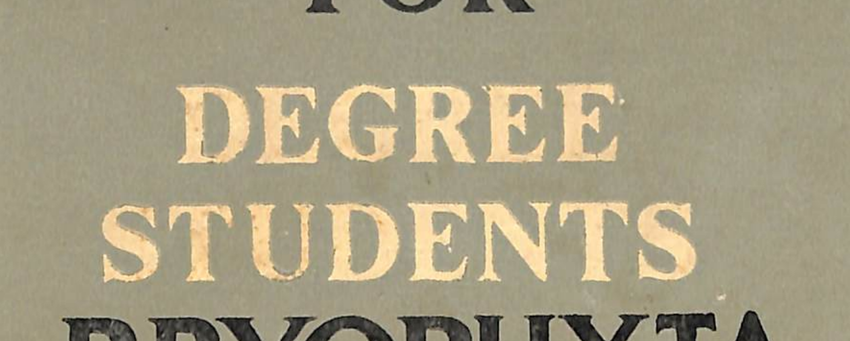
BOTANY
FOR
DEGREE STUDENTS
BRYOPHYTA



B. R. VASHISHTA

BOTANY

[For Degree Students]

PART III

BRYOPHYTA

By

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PREFACE TO THE FOURTH EDITION

The third edition of the book was published in January, 1968. All the copies were sold out by September, 1969. The encouraging response from the kind readers and the continued demand for the book has compelled the author to make the new edition more comprehensive.

With this point in view the text has been extensively revised in the light of latest research in the subject. An attempt has also been made to make it still more understandable. Some parts have been expanded and the life history of *Notothylas* has been added. A few new illustrations have been included.

It is a great pleasure to record my deep sense of gratitude to Prof. R.S. Chopra for his kind suggestions to improve the book.

B.R. VASHISHTA
CHANDIGARH

PREFACE TO THE FIRST EDITION

Part III of the series deals with a small group of primitive, thalloid plants, amphibious in habit. They are placed in the division Bryophyta. The bryophytes are peculiar in having the gametophyte as green and independent and sporophyte wholly or partially dependent upon it. The subject matter has been presented in a simple, lucid style. The obscure literary style has been avoided. The scheme followed is the same as in Parts I and II. An attempt has been made to include the latest and the significant results of botanical research on the subject. The type system is still considered the best for the undergraduate.

A simple and a clear account of structure, reproduction, function and relationships of the important members of each class is a notable feature of the book. A diagrammatic representation of the life cycle of each type gives a clear picture of the pattern of Alternation of Generations. Salient features of the division and its classes down to the orders and the type plants whose life histories have been discussed appear at the end of each respective chapter.

The bryophytes have been discussed as amphibians of the Kingdom Plantae in the first chapter which also deals briefly with the various life phenomena of this peculiar assemblage of plants whose origin is obscure even up to this age of scientific development. Chapter III deals with the structure and the various theories which attempt to explain the origin of the Marchantiaceous thallus. In the concluding chapter some general topics relating to the subject have been dealt with. It also includes exhaustive comparisons between the type plants of the various classes of the bryophytes.

All the available standard text books on the subject and research journals have been consulted. Grateful thanks are due to the authors, editors and the publishers of these books and journals The most eminent among the authors deserving special mention are Campbell, Bower, Cavers, Mehra and Proskauer. I am also grateful to Dr. Mehra for making available all his publications on the subject.

My sincerest thanks go to my colleague in the Department Dr. V.P. Dube for critically reading a portion of the manuscript and for making most of the figures of *Funaria*. Without his enthusiastic support it would not have been possible to bring out the book this year. The author alone, however, is responsible for the factual mistakes. I also owe a deep debt of gratitude to Dr. P.C. Joshi (Principal and Head of the Botany Department Government College, Rupar), Dr. A.B. Gupta (Head of the Botany Department, Christ Church College, Kanpur), Prof. D.N. Srivastava (Head of the Botany Department, Bareilly College, Bareilly), Prof. N. S. Madan (Head of the Botany Department. Government College, Rohtak) and Prof. S.P. Aggarwal (Head of the Botany Department B.S.A. Degree College, Mathura) of the encouragement and inspiration received from them. Finally I express my thanks to my publishers particularly Sri Shyam Lal Gupta and Sri Prem Nath Kapur, the production manager, for providing me all the facilities in the publication of this volume.

ROHTAK
August, 1963

B.R. VASHISHTA

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CHAPTER I

INTRODUCTORY

Bryophytes as amphibians of the kingdom plantae. Plants grow in two well defined habitats. These are the water and the land. The plants which grow in water are called the **aquatics**, and the others **terrestrial**. The best examples of aquatic plants are the **algae** and of land dwellers the **seed plants** (spermatophytes). Between these two extremes of habitats is a transitional zone. It is represented by the swamps and the areas where water and land meet. It may well be called the **amphibious zone**. Inhabiting the amphibious zone are the mosses, liverworts and hornworts which collectively constitute a group of non-vascular land plants called the *bryophytes*. The latter are simple, thallus-like plants which suggest the stages through which the green algae may have evolved to become terrestrial. Most of the bryophytes are land dwellers which inhabit damp, shaded and humid localities. A few of them, however, live in or float on water. The aquatic habit, of course, has been acquired by these plants secondarily. When the water dries up they grow equally well on the drying mud. Some, of course, can withstand long periods of drought. During the dry period they become almost brittle in texture. With the onset of rainy season the apparently dried, brittle thalli turn green and become active to carry out the normal life functions. Even these apparently xerophytic species grow actively only during the wet weather.

Evidence supports the view that these early land plants descended from alga-like ancestors which were probably green. Adaptation to land environment or sub-aerial life involved the development of certain features that were not possessed by their aquatic ancestors. These are :

1. **Development of organs for attachment and absorption of water**. Unlike algae the bryophytes which grow on land are not bathed in water. They must absorb it from the soil and be attached to it for support. For this purpose the bryophytes develop special, hair-like structures called the **rhizoids**. Like root hairs the rhizoids function as absorbing and attaching organs.

2. **Protection against desiccation**. The thick, compact, multicellular, thallus-like plant body covered with an epidermis is protected to a certain extent against the drying effects of air. Of the numerous cells constituting it only the epidermal cells, which

form only a small percentage of its total surface, are directly exposed to the dry air. Further even the free surface of the epidermal cells, in some species of liverworts, are coated with a waxy substance like **cutin** which is water proof and thus reduces the rate of water loss. Moreover total surface area of a compact body is reduced in proportion to its volume

3. **Absorption of carbon dioxide from the atmosphere for photosynthesis.** In many liverworts there are numerous pores on the upper surface of the thallus. These are called the **air pores**. They facilitate gaseous exchange between the atmospheric air and the interior of the thallus.

4. **Protection of reproductive cells from drying and mechanical injury.** The sex organs in the bryophytes are multicellular and jacketed. The jacket of sterile cells around the sperms and eggs is an adaptation to a life on land. It protects the sex cells against the drying effects of air.

The fertilized egg is retained within the archegonium. Here it obtains food and water from the parent plant and is protected from drying as it develops into an **embryo**. This adaptation is essential for the survival of the land plants. It ensures nursing of the young embryo and its protection against mechanical injury.

5. The thick-walled wind disseminated spores and the primitive vascular system in the form of a conducting strand are the other adaptations to land habit.

The bryophytes, however, connot carry on their reproductive activities without sufficient moisture. Presence of water is necessary.

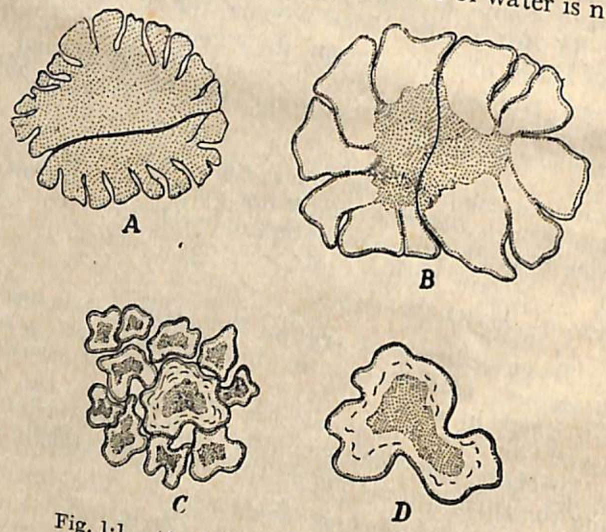


Fig. 1·1. (A—D). Riccia sp.
A—B. Riccia robusta (R. crystallina)
C—D. Riccia cruciata.

Without it the sex organs do not reach maturity and do not dehisce. Water is essential for the transfer of sperms to the archegonium. The retention of swimming sperms is an algal characteristic. The bryophytes thus rely on water for the act of fertilisation. Besides they have inefficient absorbing organs in the form of rhizoids. Consequently they are unable to grow during dry periods. They require sufficient moisture both for reproduction and successful vegetative growth. This explains why the bryophytes usually inhabit moist, shaded situations (amphibious habitat) or grow in places where water is abundant at least at some season. Since the bryophytes usually grow in amphibious situations and cannot complete their life cycle without external water they can very appropriately be called the **amphibians** of the plant world.

The bryophytes have evolved a life cycle which comprises two phases—**gametophyte** and **sporophyte**. The former is the most conspicuous of the two and independent. We start our discussion of the bryophytes with this phase of the life cycle.

GAMETOPHYTE GENERATION

(*a*) **Plant Body**. The bryophytes are a small group of most primitive land dwellers. They number about 24,000 species which are grouped under nearly 960 genera. All of them are small and inconspicuous plants. The plant body is undoubtedly more differentiated than that of a complex Alga. It is compact and better protected against desiccation. However it is relatively simple in the lower forms and still reminds one of the thallus of an Alga. It grows prostrate on the ground and is thallus-like (Fig. 1·1 A—D). It is attached to the substratum by delicate, unicellular, hair-like organs called the **rhizoids.**

In the higher bryophytes such as the Mosses the plant body is erect. It has a stem-like central axis which bears leaf-like appendages (Fig. 1·2A). It is fixed to the substratum by means of branched, multicellular **rhizoids** apparently resembling the **roots**. The rhizoids arise from the older, basal part of the stem. These organs of the bryophytes are, however, not **homologous** with those of the higher plants. They lack the vascular tissue characteristic of the stems, leaves and roots of the higher plants. Besides, they belong to the haploid generation whereas those of the higher plants represent the diploid generation. The organs which are similar in function but different in origin are said to be **analogous.** The stem, leaves and rhizoids of the bryophytes are thus analogous to the stems, leaves and roots rather root hairs of the vascular plants. The root hairs like the rhizoids of liverworts are unicellular structures. In contrast the rhizoids are borne upon the gametophyte generation and root hairs on the sporophyte. The two are thus analogous to each other. Some botanists look upon even the moss type of plant body of the bryophytes as a highly differentiated thallus.

The thallus bears the gametes. So it is called the **gametophyte** plant. It is concerned with sexual reproduction and constitutes the most conspicuous, nutritionally independent phase in the life cycle.

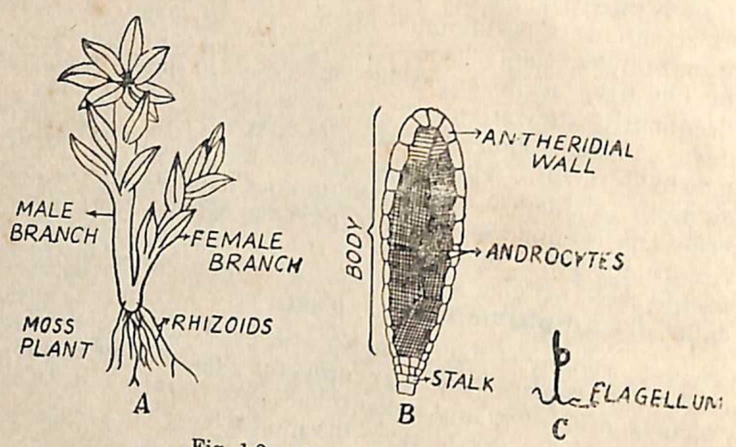


Fig. 1·2 (A—C). Funaria sp.
A. Gametophyte plant.
B. Longitudinal section of antheridium.
C. Sperm.

(b) **Reproduction**. Bryophytes show a marked advance over the thallophytes in the method of sexual reproduction. Without exception it is highly **oogamous** in the whole group. The gametes are produced in complex sex organs. They have attained a degree of complexity far above that of the thallophytes. In the thallophytes the sex organs are generally simple and unicellular. They are devoid of any wall of sterile cells. The gametes are formed directly out of the protoplasts of these sex cells. The bryophytes, on the other hand, have multicellular, jacketed sex organs. Each sex organ consists of an outer, protective wall of sterile cells surrounding the cell or groups of cells which produce the gametes. The male sex organ is still called the **antheridium**. The female, however, is known as the **archegonium** and not the oogonium or the ascogonium.

(*i*) **Antheridium**. The antheridium (Fig. 1·2 B) is a multicellular object, ellipsoidal or club-shaped in form. It is borne on a short stalk which attaches it to the gametophyte tissue. Often it is embedded in the latter. The body of the antheridium has a wall of a single layer of sterile cells. It surrounds a mass of small squarish or cubical cells called the **androcytes** (Fig. 1·2 B). The latter produce the biflagellate male gametes called the **sperms** (Fig. 1·2 C). Several sperms are produced in each antheridium. They are motile structures. Each sperm usually consists of a minute, slender, spirally curved body furnished with two long, terminal, whiplash type flagella.

(*ii*) **Archegonium** (Fig. 1·3). The female sex organ of the bryophytes is a remarkable structure. It is called the **archegonium**. It appears for the first time in the liverworts and mosses and continues in the pteridophytes. In this respect the liverworts and mosses seem to be akin to the pteridophytes than to the Algae to which they resemble in their thallus-like plant body. This common feature tempted the earlier botanists to place the bryophytes and the pteridophytes collectively in the division **Archegoniatae**. They are, however, very unlike in other features and completely unrelated to each other. Hence it is thought best to separate the Liverworts and Mosses from the Pteridophytes on one hand and the thallus bearing plants (Thallophytes) on the other. They are included in a distinct group **Bryophyta**.

The archegonium (Fig. 1·3) is a flask-shaped organ. The slender, elongated upper portion is called the **neck** and the lower saclike, swollen portion, the **venter**. The venter is attached to and often deeply embedded in the parent plant tissue. The neck has a wall of a single layer of sterile cells which surrounds a central row of elongated, naked cells. These are called the **neck canal cells**. The neck is usually projecting or freely exposed so as to be accessible to sperms. The venter also has a wall of sterile cells one or more cell layers in thickness. The venter wall encloses two cells. They are the larger **egg** cell or the **ovum** and the smaller **ventral canal cell** just above it.

(*iii*) **Fertilization** (Fig. 1·3). It occurs when the sex organs are mature. Moisture is essential for the maturing of the sex organs and also for the movements of the sperms to the archegonia. The mature antheridium ruptures at its apex liberating the sperms. At the same time the axial row of neck canal cells including the ventral canal cell in the mature archegonium disorganise. The tip of the archegonium also opens. A narrow canal opening to the exterior is formed. It acts as a passage way to the ovum in the venter. The liberated sperms swimming in a thin film of water reach the archegenia. They enter through the open necks and swim down the canals of the archegonia (Fig. 1·3). Reaching the venter one of them, probably the first one to reach there, penetrates the ovum. It fuses with the nucleus of the ovum to accomplish fertilization. With the act of fertilization the gametophyte generation ends and the sporophyte generation starts. The gemetes (sperms and eggs) are the last structures of the gametophyte generation.

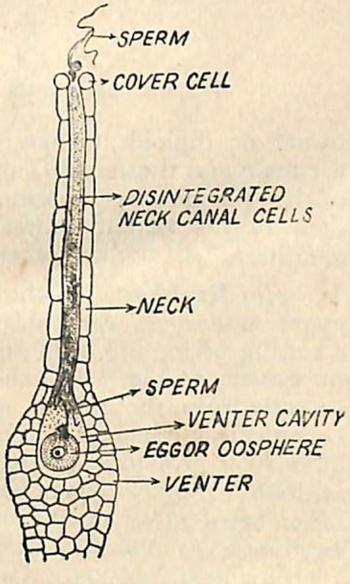


Fig. 1·3. Moss Archegonium showing fertilisation.

