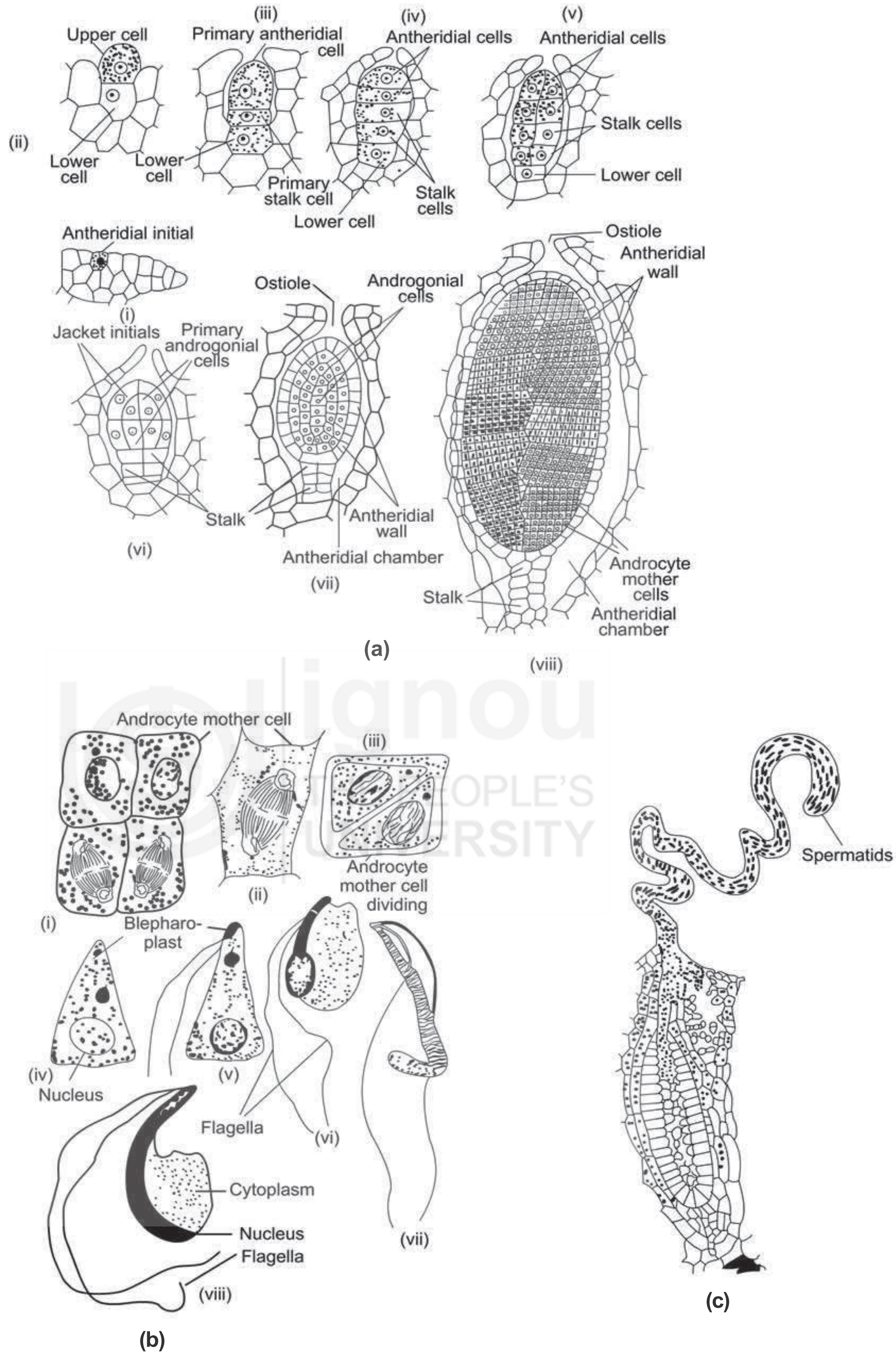

Fig. 14.6 (a-c): ***Marchantia*****: a) i-viii Stages in the development of antheridium. viii A mature antheridium; b) i-viii Development of sperms from androcyte mother cell. i-iii Diagonal division in androcyte mother cell, iv-vii stages of spermatogenesis, viii a biflagellate sperm; c) An antheridium at the time of dehiscence.**
Source**: (a, b) Vashishta, 1994, (c) Rashid, 2010.**

directed downwards, and the youngest archegonium is near the stalk and the oldest towards the periphery of the disc (Fig. 14.7 b,c). Subsequently, each group, containing 12 to 15 archegonia, is enclosed by a two-lipped pendent involucral sheath. This involucral sheath is known as perichaetium and it hangs down vertically from the lower surface of the lobe of the disc (Fig. 14.7 c). In many species green cylindrical processes arise from the periphery of the disc, between the groups of archegonia. These processes are known as rays (also see Fig. 14.7 c). In *Marchantia polymorpha* usually nine rays are present.

At maturity the archegoniophore consists of a long stalk with terminal nine-rayed disc. Archegonia are arranged on the lower surface of each lobe in radial rows and are located between the rays. Each group of archegonia is protected by a perichaetium. As mentioned above, the archegonia are in an inverted position.

The developmental stages of archegonia are shown in Fig. 14.8. A mature archegonium is a flask-shaped structure with short stalk, swollen venter and a long neck (Fig. 14.7 d, 14.8 xii). Inside the single layered venter wall is a large egg and a ventral canal cell. The neck is tubular and has six or more vertical rows of neck canal cells.

The antherozoids are transferred from the upper surface of the discs of the longer-stalked antheridiophores to the short-stalked archegoniophore by water. They swim to the archegonium and enter through the neck. One of the antherozoids fertilises the egg, and a zygote is formed (Fig. 14.9 a). Simultaneously, the stalk of archegoniophore elongates and the wall of the venter divides periclinally forming two to three-layered calyptras (Figs. 14.9 c and 14.10 f). Calyptra surrounds the developing sporogonium. An additional collar-like cylindrical outgrowth arises from the base of the venter. This is known as pseudoperianth or perigynium (Fig. 14.7 c).

The zygote divides transversely into an upper epibasal and a lower hypobasal cell. The second wall is generally formed at right angles to the first and four equal cells are formed. It is followed by one more vertical division which is at right angles to the first. At this stage embryo is composed of eight equal cells octant stage (Fig. 14.9 d). In *Marchantia polymorpha* the epibasal quadrant forms the capsule and the hypobasal quadrant forms the foot and seta.

O' Hanlon Sr. M.E. (1926) estimated that a plant of *Marchantia polymorpha* accounts for approx. 7,000,000 spore formation (24 capsules, each with 3,00,000 spores).

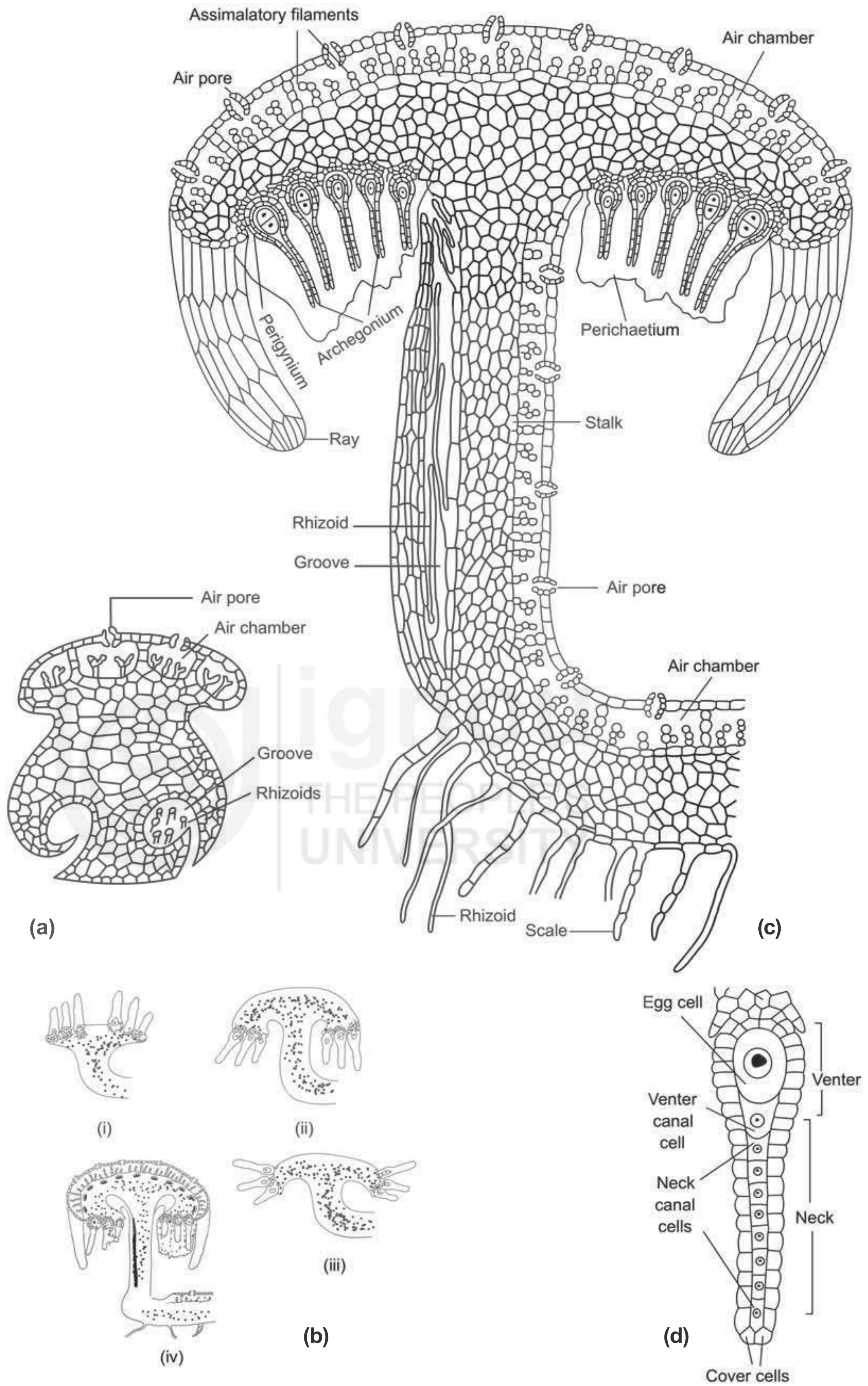

Fig. 14.7 (a-d): ***Marchantia*** **: a) A stalk of archegoniophore; b) Diagrammatic representation of l.s. archegoniophore showing various stages of development (i-iii). Inversion is shown in iv; c) L.s. archegoniophore and a portion of thallus showing structural details; d) An archegonium.**
Source**: (b-d) Vashishta, 1994.**

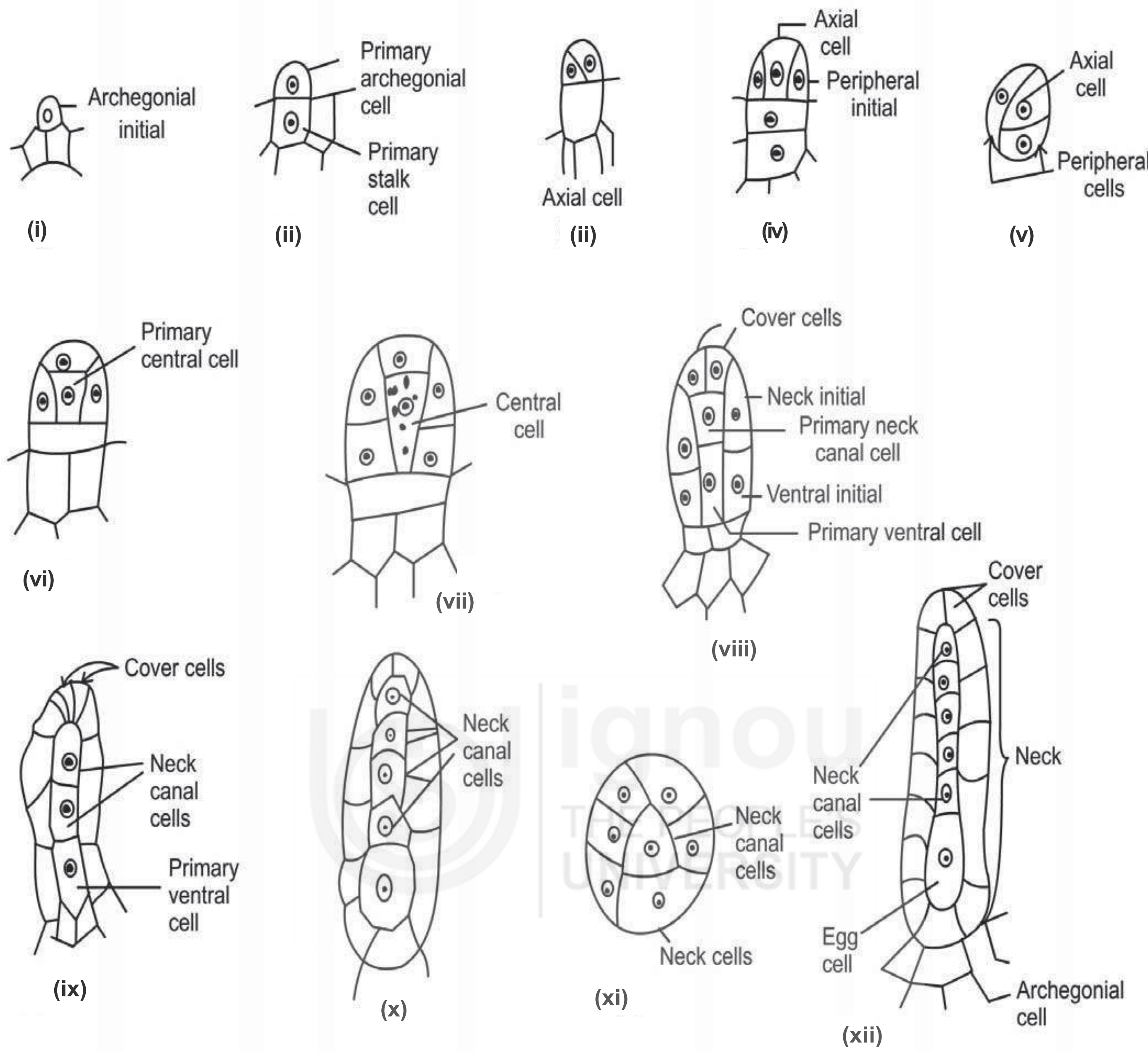

Fig. 14.8 (i-xii): ***Marchantia*. Different stages of development of archegonium. Figs. v-xi show transverse/longitudinal sections of developing archegonia. Fig. xii shows a mature archegonium.**
***Source*: Vashishta, 1994.**

Periclinal divisions in the upper capsular region of the developing sporophyte result in the formation of the outer amphithecium and the inner endothecium. The amphithecium forms the jacket of the capsule. The endothecium gives rise to the archesporium, which by repeated divisions develops into a massive sporogenous tissue. Nearly half of the sporogenous cells divide transversely a number of times to form vertical rows of more or less cubical spore mother cells. Rest of the sporogenous cells become long, have tapering ends and develop two spiral thickenings in their walls. These spindle-shaped cells are known as elaters (14.11 a).