SPOROPHYTE GENERATION

(a) **Zygote** (Fig. 1·4 A). The fertilized ovum or egg, now called the **zygote**, secretes a cellulose wall around it. It has a fusion or diploid nucleus as it contains chromatin material of both the male and the female gametes. The zygote marks the beginning of the sporophyte generation in the life cycle. It is neither independent of the parent gametophyte plant nor passes into the resting condition. In both respects it differs from the zygote of the Algae.

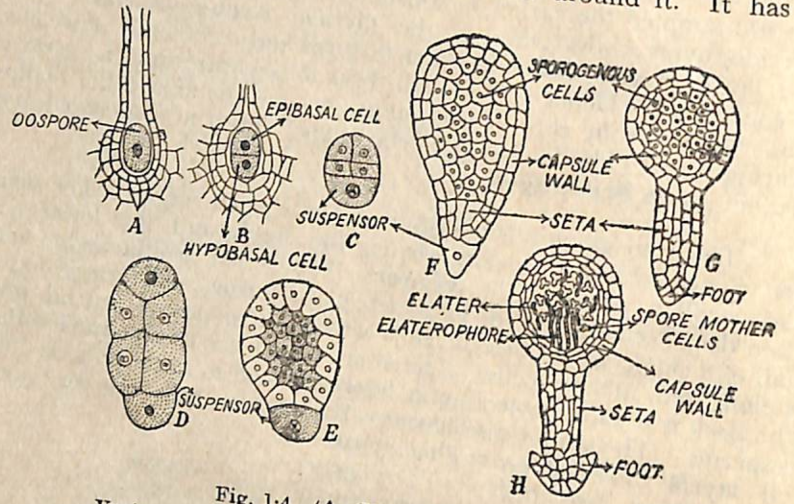


Fig. 1·4 (A—H). Pellia sp.
Various stages in the development of the sporophyte.

(b) **Embryo**. Within the venter of the archegonium the zygote undergoes segmentation (Fig. 1·4 B—D) and develops without a resting period into a multicellular, undifferentiated structure called an **embryo** (Fig. 1·4 D and Fig. 1·5). It obtains its nourishment directly from the thallus of the parent gametophyte to which it is organically attached. The zygote of the bryophytes has thus a better chance for growth as compared with the zygote of the thallophytes which is always independent. The latter accounts for the absence of embryo stage in the thallophytes. The embryo stage in the bryophytes is of short duration.

(c) **Sporogonium**. The embryo by further segmentation and differentiation finally develops into a full-fledged sporophyte individual. It is called the **sporogonium** (Fig. 1·4 H). The sporogonium is usually of a limited life span. In some bryophytes it remains embedded in the gametophyte tissue (*Riccia*). Generally it is projecting and consists of three parts, the **foot**, the **seta** and the **capsule** (Fig. 1·6). The foot is embedded in the tissue of the parent gametophyte. It absorbs nutrition for the sporogonium. The rest of the sporogonium is free and projecting to promote easy dispersal of spores. The seta conducts the food absorbed by the foot to the

capsule. The capsule is mainly concerned in the production of spores. The latter are differentiated by meiosis and are thus haploid in nature. The spores are non-motile and wind disseminated. Swimming spores characteristic of the Algae are never present in the bryophytes. With meiosis the sporophyte generation in the life cycle terminates. The meiospores thus mark the beginning of the new gametophyte generation. Each spore germinates under suitable conditions to give rise to the gametophyte plant.

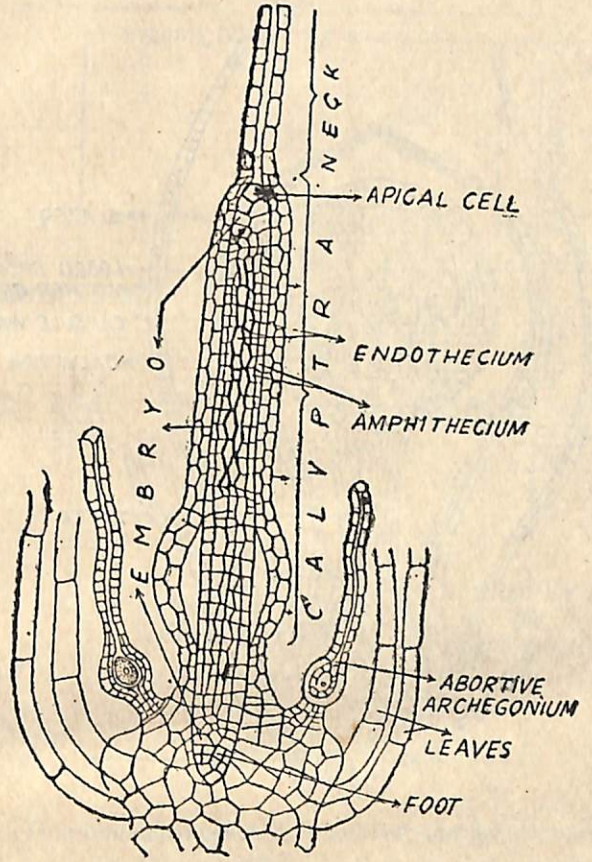


Fig. 1·5. Moss embryo.

Sporogonium is the whole product of the sexual act. It remains attached to the plant bearing sexual organs (oophyte). It is considered a **second individual** in the life cycle and not simply a part or an **outgrowth** of the parent plant (thallus or gametophyte). *The reasons are obvious.* The sporogonium is an individual with a different inheritance as it is developed from the diploid zygote. It is made up of cells containing a diploid number of chromosomes as contrasted with the haploid number characteristic of the gametophyte. Besides it differs from the parent gametophyte in its function.

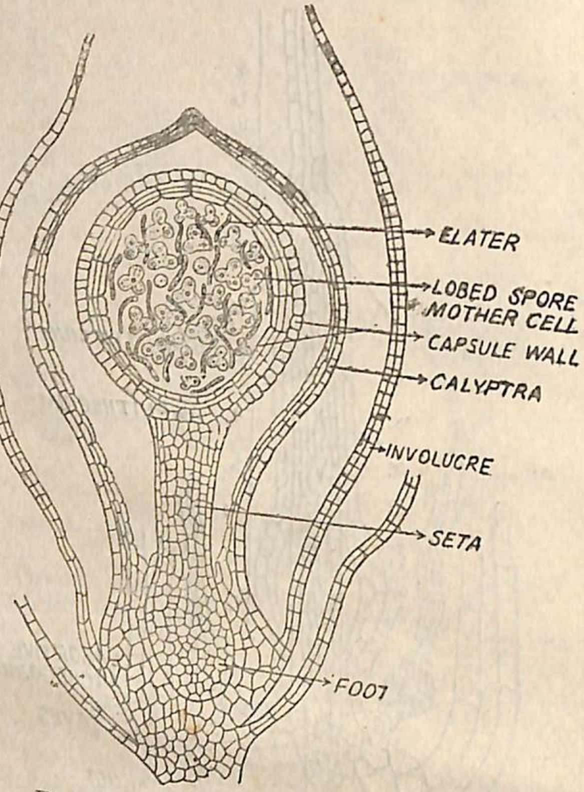


Fig. 1·6. Porella sp. V.S. Sporogonium.

It produces haploid spores. For this reason the sporogonium of the bryophytes is often called the **sporophyte**. The spores are non-motile and thus dispersed by air. In its nutrition, of course, the sporophyte is dependent partly or wholly on the gametophyte plant.

Another remarkable feature of the bryophytes in which they differ from the thallophytes, is the complete absence of asexual spores called the **mitospores** (motile as well as non-motile) in the life cycle. Asexual reproduction takes place only by the vegetative methods of fragmentation and gemmae. No true asexual spores are formed.

Alternation of Generations (Fig. 1·7). The life cycle of the bryophytes is very interesting. It is split up into two phases, each represented by a separate adult. Thus in a single life cycle there occur two distinct multicellular, vegetative individuals. One of these is the green **thalloid** (liverworts) or **leafy** (mosses) plant.

The other is the **sporogonium**. The green individual is the most conspicuous of the two. It is an independent plant. It is haploid and bears the sex organs (antheridia and archegonia) which produce the gametes (sperms and eggs). As it bears the gametes the green, independent individual is called the **gametophyte**. It is concerned with sexual reproduction. The gametophyte plant along with the structures produced by it constitutes the **gametophyte generation**. In the life cycle it starts with the formation of **spores** and consists of the **green individual** and the **sex organs**. The last structures formed during this phase are the **gametes**. The gametes fuse to form a zygote.

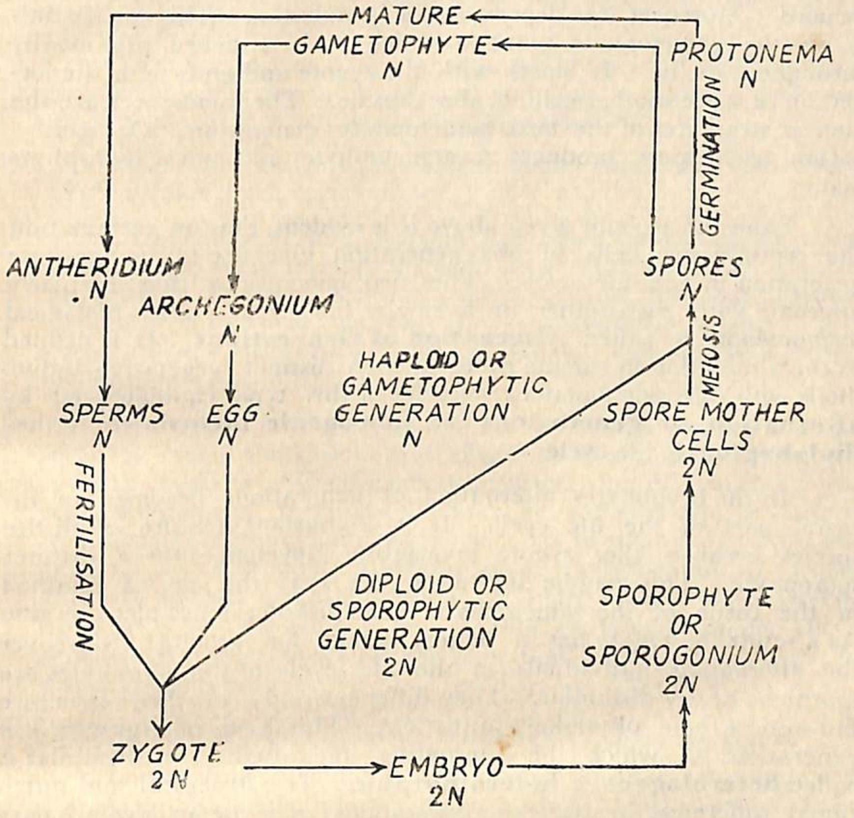


Fig. 1·7. Graphic representation of the life cycle of Bryophytes.

The zygote, on germination, does not produce the gametophyte plant. It undergoes segmentation to form an **embryo**. The embryo by further segmentation and differentiation gives rise to the second adult called the **sporogonium**. It remains diploid and is usually differentiated into **foot**, **seta** and **capsule**. In due course of time the diploid **spore mother cells** by **meiosis** give rise to haploid spores. We may refer to them as **meiospores**. As the sporogonium is concerned with the production of spores it is called the **sporophyte**. The **zygote**, the **embryo** and the **sporogonium** together constitute the **sporophyte generation**. It is less conspicuous. Moreover it is dependent for its nutrition wholly or partially on the gametophyte plant to which it is attached organically throughout its life. It starts with the zygote and ends with the formation of spore mother cells in the capsule. The meiospores are the pioneer structures of the next gametophyte generation. On germination each spore produces a gemetophyte and not a sporophyte plant.

From the account given above it is evident that on germination the reproductive cells of one generation give rise to the alternate generation in the life cycle. The two generations thus regularly alternate with each other in a single life cycle. This biological phenomenon is called **Alternation of Generations**. It is defined as the alternation in the life cycle of two distinct vegetative individuals with different functions. Cycles of this type characterized by **alternation of generations** and **sporogenic meiosis** are termed **diplohaplontic** life cycles.

In the bryophytes alternation of generations becomes an integral part of the life cycle. It is a constant feature of all the species because the zygote invariably develops into a distinct sporophyte. This may be due to the fact that the egg is retained in the tissue of the gametophyte. Fertilisation takes place *in situ*. As a result the zygote has a better chance for growth. Moreover the alternating individuals in the life cycle of the bryophytes are morphologically dissimilar. They differ not only in their structure but also in their physiology (nutrition). This kind of alternation of generations in which the alternating individuals are dissimilar is called **heterologous** or **heteromorphic**. The structural and nutritional difference in the two generations may be an evolutionary sequence due to the different modes of life. The gametophyte is independent. The sporophyte is not. It is attached and generally parasitic wholly or partially on the gametophyte. The attached condition of sporophyte can lead to dissimilarity. This viewpoint is supported by an analogy from the red algae. The attached carposporophyte of *Polysiphonia* is quite different from its free living gametophyte. On the other hand the free living tetrasporophyte is identical to the gametophyte.

In Algae alternation of generations is not a constant feature of all the species. It occurs in isolated instances. The vegetative sporophyte is generally absent. It is represented only by the single-celled zygote. The zygote being independent usually lacks enough resources to develop into a distinct sporophyte. Moreover, the sporophyte in Algae when developed is always independent of the gametophyte plant. In cases where there is alternation of generations the two alternating individuals in the life cycle generally resemble each other. Morphologically they are identical. This type of

alternation of generations in which both the alternating generations are structurally similar is called **homologous** or **isomorphic**.

Besides food the two most important biological needs of every living plant species are :—

I. Production of new individuals. Really new individuals are produced by the fusion of male and female gametes from different plants. It is called **cross-fertilization**.

II. Their dispersal to suitable places where they can find their food without much competition.

In Algae both these problems are solved by the agency of water. The gametes swim through water to fuse. The resultant zygotes are dispersed by the water currents. This accounts for the absence of structural differences between the two alternating plants in the life cycle. There is thus no division of labour. Hence the alternating generations are similar.

Among the land dwellers such as the bryophytes the two problems of cross-fertilization and dispersal are solved on the basis of division of labour. Each generation caters to and is suitably adapted to solve one of these problems. The gametophyte is concerned with sexual reproduction. It thus caters to the need of cross fertilization. The sporophyte functions in the multiplication of beneficial effects of a single sexual union. It produces minute spores which are distributed by the wind. The division of labour among the two generations thus accounts for the structural difference between them in the bryophytes. ✓

Alternation of Chromosome Number in the Life Cycle

Each cell of the gametophyte generation has a certain number of chromosomes in its nucleus. It is represented by the symbol *N*. The numerical value of *N* differs in the different species. Each gamete thus has *N* chromosomes in its nucleus. It is the basic number. At the time of fertilisation the nuclei of the **sperm** and **egg** fuse. The **paternal** and the **maternal** chromosomes, however, do not fuse. They simply become closely associated in pairs in the fusion nucleus. The fusion nucleus in the zygote now has *N* plus *N* or 2 *N* chromosomes. The single number *N* is called **haploid** or **monoploid** number. All structures with *N* chromosomes are thus **haploid**. On this basis the gametophyte generation may be called the **haploid generation** in the life cycle. The 2 *N* number is called **diploid**. The zygote with 2 *N* number of chromosomes thus is a diploid structure. The sporogonium which is developed from the zygote by repeated mitosis is a diploid individual in the life cycle. All the cells of the sporophyte generation (sporogonium) up to and including the spore mother cells are diploid. At the time of **fertilization** the haploid generation switches on to the diploid. With **meiosis** the diploid generation switches back to haploid. The **alternation of generations** is thus accompanied by the alternation of chromosome numbers from the haploid to the diploid and back to the haploid condition.

Origin of Alternation of Generations. It is still a live question. Two theories namely, **antithetic** and **homologous** have been proposed to explain how alternation of generations originated.