A mature sporogonium of *Marchantia* is differentiated into foot, seta and capsule (Fig. 14.11 a). The foot is bulbous or spreading structure directed towards the base of the archegonium. It absorbs water and nutrients from the

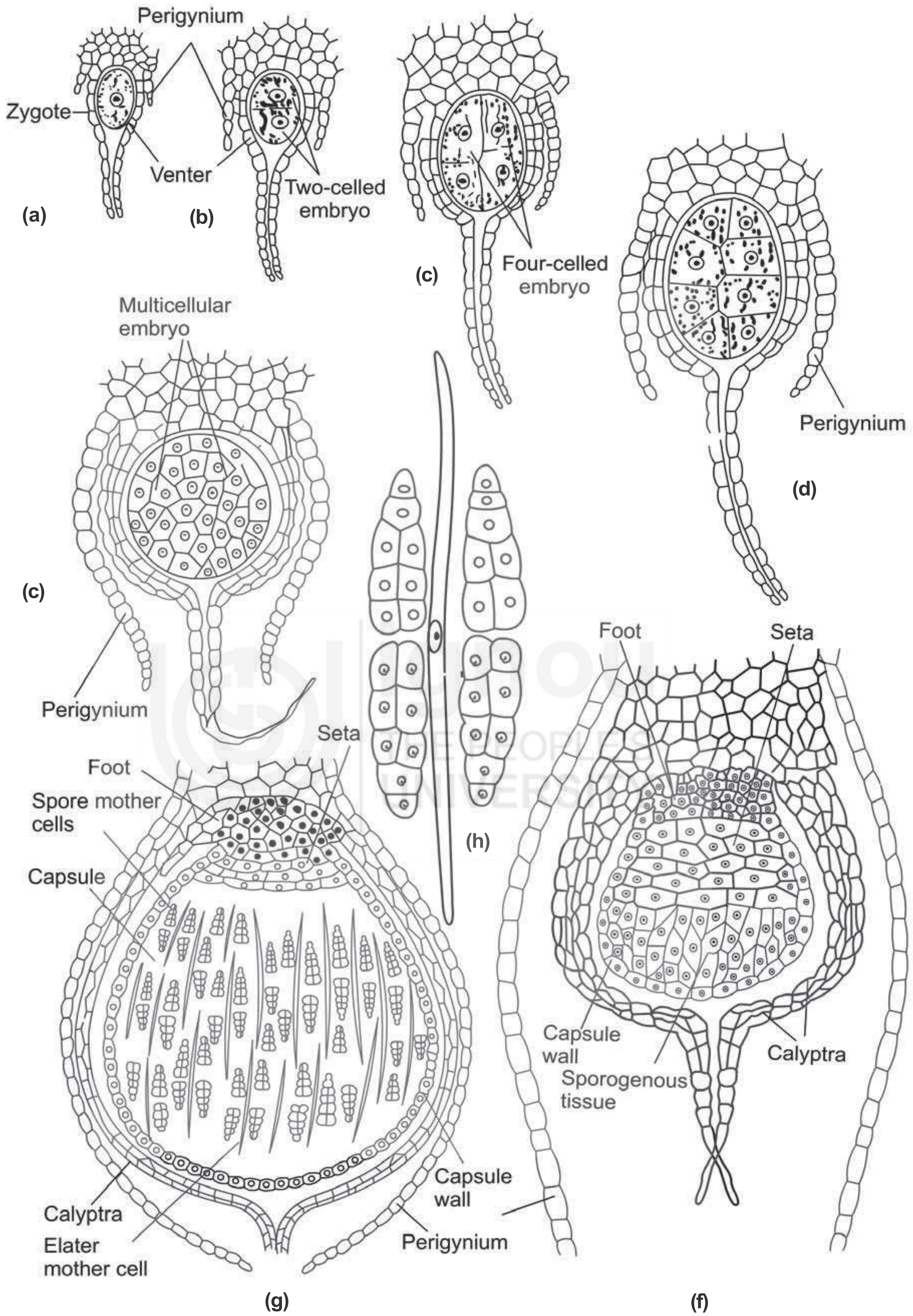

Fig. 14.9 (a - h) : *Marchantia*. Different stages of development of sporophyte : a-e) zygote in the venter; f) Differentiation of sporophyte into foot, seta and capsule. g) Capsule with spore mother cells and elater mother cells; h) Enlarged view of spore mother cells and elater mother cell. *Source*: (a - h) Vashishta, 1994.

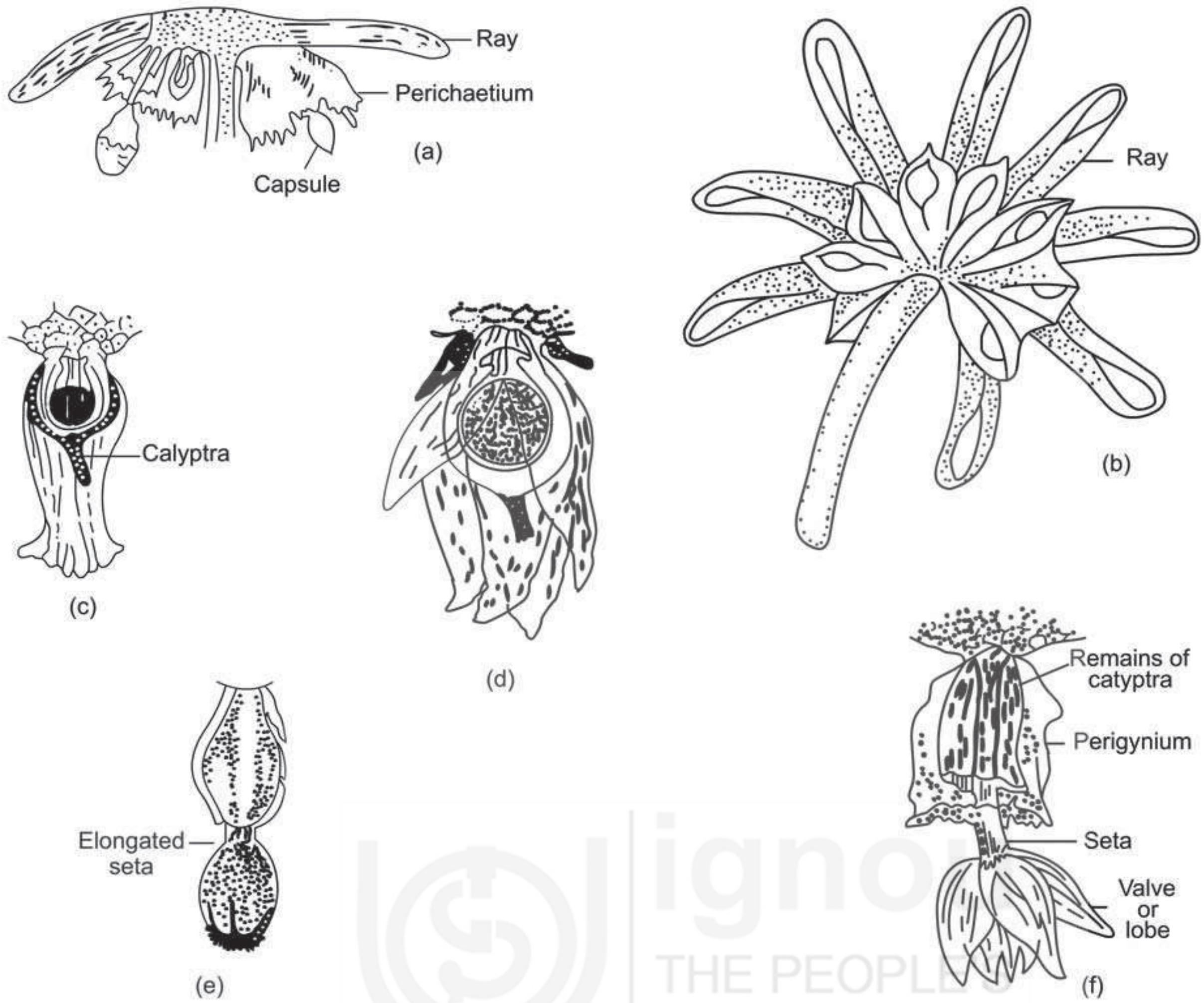

Fig. 14.10 (a - f) : ***Marchantia*. Stages of development of sporophyte : a) Archegonial disc in side view; b) Under surface of archegonial disc; c - f) Stages of developing sporophyte and its protective coverings, c, d) Early stages; e) Elongated seta; f) Capsule at dehiscence stage.**
***Source*: (a - f) Rashid, 2010.**

surrounding tissue of the gametophyte for the developing sporophyte. The seta is short and thick, and it connects the foot and capsule. The capsule is almost spherical. Its wall is composed of a single layer of cells with ring-like thickened bands (Fig. 14.11 e). Inside the capsule are spores and elaters (Fig. 14.11 a, e). The elaters are hygroscopic. They coil and uncoil with changes in the humidity of atmosphere. By these movements elaters help in separation and dispersal of spores.

After maturation of spores the seta elongates considerably. Consequently, capsule breaks through the protective coverings (calyptra, pseudoperianth and perichaetium). It hangs down from the underside of the disc of the archegoniophore (Fig. 14.9 & 14.10). After exposure to the outer atmosphere the wall of capsule splits longitudinally from apex to the middle into a number of lobes. These lobes are reflexed, exposing spores and elaters to outer atmosphere. Spores are finally dispersed by wind.

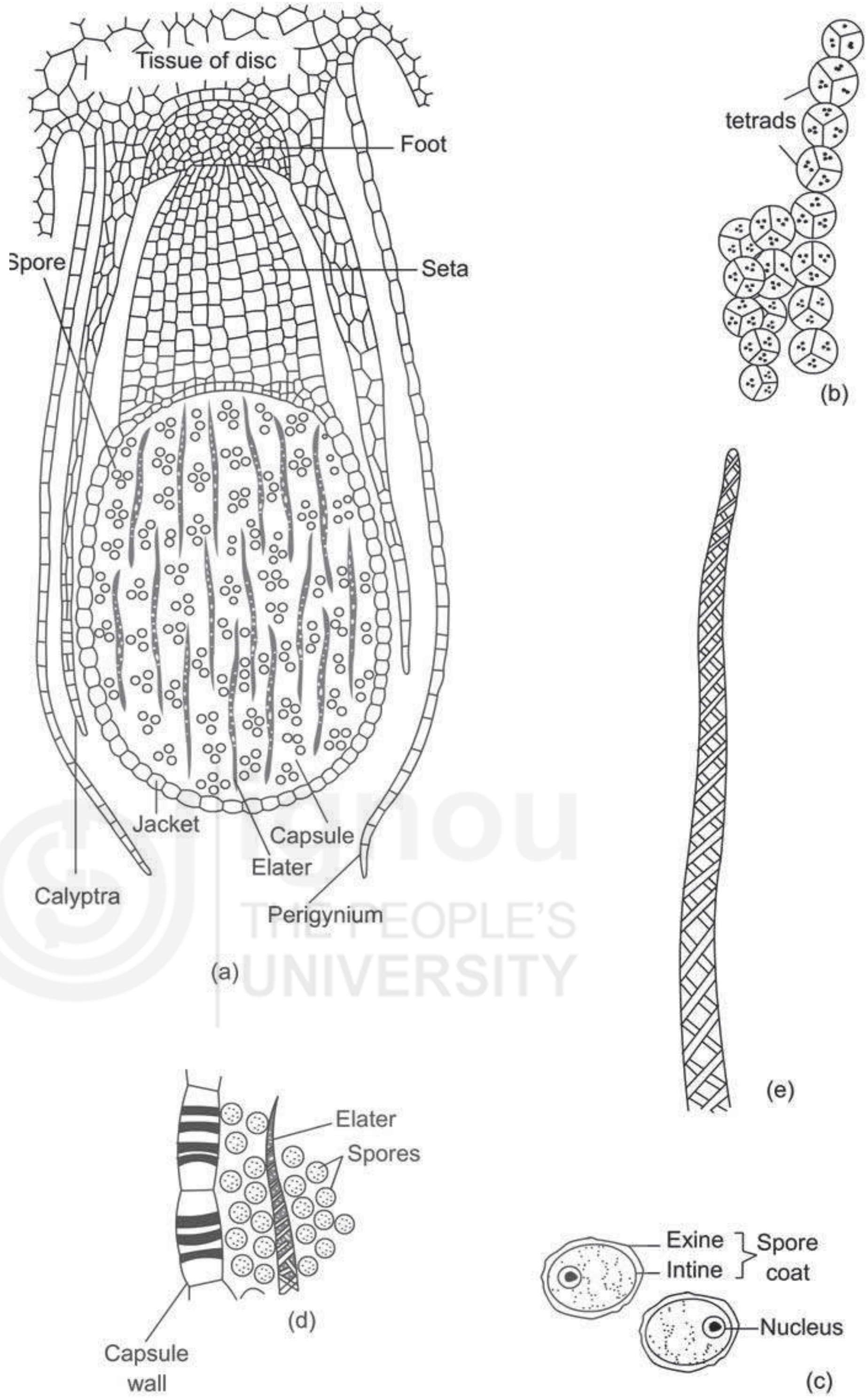

Fig. 14.11 (a - e) : *Marchantia* : a) L.s. mature sporophyte; b) Spores in tetrads; c) Enlarged view of spores; d) A portion of the capsule enlarged. Note ring-like thickenings on the cells of the capsule wall, spores interspersed with elaters; e) A portion of elater enlaged.
***Source*: (a, c - e) Vashistha, 1994, and (b) Rashid, 2010.**

A spore germinates under favourable conditions (Fig. 14.12). The exospore ruptures, and the endospore comes out in the form of germ tube which divides by transverse divisions forming a short filament. After some time the terminal cell begins to function as an apical cell and cuts off segments alternately to the right and left. Finally, the apical cell is replaced by a row of cells and a thallus is formed.

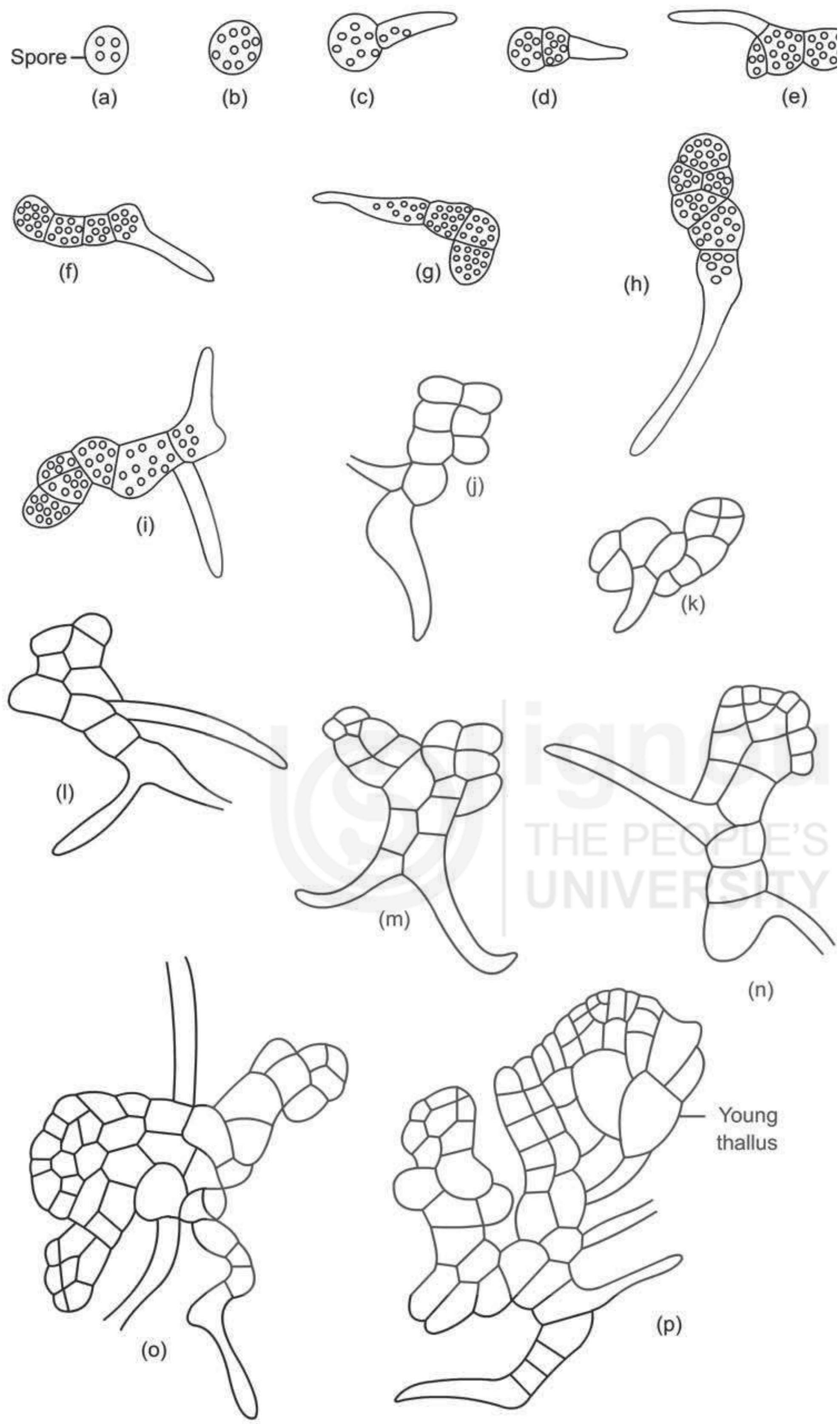

Fig. 14.12 (a - p): ***Marchantia*****. Stages in the germination of spores forming a young thallus.**
Source**: (a - p) Vashishta, 1994.**

To consolidate your understanding about the reproduction in *Marchantia*, refer to Figs 14.13 and 14.14.

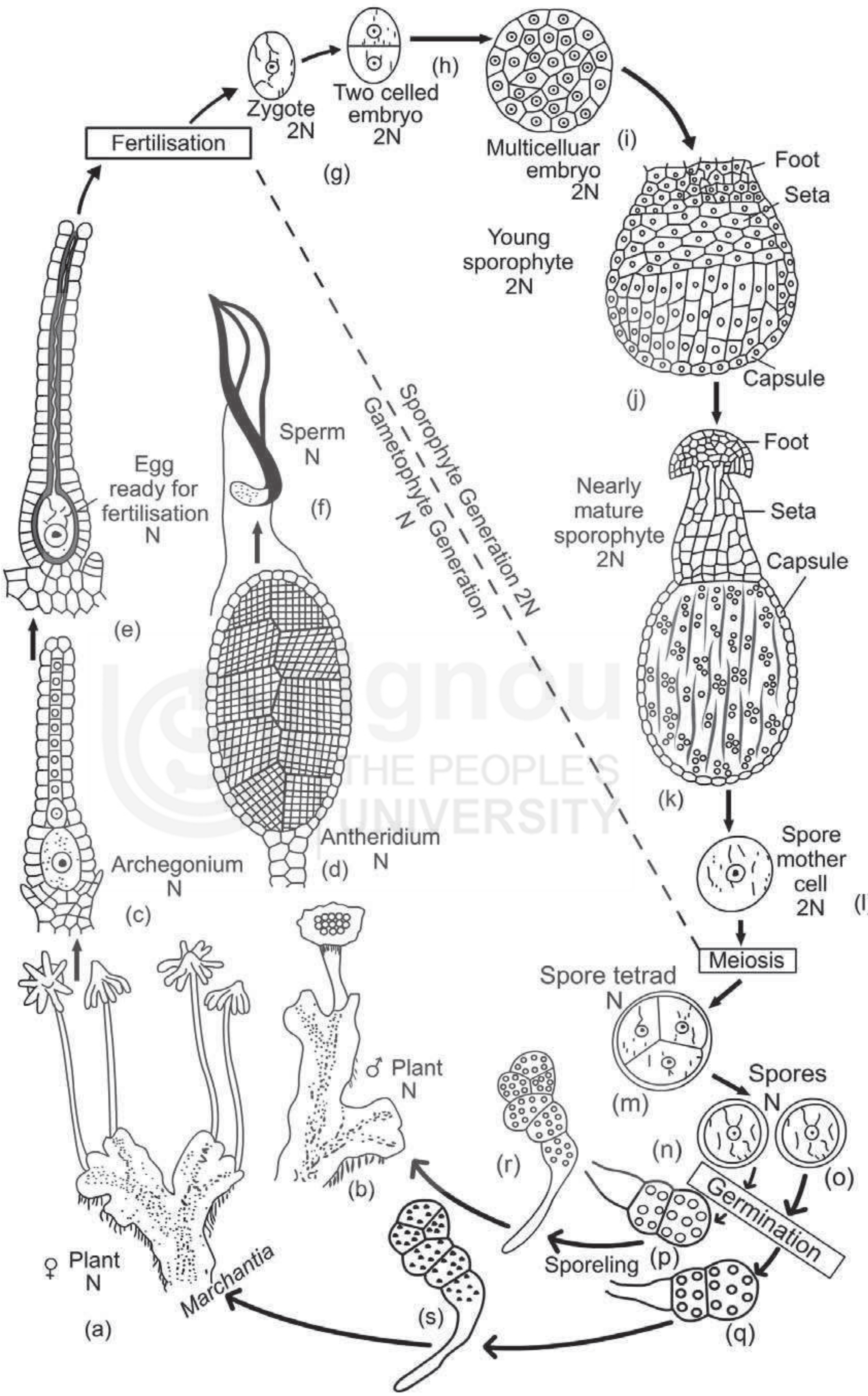

Fig. 14.13 : ***Marchantia*. Sexual life cycle (diagrammatic).**
***Source*: Vashishta, 1994.**

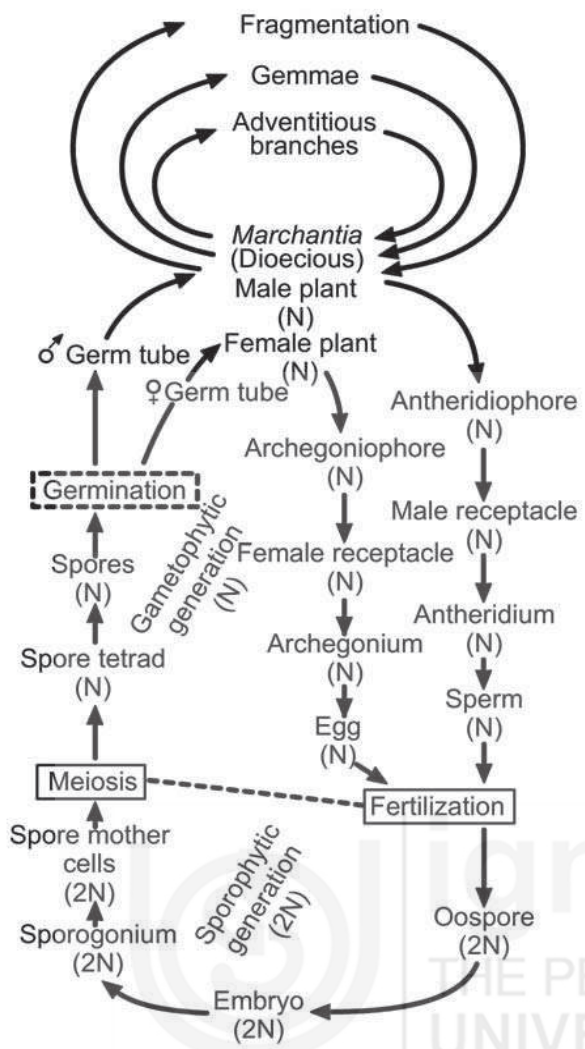

Fig. 14.14: *Marchantia*. Word diagram of various forms of reproduction.
***Source*: Vashishta, 1994.**

SAQ 3

In the following statements about *Marchantia* fill in the blank spaces with appropriate words.

i) Marchantiaceae is characterised by the presence of ………………. female receptacles.

ii) The visible ………………. markings on the dorsal surface of the thallus are actually the outlines of ………………. below.

iii) ………………. filaments are at the base of each air chamber.

iv) A few cells on the ventral surface of the thallus are filled with ………………. or contain ………………. .

v) *Marchantia* reproduces asexually by the formation of specialised discoid, bilaterally, symmetrical bodies known as ……………….. .

vi) When antheridia and archegonia are borne on different thalli, the condition is called ……………….

vii) The sex organs are borne on stalked structures called ……………….

viii) Archegoniophores represent modified ……………… systems.

ix) Antheridia are produced in antheridial chambers present on the ……………. surface of disc of antheridiophore.

x) In mature archegoniophores, archegonial necks are directed……………. .

xi) The archegonial neck is composed of ……………… neck cells.

xii) The mature capsule contains spores and ……………… .

Funaria
Division - Bryophyta
Class - Bryopsida
Order - Funariales
Family - Funariaceae

14.4 *FUNARIA*

Funaria is a very common moss. It is very widely distributed throughout the world. One species, *Funaria hygrometrica* is cosmopolitan and is the best known of the mosses.

14.4.1 Morphology

The most conspicuous form of the moss plant is the adult gametophyte (Fig. 14.15 a - h). This consists of a main erect axis bearing leaves which are arranged spirally (Fig. 14.15 a). This adult gametophyte is called gametophore. It is small, about 1-3 cm high. The leaves do not have a stalk but show a distinct midrib. The gametophore is attached to the substratum by means of rhizoids which are multicellular, branched and have oblique septae (Fig. 14.15 d). The gametophyte bears sporophyte which has foot, seta and capsule (sporogonium).

The gametophore develops from a filamentous, green short-lived protonema (Fig. 14.21 f). The protonema produces buds at certain stage of development, which initiates the development of upright leafy green axis the gametophore.

14.4.2 Anatomy

Look at the t.s. of a mature stem in Fig. 14.15 g, h. It can be distinguished into three zones: the innermost central cylinder, the middle cortex and the outer epidermis. Cells of the central cylinder are vertically elongated, and smaller in diameter than those of the cortex. A fully mature cortex usually consists of thin walled cells near the central cylinder and thick walled cells at the exterior. The cortex contains ‘leaf traces’ running diagonally from the leaves to the central cylinder. The cortical cells in the younger region of the stem usually contain chloroplasts.

A mature leaf has a well developed midrib. The midrib is several cells in thickness, while the ‘wings’ on its either sides are formed by a single layer of cells (Fig. 14.15 e, f). The cells of leaves are elongated, thin-walled, rectangular or rhomboidal and contain chloroplasts. The centre of the midrib is occupied by a small central group of narrow cells which form a single type of conducting strand. The stomata are absent.

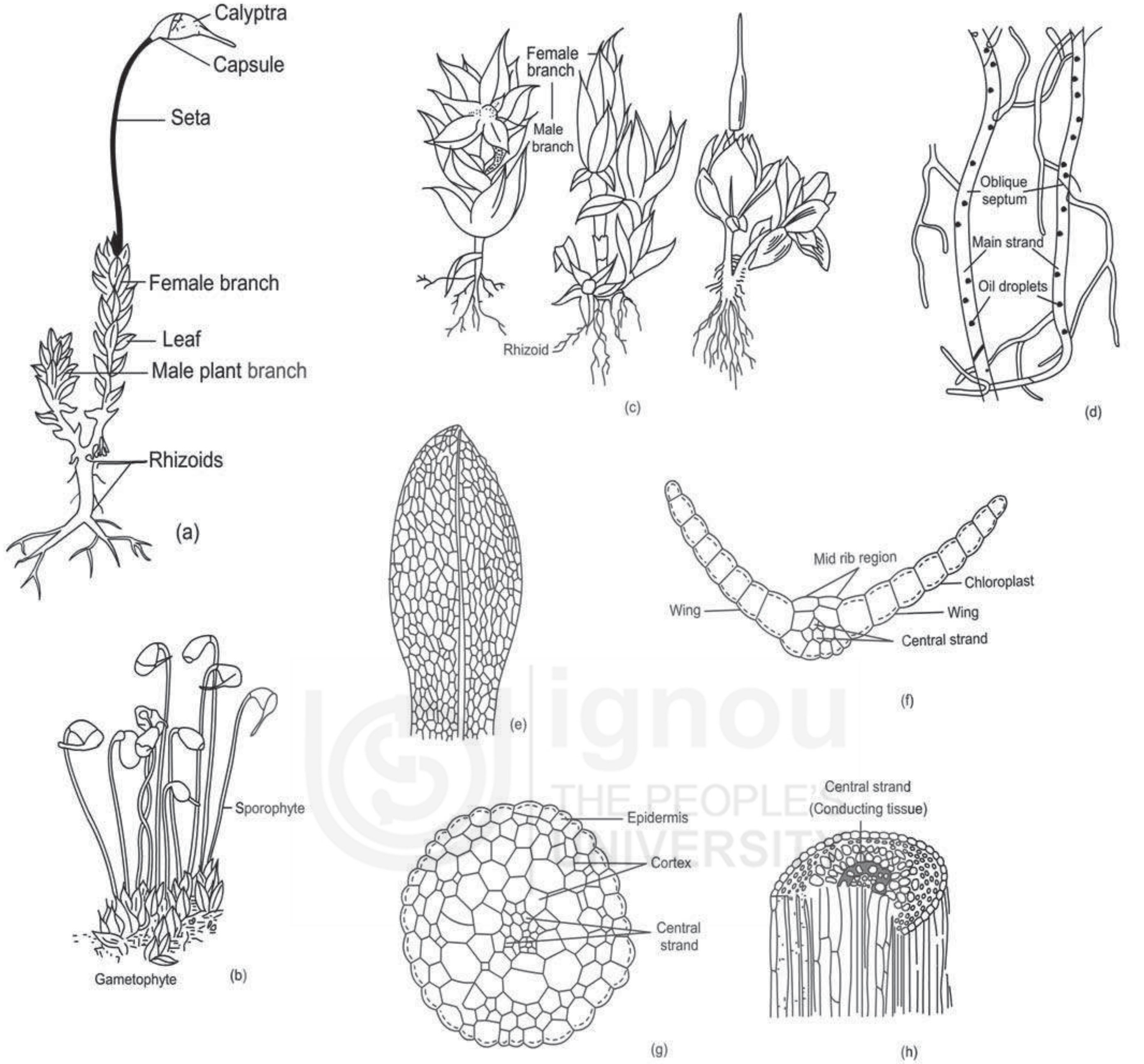

Fig. 14.15 (a- h): ***Funaria hygrometrica*** **: a) A mature gametophore with male and female branches and also a mature sporophyte (sporogonium); b) The plants grow in patches. Note gametopyhte bearing sporophytes; c) An antheridial head (left hand figure), archegonial head (middle figure) and an archegonial branch bearing a developing sporophyte that is enclosed by calyptras (right-hand figure); d) Multi-celled, branched rhizoid; e) Whole mount of a leaf. Note its wing, midrib and leaf base; f) Cross section of a leaf; g) Cross section of a stem; h) Diagrammatic three-dimensional representation of stem. Note the central strand that is composed of hydroids and leptoid-like cells around it. Source: (b, c, e, h) Rashid, 2010; (a, d, f, g) Vashishta, 1994.**