Antithetic Theory. It was the first to be proposed. On the basis of this theory the gametophyte or sexual plant represents the original generation. The sporophyte or the non-sexual organism is a new and different phase evolved by progressive elaboration of the diploid zygote of some algal ancestor like *Coleochaete*. It is interpolated in the life cycle of the gametophyte of primitive land plants between the two crucial points, **fertilisation** and **meiosis** in response to a life in a drier environment. The factors which caused its origin are prompt germination of the zygote accompanied by delayed meiosis.

The result is the production of a small sporophyte of *Riccia* consisting simply of a spore case. With further elaboration and increased sterilisation of the spore producing tissue a larger sporophyte with differentiation into a foot, a seta and a capsule is finally evolved.

Homologous Theory. On the basis of this theory the sporophyte is simply a modification of the gametophyte and not a new generation evolved in response to a life in a drier environment. The advocates of this theory point to the fact that among the green algae the gametophyte plant reproduces by both the methods of reproduction. It bears spores and also the gametes. In the course of evolutionary sequence these two functions became separated in two distinct individuals. One of these produced the spores and the other produced gametes. The former came to be known as the **sporophyte** and the latter **gametophyte**. These two individuals occur regularly one after the other in the life cycle. The occurrence of two similar generations in most of the algae furnishes a strong argument in favour of this theory. The phenomenon of apospory and apogamy is another. Both the individuals in primitive land plants were photosynthetic and free living. Gradually the sporophyte became attached to and partly parasitic on the gametophyte. Consequently it became reduced.

Salient features 1. The bryophytes are a small group of primitive **land dwellers**. They have a **leafy** or **thalloid**, green plant body which is small in stature, rarely more than 5 inches.

2. In their vegetative structure they have become completely adapted to the land habit. However they still rely upon water for sexual reproduction because the swimming habit is retained by their sperms.

3. The plant body lacks the true roots, stems or leaves. It is relatively simple in the lower forms and still reminds of the **thallus** of an alga. It grows prostrate on the ground and is attached to the

substratum by delicate, unbranched, unicellular hair-like organs called the **rhizoids**. In the higher bryophytes (mosses) the plant body is erect. It consists of a central axis which bears leaf-like expansions. It is attached to the substratum by branched, multicellular rhizoids.

4. Like the thallophytes the most conspicuous phase in the life cycle is the **gametophyte**. It is independent and concerned with sexual reproduction.

5. The bryophytes like the thallophytes lack the vascular tissue (xylem and pholem) characteristic of the higher plants.

6. In sexual reproduction they show a marked advance over the thallophytes. It is invariably highly **oogamous**. The sex organs are **jacketed** and **multicellular**. In Algae they are **non-jacketed** and **unicellular**.

7. Female sex organ in the form of an **archegonium** appears for the first time in the bryophytes in the plant world.

8. The sperms are **biflagellate**. Both the flagella are of **whiplash** type.

9. Fertilization takes place in the presence of water.

10. The fertilized egg is retained within the venter of the archegonium. It neither becomes independent of the parent gametophyte nor passes into the resting period. In both these respects the bryophytes differ from the algae.

11. The zygote undergoes repeated division to form an undifferentiated, multicellular structure called the **embryo**. The first division of the zygote is transverse and the apex of the embryo develops from the outer cell. Such an embryogeny is called **exoscopic**. It is characteristic of the bryophytes. No embryo stage exists in the thallophytes.

12. The embryo by further division and differentiation produces a relatively small spore producing structure which is not independent. It is called the **sporogonium** (sporophyte). It consists of a foot, a seta and a capsule. In some the seta is absent (*Corsinia*) and rarely both, the foot and the seta (*Riccia*).

13. The sporophyte is thus simpler than the gametophyte and is organically attached to the parent gametophyte throughout its life. It is dependent upon it partially or wholly for its nutrition. In Algae the sporophyte generation when present is always independent of the parent gametophyte.

14. The sporogonium is concerned with the production of wind disseminated, non-motile, cutinized spores which are always gonospores or meiospores.

15. The meiospores are all of one kind. Hence the bryophytes are **homosporous**.

15. Each spore on falling on a suitable soil germinates to give rise to the gametophyte plant either directly or indirectly as a lateral bud from the **protonema**.

16. The occurrence of **heterologous** type of **alternation of generations** is a constant feature of the life cycle of bryophytes. In Algae when present it is of **homologous** type.

The differences between the thallophytes and bryophytes are tabulated below:

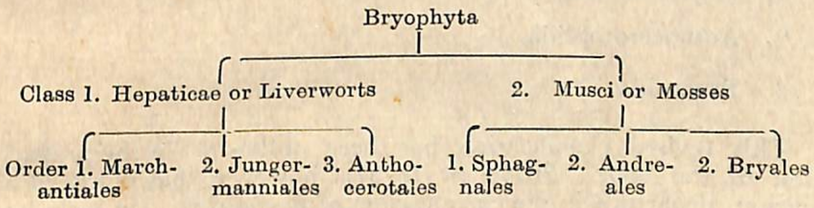
Thallophyta	Bryophyta
1. Mainly aquatic.	1. Chiefly terrestrial.
2. The thallus generally consists either of a single cell or a filament of cells or of intertwining filaments. Layers of parenchyma occur in a few.	2. The thallus, excepting in the protonema stage, is never filamentous. It is made up of sheets of parenchyma cells.
3. Asexual reproduction by the formation of mitospores common in the growing season.	3. Complete absence of mitospores in the life cycle. Asexual reproduction takes place by vegetative methods only.
4. Reproduce by meispores in addition to mitospores.	4. Reproduce entirely by meiospores.
5. The sex organs are usually single celled, sometimes of groups of single cells but always without a jacket of sterile vegetative cells.	5. The sex organs are always multicellular protected by a jacket of sterile vegetative cells.
6. Sexual reproduction ranges from **isogamy**, through **anisogamy** to **oogamy**.	6. Sexual reproduction is invariably **oogamous**.
7. The female sex organ is the **oogonium** or **ascogonium**.	7. The female sex organ is the flask-shaped **archegonium** which is characteristic of land plants only.
8. The zygote is usually liberated and frequently passes into the resting stage.	8. The zygote is neither liberated nor passes into the resting stage.
9. No embryo formation after gametic union.	9. All bryophytes develop embryo after gametic union.
10. Many exhibit alternation of generations but it is of **homologous type**,	10. All exhibit alternation of generations but it is always of **heterologous type**.
11. Both the gametophytes and sporophytes are independent.	11. The sporophyte is organically attached to and is nutritionally dependent upon the gametophyte.

Resemblances between the bryophytes and the Algae :—

1. Thallus-like plant body.
2. Lack of vascular tissue.
3. Absence of roots.
4. Conspicuous plant in the life cycle being the gametophyte.
5. Autotrophic mode of nutrition.
6. Retention of the swimming habit by the sperms which indicates the algal ancestry of the bryophytes.
7. The early stages of development in the gametophyte of many bryophytes are green filaments which strikingly resemble the filamentous thallus of green algae.
8. The chloroplast pigments in the vegetative cells of bryophytes are identical with those of green algae.

The above mentioned similarities give support to the view that the Bryophytes have evolved from the algal ancestors particularly the green Algae.

Classification. The rank of a division Bryophyta to this well-defined group of plants was first given by Schimper in 1879. Later Eichler in 1883 recognised two groups, **Hepaticae** and the **Musci** in the Bryophyta. Since then these two classes remained as separate, major entities within the division. Engler 1892 subdivided each of the two classes into three orders as follows :—



This system of classification with slight modifications is still followed by many eminent bryologists.

The anomalous position of Anthocerotales as an order of the class Hepaticae was pointed out by many investigators very early. The important among them were deBary, ex Janczewski (1872), Leitgeb (1879) and Underwood (1894). However it was Howe who in 1899 gave the class status to the order Anthocerotales. He named it **Anthocerotes** and divided the Bryophyta into three classes, **Hepaticae**, **Anthocerotes** and **Musci**.

Many eminent hepaticologists like Campbell (1918, 1940), Smith (1938, 1955), Takhtajan (1953) followed him and supported his move to divide the Bryophyta into three classes but Smith, Takhtajan and later Wardlaw (1955) and Schuster (1958) called the Anthocerotes as **Anthocerotae**.

The consensus of opinion at present favours this view and the Bryophyta is classified as follows into three classes :

Bryophyta

Classes 1. Hepaticae 2. Anthocerotae 3. Musci

Rothmaler in 1951 suggested the following class taxons for the old ones :

1. **Hepaticopsida** for Hepaticae.
2. **Anthoceropsida** for Anthocerotae.
3. **Bryopsida** for Musci.

The new names suggested by Rothmaler have been recognised by the International Code of Botanical Nomenclature. Proskauer in 1957 suggested the name Anthocerotopsida for Anthoceropsida. The modern bryologists thus classify Bryophyta into the following three classes :—

1. Hepaticopsida.
2. Anthocerotopsida.
3. Bryopsida.

This revised classification has been followed in the present edition of the book. Proskauer (1957), however, has proposed a significant departure in the classification of Bryophyta. He includes the green algae and all green land plants in the division **Chlorophyta**. The bryophytes are thus included in this division as a class **Bryopsida** which is further divided into three subclasses as follows :—

1. Hepaticidae.
2. Anthocerotidae,
3. Bryidae.

REVISION QUESTIONS

1. "The bryophytes are the amphibians of the plant world." Comment upon the statement.
2. Define Alternation of Generations. Point out the differences between the Alternation of Generations met with in the algae and the bryophytes.
3. List the salient features found in the life cycle of bryophytes.
4. In what respects do bryophytes, (*a*) differ from algae and (*b*) resemble algae.
5. Is the sporogonium a new individual or an outgrowth of the gametophyte plant ? Give reasons in support of your answer.
6. Are the so-called leaves, stems and rhizoids of a moss plant (*a*) homologous with or (*b*) analogous to the leaves, stems and roots respectively of a vascular plant ? Give reasons in support of your answer.

CHAPTER II

HEPATICOPSIDA (HEPATICAE) OR LIVERWORTS

Liverworts as inefficient land dwellers. The liverworts are bryophytes in which the plant is a green, dorsiventral thallus. It frequently grows close to the ground to which it is secured by the delicate, simple processes called the **rhizoids**. The rhizoids supply water and minerals needed for the plant's growth. The liverworts have thus completed migration to land. The aerial habit in plants, in general, seems to have been established through them. The fossil record indicates that about 350 million years ago there were found plants resembling the liverworts. Very little, however, is known about their structure and reproduction. For a life on land the first requirement is the presence of efficient absorbing organs. The second requirement is a compact plant body protected against desiccation. The third is a change from motile to non-motile aerial reproductive cells. The rhizoids which function as absorbing organs in the liverworts are short, delicate structures. They are inefficient absorbing organs because they have none of the complex features exhibited by the roots.

The plant body, no doubt, is more compact and better protected. The surface area is reduced as much as possible as compared with the filamentous, colonial or huge bodies of aquatic algae. The bulk of the cells constituting the thallus are protected by the epidermis. Fewer cells are directly exposed to water loss by transpiration. The prostrate habit is another advantage. However, the thallus is not completely protected against desiccation. The epidermal cells lack special, waterproof thickening. Besides, the epidermal layer is not continuous. It has unguarded pores. The latter allow aeration of thallus with miniature dehydration. The thallus is, therefore, not completely protected against desiccation. Consequently the liverworts must live in very moist habitats. They are unable to withstand the drying effect of the direct rays of the sun for any length of time. This accounts for their preference to grow in moist, shaded places on the ground, on the banks of rivers, on moist rocks, on tree trunks or floating on the surface of water or even submerged. In fact the factors which favour their growth, are the combination of high humidity, shade and abundant moisture in the soil.

From the foregoing account it is evident that the liverworts have not become completely adapted to the land life. They are still in a transitional stage and in the process of becoming adapted to land environments. Although the sex organs are jacketed and thus protected against the drying influence of air yet the dependence of liverworts on water is even more pronounced in the case of sexual reproduction. Their sperms have retained swimming habit. The presence of external water is a necessary condition for the sperms to swim to the egg. In fact the male gametes (sperms) produced by the liverworts are characteristic of water plants and not land plants. They furnish a clear sign of their aquatic ancestry. The spores, however, are non-motile and wind disseminated.

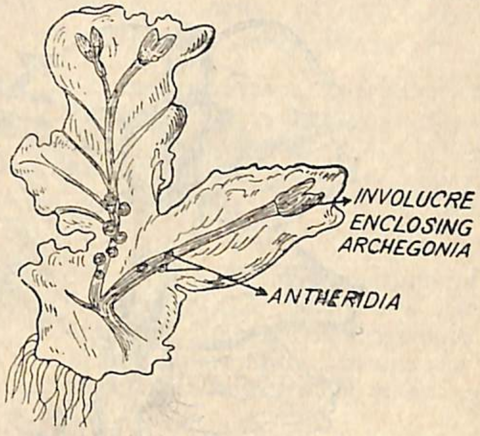


Fig. 2·1. Pellia epiphylla (monoecious).

Plant Body. The dominant plant in the liverworts is a gametophyte. It is a dorsiventral thallus-like structure. It remains small in size. Why does it remain small ? The study of the thallus structure reveals that the tissues required for large growth are lacking. It lacks the vascular tissue which is essential for conduction of water and minerals. It has no supporting or mechanical tissue in the form of long, thick-walled fibres. Besides the absorbing organs in the form of rhizoids are inefficient. Secondary meristems which provide increase in girth and additional cortical cells are absent. Consequently a vegetative plant body remains a thin-walled, porous, flat, thallus-like structure which grows prostrate and close to the surface of the substratum. In land plants in which the corticating tissues, which consume water, are lacking the prostrate habit is useful. It reduces the exposed surface and the major portion of the plant body remains in direct contact with soil moisture. Besides it furnishes maximum surface area for fixation and absorption of water.

The gametophyte of liverworts is an independent plant. Some liverworts have a thalloid plant body (Fig. 2·1). It is flat and dichotomously branched very much resembling the thallus of a foliacous lichen. However, the rich green colour of the liverwort thallus distinguishes it from the gray or grayish green colour of the lichen thallus. The different types of fruiting bodies in the two is another distinctive feature.

There are other liverworts in which the gametophyte plant is leafy (Fig. 2·2). It consists of a central branched axis (stem) bearing leaf-like expansions (leaves). Both the so-called leaves (Fig. 2·2 B and C) and the stem lack vascular tissues. The leafy or foliose liverworts are more numerous. Both the thalloid and the leafy gametophytes are anchored to the substratum by unicellular rhizoids.

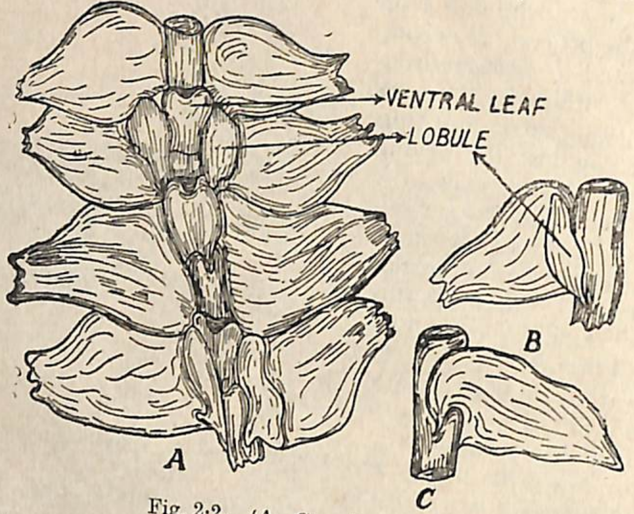


Fig. 2·2. (A—C). Porella sp.
A. A portion of the leafy gametophyte from the ventral side.
B. A dorsal leaf from the ventral side.
C. A leaf from above.

Habitat. The liverworts do not grow in dry habitats as the plant body is not completely protected against serious desiccation. They prefer to grow in situations where there is high humidity, shade and abundant moisture in the soil. Thus they thrive in moist shady habitats such as banks of streams, marshy ground, damp soil and rocks, deep shaded ravines, deep in the woods, on the bark of trees in diffuse light as epiphytes. There the dense shade protects them from the intense rays of the sun. A few live submerged in (*Riella*) or floating on water (*Riccia fluitans*). They often form soft, bright, green mats over the substratum.

Distribution. The liverworts are widely distributed over the earth's surface but are far more numerous in the tropics than in other parts of the world. Some of them are cosmopolitan in their distribution. They extend in their distribution from the arctic, through the temperate zones to the tropical forests. In India they abound in the outer Himalayas where rainfall is the heaviest. It is the home of the liverworts particularly within a range between 5,000 ft. to 8,000 ft. above sea level. The thallose forms are met with on the exposed slopes. The foliose liverworts are confined to the shady, moist situations. They occur on rocks or as epiphytes on tree trunks. Simla, Dalhousie, Mussourie, Garhwal, and Almora are some of the hilly places rich in them. The liverworts are not found in Western Tibet. They show active growth during summer and rainy season from May to September. Winter is the resting period. August to September is the fruiting season. The Hepaticae number about 9,500 species. They are grouped under 280 genera.

Asexual Reproduction. In liverworts asexual reproduction takes place by vegetative methods only. Like other land plants true asexual spores are lacking. Vegetative reproduction takes place during the growing season. It is brought about in a variety of ways. The most important methods of vegetative propagation in the Himalayan **liverworts** are :—

1. **Fragmentation**. The cells in the posterior portions of the branched thalli die of old age and eventually disorganise. As a result the younger branches are set free. Each of the detached branches, by apical growth, grows into a new plant. In this way the number of plants increases from time to time. The common examples are *Riccia, Marchantia, Pellia*, etc.

2. **Gemma Formation**. Many species of liverworts produce green, multicellular asexual buds called the **gemmae**. The gemmae become detached from the parent plant. On falling on a suitable substratum the green gemmae (Fig. 2·3) grow into new individuals immediately. In *Marchantia* and *Lunularia* the gammae are developed in small receptacles called the **gemma cups**. The gemmae cups are circular in *Marchantia* and crescent-shaped in *Lunularia*. They are developed on the dorsal surface of the thallus.

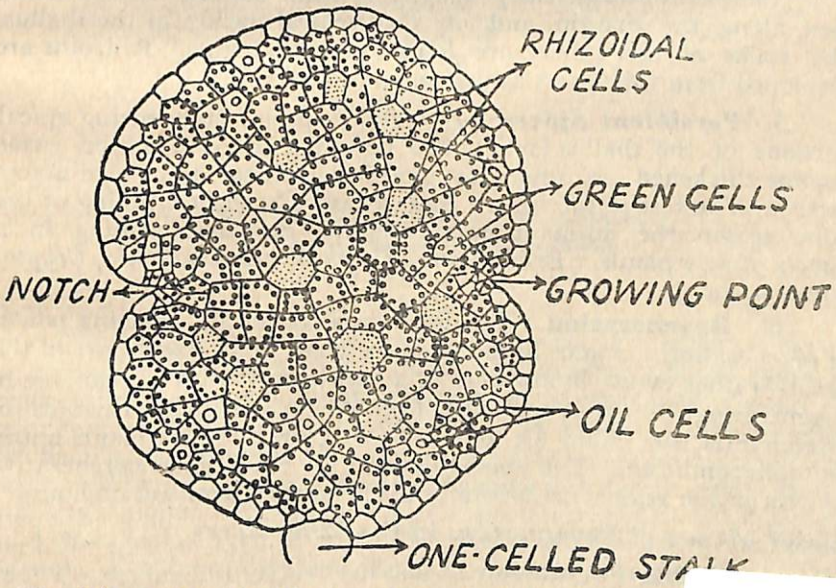


Fig. 2·3. Marchantia sp. A single gemma.

In *Blasia* the gemmae are produced in flask-shaped receptacles. Two-celled gemmae may be produced within any cell of the thallus in *Riccardia*.

3. **Adventitious Branches**. Vegetative propagation also takes place by the production of adventitious branches. They arise from the ventral surface of the thallus and become separated by death and decay of the tissue connecting the branch with the parent plant. The detached adventitious branch grows into a new plant. Examples are *Riccia fluitans*, *Targionia* and *Reboulia*, etc.

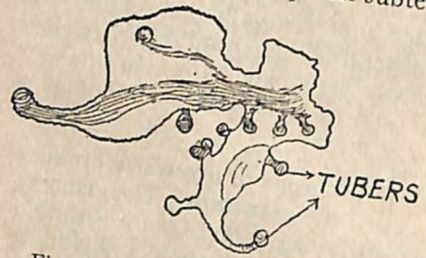


Fig. 2·4. Anthoceros himalayensis. A sterile plant bearing tubers.

4. **Tuber formation**. In some liverworts, especially those exposed to desiccation, special subterranean branches are formed towards the end of the growing season. These branches get swollen at their tips to form **tubers**. The tubers are usually buried underground. The plant dies at the onset of the period unfavourable for growth, the tubers remain dormant. Being buried they are not affected by drought. With the return of the favourable season the tubers resume growth. *In Petalophyllum* and *Sewardiella* the tubers are formed at the growing apices. In *Anthoceros* the tubers are found embedded in the thallus.

Anthoceros himalayensis (Fig. 2·4) bears stalked tubers at the apex, along the margin and on the ventral surface of the thallus. The stalks of the tubers are long and cylindrical. Rhizoids are developed from the tubers as well as their stalks.

5. **Persistent Apices**. In certain species the growing apical portions of the thallus lobes with a certain amount of thallus tissue become thickened or otherwise modified. These thickened apices persist. The rest of the plant dies away. At the beginning of the rainy season the dormant apices resume growth resulting in a rosette of new plants. Examples are *Cyathodium*, *Athalamia*, *Cryptomitrium*, etc.

6. **Regeneration**. The liverworts possess an amazing power of regeneration. Some hepaticologists state that every part of the plant—rather every living cell of a liverwort thallus—is capable of regenerating the entire plant. Isolated scales and rhizoids of Marchantiaceae could be induced to grow into new plants under suitable conditions. The implications of the exceptional regenerative powers in the vegetative spread of the liverworts are thus obvious.

Chief Means of Perennation in the Liverworts.

1. **Tuber Formation**. Some liverworts form tubers. Tubers being buried underground are unaffected by drought and extremes

of temperature. Moreover the outer two to three layers of cells of the tubers possess corky, hyaline walls which are waterproof. The inner or central cells are packed with food reserves such as starch grains and oil globules. The tubers, therefore, serve as a means of perennation.

2. The thallus of some liverworts such as *Reboulia*, *Grimaldia*, etc., dries up in winter or extreme dry season. The margins of the thallus roll upwards. As a result the upper surface is protected and the ventral surface with the scales is exposed. With the onset of the rainy season these thalli resume growth.

3. **Persistent Apices**. In a few of the liverworts the whole of the thallus dries up with the approach of unfavourable period. Only the apices of the thalli remain alive. They become dormant as they get thickened or otherwise modified. The surviving persistent thickened apices resume growth with the advent of rainy season.

4. In most of the leafy Jungermanniales the whole plant dries up. With the approach of the favourable season it resumes growth.

Sexual Reproduction. The student must bear in mind that asexual reproduction by vegetative methods is entirely a secondary phenomenon in the basic life cycle of a bryophyte. It simply serves to propagate the gametophyte phase in the life cycle and plays no role in the phenomenon of **alternation of generations**. Sexual reproduction which consists in the union of gametes and subsequent production of **meiospores** is the usual method of reproduction. The male and the female sex organs in some species are developed on different plants. Examples are *Pellia calycina* (Fig. 2·5 B and C) and *Marchantia* (Fig. 5·1 A and B). Such species are called **dioecious**. In others they are developed on the same thallus. They are called **monoecious**. The sex organs may be borne dorsally

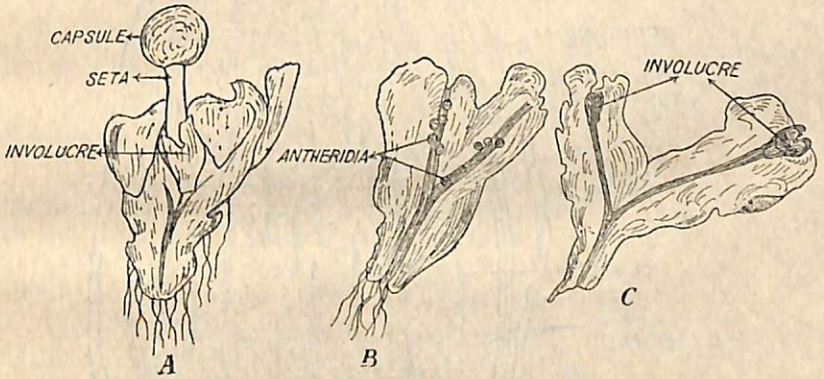


Fig. 2·5. (A—C). Pellia calycina (Dioecious)
A. A plant bearing a sporogonium.
B. A male plant.
C. A female plant.

or at the enterior end. They are either embedded in the tissue of the thallus (*Riccia*) or raised on special upright branches (*Marchantia*) called the **gametophores** (Fig. 5·1 A and B).

Following fertilization the zygote develops into the second individual in the life cycle called the **sporophyte**. It receives a special name **sporogonium** in the bryophytes. The sporogonium is without differentiation. Consequently it suffers from certain disabilities. It lacks direct contact with the soil as it has no roots or other basal appendages of any kind. It remains (Fig. 2·5 A) attached by the foot to the parent gametophyte (thallus) which provides for its nutrition from its own resources. Owing to the limited ability of the parent gametophyte plant for absorption and conduction the possibilities of the development of the parasitic sporogonium in the liverworts are limited. Moreover it has no stem to bear leaves or to elevate and support photosynthetic appendages. Naturally it is doomed to remain small. The other disabilities it suffers from are :—

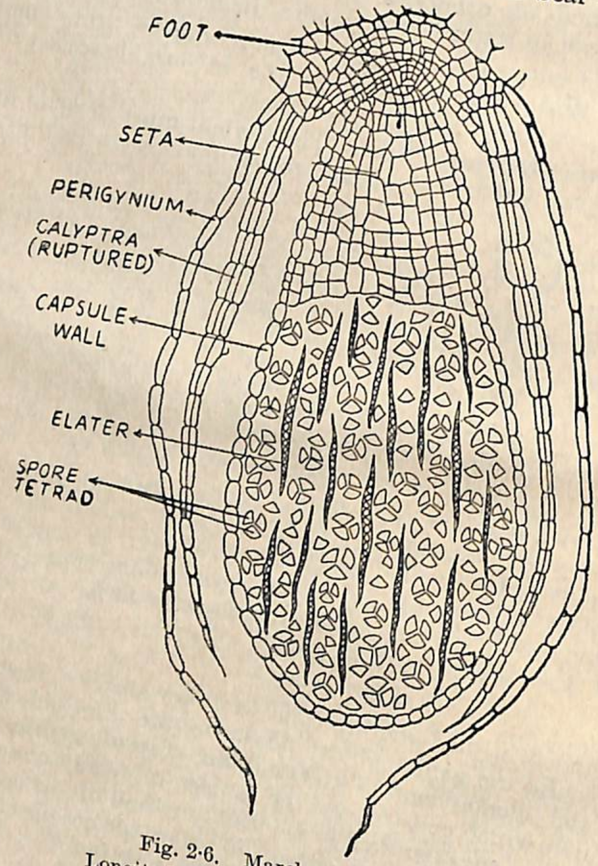


Fig. 2·6. Marchantia sp.
Longitudinal section of sporophyte.

(*i*) Absence of meristematic tissue.

(*ii*) Absence of any kind of lateral appendages and of branching habit.

(*iii*) Continuity of the archesporium leading to simultaneous ripening of spores.

All these factors collectively account for the liverwort sporogonium not progressing beyond a limited size. It remains dwarfed.

In some species the sporogonium is differentiated into three parts, a **foot**, a **seta** and a **capsule** (Fig. 2·6). In a few others (*Riccia*) both the foot and seta are absent. The sporogonium is a specialised body which is solely devoted to the production of meiospores and their dispersal. A large proportion of the cells of the endothecium are devoted to spore formation as compared with the other two classes of the bryophytes. The columella is absent. The spores are differentiated by meiosis. They are haploid in nature. On germination each spore produces the alternate plant in the cycle. It is the thallus (gametophyte) and not the sporogonium (sporophyte).

Distinctive Features

1. All the hepatics, with of course a very few exceptions, are dorsiventral in structure.

2. They are comparatively small in size never more than a few inches in length.

3. The plant body, which is always a **gametophyte**, is an independent plant. It is either thallose in form or leafy in nature. In the latter case it is differentiated into a branched central axis. Both the axis and the branches bear leaf-like expansions. They are all without the vascular tissue. The leaf has no midrib.

4. The gemetophyte is secured to the ground by simple, one-celled, absorptive processes called the **rhizoids**.

5. Internally the gametophyte always has a photosynthetic tissue. The cells constituting it have numerous, small chloroplasts each. The chloroplasts lack pyrenoids.

6. The sex organs are either dorsal in position or terminal. Each develops from a single **initial cell**.

7. The sporogonium is small and generally without chlorophyll. It is attached to and lives almost entirely as a **parasite** on the parent gametophyte.

8. The sporogonium is either differentiated into *foot*, *seta* and *capsule* or is very simple with both the foot and seta lacking (*Riccia*).

9. The sporogonium has no meristematic tissue.

10. The sporogenous tissue is endothecial in origin. A major portion of the sporogenous tissue forms the spores as compared with the other two classes.

11. The columella is absent.

12. The spores, on germination, generally directly and in some indirectly develop into the gametophyte plants.

Classification. Engler (1892) subdivided the class Hepaticae (Hepaticopsida) into three orders namely, Marchantiales, Anthocerotales and Jungermanniales. Many early hapatocologists considered that the Anthocerotales stand apart from the other two orders. Howe (1894) thus suggested class status to the order Anthocerotales. Many eminent bryologists such as Campbell, Smith and Takhtajan supported Howe's suggestion to elevate order Anthocerotales to the rank of a class, Anthocerotae, Cavers, Leilgeb and Jones recognized the anomalous position of the Anthocerotales but were opposed to the idea of giving it the status of a class. Many bryologists, however, have followed in line with the new move. With the raising of the order Anthocerotales to the rank of a class, only two were left. Cavers in 1910 added a third to the list. He separated family *Sphaerocarpaceae* from the order Jungermanniales and gave it the status of an order naming it as *Sphaerocarpales*. Later in 1936 Campbell suggested another change. He proposed to establish another order *Calobryales*. The consensus of opinion favoured this view. So at present majority of the hepaticologists classify the class **Hepaticopsida** into four **orders** as follows :—

Class **Hepaticopsida** (**Hepaticae**)

(Gametophyte practically always dorsiventrally differentiated, develops directly from the spores, sporophyte without any meristematic tissue, sporogenous tissue endothecial in origin, columella absent)

↓ Order 1 **Marchantiales**	↓ Order 2 **Sphaerocarpales**	↓ Order 3 **Jungermanniales**	↓ Order 4 **Calobryales**
Thallus flat, dichotomously branched, internally differentiated into dorsal region of air chambers and ventral parenchymatous storage portion, archegonial neck composed of 6 vertical rows of cells, capsule with a jacket of sterile cells one cell thick.	Thallus without any internal differentiation of tissues, each sex organ surrounded by an involucre, archegonial neck composed of 6 vertical rows of cells, capsule wall one cell in thickness.	Plant body thallose or foliose, no internal differentiation of tissues, archegonial neck made up of 5 vertical rows of cells, capsule wall more than one layer of cells thick.	Plant body erect, leafy with leaves in 3 vertical rows, neck consists of 4 vertical rows of cells, capsule wall one cell in thickness.

Some hepaticologists still recognize six orders in the liverworts namely, Anthocerotales, Sphaerocarpales, Marchantiales, Metzgeriales, Calobryales and Jungermanniales.