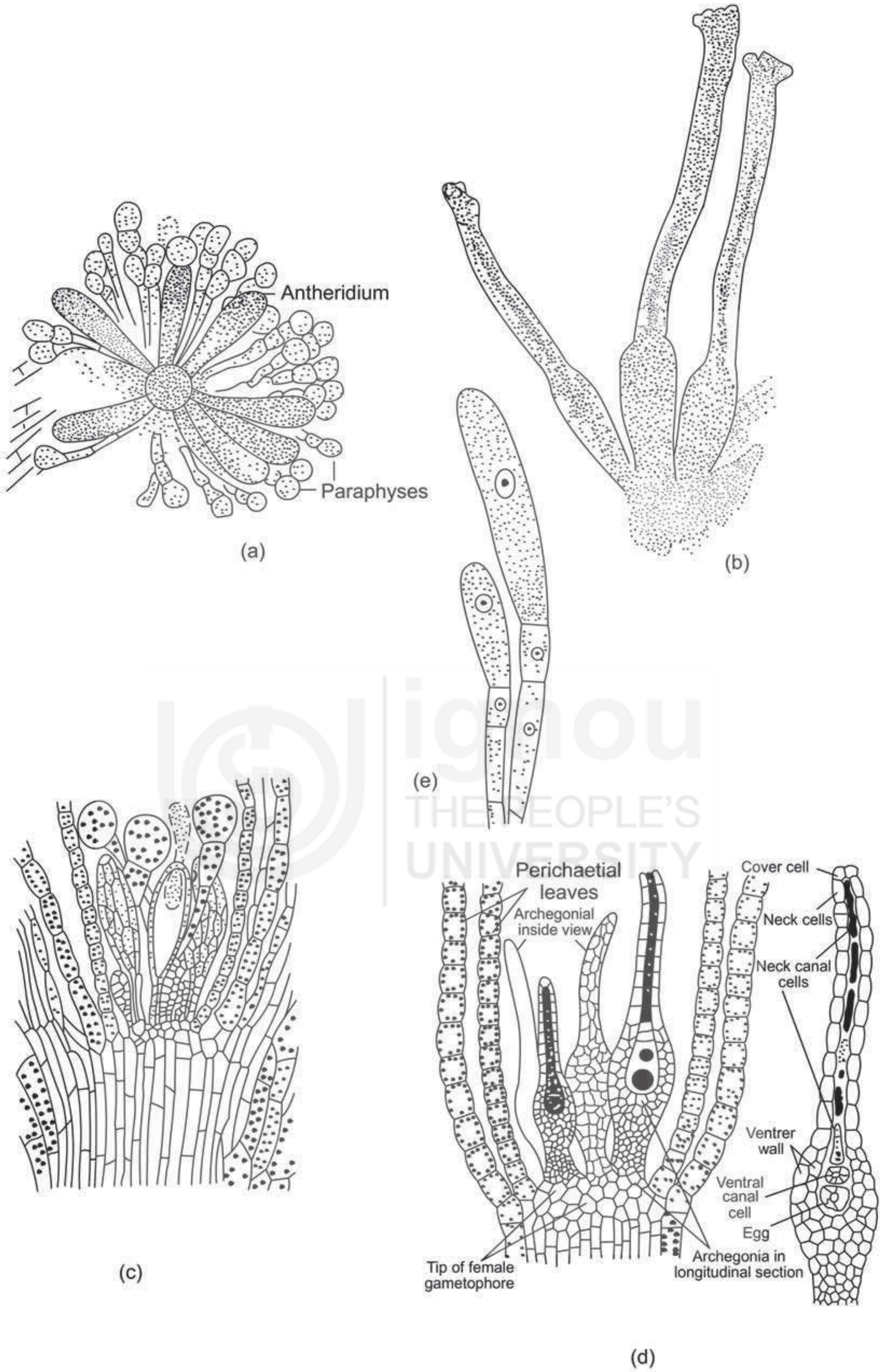

Fig. 14.16 (a - e): ***Funaria*: a) W.m. antheridia and paraphyses; b) W.m. of archegonia; c) L.s. through the tip of male branch showing developing and dehiscing antheridia; d) L.s. through the tip of female branch showing perichaetial leaves, archegonia in side view and paraphyses (left hand) and a mature archegonium (right hand); e) Paraphyses in enlarged view.**
***Source*: (a - c) Rashid, 2010; (d, e) Vashishta, 1994.**

14.4.3 Reproduction

In this section you will learn about reproduction in *Funaria*.

Vegetative Reproduction

Funaria may reproduce vegetatively by producing branches which are detached from the parent plant by decay and give rise to independent plants. Vegetative reproduction also occurs by the development of secondary

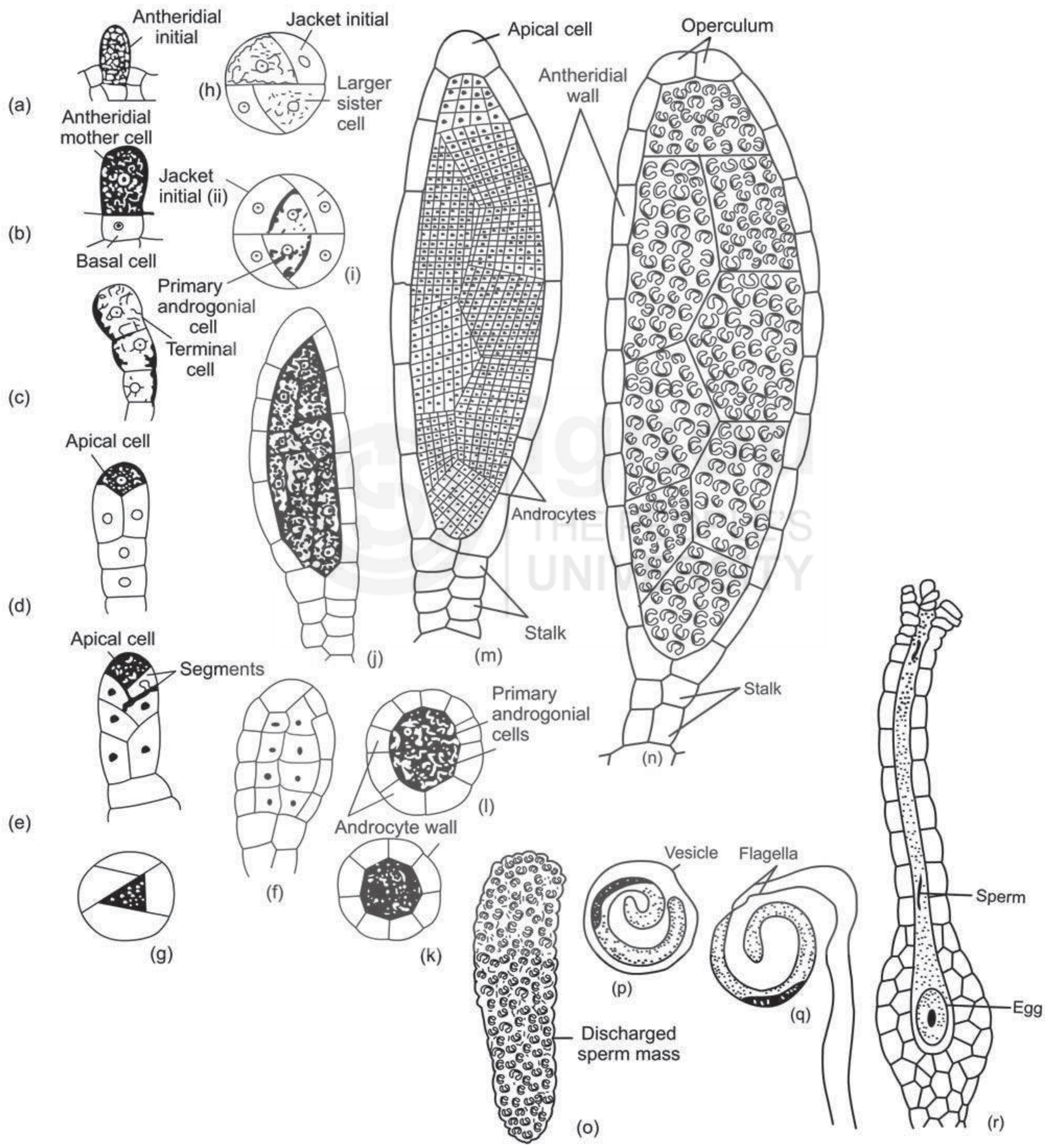

Fig. 14.17 (a - q): ***Funaria*** **: a - q) Different stages of development of antheridium; g - i) T.s. of early developmental stages; o) A discharged mass of sperms; p) A sperm within the vesicle; q) A free sperm after dissolution of vesicle; r) A mature archegonium showing passage of sperms.**
Source**: Vashishta, 1994.**

protonema from different parts of the gametophyte (Fig. 14.21 f). On this protonema buds are borne which develop into leafy gametophores.

Sexual Reproduction

Funaria is monoecious and autoecious, i.e., antheridia and archegonia develop on the same plant but on separate branches (Fig.14.15 a). Antheridia are borne on the main shoot, whereas archegonia develop on lateral branches. However, after fertilization archegonial branch grows more vigorously and soon becomes higher than the main shoot (Fig. 14.15 a).

In the antheridial shoot (Fig. 14.16 a, c) many club-shaped, stalked antheridia are surrounded by perigonial leaves. Note many multicellular, uniseriate structures among antheridia. These are paraphyses (Fig. 14.16 e). Their tips are swollen.

The archegonia develop in clusters acropetally on archegonial shoots (Fig.

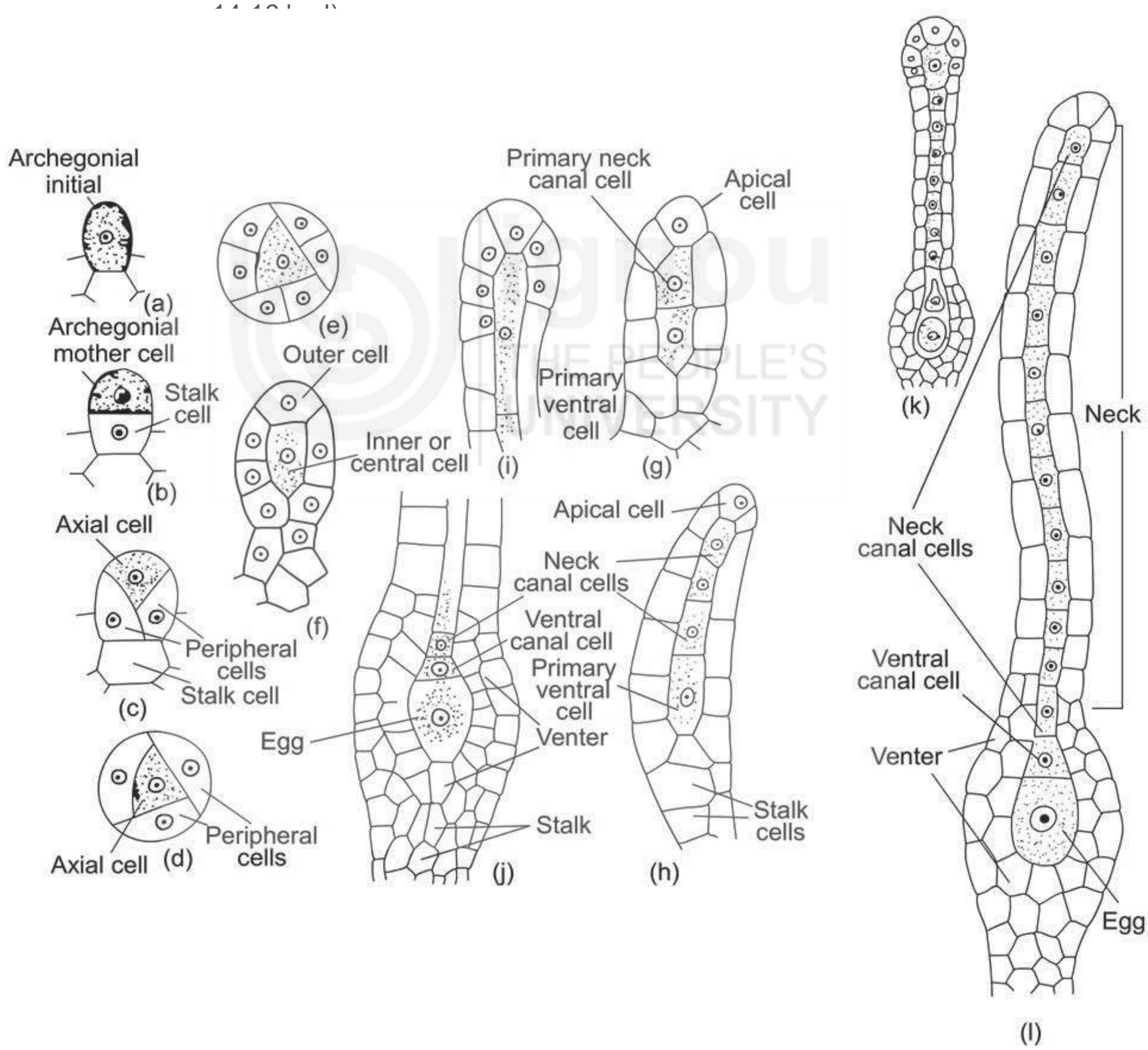

Fig. 14.18 (a - l): ***Funaria*** **: a – c, f - h) L.s. of early stages of development of archegonium; d, e) T.s. of early stages of development: i, j) Longitudinal sections of upper; i) and lower; j) part of the archegonium; k) Young archegonium. l) Mature archegonium.**
Source**: (a – l) Vashishta, 1994.**

As in other mosses, the development of an antheridium begins with an antheridial initial cell (Fig. 14.17). This cell forms an antheridium bearing androcytes covered with a layer of sterile cells. This is called jacket. An antheridium possesses a multicelled stalk.