Recently Hattori and Mizutani (1958) suggested the inclusion of a new order, *Takakiales* with a single family *Takakiaceae* in the class **Hepaticopsida**. Their suggestion is based on the discovery of a curious, new liverwort, *Takakia lepidozioides* in Japan in 1951 and later in Canada (Persson, 1956). *Takakia* approaches the *Calobryates* in the following features :—

(*a*) Erect leafy thallus.

(*b*) Branching of the stem.

(*c*) Certain features of cell structure.

(*d*) Absence of rhizoids.

It, however, differs from the Calobryales in :—

1. Large archegonia borne in terminal clusters.

2. Unique form of the leaves. Each leaf is usually divided into two rarely three cylindrical structures which are solid and parenchymatous.

3. Low chromosome number which is $n=4$.

The bryologists, in general, are reluctant at present to accept Hattori and Mizutani's suggestion. They hold that the final assessment of the taxonomic importance of *Takakia* can be deferred until the sporophytic material is known.

In this book only two of these orders have been discussed. These are the *Marchantiales* and *Jungermanniales*.

REVISION QUESTIONS

1. The liverworts are inefficient land dwellers. Discuss this statement.
2. Describe the habitat and distribution of liverworts.
3. Give an account of the plant body of the Hepaticae (Hepaticopsida).
4. Describe, giving examples, the various methods of vegetative reproduction and perennation found in the Himalayan liverworts.
5. List the distinctive features of the class Hepaticopsida.
6. Give a brief account of the classification of the Hepaticae (Hepaticopsida) into orders and state the diagnostic characters of each order.
7. Justify the truth or falsity of the following giving reasons :—
   (*a*) The thallus of the liverworts represents a transition stage in the migration of plants from water to land.
   (*b*) The rhizoids of liverworts are homologous to the root hairs of the higher plant.
8. Why does the sporogonium remain small in the liverworts ?

CHAPTER III

HEPATICOPSIDA (HEPATICAE)—MARCHANTIALES

Morphology of the Gametophyte

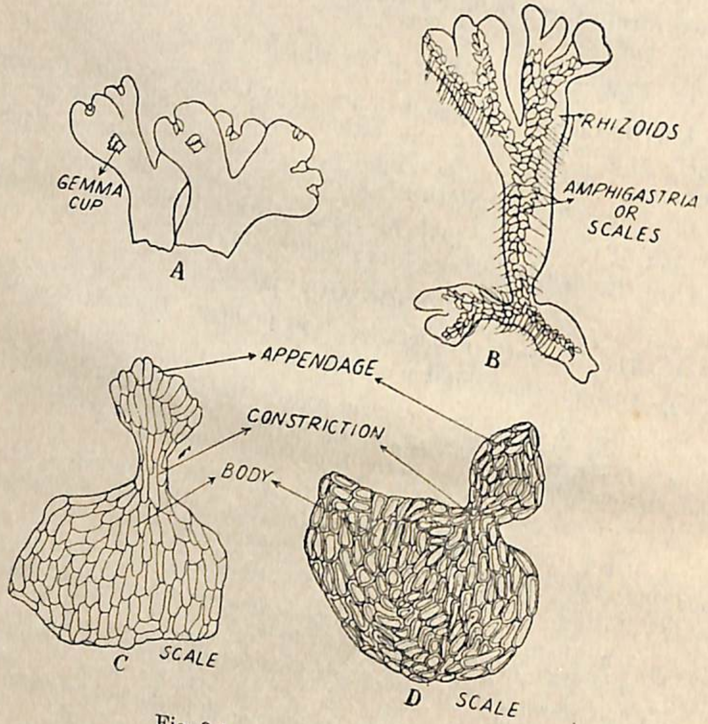


Fig. 3·1 (A—D). Marchantia sp.
A. Thalli bearing gammae cups.
B. Thallus as seen from the lower surface.
C and D. Scales of two different species.

(a) *External Characters.* Externally the gametophyte of the *Marchantiales* is very simple. It is a green, fleshy, broad thallus-like structure with more or less a distinct midrib. Without exception the thallus shows dorsiventral differentiation. It branches dichotomously once or a few times. Being plagiotropic it grows prostrate on the ground and is secured to it by two kinds of rhizoids, namely **smooth walled** and **tuberculate**. Associated with the rhizoids on the ventral surface of the thallus are the membranous **scales** (Fig. 3·1 B). The scales are arranged in rows.

The sex organs (antheridia and archegonia) in the lower members of the order (Ricciaceae) are scattered on the dorsal surface of the thallus. They develop in acropetal order. In the higher members they are borne on special structures called the **receptacles** (Marchantiaceae). The receptacles may be sessile or stalked. Some genera are **monoecious** and others **dioecious**. The sex organs in their structure and development resemble those of the Sphaerocarpales but differ from that of all the other Hepaticae.

Some members of the order are strictly hygrophilous. They grow in very moist situations. A few occur actually in water, floating or submerged. Some with a larger thallus are capable of growing in exposed places. Still other can live under conditions of temporary drought.

(b) *Internal Structure* (Fig. 3·2 A—C). Though the general plan of construction of the thallus in the Marchantiales is the same yet it presents a wide range of variation in details. It is differentiated into various tissues. These tissues are arranged in two distinct regions, **dorsal** and **ventral**.

The deep, green, dorsal assimilatory region encloses air chambers. The chambers are roofed by a single layered epidermis. In the family Ricciaceae the chambers are reduced and are in the form of deep canals or channels. The chambered condition is represented in a relic condition in *Dumortiera* and is absent in *Monoselenium*. In species in which the chambers are present they may be in one or more than one layer. Each chamber is separated from its neighbours by partitions which are generally one cell thick. It may be empty or contain assimilatory filaments. When multi-layered the chambers are invariably empty. Each chamber opens to the outside by a pore. These pores vary widely in structure in different genera. In *Stephensoniella* the pores are simple and wide. They are large and barrel-shaped in *Marchantia* and *Preissia*. In *Targionia* they are barrel-shaped.

The ventral zone of the thallus functions as the storage region. It lies below the air chambers and consists of colourless parenchyma. The parenchyma cells are compactly arranged. They lack chloroplasts but contain starch. Here and there are present the **oil cells**. The lowermost layer of this region bears two kinds of rhizoids and scales.

On the basis of anatomy Mehra divides the thalli of the Marchantiales into the following three categories :—

1. *Marchantia Type* (Fig. 3·2 A). The midrib region is expanded. The ventral storage zone is several layers thick. It

gradually thins on either side towards the margins where it is 3 or 4 layers thick. The parenchyma cells constituting it are colourless. They contain starch grains. There are oil cells here and there. The lowermost layer bears two kinds of rhizoids and scales. The upper assimilatory zone contains air chambers arranged in a single layer. The chambers are separated from each other by single layered partitions. From the floor of the chambers arise chlorophyllose filaments. Each chamber communicates with the outside either by a barrel-shaped pore (*Marchantia*) or by a semi-

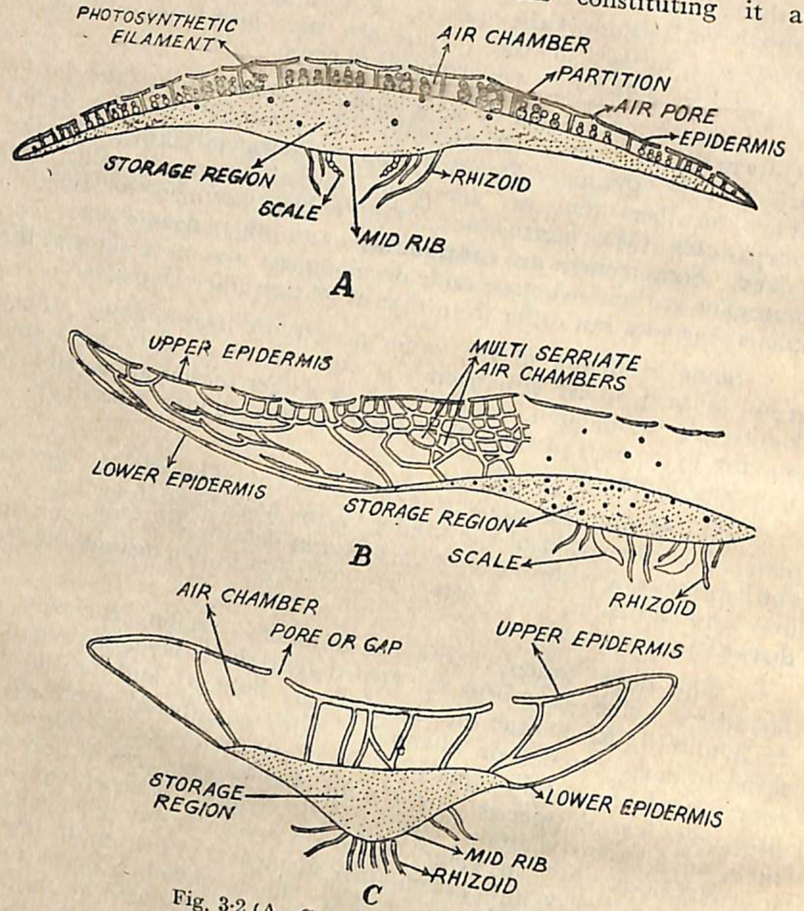


Fig. 3·2 (A—C). Marchantiales. Transverse sections of Thalli. (Thick dots represent oil cells).
A. Marchantia nepalensis (outline sketch).
B. Plagiochasma appendiculatum (outline sketch of a portion of the thallus showing the disposition of chambers).
C. Stephensoniella brevipedunculata (outline sketch).
(After Mehra).

barrel shaped pore (*Targionia*). To this category belong the species of *Marchantia* and *Targionia hypophylla*.

2. *Plagiochasma Type* (Fig. 3·2 B). The midrib is not much flattened. Consequently the storage region is thickest in the centre. In the wings it consists of a single layer of cells which represents the lower epidermis. The assimilatory zone consists of air chambers arranged in several layers one above the other. The chambers are empty and are separated by single layered partitions. The air pores are either star-shaped or semi-barrel shaped. Examples are *Plagiochasma appendiculatum*, *P. articulatum*, *Reboulia hemisphaerica*, *Asterella mussouriensis*, *Grimaldia indica* and *Athalamia pinguis*.

3. *Stephensoniella Type* (Fig. 3·2 C). The midrib is least expanded and the ventral storage region consists of colourless cells which contain starch or protein granules. The wing on either side consists of the lower epidermis and a layer of air chambers above it. The chambers are spacious and empty. They communicate with the exterior through large gaps or pores of extremely primitive type. To this type belong *Stephensoniella brevipedunculata*, *Sauchia spongiosa*, *Asterella blumeana*, *A. reticulata*, *Riccia crystallina and Cryptomitrium himalayensis*.

Origin of the Marchantiaceous Thallus. Two widely divergent views have been put forth to explain the origin of the Marchantiaceous thallus. Some bryologists consider that the simple gametophyte of the Marchantiales is the result of **retrogressive evolution**. Others hold that it is the result of **progressive evolution** or **elaboration**.

(1) **Mechanism of Retrogressive Evolution**. The supporters of this hypothesis are divided into two camps. Majority of them particularly the older bryologists hold that retrogressive evolution has been brought about by progressive simplification also called **reduction**. The latest view put forth by Mehra is that it has been brought about by **condensation**.

(a) **Reduction Theory**. The reduction theory to explain retrogressive evolution (regression) was first proposed by Von Wettstein in 1908. He held that the primitive gametophyte of the Hepaticae was nearest the erect, leafy Acrogynous Jungermanniaceous forms. His theory with slight modifications received support from many eminent bryologists. The chief among them were Church (1919) and Evans (1939). Von Wettstein placed the Acrogynous Jungermanniales of the *Calobryum* type first. It is an erect, leafy gametophyte radial in symmetry and with leaves in three rows. The first step towards reduction was the adoption of the prostrate habit. With the appearance of dorsiventrality the leaves on the ventral side gradually diminished in size and finally disappeared in some cases. The changes in habit and diminishing size of the ventral leaves were accompanied by the flattening of the central axis. Associated with these changes was the gradual and complete elimination of the lateral leaves. These changes resulted in the formation of a leafless, flat, dorsiventral Anacrogynous Jungermanniaceous gametophyte of *Pellia* type. The latter by gradual progressive internal differentiation of tissues finally led to the formation of externally simple but internally highly differentiated thallus of the Marchantiales. The scales on the ventral surface of the thallus of the Marchantiales are considered as modifications of the leaves of the ventral row of the prostrate, foliose ancestor. Goebel (1930) and Kashyap (1919) were the other champions of retrogressive evolution by reduction in the Liverworts.

Kashyap, however, postulated the theory of the *Pteridophytean origin* of the Marchantiales by reduction. He was greatly struck by the resemblance in external form and structure between the radial prothallus of *Equisetum debile* and *Lycopodium cernuum* with the liverwort thallus in general and Marchantiaceous thallus in particular. The upright, chlorophyllose branched lobes of the dorsal photosynthetic region of these genera of the Equisetales and Lycopodiales respectively agree with the upright chlorophyllose filaments and walls of the air chambers in the Marchantiales. This resemblance tempted Kashyap to guess that the Marchantiales probably arose by reduction from these pteridophytean ancestors. Mehra has developed the following arguments against this hypothesis :—

(*i*) It is difficult to reconcile the highly differentiated sporophyte of *Equisetum* or *Lycopodium* with the simple liverwort sporophyte.

(*ii*) Absence in the entire class of liverworts including the Marchantiales of any relic of the lost vascular system.

(*iii*) Absence of any structure on the undersurface of the prothallus of these Pteridophytes which could be interpreted as having been reduced to scales so characteristic of the thallus of the Merchantiales.

(*iv*) It is difficult to explain the origin of the upright, specialised, sexual branches of *Marchantia* from the ancestral prothalli particularly when Kashyap considers forms like *Marchantia* to be primitive or ancestral in the Marchantiales.

(*b*) **Condensation Theory**. Mehra and Vasisht (1950) suggested the derivation of the thalloid structure in the liverworts from the foliose forms by **condensation**. Later in 1957 Mehra adduced evidence in support of a real phylogenetic connection between the Jungermanniales and the Marchantiales. He propounded a theory explaining the origin of the Marchantiaceous thallus from the foliose Jungermanniales by "compaction, condensation and fusion of leaves". The outlines of his theory are :—

1. The overlapping of the lateral leaves succubously or incubously in the foliose ancestor.

2. Fusion of the lower portions of these leaves at the points of contact resulting in the formation of single layered wings on either side of the central axis and lamellae on the upper surface of each wing.

3. The one-cell thick lamellae were directed obliquely outward and as a whole formed open chambers of linear type.

4. The next step was the roofing of the air chambers by inward growth of the margins of the cavities of the chambers.

5. The roofed chambers, at first, communicated with the outside by large gaps. The gaps were later replaced by definite pores —a protection against loss of water by transpiration.

6. All these changes were accompanied by gradual flattening of the central axis till it reached the margin of the wings.

7. Formation of secondary partitions occurred across the chambers as the flattening of the thallus occurred.

8. In some genera adapted to xerophytic conditions like *Plagiochasma* horizontal partitions were also formed between the lamellae forming multi-layered chambers.

9. Subsequent changes were the development of the assimilatory filaments from the floors of the chambers in members like *Marchantia* and the formation of barrel-shaped pores characteristic of some of the Marchantiales.

Progressive Evolution. The adherents of this hypothesis hold that the Hepaticopsida originated from a simple, thallose gametophyte. The ancestral thallus was simple, prostrate and showed no external or internal differentiation. The theory of progression was originally suggested by Schiffner. The chief supporters are Cavers, Campbell, Fritsch, Bower, Smith, etc. Caver's suggested *Sphaerocarpus* and Campbell thought forms like *Metzgeria* as the present day Hepaticae which show a nearest approach to the primitive hepaticean gemetophyte. From these primitive types progressive evolutionary sequence followed two diametrically opposed directions. This resulted in the evolution of the following two types of gametophytes :

(*a*) *Marchantiaceous Gametophyte*. It is suggested to have evolved from the primitive thallose gametophyte by the following changes :—

(*i*) Retention of external, simple, prostrate, thallus-like form.

(*ii*) Gradual but progressive internal differentiation of tissues. It finally resulted in the formation of a thallus internally composed of a definite epidermis, pores leading into the air chambers containing chlorophyllose filaments and a parenchymatous, compact storage tissue.

(*iii*) Aggregation of sex organs into localized areas called the **receptacles**.

(*b*) *Jungermanniaceous Gametophyte*. It involved the following changes :—

(*i*) Retention of simple internal structure.

(*ii*) Gradual but progressive elaboration of the external form resulting in the formation of a leafy, prostrate thallus characteristic of the Jungermanniales.

Sporogonium It represents the sporophytic or diplophase. It is very simple in structure and radial in symmetry. It bears no appendages. All its life it remains organically connected with the parent thallose gametophyte and is nourished by it. It is concerned with the production and dispersal of spores. In the lower Marchantiales (Ricciaceae) it consists of a spherical capsule only whereas in the higher members it is differentiated into a **foot**, a small **seta** and a **capsule**. The capsule has a single layered wall. All the cells within the capsule wall, in some species, are fertile and form spores whereas in others some of them remain sterile and form **elaters** (Fig. 2·6).

DISTINCTIVE FEATURES OF MARCHANTIALES

The Marchantiales are the liverworts characterised by the following features :—

1. The plant body, which is a gametophyte, is a green, thick, flat, dichotomously branched, dorsiventral thallus with a more or less marked midrib.

2. Internally it is differentiated into two distinct portions, the **dorsal** and the **ventral** regions.

3. The dorsal, green region generally encloses air spaces also called the **air chambers**.

4. The air chambers communicate with the exterior generally through **pores**.

5. The ventral region is composed of compact, colourless, parenchymatous **storage** tissue.

6. Scales are usually present on the ventral surface of the thallus.

7. The thallus is secured to the substratum generally by means of two kinds of unbranched, unicellular rhizoids, **smooth walled** and **tuberculate**.

8. The sex organs in a few species are scattered on the dorsal surface of the thallus (*Riccia*) but more usually assembled in **receptacles**.

9. The receptacles are generally elevated on slender stalks but are sometimes sessile.

10. The sporogonium is simple in structure and small, either with or without seta. It has a capsule wall one cell in thickness. Columella is absent.

Classification of Marchantiales. The order includes about 420 species. They are placed under about 35 genera. Campbell (1918) recognized only three families namely Ricciaceae, Corsiniaceae and Marchantiaceae in this order. He included the genus *Monoclea* and *Targionia* in the family Marchantiaceae. He, as early as 1898, was the first hepatocologist to point out *Monoclea's* relationship with the Marchantiales. This viewpoint was later challenged by Schiffner (1913). Verdoorn, Evans and some others supported him.

Verdoorn (1932) and Evans (1939) each recognised six families in the order Marchantiales. The former made out Marchantiaceae, Operculatae, Astroporae, Targionaceae, Corsiniaceae and Ricciaceae. Evans recognized Marchantiaceae, Sauteriaceae, Rebouliaceae, Targionaceae, Corsiniaceae and Ricciaceae. Both of them excluded *Monoclea* from this order and placed it in the suborder Anacrogynous Jungermanniales.

Later Campbell (1940) revised the classification of Marchantiales basing it on the following features :—

1. Nature of the receptacle.
2. Manner in which it is borne.
3. Structure of the sporophyte.

On the basis of the above mentioned features he divided the order into the following five families :—

1. Ricciaceae.
2. Corsiniaceae.
3. Targionaceae.
4. Monocleaceae.
5. Marchantiaceae.

It is evident that the families Ricciaceae, Corsiniaceae and Targionaceae are common in Verdoorn, Evans and Campbell's systems of classification. The families Marchantiaceae, Operculatae and Astroporae of Verdoorn and Marchantiaceae, Sauteriaceae and Rebouliaceae of Evans are equivalent to family Marchantiaceae of Campbell.

As stated above Verdoorn and Evans excluded Monocleaceae from Marchantiales and placed it in the suborder Anacrogynous Jungermanniales whereas Campbell included it in the Marchantiales. To clear this tangle Proskauer (1951) made a critical study of the taxonomic position of *Monoclea* and suggested that the inclusion of the Monocleaceae in the Jungermanniales is unwarranted. According to him *Monoclea* shows affinities with the dumortieroid line of the Marchantiales.

Professor Kashyap reduced the number of families in the Marchantiales to three. In his extensive collections of the Himalayan liverworts he found many intermediate forms which connect the families Targionaceae and Corsiniaceae with the Marchantiaceae. Consequently he recognised only the following families in this order :—

1. Ricciaceae.
2. Monocleaceae.
3. Marchantiaceae.

Carr (1956) added another family Monocarpaceae (=Carrpaceae) to the list. This family includes a single thollose hepatic *Monocarpus sphaerocarpus*. It was discovered by Carr in 1956 and renamed as *Carrpos sphaerocarpos* (Carr) Prosk by Proskauer in 1961. This hepatic has an odd combination of characters. Like the genus *Sphaerocarpos* it has a small simple thallus and relatively a large involucre. The presence of reduced photosynthetic air chambers opening by wide air pores on the dorsal surface, shortly stalked female receptacle with roofed air chambers opening by barrel shaped pores, each consisting of two tiers of cells, sporogonium with a short seta, bulbous foot and lack of functional elaters suggest a close relationship with the Marchantiales. These features led Carr to assign *Monocarpus* (=*Carrpos*) to a new family Monocarpaceae (=Carrpaceae) within the order Marchantiales. Proskauer (1961) and Schuster (1963) endorsed his viewpoint.

The consensus of opinion, at present, is in favour of dividing Marchantiales into six families namely Ricciaceae, Corsiniaceae, Targionaceae, Monocleaceae, Monocarpaceae (=Carrpaceae) and Marchantiaceae.

REVISION QUESTIONS

1. Describe the external features and anatomy of the gametophyte of the Marchantiales.
2. List the distinctive features of the order Marchantiales.
3. Give a brief account of the classification of the order Marchantiales.
4. In the light of recent researches discuss the structure and origin of the Marchantiaceous thallus.

CHAPTER IV

MARCHANTIALES—RICCIACEAE : RICCIA

Ricciaceae

General Characters :

The family Ricciaceae includes the simplest members of the order Marchantiales. They are characterised by the following features :—

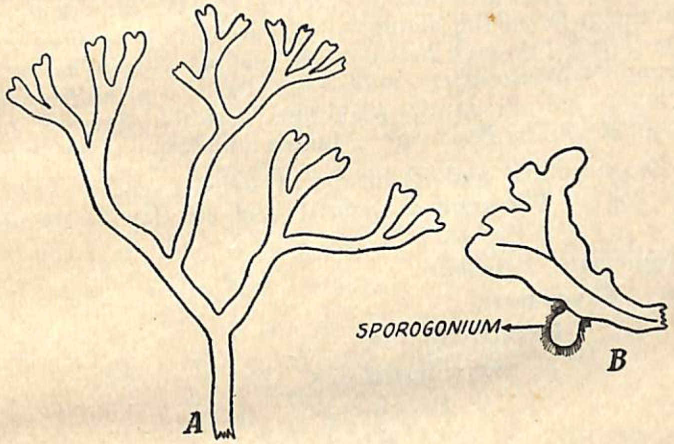


Fig. 4·1 (A – B). Riccia fluitans.
A. Floating form.
B. Land form.

1. The gametophyte is a flat, ribbon-shaped somewhat fleshy, green thallus.

2. The dorsal photosynthetic region contains fine air channels which in some species are large but generally greatly reduced in width. In the latter case they occur as deep narrow **canals** or **channels** separated by long columns of green cells.

3. The air channels or canals lack special assimilatory filaments and thus are **empty**.

4. The upper superficial layer, the so-called **epidermis**, lacks definite **pores**. The pores are either absent or are redimentary and unspecialized structures.

5. The **sex organs** occur in the **median furrow** on the upper surface of the thallus in longitudinal rows extending the entire length of the thallus from the apex backwards.

6. They occur singly in the open cavities at the bottom.

7. The sporophyte or sporogonium is the simplest among the liverworts. It lacks both the **foot** and **seta** and thus consists of a spherical **capsule** only.

8. The capsule remains permanently locked in the calyptra.

9. The spores are set free by the decay of the surrounding sterile tissue.

10. Practically all the cells of the archesporium are devoted to spore formation.

11. The sterile cells or elaters are wanting.

The family includes about 140 species. They are placed under three genera. These are *Tesselina* (*Oxymitra*), *Ricciocarpus* and *Riccia*. The first two are represented by a single species each. All the rest are included in the genus *Riccia*. Practically all the Ricciaceae grow on the damp soil. The only exceptions are *Riccia fluitans* (Fig. 4·1 A) and *Ricciocarpus natans* (*Riccia natans*). They are aquatic. *Ricciocarpus natans* has been reported from Kashmir (Dal lake) and Peshawar (Pakistan). *Riccia fluitans* occurs in Garhwal, Kashmir, Peshawar, Madras and Kapurthala (Punjab).

The structure and life history of the type genus *Riccia* is considered here. The genus is named after an Italian botanist F. F. Ricci.

Systematic Position :

Bryophyta
Hepaticopsida
Marchantiales
Ricciaceae
Riccia (Mich.) **L.**

Distribution and Habitat. It is the most widely distributed genus of the family Ricciaceae. It comprises about 138 species. They are found practically over all parts of the earth. More than 18 species have been recorded from different parts of India both from the hills and the plains. Most important among these are *R. himalayensis* (*R. discolor*, Fig. 4·2), *R. robutsa* (*R crystallina*, Fig. 1·1 A), *R. pathankotensis* (Fig. 4·3), *R. sanguinea* (*R. frostii*), (Fig. 4·8), *R. cruciata* (Fig. 1·1 C), *R. melanospora*, *R. fluitans* (Fig. 4·1), etc. With the exception of *R. fluitans* which is aquatic all others are terrestrial. The terrestrial species generally grow for short seasons on clayey damp soil forming rosettes. *R. fluitans* occurs floating or partly submerged in still water in pools, ponds or lakes. It continues to live and grow but fruits only (Fig. 4·1 B) when it comes in contact with the mud at the bottom.

GAMETOPHYTE PHASE

It has its origin in the life cycle with the maturation of spores. Each spore germinates to give rise to the gametophyte plant which is thallose in form.

Adult Gametophyte (Fig. 4·2 A and B).

(*a*) **External Features**. The plant body is a thallus. It is small, green, flat and rather fleshy. It grows prostrate on the ground and branches freely by dichotomy. Consequently it generally takes up a rosette form (Fig. 4·8). The branches of the thallus are called the **thallus lobes**. According to the species the thallus lobes are linear to obcordate. Each lobe is thickest in the middle and gradually thins toward the margins. The thick middle portion constitutes the **midrib** region. On the upper surface of each lobe there is generally a median **groove** or **furrow**. It is in the form of a broad channel in *R. pathankotensis* (Fig. 4·3 B) and a narrow longitudinal furrow near the apex in *R. melanospora*. In *R. sanguinea* (*R. frostii*) the upper surface is flat or slightly convex.

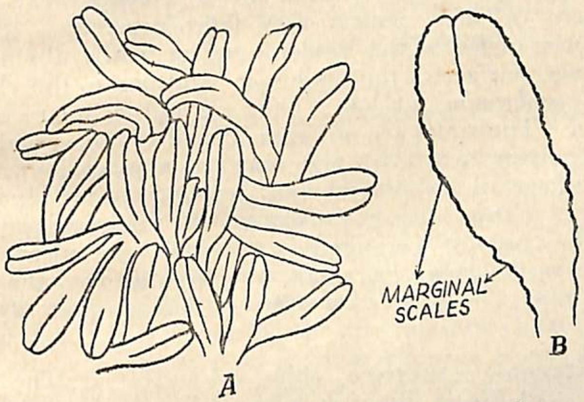


Fig. 4·2 (A—B). Riccia himalayensis (R. discolor)
A. A patch of plants.
B. A single plant.

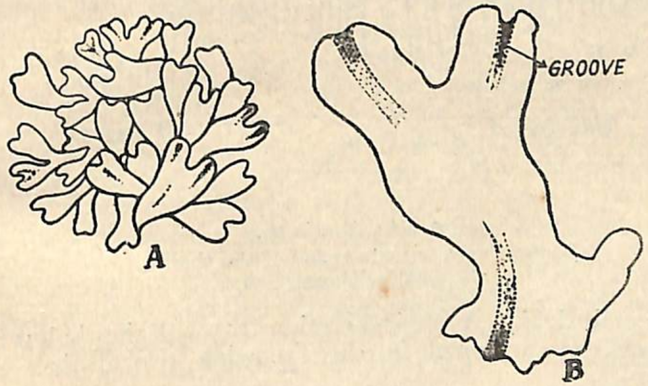


Fig. 4·3 (A – B). R. pathankotensis.
A. A patch of plants.
B. A single plant showing a dorsal furrow or groove.

Each thallus lobe usually ends in a terminal notch in which lies the growing point. The terminal notch is absent in *R. frostii*.

The thallus is attached to the substratum by slender, simple, unicellular processes called the **rhizoids**. The latter arise from the lower surface of the thallus. They are of two kinds, **smooth walled** and **tuberculate**. The tuberculate rhizoids are narrower and lack protoplasm at maturity. They have peg-like outgrowths projecting inwards into the lumen from the wall. The rhizoids in form and function somewhat resemble the root hairs. The two, however, are analogous to each other and not homologous. They function as organs of attachment and also absorb water and soil solutes. The tuberculate rhizoids in *R. sanguina* (*R. frostii*) are either absent or they possess very faint tubercles. In the submerged species of *Riccia* the rhizoids are generally absent. Arising from the lower surface of the thallus, in addition to the rhizoids, are the violet, *membranous* **scales**. They are multicellular and one cell in thickness. The scales are not appendaged and are usually arranged in one transverse row near the apex. They are situated closely and project forward to protect the growing point. In the older portion of the thallus lobes the scales split in the median line. Consequently they become arranged in two rows, one near each lateral margin. *R. melanospora* has small, purple scales near the apex only. They are absent in *R. robusta* (*R. crystallina*) and *R. sanguinea* (*R. frostii*).

(b) **Internal Structure** (Figs. 4·4 and 4·5). The externally simple thallus of *Riccia* shows a more elaborate internal structure.

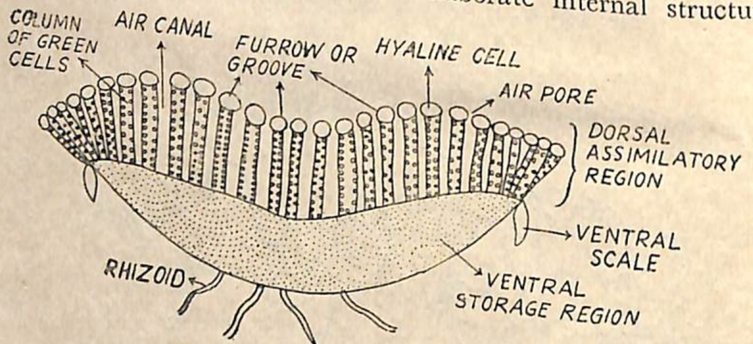


Fig. 4·4. Riccia sp.
Transverse vertical section of the thallus.
(Outline sketch).

It is many cells deep. A vertical section through the thallus reveals that these cells are arranged in the following two distinct regions (Fig. 4·4) :—

(*i*) An upper or dorsal **photosynthetic region**.

(*ii*) A lower or ventral **storage region**.