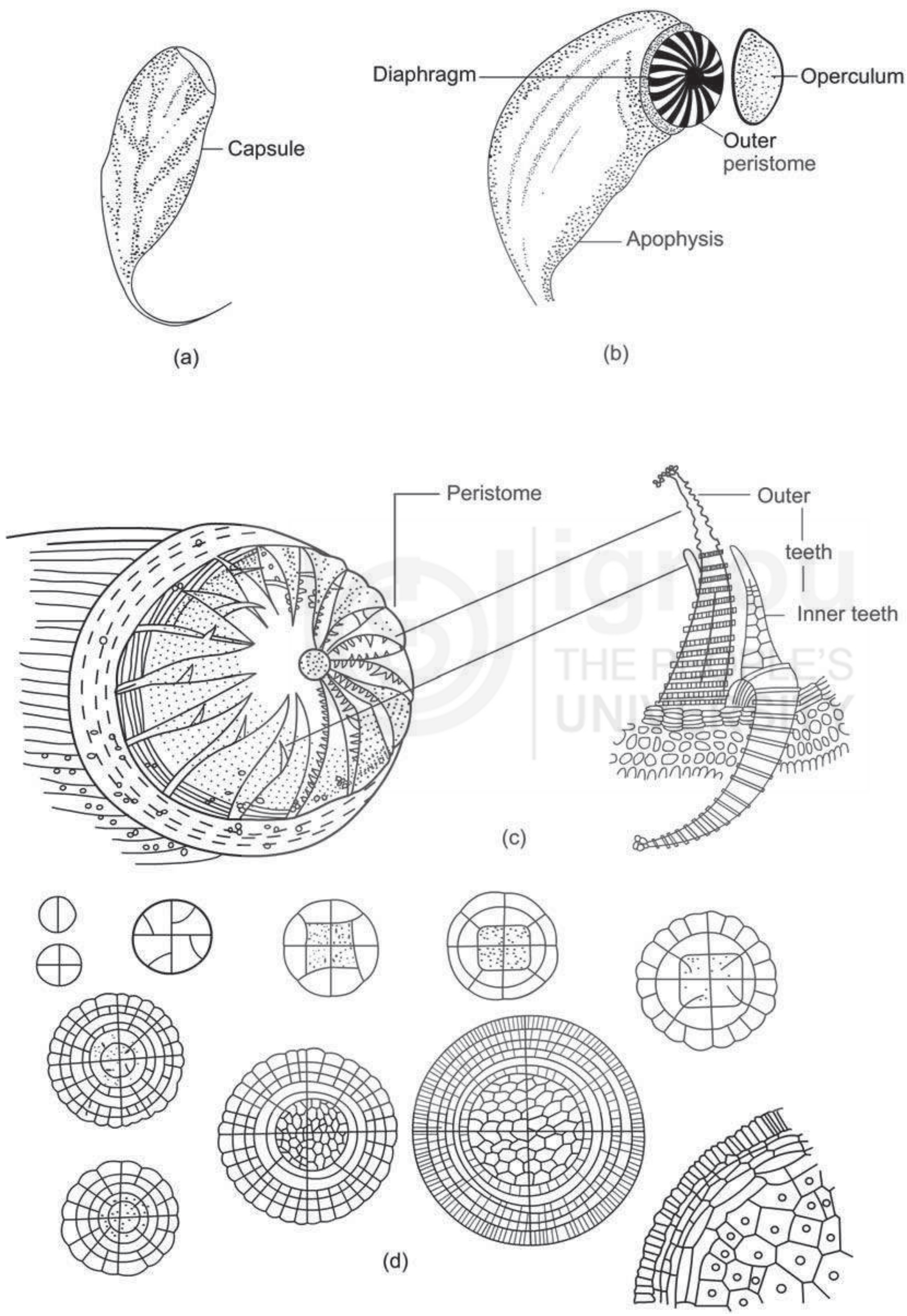

Fig. 14.19 (a – d): ***Funaria*: a) A mature capsule with ridged boundary; b) A capsule after removal of operculum; c) An enlarged view of peristome teeth; d) T.s. of stages in the development of capsule. The endothecial cells are shaded. *Source*: (a, c, d) Rashid, 2010; and (b) Santra et al., 1993.**

During initial stages of archegonial development an apical cell forms the stalk of an archegonium (Fig. 14.18). An archegonium is exposed, with a massive, multicellular multilayered stalk. It is flask-shaped structure with swollen base, the venter. Neck is very prominent and long. An archegonium contains an egg cell in venter cavity, a venter canal cell and a number of neck canal cells.

After fertilisation the zygote divides by a transverse wall into an epibasal cell and a hypobasal cell. Futher divisions give rise to a spindle-shaped young embryo with an apical cell at each end. The lower end forms the foot and the upper end gives rise to seta and capsule. The mature sporophyte shows a poorly developed conical foot, embedded in the apex of the archegonial branch, a long, reddish-brown and twisted seta and a pear-shaped, asymmetrical, slightly curved, bright orange capsule at the tip (Fig.14.19).

The lowermost portion of the capsule is known as apophysis and it is connected with seta. The lower part of the axis of the apophysis is composed of thin-walled elongated cells and it merges with columella present above it. The axis is surrounded by a green spongy tissue formed out of the endothecium. This spongy tissue is photosynthetic and has numerous air spaces. The spongy tissue is surrounded by an epidermis having stomata which are connected to air spaces below them. The main upper part of the capsule is a slightly curved cylindrical structure. It consists of columella in the centre surrounded by spore sac in which single-layered archesporium is

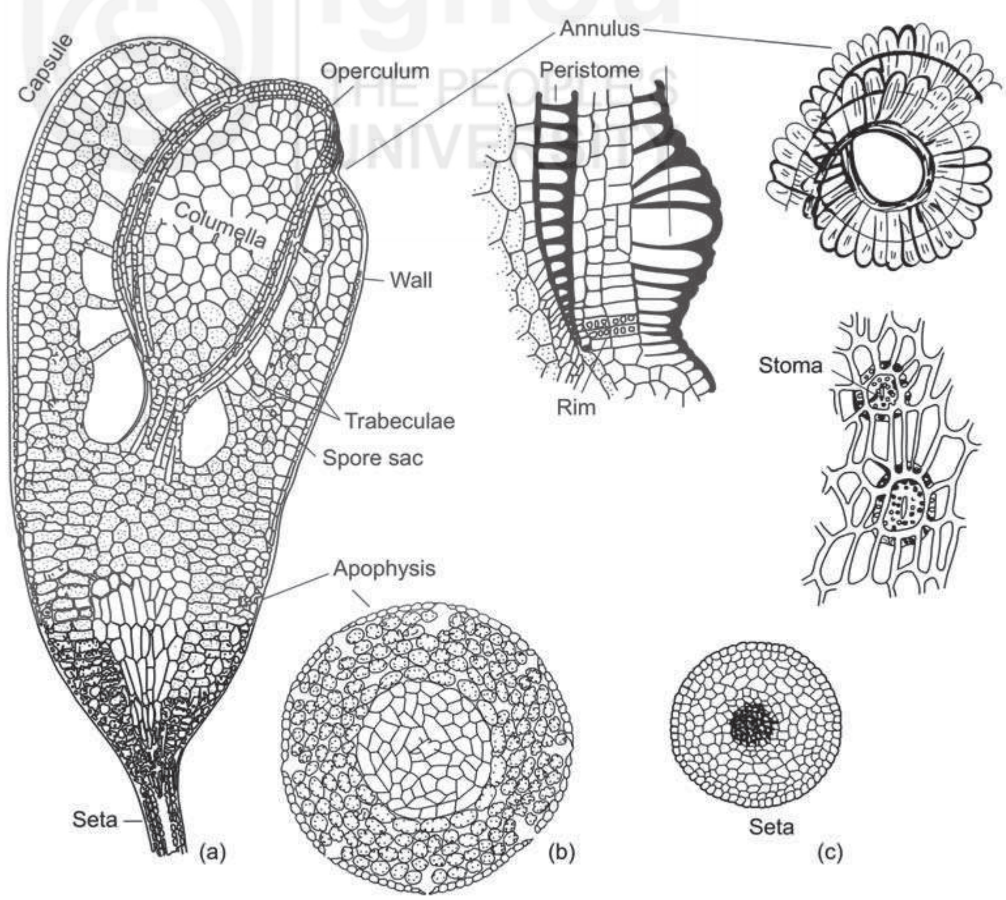

Fig. 14.20 (a – c): ***Funaria*. Details of capsule: a) L.s. capsule showing annulus and apophysis with stoma. T.S. through apophysis; b) and seta; c). Source (a – c): Rashid, 2010.**

located. The columella and the inner wall of the spore sac are derived from common initials called endothecium, whereas the outer wall of the spore sac and the tissues surrounding it develop from the initials called amphithecium. A big cylindrical cavity is present on the outer side of the spore sac. This space is traversed by numerous green, elongated filaments known as trabeculae. The capsule wall is composed of parenchymatous cells. Its outermost layer is epidermis which is devoid of stomata, initially it is green but becomes dark-brown or orange when mature.

The upper region of the capsule is highly modified for dispersing spores. It possesses operculum and peristome. This region is marked off from the fertile portion or theca by a constriction. Just below the constriction there is a rim which stretches inwards from the epidermis of the capsule wall and joins the peristome to the epidermis. Immediately above the rim is the annulus. It is composed of 5-6 superimposed layers of epidermal cells. It helps in

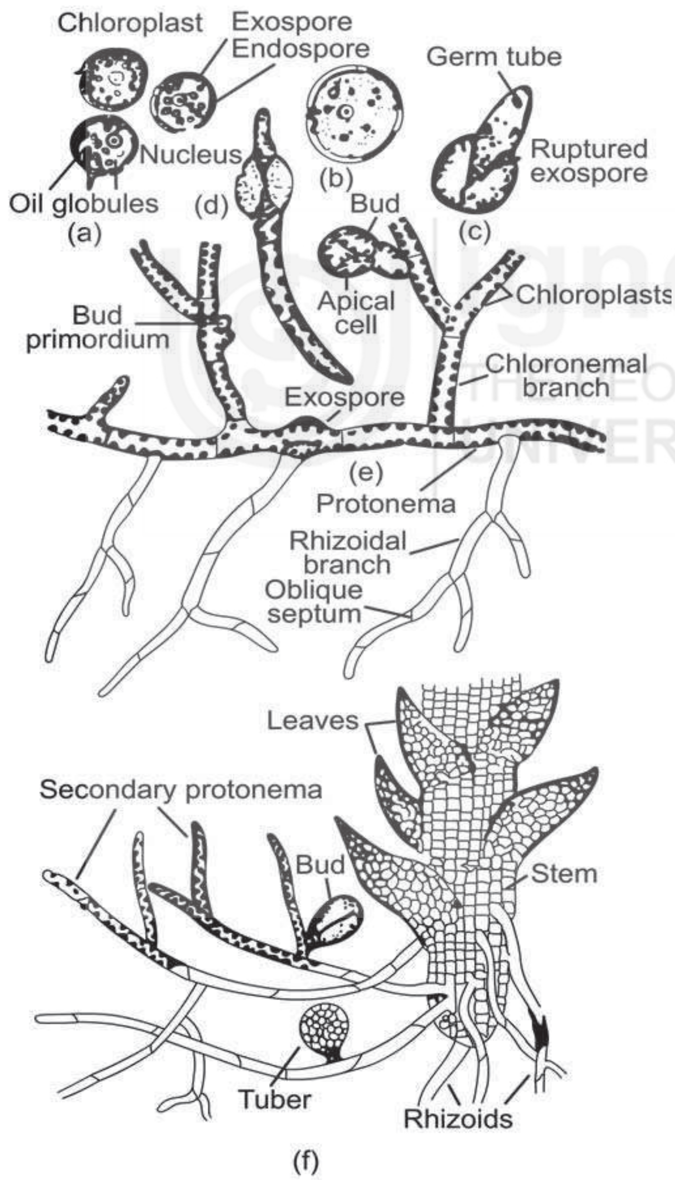

Fig. 14.21 (a – f): ***Funaria*** **: a) A spore; b - e) Stages in germination of spore forming primary protonema; f) A gametophore. Note some rhizoids come above ground and form secondary protonema. Source (a – f): Vashishta, 1994.**

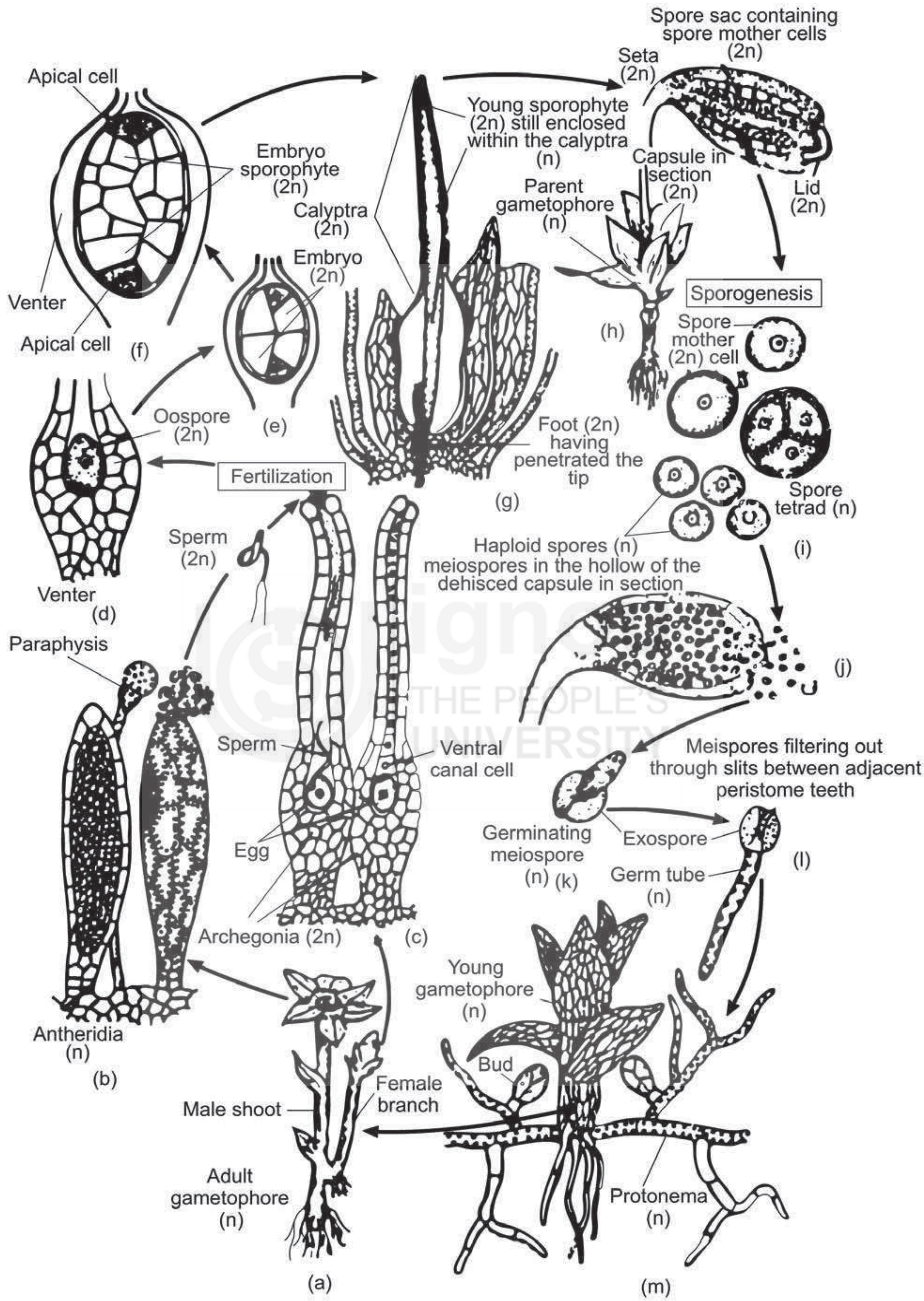

Fig. 14.22 (a – m): ***Funaria*****. Outline diagram of various stages of sexual life cycle.**
Source (a – m): Vashishta, 1994.

dehiscence of capsule. The peristome consists of two rows of curved narrow triangular plate-like teeth. In each row sixteen teeth are present and these teeths are twisted spirally to the left (Fig. 14.19 c). The teeth of outer row (exostome) are red and are ornamented with thick transverse bars, whereas teeth of inner row (endostome) are colourless, shorter and delicate. The mouth of the capsule is covered by the operculum (Fig. 14.20).

At maturity, the cells of the annulus absorb moisture and swell rapidly. This results in the breaking of the annulus from the rim and also in the detachment of operculum. Consequently, the peristome teeth are exposed. The members of the exostome are hygroscopic. They move out and in with changes in relative humidity of the atmosphere, and help in the dispersal of spores.

The spores germinate under favourable conditions (Fig. 14.21 a - e). The exine or exospores rupture after absorbing water. Intine or endospore comes out in the form of germ tube which elongates. It divides by transverse divisions forming multicellular, branched, filamentous green protonema. After sometime the protonema turns brown and its cross walls becomes obliquely oriented (Fig. 14.21 f). Buds arise on this protonema and finally develop into leafy gametophores.

The diagrammatic representation (Fig. 14.22) and outline diagram (Fig. 14.23) would help you to understand the reproduction in this moss.

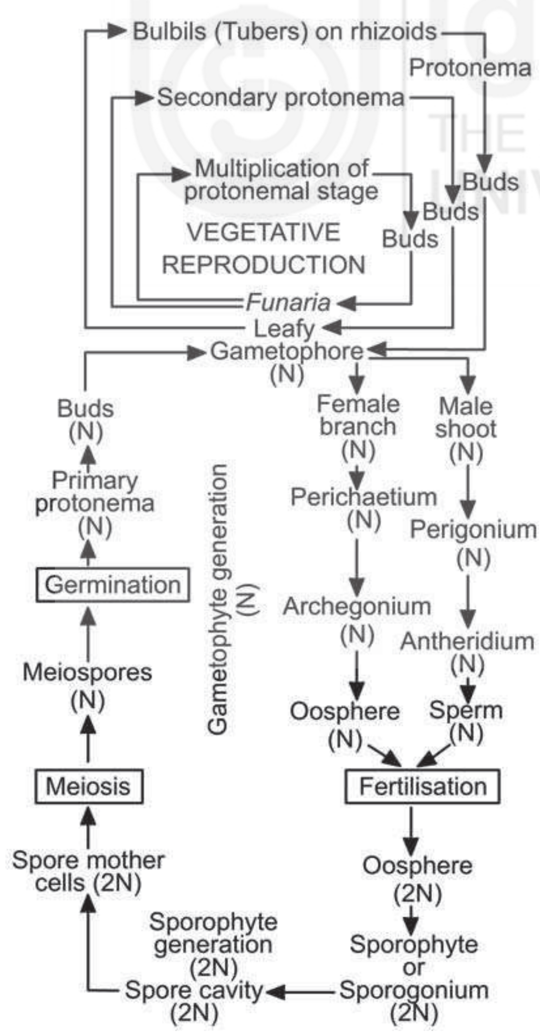

Fig. 14.23: ***Funaria*****. Word diagram of life cycle. Source: Vashishta, 1994.**

SAQ 4

Indicate which of the following statements regarding *Funaria* are true.

i) Sporophyte is differentiated into foot, seta and capsule.

ii) The antheridia and archegonia are formed on the same plant but on its different branches.

iii) In between antheridia in antheridial heads, many multicellular hair-like structures are present.

iv) Capsule of *Funaria* is spherical and straight.

v) Archesporium in *Funaria* is spherical and straight.

vi) Peristome teeth present near the rim of capsule help in providing nutrition.

vii) The adult gametophyte of *Funaria* is called gametangiophore.

viii) The rhizoids in *Funaira* are different from *Marchantia* because in the latter they are multicellular and have oblique septae.

ix) The wings of the leaf are formed by several layers of cells.

x) The leaves have prominent midrib.

14.5 SUMMARY

In this unit you have learnt that:

- The gametophytes of bryophytes could be: thalloid or erect. The thalloid liverworts could be: expanse of undifferentiated chlorophyllous cells; partly differentiated; dorsiventrally differentiated; leafy.
- The thalli of *Sphaerocarpos*, *Pellia*, *Anthoceros*, *Marchantia*, and *Porella* are representative of various forms of gametophytic organization in bryophytes.
- Gametophytes of bryophytes grow through apical initial(s).
- The gametophyte of *Marchantia* is doriventral, thalloid, dichotomously branched and is internally differentiated. The pores on the dorsal surface allow exchange of gases. They bear multicellular, appendiculate, dark, non-chlorophyllous scales and simple and tuberculate rhizoids along the midrib ridge on the ventral surface.
- In *Marchantia* antheridia and archegonia are borne on stalked receptacles, antheridiophore and archegoniphore respectively. Sporophyte is differentiated into foot, seta and capsule. The capsule has one-layered thick wall. Besides spores the capsule has elators which help in dispersal of haploid spores.
- The moss, *Funaria* have erect axes and bear leaf-like structures. The axis is branched. *Funaria* stem is differentiated internally with central core of conducting tissue. The leaves are with mid-rib and wings.

- In *Funaria* antheridium and archegonia are produced on separate branches on the same plant. Paraphyses are present among the sex organs which are produced in terminal clusters. Sporophyte is differentiated into foot, seta and capsule. Seta is substantially long and the capsule is pear-shaped, and slightly bent. Capsule has columella in the centre surrounded by one-celled thick capsule wall. On the upper part of the capsule two rings of peristome teeth are present which are covered by an operculum.

14.6 TERMINAL QUESTIONS

1) Describe briefly the structure of sporophyte in *Marchantia*.
2) Draw a labelled diagram of l.s. of a capsule of *Funaria*.
3) Compare the structure of rhizoids in *Marchantia* and *Funaria*.
4) Enumerate major steps in the life cycle of *Funaria*.
5) Describe briefly the range of thallus organization in bryophytes.

14.7 ANSWERS

Self-Assessment Questions

1. i) thalloid
   ii) *Marchantia*
   iii) *Anthoceros*
   iv) moss
2. i) F
   ii) F
   iii) T
   iv) F
3. i) stalked
   ii) hexagonal, air chambers
   iii) Photosynthetic
   iv) mucilage, oil bodies
   v) gemmae
   vi) dioecious
   vii) gametangiophores
   viii) branch
   ix) upper / adaxial
   x) downwards
   xi) six
   xii) elators

4. (i) T
   ii) T
   iii) T
   iv) F
   v) F
   vi) F
   vii) F
   viii) F
   ix) F
   x) T

Terminal Questions

1) Refer Sub-section 14.3.3.
2) Refer Figure 14.20 a.
3) Refer Sub-sections 14.3.1 and 14.4.1.
4) Haploid spore → protonema → male and female heads → antheridia / archegonia → sperm / egg cell → fertilization → syngamy

   Diploid zygote → sporophyte → foot, seta, capsule → sporogenous tissue → meiosis → haploid spore.

   (Elaborate the above points and supplement with figures, Sub-section 14.4.3)
5) Refer Section 14.2

   Hint: Thalloid liverworts, leafy liverworts, mosses.

14.8 GLOSSARY

Amphigastria : Under leaf in leafy liverworts.

Androcyte : Antherozoid mother cell. The cell which later develops into the antherozoid.

Antherozoid : Small, motile male gamete with flagella.

Archegonium : Egg-producing multicellular organ of embryophytes.

Calyptra : An enlarged portion of the venter of the archegonium that serves to protect the developing embryo in the sporophyte of most mosses.

Capsule : In bryophytes, the sporangium that contains meiospores.

Columella : In mosses, the central column of sterile sporophytic cells in the sporangium that is surrounded by the meiospore-bearing region or sporogenous layer.

Dioecious	:	Plants/organisms, bearing male and female gametes on different plants.
Elater	:	An elongate, hygroscopic cell with spiral wall thickenings that aid in the release of spores from capsule/sporangia.
Exine	:	Outer layer of the cell wall of spore.
Gemma	:	A vegetative propagule produced in bryophytes.
Gemma cup	:	A specialized structure in which vegetative propagules (gammae) are produced in bryophytes. Also called splash cup.
Homospory	:	A condition in which an organism produces one type of haploid meiospores.
Hydroid	:	Specialized, elongate, living, water-conducting cell in many moss gametophytes, a few liver-worts, and the setae of some moss sporophytes.
Intine	:	Inner layer of the cell wall of a spore.
Leaf trace	:	A bundle of transport tissue that enters a leaf from the stem.
Leptoid	:	A conducting cell of mosses that is considered to transport metabolic products.
Monoecious	:	Organisms, bearing male and female gametes on the same plant.
Operculum	:	A cup or cover at the apex of the capsule in true moss sporophytes.
Plagiotropic	:	Growth of a plant part at an oblique angle to the stimulus, such as gravity.
Protonema	:	The filamentous or thalloid gametophyte stage of bryophytes. It usually appears as the haploid spore germinates.
Rhizoid	:	Unicellular or multicellular root-like filament(s) that functions in nutrient and water uptake and anchoring in bryophytes.
Spore mother cell	:	Diploid cell in which meiosis occurs to produce haploid meiospores.
Tuberculate rhizoids	:	Rhizoid of some bryophytes with peg-like thickenings in inner wall.

14.9 FURTHER READING

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UNIT 15

BRYOPHYTES: ECOLOGY AND ECONOMIC IMPORTANCE

Structure

15.1 INTRODUCTION

In Units 12, 13 and 14 of this block you have learnt that bryophytes are small, non-vascular, green plants. You have also learnt that they exhibit distinct heteromorphic alternation of generations. Studies on the distribution, general characteristics and reproductive structures of bryophytes have helped plant biologists to understand the adaptations needed by plants to establish on land habitat and the relationship between the female sex-organ - archegonium and matrotrophy.

In this unit, you will study about the ecological role the bryophytes play in terrestrial habitats and their economic importance.

Objectives

After studying this unit, you should be able to:

- discuss the role of bryophytes in soil formation;
- describe the role of bryophytes in preventing soil erosion and as pioneers of vegetation;
- appreciate the importance of bryophytes in nutrient and water recycling; as carbon sinks; as indicators of mineral deposits, pH, pollution; and in peat formation;
- enumerate and describe the economic uses of bryophytes in medicines, horticulture, and households; and
- discuss the role of bryophytes in the provision of food and shelter for animals.

15.2 ECOLOGICAL ROLE

15.2.1 Pioneers of Vegetation

Many bryophytes are the first ones to appear on open and often nutrient-poor sites where no other plant is able to grow (Fig. 15.1). For instance a liverwort, *Nardia esculenta* grows on bare rocks and on recently deposited volcanic ash. Gradually, the bryophytes build up an organic layer that is invaded by microorganisms, resulting in changes in the mineral substratum beneath. This increased nutrient availability makes the site suitable for invasion by vascular plants. In this way, bryophytes help in succession of plants on bare rocks by becoming pioneer plant community (pioneers - first to appear). Some bryophytes like *Andreaea* are restricted mainly to bare rock surfaces. Most of these bryophytes are highly tolerant to extended periods of desiccation.

The mosses are also pioneer species on burnt sites. Every year large areas of grasslands, temperate and tropical forests catch fire. The resulting tracts of land provide habitats for a line of succession (seres) of mosses like *Funaria, Ceratodon* and *Polytrichum*.

Mosses are pioneers in dune systems as well. They help in retaining moisture and stabilizing dunes that otherwise are at the mercy of wind, e.g., *Ceratodon* and *Tortula*.

15.2.2 Prevention of Soil Erosion

You have learnt that bryophytes grow as compact cushions forming a carpet on the forest floor. Actually, their rhizoids bind soil particles together and also interweave with the rhizoids of adjacent plants keeping the whole cushion compact and difficult to detach from the soil. The soil particles thus trapped do not flow along with water during floods.

Fig. 15.1: Algae, liverwort (*Riccia*) and mosses colonise the spaces between floor tiles.

***Courtsey*: Kavathekar, 2017.**

Bryophytes help play crucial role in mediating soil-temperature and soil-moisture. Being effective insulators in frozen areas they promote permanent permafrost by shielding soil from heat during summer when air temperatures are above freezing.

The colonization of bryophytes on the roadside is important in stabilizing these sites. Species of *Barbula*, *Weissia*, and *Bryum* (Fig. 15.2a-c) are pioneers on new road banks.

Extensive sand dune systems occur along many sea coasts of the world. Mosses play a very important role in helping to retain moisture and stabilize dunes. Such mosses can survive even if they get covered by sand. An example of such a moss is *Ceratodon purpureus*.

Bryophytes protect soil in arid areas as components of cryptogamic crust consisting of assemblage of lichens, bryophytes, cyanobacteria, green algae, fungi and upper moist soil layers. Such cryptogamic crusts are common in arid/semi-arid landscapes.

Mosses have potential role as inhibitors of soil erosion due to their trample-resistant structure and their high regenerative ability.

In present times, certain mosses like *Polytrichum*, *Atrichum*, and *Ceratodon* are grown to prevent soil erosion around fruit trees such as apples and pears.

Fig. 15.2 (a-c): ***Bryum*. A patch with sporophytes: b) Enlarged view of capsules. Note the morphology of the capsules; c) A leaf enlarged, a part of another leaf is also seen in this figure. A prominent mid-rib is present in the leaf.**

Source : **a) https://www.google.co.in/search?q=bryum&source=lnms&tbm=isch&sa=X&ved=0ahUKEwjs6cD18t_VAhUHLI8KH TAaDKEQ_AUICigB&biw=1366&bih=627#imgrc=4gcb1imdUxaCWM: b) https://www.google.co.in/search?q=bryum&source=lnms&tbm=isch&sa= X&ved=0ahUKEwjs6cD18t_VAhUHLI8KHTAaDKEQ_AUICigB&b iw=1366&bi h=627#imgrc=VoGKfyvFf-aJ3M: c) https://www.google.co.in/search?q=bryum&source=lnms&tbm=isch&sa=X&ved=0ahUKEwjs6cD18t_V AhUHLI8KHTAa DKEQ_AUICigB&biw=1366&bih=627#imgrc=I7mR0vT84sYRUM:**

15.2.3 Recycling of Nutrients

Bryophytes release nutrients by leaching and decomposition. Such nutrients are made available to other organisms. As symbionts with cyanobacteria, they help fix atmospheric nitrogen. For example, feather moss, *Pleurozium schreberi* with *Nostoc* as symbiont can fix about one-third to one-half of 3 kg of atmospheric nitrogen, fixed per hectare, in boreal forests.

A tree-biomass represents many years of growth and thus prevents recycling of minerals for years. In contrast, rapidly growing and decomposing biomass of bryophytes recycle minerals in the ecosystem relatively much faster.

The bryophytes contribute substantially to global biomass and thus help recycle of carbon and other nutrients through growth and decomposition.

15.2.4 Carbon Sinks

Moss photosynthesis can represent upto 50 per cent of total photosynthates in swampy spruce forests. A large portion of carbon fixed long-term, e.g., in *Sphagnum* (Fig. 15.3 a, b). Since in a peat-land, where almost 90 per cent of ground cover is *Sphagnum* it is estimated that in the past millennium a very significant quantity of total carbon has been accumulated in organic deposits of peat lands (see Sub-section15.2.11).

(a) (b)

Fig.15.3(a,b): ***Sphagnum*. a) A portion of the patch. Note the closely growing plants; b) A few plants with sporophytes in enlarged view.**
Source : **a) https://www.google.co.in/search?biw=1366&bih=627&tbm=isch&sa=1&q=sphagnum+&oq=sphagnum+&gs_l=psy-ab.12..0j0i67k1l2j0.27544.27544.0.29645.1.1.0.0.0.0.207.207.2-1.1.0....0...1.1.64.psy-ab..0.1.206.JiQUQ2zblJs#imgrc=81lXfwSt7lNP2M: b) https://www.google.co.in/search?biw=1366&bih=627&tbm=isch&sa=1&q= sphagnum+&oq= sphagnum+&gs_l=psy-ab.12..0j0i67k1l2j0.27544.27544.0.29645.1.1.0.0.0.0.207.207.2-1.1.0....0...1.1.64.psy-ab..0.1.206.JiQUQ2zblJs#imgrc=UBzmvCkhHquAKM:**

5.2.5 Recyling of Water

Bryophytes are poikilohydric (able to dry out). They become dormant under dry conditions and can resume physiological activity upon remoistening. They possess very-high water-holding capacity, as much as almost 1500 per cent of their dry weight. In tropical and temperate forests with epiphytes, the bryophytes may collectively retain 15000 kg of water per hectare. As epiphytes, bryophytes intercept considerable amount of rainfall and thus influence water budget of a watershed region.

15.2.6 Grassland and Heathland

This moss cover in a grassland and heathland discourages or prevents the seedling establishment. This results in limiting the invasion of alien species in the area.