(*i*) *Photosynthetic Region*. The photosynthetic region consists of a loose, green tissue. It is composed of parenchymatous cells rich in chloroplasts (Fig. 4·5). These green or chlorenchymatous cells are arranged in vertical rows or columns. Generally between the columns of green cells are very narrow, deep, vertical slits. These slits are called the **air canals** or **air channels**. They are wide and larger in the form of air chambers in *R. cruciata* and *R. robusta* (*R. crystallina*). In *R. himalayensis* (*R. discolor*) and *R. sanguinea* (*R. frostii*) they are narrow, slit-like. The air canals or chambers in *Riccia* lack **assimilatory filaments** (Fig. 4·5) characteristic of *Marchantia*. The walls separating the air canals or channels consist of four vertical rows of green cells in some species, In others they are bounded by six to eight vertical rows of cells (*R. vesiculosa*). The superficial or uppermost cell of each row is somewhat distended. The distended or enlarged terminal cells are hyaline. They do not contain chloroplasts. Together these usually colourless, superficial cells of the neighbouring rows form an ill defined, discontinuous layer, the so-called **upper epidermis**. It is one cell in thickness. The air canal or channels communicate with the exterior through gaps in the upper epidermis. These gaps are called the **air pores**. The air pores in *Riccia* are thus very unspecialized and rudimentary structures. They are simple, intercellular spaces bounded by 4 to 8 so-called epidermal cells. No true or well defined air pores characteristic of *Marchantia* are developed in *Riccia*. The wide air canals in *R. crystallina* communicate with the outside by their whole width. This upper region of air channels functions in photosynthesis. In the sterile thallus of *R. fluitans* floating under the water surface the upper epidermis is continuous. The air chambers are large but closed.

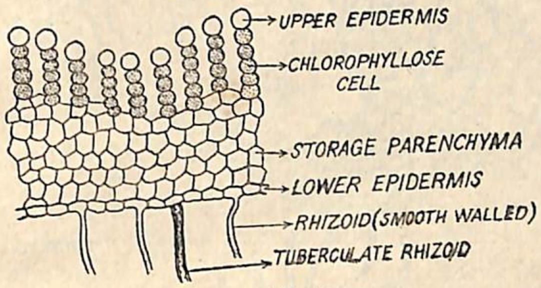


Fig. 4·5. Riccia sp.
Portion of a transverse vertical section of the thallus.

The assimilatory region in *Ricciocarpus natans* (Fig. 4·6 A and B) consists of large, irregular air chambers. They are arranged in several layers one above the other. The chambers of the upper layer communicate with the exterior through air pores.

(*ii*) *Storage Region* (Fig. 4·5). The lower or the ventral portion of the thallus is colourless. It consists of closely packed, undifferentiated parenchymatous cells without intercellular spaces. The cells are colourless and may contain starch but no chloroplasts. They serve for water and food storage. The lowermost cells of this region

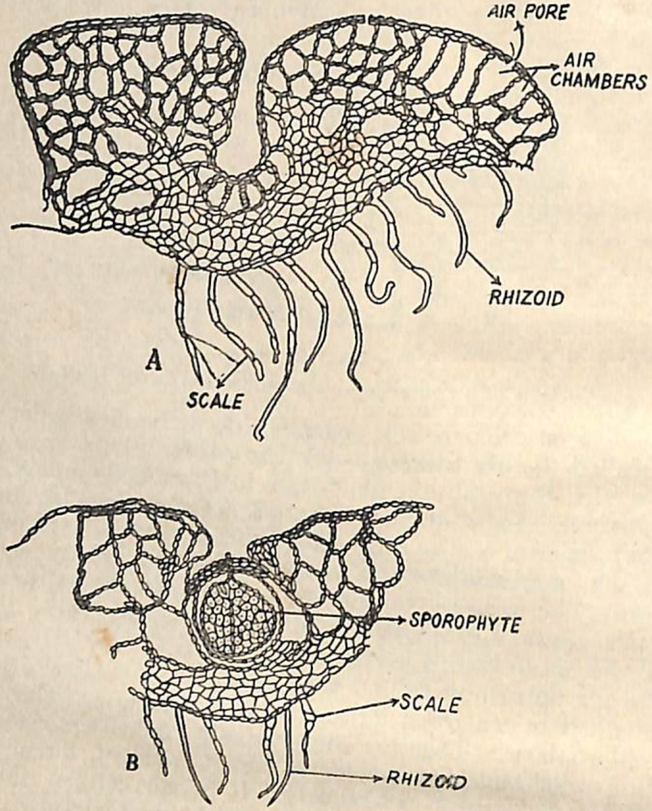


Fig. 4·6 (A—B). Ricciocarpus natans.
A. A transverse vertical section of a thallus lobe.
B. The same bearing a young sporophyte.

are small in size and regularly arranged to form the so-called **lower epidermis**. From the latter arise the rhizoids and the thin scales.

Origin of Air Chambers. There are two views with regard to the development of air chambers. Leitgeb (1879), Hirsch (1910), Black (1913) and others hold that the air chambers arise by **surface-involution**. They originate as depressions of the surface. These depressions are formed by cessation of upward growth in certain portions of the thallus and vigorous upgrowth in the adjoining portions. In this way depressions are formed in between.

Barnes and Land (1907), Evans (1918), Campbell (1918), Bower and others hold that the air chambers arise **schizogenously**. They originate as depressions formed by splitting of the cell

walls. The young embryonic thallus tissue just back of the thallus apex is compact. Air chambers arise later by the splitting of the vertical cell walls. The consensus of opinion favours the second hypothesis. The supporters of this hypothesis are further divided into the following two camps :

(*i*) Some hold that the schizogenous splitting is **exogenous**. It starts from without inwards. It begins from the surface and extends downward. The ardent supporters of this view are Black, Orth, etc.

(*ii*) Many hold the opposite view. The chief among them are Barnes, Land and Pietsch. They contend that the splitting is **endogenous**. It starts within the tissue of the thallus below the surface. It begins from below and gradually extends upward right up to the epidermal layer.

Apical growth (Fig. 4·7 A). The growth in length of the thallus lobes takes place by means of a group of **apical initials**. They are arranged in a horizontal row and vary in number usually from 3 to 5, sometimes more. The growing point containing the apical initials is located at the bottom of a notch at the tip of each lobe. Once the apical initials are established in the young thallus all further growth is brought about by their activity and division and growth of the daughter cells. The growing region comes to lie in a

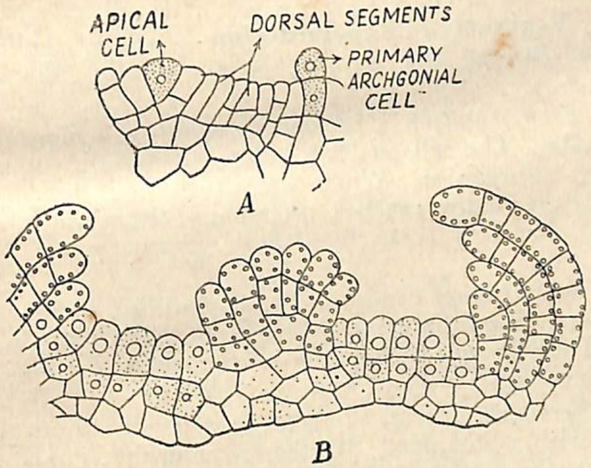


Fig. 4·7 (A – B). Riccia sp.
A. Vertical section through the growing point.
B. Section through the growing point showing dichotomy.
(Diagrammatic)

depression because the embryonic cells on the sides of the apical cells divide and grow more vigorously than the embryonic cells posterior to the apical initials. Each apical initial is wedge-shaped It has four cutting faces but segments are usually cut off from the dorsal and the ventral faces. A major portion of the thallus is however formed from the segments produced at the dorsal face. Each dorsal segment divides by a wall parallel to the surface of the thallus. The outer and the inner daughter cells divide and redivide. The segments derived from the outer daughter cell differentiate into the upper photosynthetic region of the thallus and the sex organs. The derivatives of the inner cell give rise to the ventral, colourless, storage region. According to Pietsch the segments cut off parallel to the ventral face of the apical initials give rise only to the **lower epidermis**, the **rhizoids** and the **scales**.

Dichotomy (Fig 4·7B). Now and then some of the median cells of the row of apical initials divide vertically to form a tissue which separates the growing point into two sets of apical initials. Each set functions as the growing point of a new thallus lobe. It is the beginning of dichotomy. It becomes more marked by the addition of more and more tissue between the two sets of apical initials.

REPRODUCTION

Riccia starts reproducing when it has reached a certain stage of maturity. It reproduces vegetatively and by meiospores formed following a sexual process. The thallus reproduces by vegetative methods and is also concerned with the sexual process. Meiospores are produced by the non-sexual individual in the life cycle. It is the **sporogonium**.

A. Vegetative Reproduction. *Riccia* thallus multiplies vegetatively during the growing season by the following first two methods :—

1. *Fragmentation*. It depends upon the ageing of the **vegetative cells**. The cells in the older portions die of old age and eventually disorganise. When the death and decay of the older portions of the thallus reaches dichotomy the young lobes become separated. Each of these by apical growth grows into a new thallus.

2. *Adventitious Branches*. In *R. fluitans* special adventitious branches arise from the ventral surface of the thallus in the midrib region. They become detached from the parent thallus by the decay of the connecting tissue and form new plants.

3. *Persistent apices*. In many species of *Riccia* which grow in regions with a prolonged dry season, as in the Punjab, the whole plant except the growing apices of the thallus lobes is killed. The surviving persistent apices resume growth in the succeeding rainy season. Kashyap reported that in *R. himalayensis* (*R. discolor*) at the end of the growing season the apices of the thallus lobes grow down into the soil and become thickened. The rest of the plant dies. During the next growing season the apices grow up and form new plants.

4. *Tuber formation*. It has been reported in *R. perennis*, *R. discolor*, *R. vescata*, etc. The apices of the thallus lobes become

thickened to form tubers at the end of the growing season. With the advent of unfavourable conditions the plant perishes. The tubers remain dormant and resume growth under suitable conditions.

B. Sexual or Gametic Reproduction.

1. *Distribution of Sex Organs*. The sex organs are developed on the thallus lobes which are not in any way specialised for the purpose. They are developed in lines extending back from the growing points. Generally they lie in the dorsal furrow or groove sunk deeply, each in a separate cavity. They are developed in an acropetal order. The younger ones are thus near the tip or near the growing point and the older are away from it. The antheridia and archegonia, in some species, are developed on the same thallus. Such species are known as **monoecious**. In others the two kinds of sex organs are developed on different thalli. They are referred to as **dioecious**. *R. robusta* (*R. crystallina*), *R. billardieri*, *R. gangetica* and *R. pathankotensis* are monoecious while *R. himalayensis* (*R. discolor*) and *R. sanguinea* (*R. frostii*, Fig. 4·8) are dioecious. In the monoecious forms the antheridia are formed first and archegonia later. In a few cases they are formed successively, a few antheridia and then a few archegonia. The sex organs arise singly and each lies in a separate pit. The site of a sunken antheridium is usually marked by a tiny tower-like projection of surrounding thallus tissue. The thallus af *Riccia*, as it bears the sex organs, is known as the **gametophyte** plant. The sperms and the eggs are the last structures developed during the gametophyte phase.

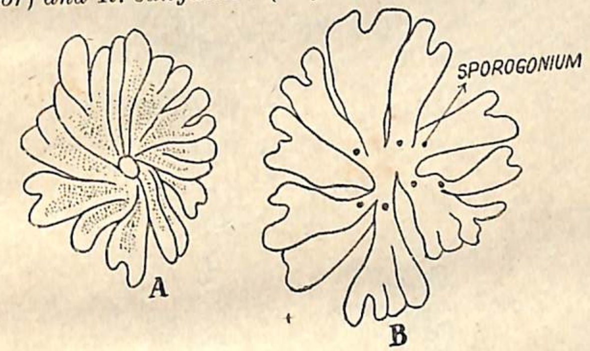


Fig. 4·8 (A—C). Riccia sanguinea (R. frostii)
A. Male plant.
B. Female plant.

Structure and Development of Sex Organs.

(*a*) **Antheridium** (Fig. 4·9, I).

(*i*) *Structure*. The mature antheridium (Fig. 4·9, I) is an elongated structure. It consists of an ovoid or a pear-shaped body seated on a short, few-celled stalk. It stands in a deep pit (**antheridial chamber**) and is attached to its bottom by means of its multicellular stalk. Each antheridial chamber opens at the upper surface of the thallus by a narrow pore. The body of the antheridium has an outer, jacket layer of sterile cells. It is called the **antheridial wall**. The antheridial wall is protective in function and one cell in thickness. It encloses a mass of small, fertile cubical cells called the **androcyte mother cells**. Each androcyte mother cell has a denser cytoplasm and a relatively larger nucleus. It divides diagonally to form two sperm cells known as the **spermatids** or **androcytes** (Fig. 4·10 A). The protoplast of each androcyte gets metamorphosed into a single sperm (Fig. 4·10 E). In this way several hundred biflagellate sperms are produced in each antheridium. When mature the walls of the spermatids or androcytes dissolve. The sperms lie free in the viscous fluid in the cavity of the antheridium surrounded by the jacket layer.

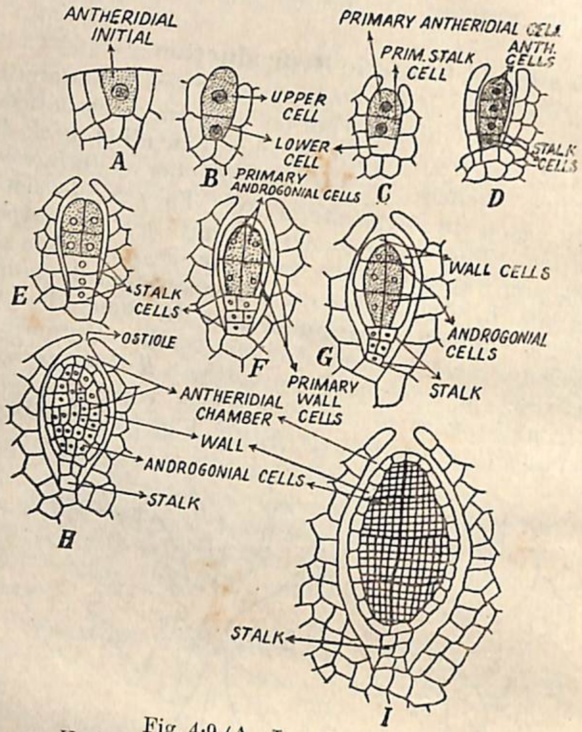


Fig. 4·9 (A—I). Riccia sp. Various stages showing the development of antheridium. (Diagrammatic). Explanation in the text.

Each sperm (Fig. 4·10 E) is a minute, slender, curved structure. It is furnished with a pair of flagella at its anterior end. The body consists of an elongated nucleus. The portion of the cytoplasm not utilized in the formation of flagella remains attached to the posterior end of the body of the sperm as a tiny vesicle. The sperms do not leave the antheridium until enough moisture is present to permit them to swim about.

(*ii*) *Dehiscence*. Presence of moisture is essential for the dehiscence of an antheridium. Water enters the narrow pore of the antheridial chamber and finds its way into its cavity. The cells of the antheridial wall at the apex of the antheridium absorb this water by imbibition. They get softened and eventually disintegrate to form a distal pore. The sperms may be shot with considerable force or extruded slowly in a single viscous mass through the pore. Eventually they escape through the narrow canal of the antheridial chamber to the upper surface of the thallus. Here they swim freely in a thin film of water in the dorsal furrow.

(*iii*) *Development* (Fig. 4·9 A—H). Each antheridium develops from a single superficial cell called the **antheridial initial** (Fig. 4·9 A). It lies on the dorsal surface of the thallus immediately behind the growing apex. The antheridial initial increases in size and becomes papillate. It then divides transversely into an **upper cell** and a **lower cell** (Fig. 4·9 B). The lower cell undergoes a few divisions to form the embedded portion of the antheridial stalk. The upper cell enlarges and undergoes parallel cleavage to form a row of four cells (Fig. 4·9 D). The two lower cells of this row function as the **primary stalk cells** (Fig. 4·9 D). They undergo a few further divisions to form the stalk of the antheridium. The two upper cells of the row function as **primary antheridial cells** (Fig. 4·9 D). Each primary antheridial cell divides by two successive vertical divisions at right angles to each other forming four cells (Fig. 4·9 E).