15.2.7 Indicators of Mineral Deposits

Some mosses are restricted to the soil rich in a particular metal(s). The metal(s) often get(s) accumulated in the plant. By studying the distribution of such plants or analyzing their metal contents, it is possible to discover new mineral deposits. This technique is known as geobotanical prospecting. In Almora, Nainital and Pithoragarh districts in the Kumaon region of North Western Himalayas various mineral-rich substrates have been recognised. Each mineralized area has a characteristic bryoflora of its own. The distinction is so pronounced that the bryoflora provides an idea of the precise nature of the underlying substrate. Some of the examples are as follows:

a) Granite and Mica – Bryophytes belonging to order *Grimmiales* are the invaders and sole colonizers of smooth, polished surfaces of mica rocks, granites and other rocks. Hard granite surfaces are always colonized by *Grimmia* spp. and *Rhacomitrium himalayanum*. The colonization is so sharply delimited that one can predict the substrate by merely studying the moss.

b) Dolomite rocks – These rocks are a characteristic feature of the Himalayan geology. The substrates are calcium-rich. The mosses growing on these substrates have a remarkable capacity to absorb and accumulate different amounts of calcium from the substrate. The mosses which are always present on such sites are – *Hyophila involuta*, and *Tortella tortuosa*.

c) The magnesite ($MgCO_3$) – one of the largest deposits of this mineral in India is at Kumaon. At all sites, the large magnesite deposits present a strikingly barren appearance. The only species of moss growing on these sites is *Hymenostylium recurvirostrum*.

d) Copper – Some species of mosses serve as indicators of high copper concentration in the substrate and are known as 'copper mosses'. The copper concentration tolerated by the 'copper mosses' is lethal to other plants and thus bryophytes have no competition on such sites. The important copper mosses are – *Mielichhoferia elongata* and *Scopelophila cataractae* which can serve as indicator of copper.

e) The occurrence of *Funaria* (Fig. 15.4) is associated with potash, especially in areas devastated by fire.

15.2.8 Indicators of pH

Some bryophytes grow only on the soil that is at particular pH. So, the presence of a particular species indicates the acidic or alkaline condition of the soil.

a) The mosses also grow on haematite (ore of iron) with alkaline pH (7.3 -7.6). It is a well known fact that in an alkaline medium, iron remains unavailable to most of the plants.

b) Some bryophytes grow only on strongly acidic, highly soluble, iron enriched limonitic substrates. Iron is readily available on such substrates. These substrates have pH 2.9 - 4.1.

   Polytrichum (Fig. 15.7 a, b) and *Rhacomitrium* is a reliable indicator of acidic conditions. In contrast the mosses *Ditrichum flexicaule*, *Funaria* spp. (Fig. 15.4 a) and *Encalypta streptocarpa* are indicators of basic pH conditions.

(a) (b) (c)

Fig. 15.4 (a-c) : ***Funaria hygrometrica*: a) A few plants with capsules; b) A capsule enlarged; c) A part of the leaf enlarged.**

***Source*: a) https://commons.wikimedia.org/wiki/File:Sporophytes_of_the_moss_Funaria_hygrometrica_-_USGS_Bee_Inventory_and_Monitoring_Laboratory.jpg b) https://www.google.co.in/search?biw=1366&bih=627&tbm=isch&sa=1&q=funaria+hygrometrica&oq=funaria+hygrometrica&gs_l=psy-ab.3..0l2.5427.11473.0.12065.22.21.1.0.0.0.221.3499.0j13j5.18.0....0...1.1.64.psy-ab..3.19.3527...0i67k1j0i24k1j0i13k1.V94p28glubQ#imgrc=DZevpa1a4Jnu8M: c) https://www.google.co.in/search?q=funaria+hygrometrica&source=lnms&tbm=isch&sa=X&ved=0ahUKEwiHuee0sOLVAhUUSY8KHXOAAYIQ_AUICigB&biw=1525&bih=700#imgrc=6vnFmjeuuYmgRM:**

c) Gypsum containing areas are alkaline to varying degrees and even contain acidic pockets. The moss *Campylopus gracilis* serves as an example of a species that is tolerant to both acidic and basic conditions over a pH range of 4.9 - 7.8.

15.2.9 Indicators of Seed Plant Community

Some bryophyte species are consistent inhabitants at the sites where a particular seed plant community is growing, so these species can be used as indicator species. While some others persist at localized sites though the original vascular plant vegetation gets destroyed due to some reason. Consequently, they become useful remnants to indicate the past existence of a forest or non-forest vegetation and can be used as indicators as to which vegetation could be effectively regenerated on that site.

15.2.10 Indicators of Pollution

Air Pollution

Bryophytes can also be used as bioindicators of pollution as they are sensitive to SO_2, fluorides and heavy metals. They show symptoms of injury when exposed to minute quantities of pollutions. Exposure to SO_2 results in loss of green colour. The leafy liverwort *Radula complanata* (Fig. 15.5) changes its colour within ten minutes and its chloroplasts are destroyed at concentration of 120 ppm. Bryophytes are also very sensitive to hydrogen fluoride and show symptoms of injury at concentrations as low as 0.001 to 0.1 ppm. The colour of leaves of moss *Pylaisiella polyantha* changes to brown at low concentration and appears burnt at higher concentration.

Fig. 15.5: *Radula complanata*.
Source : **https://www.google.co.in/search?q=Radula+complanata&source=lnms&tbm=isch&sa=X&ved=0ahUKEwjvmcO_ueLVAhVCPo8KHahxCrAQ_AUICigB&biw=1525&bih=700#imgrc=JRF4VxvodW8ywM:**

Some bryophytes have the capacity to absorb and retain pollutants in quantities much higher than those absorbed by other plants growing in the same habitats. These can be used to lower the concentration of certain pollutants in the environment. Analysis of such bryophytes can also provide the idea of the degree of pollutants present in that area. Heavy metals constitute a very important class of pollutants. The most significant among these are lead, cadmium, arsenic and chromium. Lead is most toxic metal. You may know that it is used as anti-knock compound and is released in the automobile exhaust. It is found that lead content of mosses growing at a distance of 2 metre away from anti-knock manufacturing factory was found to be 320 ppm. Similarly, Zinc was accumulated 1315 ppm in moss (*Hypnum cupressiforme*) growing at a distance of three miles away from the manufacturing factory.

Herbarium specimens of three mosses which were collected at intervals during 1860 to 1968 were tested for lead contents.

The results are given below :

Table 15.1 : Lead Content in HerbariumSpecimens of Bryophytes

Time period in years	lead content in ppm
1860-1875	20
1875-1900	40
1900-1950	45
1950-1960	80-90

These results coincide with the amount of lead released in the atmosphere during those periods.

Water Pollution

Bryophytes can also act as indicator of water pollution. For example, *Amblystegium riparium* was found to be absent in the upper part of the river with clean water. However, it appeared at a place where the quality of river water deteriorated due to joining of a polluted tributary coming from a village. This species seems to be an indicator of more or less polluted water. Aquatic bryophytes can be used for monitoring heavy metal pollution as they accumulate them in high concentration. *Jungermania* spp. and *Scapania* spp. accumulate mercury and thus can be used for monitoring its concentrations.

Bryophytes, *Palustriella commutata*, *Cratoneuron filicinum*, *Fissidens viridulus* show high preferences for clear, turbulent fast-flowing water with high specificity for water temperature and phosphate and ammonium concentrations. They are indicators of water quality.

(a) (b)

Fig. 15.6 (a, b): ***Amblystegium riparium*. a) A few plants with sporangia; b) A few leaves in enlarged view.**
Source : **a) https://www.google.co.in/search?q=Amblystegium+riparium&source=lnms&tbm=isch&sa=X&ved=0ahUKEwiJzab8vuLVAhUhTI8KHf9cAVQQ_AUICygC&biw=1525&bih=700#imgrc=4I4KHtXgoOmcSM: b) https://www.google.co.in search?q=Amblystegium+riparium& source=lnms&tbm=isch&sa=X&ved=0ahUKE wiJzab8vuLVAhUhTI8KHf9cAVQQ_AUICygC&biw=1525&bih=700#imgrc=oPLOgBwRXAsvaM:**

15.2.11 Peat Formation

You may have heard about peat bogs. A peat land is a peculiar ecosystem. They are formed when organic matter gets accumulated as a consequence of an imbalance between net-primary production and decomposition. The cell walls of bryophytes possess lignin-like substances. There along with high carbon nutrients, low temperatures, low pH, anaerobic soil all together prevents complete organic decomposition. The moss *Sphagnum* (Fig. 15.3 a, b) accelerates the peat formation. It is

Doctrine of Signature:

In medieval times there was a curious superstition that God would mark each plant in some way to indicate its medicinal value. The external form of a plant gave a clue as to which body organ would be benefitted by treating with its preparation. For example, plants resembling liver (Hepaticae), were supposed to be good for liver.

The following bryophyte genera inhibit the growth of micro-organisms.

Sphagnum portoricense,

S. strictum, Conocephalum,

Reboulia,

Pallavicinia conicum, Dumortiera hirsute, Atrichum,

Mnium,

Polytrichum,

Dicranum,

Barbula,

Timmiella,

Radula.

estimated that litter decomposition rate as percentage of initial litter-mass after one year of burial is less than 15

percent in *Sphagnum*. It contrasts with a rate of 25-70 percent in grasses and shrubs. Thus, *Sphagnum* plays an important role in sequestering large amount of carbon.

Wetlands of *Sphagum* are maintained by a process called *paludification*. Paludification is referred to as a dynamic process of peat accumulation over a former dry mineral soil, involving formation of waterlogged conditions. During peat formation, *Sphagnum* acts as an ecological switch. It modifies environment to its own advantage through acidification, decrease in species diversity and more peat accumulation. Acidification occurs due to an increased cation exchange capacity (it enables it to take up nutrients and replace them with protons). By reducing pH and along with low soil temperature, the microbial activity decreases resulting in lowered nutrient recycling and availability and increased organic matter content in a peat land.

The accumulation of peat may eventually expand to the surroundings. It causes sharp drop in growth of neighbouring trees and forest productivity; inhibition of seedling establishment of other plants and the *Sphagnum* dominates swamp community. *Sphagnum* therefore is also referred to as 'ecosystem engineers', because under certain conditions they can create, modify and maintain certain habitats in which only they themselves can thrive. The area of earth covered by peat bog is also known as 'mires' especially in temperate and sub-Arctic regions.

Peat bogs are of great importance to biologists because a number of well preserved fossils of organisms or their parts have been found in them. Pollen grains of several plants are found in them. These findings help scientists in characterizing flowering plants and establishing flora and fauna of a particular geological period.

SAQ 1

a) Given below in Column I are the names of few mosses. Match them with their occurrence as pioneer moss community given in the Column II.

Column I	Column II
i) *Ceratodon*	1) bare rocks
ii) *Andreaea*	2) burnt sites
iii) *Funaria*	3) dune systems

b) Explain how mosses as pioneer plant communities help in succession of other vegetation.

c) How do bryophytes help prevent soil erosion?

d) Fill in the blank(s) with suitable example (generic name).

i) The moss ………………… is a very effective carbon-sink.

ii) ………………… is also known as 'copper-moss'.

iii) Bryophytes are very sensitive to ………………… concentration in the atmosphere.

e) What is meant by 'geobotanical prospecting'?

15.3 ECONOMIC IMPORTANCE

Bryophytes form an important part of vegetation in cold temperate regions of the world including Himalayas. Studies on the uses of bryophytes in the daily lives of the native people have revealed that in these regions bryophytes are widely used as medicine, construction materials, insect repellents, pads and stuffing, packing, chinking materials and smoke filters. In the following account you will study these uses of bryophytes in detail.

15.3.1 Medicines

In ancient times bryophytes have been used as herbal medicines in various parts of the world. Dioscorides ascribed medicinal properties to *Marchantia polymorpha*. During the middle ages, the large thallose liverworts were interpreted according to the Doctrine of Signatures. The decoction of liverworts was supposed to be effective in the treatment of disorders of liver, and that of the 'hairy-cap moss', *Polytrichum commune* to beautify ladies hairs.

In Northern Montana (USA) *Polytrichum juniperinum* is still used for preparing various medicines. In Kumaon region (North-Western Himalayas) liverworts *Marchantia polymorpha* and *M. palmata* are used as medicine for boils and abscesses whereas mosses are used in the preparation of an ointment for cuts, burns and wounds. In China, more than 30 species of bryophytes have been recognised as curative agents.

Clinial researches are also being carried out to confirm the effectiveness of these medicines and it has been observed that the extract of moss *Rhodobryum giganteum* which is used to cure angina (an attack of intense constricting pain), increased the rate of flow in aorta of white mice by over 30% causing a reduction in the amount of oxygen resistance (Table 15.2).

Modern phytochemists and biochemists have isolated a vast number of biologically active organic compounds from bryophytes which are of potential use in pharmaceutical industry. It has been demonstrated that certain products of bryophytes inhibit the growth of micro-organisms. Three prenylbibenzyls from *Radula* spp. inhibit the growth of *Staphylococcus aureus*.

Many species of bryophytes have been shown to posses antitumor activity. The first antitumor active compound, diplophylline, was obtained from liverworts. This compound shows significant activity against human carcinoma. Antitumor sesqueterpenoids have also been isolated from many liverworts.

The following antitumor sesquiterpenoids have been isolated from various bryophytes (Table 15.3).

Table 15.2 : Medicinal Uses of Bryophytes

Species	**Medicinal value**
Rhodobryum giganteum and *R. roseum*	For the treatment of cardio-vascular diseases and nervousness.
Polytrichum commune (Fig. 15.7)	To reduce inflammation, as an antifever agent, diuretic (causing increased output of urine), laxative and hemostatic agent.
Haplocladium microphyllum	For tonsillitis, bronchitis, tympanitis, and cystitis (an inflammation of the urinary bladder).
Conocephalum conicum and *Marchantia polymorpha*	(mixed with vegetative oils) an ointments for boils, eczema, cuts, bites, wounds and burns.
Fissidens	As an antibacterial agent for swollen throat.

(a) (b)

Fig. 15.7 (a,b) : *Polytrichum commune*. a) A patch. Its size can be gauged by the lady bug insect in the background; b) A few leaves in enlarged view.
Source: (a) https://commons.wikimedia.org/wiki/File:Polytrichum_commune_in_natural_monument_Knez_u_Hrazan_(2).JPG, (b) https://www.google.co.in/search?q=Polytrichum+commune&source=lnms&tbm=isch&sa=X&ved=0ahUKEwjWu6HtwOLVAhXH s48KHbpKD1IQ_AUICigB&biw=1525&bih=700#imgrc=cuSHdSzm_iwmWM:

Table 15.3: Antitumor sesquiterpenoids isolated from bryophytes.

Diplophyllin	*Diplophyllum albicans, D. taxifolium*
Marchantin A	*Marchantia polymorpha, M. tosana, M. paleacea*
Riccardin C	*Riccardia multifida*
Perrottetin E, F & G	*Radula perrottetii*
Plagiochiline A	*Plagiochila sp.*
Pingisane	*Trocholejeunea sandvicensis*

Sphagnum has been used as absorbent dressing for centuries. *Sphagnum* dressings were first used on a large scale during the Russo-Japanese war, 1904-1905. The following were the advantages of *Sphangum* dressing over cotton.

i) They absorbed 16-20 times their own dry weight of liquid, whereas cotton dressings could only absorb 4-6 times.

ii) They were cool and soothing because the moss is porous. A dressing was found to be comparatively dry for 24 hours after an operation in cases where the wound had bled quite freely.

iii) The dressing could be left on for up to 2-3 days which is much longer than cotton dressings.

iv) *Sphangum* itself has mild antiseptic properties not possessed by cotton.

Effective against plant pathogens: Bryophytes also show activity against some plant pathogens. Extract of the liverwort – *Herbertus aduncus* inhibits the growth of some plant pathogenic fungi. Many species of mosses (e.g. *Dicranum scoparium* and *D. japonicum*) contain some rare fatty acids which completely inhibit the growth of the fungus causing rice blast, *Pyricularia oryzae*.

15.3.2 Construction Materials

In areas where woody plants are scarce, the tiny bryophytes have commonly been utilized in number of ways. They are also used in the construction of houses and for their furnishings.

The aquatic moss *Fontinalis antipyretica* is used by Nordic people for filling spaces between the chimney and walls to prevent fires. Several mosses are used as chinking (chink – a crack or narrow fissure) materials. Similarly, in Alaska, chinking of wooden and log cabins is done using bryophytes. The shepherds in the Himalayan highlands also use bryophytes for chinking. In northern Europe *Sphagnum* is stuffed between timber used in houses to deaden the sound. Mosses have also been used in making huts by herdsman in Alps. *Neckera complanata* and other mosses are used for plugging the seams and cracks of boats.

In the Scottish highlands *Sphagnum* mixed in tar is used for plugging the seams. In Russia, pressed and heated raw peat is used for making slabs which are used for insulation of domestic housing and refrigeration.

Recently, new construction materials like 'peat crete', 'peat wood', and 'peat foam' have been developed from *Sphagnum* using certain binders for solidification and strengthening.

15.3.3 Decorative Materials

In decorative industry and floral trade mosses play significant role. In countries like Japan, England, France, Finland and America mosses are used for decoration of ladies hats. In the floral trade mosses are marketed as 'sheet moss' or 'blanket moss' and are used commonly in this industry the year-round. The moss sheets form blanket material for Christmas tree yards and nativity scenes. The decorative uses of mosses are as follow :

i) *Dicranum scoparium* – for forming banks of green, in-shop window displays.

ii) *Rhytidiadelphus loreus, R. triquetrus* and *Hylocomium splendens* – as green carpets for floral exhibitions.

iii) *Climacium americanum* (Fig. 15.8) – fashioned into wreaths and crosses.

iv) *Hylocomium splendens* – for making moss roses.

v) *Climacium dendroides* – (dyed) for decorating women's hat.

Some aquatic bryopohytes are used in aquaria. These bryophytes are also useful to fishes because they provide oxygen and egg-laying substrata.

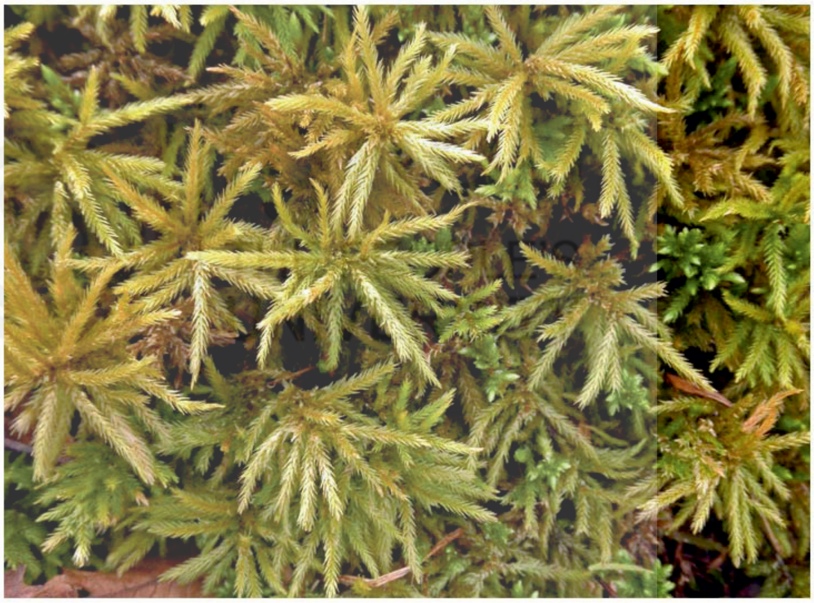


Fig. 15.8: *Climacium americanum.*

***Source*: https://www.google.co.in/search?q=iii)%09Climacium+americanum&source=lnms&tbm=isch&sa=X&ved=0ahUKEwiu5lPqw-LVAhUEu48KHZzXD98Q_AUICigB&biw=1525&bih=700#imgrc=cQdwZ1g_5v6-oM:**

15.3.4 Packaging Materials

Mosses are suitable for packing purposes because they have soft elastic texture and are not easily attacked by microorganisms. In the western United States mosses are used for packing vegetables. In tropics, leafy liverworts are used for packing, largely because of their abundance. In the Himalayas, apples and plums in particular are wrapped in mosses. Nurserymen in India use wet *Sphagnum* for sending or supplying live plants and also for shipment of vegetables, cacti, ferns and other delicate plants. Moist *Sphagnum* is used for packing live frogs, snakes, lizards, worms and some insects for shipment.

15.3.5 Household Uses

As Absorbent

A layer of *Sphagnum* is used in hiking boots for cushioning the foot and absorbing moisture and odour. Dry *Sphagnum* is usd as diapers and in cradles to keep babies clean and warm.

In Azores, mosses are used in making moss beds and pillows. Laplanders use *Polytrichum commune* (Fig. 15.7 a, b) for this purpose. In alpine regions of the North Western Himalayas Indians make beddings, mattresses, cushions and pillows by stuffing mosses into coarse linen sacks or by spreading them on muddy floor of huts. Mosses are preferred due to their soft texture, insect-repellent property and resistance to rotting.

Insect Repellents

It is generally known that bryophytes, even as herbarium specimens, are hardly ever attacked by microorganisms and insects. Many bryophyte species have their own peculiar odour and taste. In many villages of Nainital and Pithoragarh, mosses in particular are used as insect repellents. The locally available mosses and liverworts are dried and coarsely powdered. The moss power is sprinkled over the grains and pulses that are to be stored in containers.

Bryophytes have high concentrations of polyphenolic compounds and high concentrations of accumulated heavy metals in their cell walls in addition to many secondary metabolites, terpenoid oils in their cells. These chemicals make bryophytes repellent as food especially against snails and browsing invertebrates.

Smoke Filters and Pads

Bryophytes are used as smoke filters in the hubble-bubble or 'hookah' in the Kumaon Himalayas.

Women who have to fetch water from long distances in the villages of Kumaon, make a round base of moss mats called 'sirona' which is kept on the head to hold the pitcher.

15.3.6 Treatment of Waste Waters

Sphagnum (Fig. 15.3 a,b) has been used as an effective filtering and absorptive agent for the treatment of waste water and effluents of factories with acidic and toxic discharge containing heavy metals, and many organic substances. Peat can also be used as an absorbent for oil spills and as filtering agent for oily waste water in vegetable oil factories.

15.3.7 Animal Food and Shelters

Food

The biomass of mosses in many vegetational zones of the world is considerable. However, it is in tundra that they are most abundant. The caloric content of mosses from the Canadian Tundra is about 4.5 - 5.0 kcal/g. This is comparable to higher plants growing in the same habitat.

Other than proteins and fats mosses contain a large amount of lignin-like compounds. It is reported that they are rich in vitamins, especially B_2.

Mosses are consumed by many Arctic and Alpine vertebrates like bison, reindeer, caribou, musk ox, arctic geese, lemmings, and rodents.

Another interesting use is feeding of mosses to baby pigs. If pigs are born anemic, the milled *Sphagnum* feed is ideal for binding the iron and vitamins fed to baby pigs. It has ability to absorb and hold nutrients.

Shelter

Bryophytes form shelter for vast array of microorganisms especially slime moulds. Several aphids, nematodes, rotifers and tardigrades get shelter in moss colonies. They provide buffered temperatures and suitable humidity to these organisms. They possess chemicals that deter herbivores.

15.3.8 Horticulture

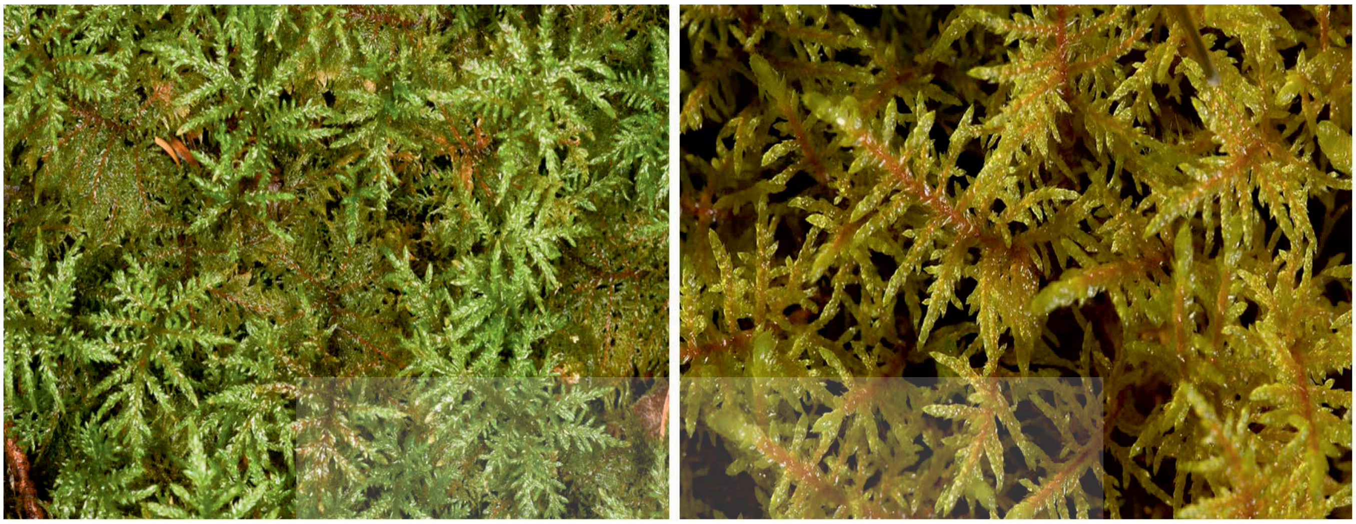
Bryophytes are useful in horticulture because of their high water holding capacity. You may have observed money plant or other climbers growing in pots around sticks. They are used for providing moisture to the plant.

Gardners use moss wrapped hanging baskets and pots for cultivating *Begonia*, *Fuchsia* and Orchids. It is observed that when plants are grown in a pot with a layer of moss sandwiched between the humus-rich top and bottom soil, they grow well and produce buds and flowers more profusely in comparison to the ones grown without it.

Mosses are used as soil additives. Moss carpet serves to stabilize the soil and retain its moisture. When *Sphagnum* (Fig. 15.3 a, b) is mixed with soil or spread over the ground it lightens soil mixture, discourages weed growth and prevents excessive drying of the upper soil layers. Mosses are used as ground cover for making Bonsai.

In Japan mosses have long been used as precious attributes of gardens. They are useful as an evergreen ground cover in much the same way as lawn grasses.

In some countries mosses are used as seed beds. It has been reported that pioneer white spruce in Nova Scotia (Canada) germinates most prolifically in carpets of *Polytrichum*. Similarly, the mosses, especially *Hypnum imponens* provide the seedling bed for *Tsuga* and *Betula*. Extract of *Sphagnum* promotes germination of Jack Pine seeds. Mosses such as *Pleurozium schreberi* (Fig. 15.9 a, b) has been found to act as good seed beds for the germination of seeds of pines.



(a) (b)

Fig. 15.9 (a,b): ***Pleurozium schreberi*****: a) A small patch; b) An enlarged view.**

Source**: a) https://www.google.co.in/search?q=Pleurozium+schreberi&source=lnms&tbm=isch&sa=X&ved=0ahUKEwjJ5-3FxuLVAhULLo8KHbvNAJ8Q_AUICigB&biw=1525&bih=700#imgrc=z9_radFd3OkoAM:**
b) https://www.google.co.in search?q=Pleurozium+schreberi&source=lnms&tbm=isch&sa=X&ved=0ahUKEwjJ5 3FxuLVAhULLo8KHbvNAJ8Q_AUICigB&biw=1525&bih=700#imgrc=1ZTJe6sYwBV24M:

SAQ 2

a) Why *Sphagum* dressing is more absorbent than cotton dressing?

b) Choose the correct alternative from those provided in parentheses.

i) (Mosses/Liverworts) are used for stuffing beddings, mattresses and pillows.

ii) (*Climacium*/*Sphagnum*) are fashioned into wreaths and crosses.

iii) Seeds of pines are sown in seed beds made up of (*Funaria*/*Pleurozium*).

iv) Active substance diplophylline obtained from a liverwort is an (antiallergen/antitumour) compound.

v) Cracks in wooden boats are plugged with aquatic moss (*Fontalis*/*Neckera*).

15.4 SUMMARY

In this unit you have learnt that:

- Bryophytes serve as important and significant carbon-sink and play important ecological role in water and nutrient recycling.
- Bryophytes help maintain grasslands and heathlands.

- Bryophytes are pioneers of vegetation on bare rock surfaces, burnt sites where no other plant can grow. They make the substratum suitable for invasion of vascular plants.
- A moss *Sphagnum* plays an important role in the formation of peatlands that serve as reservoir of life of the past.
- Bryophytes help in controlling soil erosion on river banks, forest floors and road sides. They form compact cushions and their rhizoids bind soil particles so tightly that they do not flow along with running water.
- Some bryophytes serve as indicators of certain minerals, pH condition of soil, air and water pollution, whereas some others can be used as indicator species because they are associated with some vascular plants.
- Bryophytes have been used by many vertebrates and invertebrates as food and shelter. Many birds use them for making nests.
- In cold temperate regions of the world native people widely use bryophytes as medicines; insect repellents; pads; stuffings-, packing-, and chinking- materials; and smoke filters.
- They are used for horticultural purposes because of their water holding capacity.

15.5 TERMINAL QUESTIONS

1. Explain the role of Bryophytes in soil erosion.
2. Give a brief account of the various uses of bryophytes.
3. Discuss role of *Spagnum* in peat bog formation.
4. Why are bryophytes used for horticultural purposes?
5. Discuss the role of bryophytes as indicators of pollution.
6. How do bryophytes help recycling of nutrients?

15.6 ANSWERS

Self-Assessment Questions

SAQ 1

a) (i) (3)

(ii) (1)

(iii) (2)

b) Bryophytes build up organic layer in soil. The microorganisms invade this layer and make it nutrient rich, so the site becomes suitable for various plants.

c) Refer Sub-section 15.2.2

d) (i) *Sphagnum*; (ii) *Mielichhoferia*; (iii) SO_2

e) Refer Sub-section 15.2.7

SAQ 2

a) Refer Sub-section 15.3.1

b) (i) Mosses

(ii) *Climacium*

(iii) *Pleurozium*

(iv) antitumour

(v) *Neckera*

Terminal Questions

1. Refer to Sub-section 15.2.2
2. Hint: elaborate Section 15.3
3. Refer to Sub-section 15.2.11
4. Hint: Water-holding capacity, elaborate Sub-section 15.3.8
5. Refer to Sub-section 15.2.10, and elaborate each point in 3-4 lines.
6. Refer to Sub-section 15.2.3

15.7 GLOSSARY

Active compound : A chemical of medicinal value, obtained from an organism.

Alien : A species that is not commonly present in a given region.

Ecosystem engineers : Those organisms that create, modify and maintain certain habitats that are best suited for themselves to thrive, e.g., *Sphagnum* and peatland.

Dolomite : Calcium-rich soils/rocks.

Magnesite : Magnesium carbonate-rich rocks.

Matrotrophy : The first cell of a sporophytic generation (zygote) and young embryo retained in an archegonium and nourished by gametophytic maternal tissue.

Paludification : A dynamic process of peat accumulation over a dry former mineral soil involving formation of water-logged conditions.

Poikilohydric : Organisms that are able to dry out and become physiologically inactive and get physiologically active upon rehydration.

Symbionts : Two organisms that cohabit and are beneficial to each other, a mutualistic relationship.

15.8 FURTHER READING

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