The body of the antheridium at this stage consists of two tiers of four cells each (Fig. 4·9 E). Periclinal divisions now appear in all the cells of each tier. The young antheridium is now differentiated into an outer layer of eight sterile **jacket** or **wall initials** enclosing the eight fertile inner cells (Fig. 4·9 F). The inner fertile cells are called the **primary androgonial cells**. The latter divide further. Eventually a mass of small cubical cells is formed. These are the **androgonial cells** (Fig. 4·9 H). The latter undergo further division. The cells of the last cell generation of androgonial cells are sometimes referred to as the **sperm mother cells** or **spermatocytes**. Smith calls them **androcyte mother cells**. As the androgonial tissue increases anticlinal walls appear in the jacket or wall initials. This results in the formation of a jacket layer of sterile cells one cell in thickness. It constitutes the wall of the antheridium. Each androcyte mother cell divides diagonally without the formation of a wall into two triangular **sperm cells** or **androcytes** (Fig. 4·10 A). Each of these gives rise to a minute, biflagellate **sperm**.

Coincident with the early development of the antheridium the neighbouring cells of the thallus tissue exhibit rapid upgrowth. They divide and grow upward around the antheridium The latter at maturity becomes completely enclosed in a cavity. This cavity or pit is called the **antheridial chamber** (Fig. 4·9 H and I). It opens by a small pore at the upper surface of the thallus.

(*iv*) *Formation of sperms or spermatogenesis* (Fig. 4·10 A—D). The sperms are formed from the triangular androcytes. Each androcyte (Fig. 4·10 B) has a dense protoplast. It has a distinct relatively large nucleus. There appear near the periphery of the protoplast a small granule. It is called the **blepharoplast**. Gradually the androcyte becomes more or less spherical (Fig. 4·10 C). Accompanied by this change in the form of the androcyte is the elongation of the blepharoplast and the nucleus. The blepharoplast forms a thin cord-like structure with a thickened head. The nucleus becomes sickle-shaped (Fig. 4·10 D). The sickle-shaped nucleus moves to the periphery of the protoplast. The cord-like blepharoplast encircles the protoplast up to about $\frac{3}{4}$ of the distance. The thickened head of the blepharoplast produces the two **flagella**. The electron microscopy reveals the standard 9—2 fibrillar organisation of the flagellum. The curved nucleus forms the body of the sperm with the blepharoplast forming the apex furnished with two flagella. The unused portion of the cytoplasm of the androcyte forms a small **vesicle**. The latter remains attached to the posterior end of the sperm (Fig. 4·10 E).

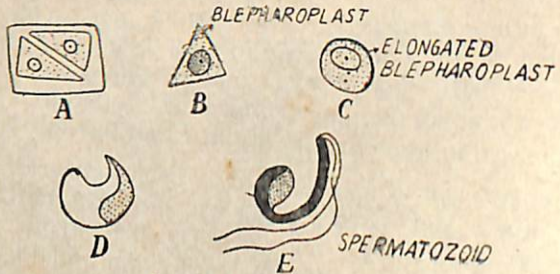


Fig. 4·10 (A—D). Riccia sp.
Stages in the development of sperms
A. Diagonal division of androcyte mother cell into two androcytes.
B—D. Metamorphosis of androcyte into a sperm.
E. A biflagellate sperm. (After Black)

(*b*) **Archegonium**. (*i*) *Structure*. The archegonium is a flask-shaped organ. It consists of two parts, the basal swollen portion called the **venter** and a long, slender **neck**. (Fig. 4·11 I). The venter is directly attached to the tissue of the thallus. There is usually no visible stalk. The neck consists of a vertical row of four cells, the **neck canal cells** surrounded by a layer of sterile cells forming a protective jacket. The jacket or neck cells are arranged in six longitudinal rows. Each row is 6—9 cells in height. The tip of the neck is made up of four specialised large **cap**, **cover** or **lid cells** with greater diameter than the neck cells. The venter also has a jacket of sterile cells continuous above with the jacket of the neck. It is the **venter wall**. The venter wall is also one cell in thickness. It encloses the venter cavity which is filled with two cells. They are the lower, larger **egg cell** and the upper smaller **ventral canal cell**. The latter functions like a plug holding the former in place in the venter. The egg cell is the largest of the axial row. Each archegonium lies within a cavity. The distal portion of the archegonial neck, however, projects above the surface of the thallus into the dorsal furrow. *R. Sanguinea* (*R frostii*) is an exception in which the neck almost reaches the surface of the thallus.

(*ii*) *Dehiscence*. When the archegonium reaches maturity the neck canal cells and the ventral canal cell degenerate. Their products, when hydrated, form mucilage. The mucilage imbibes water and swells. The pressure thus set up forces the cover cells to separate from one another. In this way a narrow passage, the **neck canal** is formed. It connects the cavity of the venter containing the egg with the outer world. The neck canal is now filled partly with water and partly with the mucilage formed by the disintegration of the axial row of cells except the egg cell.

(*iii*) *Development*. The archegonium springs from a single cell called the **archegonium initial** (Fig. 4·11A). It is the superficial cell derived from the younger dorsal segment of the apical cell. The archegonial initial grows and projects above the surface of the

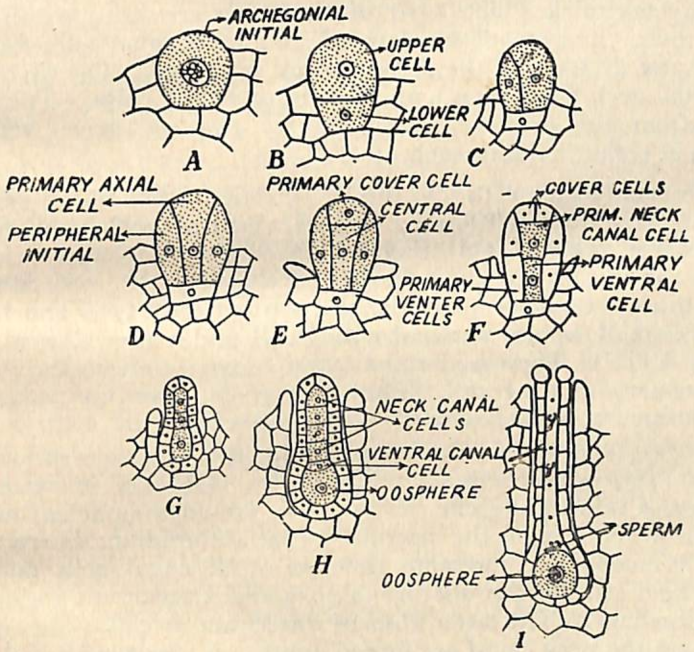


Fig. 4·11 (A—I). Riccia sp.
A—H. Various stages in the development of archegonium. Explanation in the text.
I. Mature archegonium illustrating fertilisation. (Diagrammatic)

thallus. It then divides by a transverse wall separating a lower cell from an upper cell (Fig. 4·11B). The lower cell takes no further part in the development of the archegonium. The upper cell functions as a **primary archegonial cell** (Fig. 4·11C). It enlarges and divides by three eccentric vertical walls (Fig. 4·11D). They separate three sterile, **peripheral initials** surrounding a middle fertile cell. The latter functions as the **primary axial cell**. It slightly overtops the peripheral initials. Each of the three peripheral initials divides longitudinally to form six **jacket initials** or **envelope cells**. The primary axial cell now undergoes a transverse cleavage. This separates an upper **primary cover cell** from an inner **central cell** (Fig. 4·11E).

At this stage a transverse division appears in the six jacket initial and the single central cell. The division differentiates the archegonium into two halves or two tiers of cells (Fig. 4·11F). The six jacket cells of the upper tier function as **neck initials**. The outer cell separated from the central cell functions as the **primary neck canal cell** (Fig. 4·11 F). Further transverse divisions of the six neck initials and their daughter cells produce a slender, tubular neck one cell thick. The cells of the neck are arranged in six vertical rows. They enclose a row of four neck canal cells formed by transverse divisions of the primary neck canal cell. The tip of the archegonial neck has a rosette of four **lid** or **cover cells**. They are formed from the primary cover cell by two successive vertical divisions at right angles to each other.

The six jacket cells of the lower tier function as **venter initials**. The inner cell formed from the central cell functions as the **primary ventral cell** (Fig. 4·11F). The transverse divisions of the venter initials and their daughter cells form the **venter wall** one cell thick. It encloses a cavity the, **venter cavity**. The latter contains a small upper **ventral canal cell** and a large lower **egg cell** (Fig. 4·11H). They are formed by an unequal transverse division of the primary ventral cell. The archegonia have no protective sheaths around them. Each archegonium lies in a pit.

(c) *Fertilisation*. It takes place in the presence of water. The dorsal furrow serves as a capillary tube. It takes in water in the form of a thin film. The heavy dew provides sufficient water to permit movements of the sperms. The antheridium bursts and the sperms escape. At the same time the neck canal cells and the ventral canal cell in the mature archegonia degenerate to form a mass of mucilage. The latter absorbs water and swells. The cover cells closing the neck canal are forced apart. A passage way to the egg is thus formed. A bit of this mucilage oozes out of the open necks. The exuded mucilage contains certain chemical substances such as soluble proteins and inorganic salts. At the same time the liberated sperms swim about in all directions and in great numbers in the water film that covers the thallus in the region of the dorsal furrow. Some will chance to come near the open necks of the archegonia. Of these some gain entrance into the open necks. This

is perhaps in response to certain chemical substances (proteins and inorganic salts) present in the mucilage which diffuses from the neck of each archegonium. Several of the sperms may swim downward in the liquid in the neck canal. They enter the venter. Usually one, probably the first to arrive, penetrates the egg. The nucleus of the sperm travels to that of the egg and unites with it to accomplish fertilisation. The act of fertilisation ends the gametophyte phase.

SPOROPHYTE PHASE

This phase in the life cycle is the direct result of the sexual process. It comprises the **zygote**, **embryo** and the **sporogonium**.

(*a*) **Zygote**. It is the fusion cell formed by the union of the sperm with the egg and is the pioneer structure of the sporophyte phase. It secretes a wall around it and enlarges in size. The zygote is retained within the venter where it begins to grow immediately. It enters upon no resting period. The zygote differs from the unfertilized egg in the following two respects :

1. It has a diploid nucleus.
2. It has a cellulose cell wall around it. The egg before syngamy has a haploid nucleus and is naked.

(*b*) **Development of Embryo**. The zygote (Fig. 4·12A) lying in the venter undergoes repeated cell division and cell enlargement. A spherical mass of undifferentiated cells called an **embryo** (Fig. 4·12 C) is formed. It fills the venter cavity. The archegonium is persistent. The venter expands as a close envelope over the developing embryo (Fig. 4·12 C). It becomes two cell layers thick and is known as the **calyptra**. The neck of the archegonium later withers.

The first division of the zygote is by a nearly horizontal wall (Fig. 4·12 B). It is in a plane at right angles to the long axis of the archegonium. The next division is at right angles to the first. The young embryo now consist of four cells. It is the **quadrant stage** (Fig. 4·12C) of the embryo. All the four quadrants are nearly equal. Each quadrant, as a rule, divides by a vertical wall at right angles to the preceding ones. The embryo at this stage consists of eight nearly equal cells. It is the **octant stage**. Garber and Lewis reported the formation of a four-celled filamentous instead of a quadratic type of embryo in some species of *Riccia*. Succeeding divisions in the eight-celled embryo are in an irregular sequence. A more or less spherical mass of 20 to 40 undifferentiated, colourless cells is produced.

(*c*) **Young Sporogonium**. Each of the outer cells of the undifferentiated spherical embryo divides by a periclinal wall (Fig. 4·12D). A single layer of outer cells is separated from an inner, central mass of cells. The former is called **amphithecium** and the latter **endothecium**. The cells of the amphithecium are large and flat. They divide only by anticlinal walls to form the protective, sterile, **jacket layer** which remains one cell thick and constitutes the wall of the young sporogonium. The cells of the endothecium are all alike. They constitute the first cell generation of the sporogenous tissue. It is called the **archesporium**. As the sporogonium advances towards maturity the archesporial cells divide and re-divide to form a mass of sporogenous cells (Fig. 4·12E). The cells of the last cell generation of the sporogenous mass function as

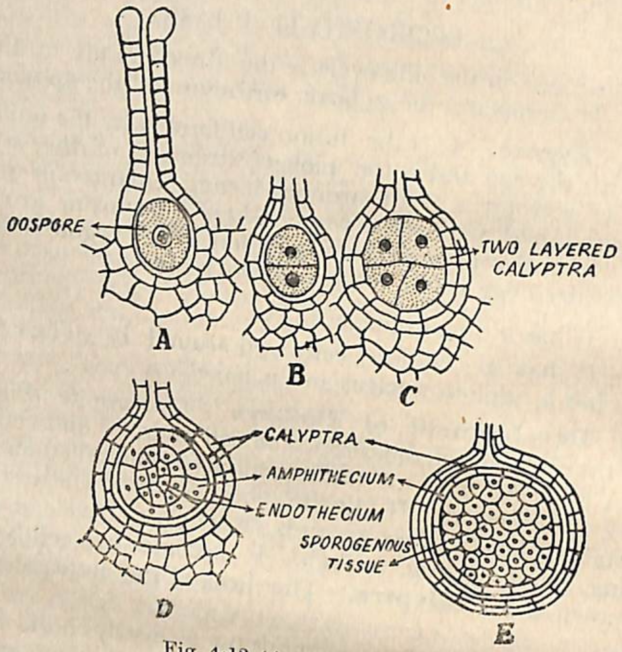


Fig. 4·12 (A – E). Riccia sp.
Various stages in the development of sporogonium.

A. Mature oospore ready for division.
B. First division of zygote, two-celled embryo.
C. Quadrant and octant stages of the embryo enclosed in a two-layered calyptra.
D—E, Differentiation of amphithecium and endothecium.
(Diagrammatic).

potential **spore mother cells** or **sporocytes**. The spore mother cells are the last structures of the sporophyte phase. During further development of the sporogonium the sporocytes begin to separate and become more or less rounded. Their walls become mucilaginous and contents densely granular. Practically all the sporocytes divide meiotically to form spores. A few, however, are said to disintegrate to form a nutritive fluid (Fig. 4·13D). They are called the **nurse cells**. Some bryologists consider the nurse cells as the **fore-runners** of the **elaters** of the more advanced members of the Marchantiales.

As the spore mother cells enter upon meiotic division their walls disintegrate. The wall of the sporogonium and the cells of the inner layer of the calyptra also disintegrate (Fig. 4·13E). The rounded spore mother cells lie free in the cavity of the sporogonium surrounded by the single layered calyptra. The developing

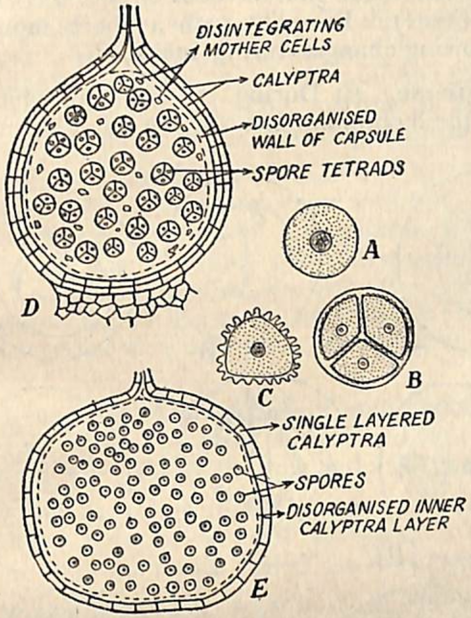


Fig. 4·13 (A—E). Riccia sp. Formation and maturation of spores.

A. A spore mother cell.
B. A spore tetrad with a common sheath around it.
C. A mature spore.
D. L.S. Sporophyte containing spore tetrads, degenerating spore mother cells and the disintegrated sporogonium wall.
E. Spores lying in a cavity surrounded by an outer layer of calyptra.

spores are bathed and nourished by the nutritive fluid formed by the disintegration of :—

(*i*) walls of spore mother cells.
(*ii*) non-functional spore mother cells.
(*iii*) jacket layer of the sporogonium.
(*iv*) inner layer of the two cell thick calyptra.

(*d*) **Sporogenesis** (Fig. 4·14 A—H). It is the process whereby the spores are formed from the spore mother cells. Each functional spore mother cell (Fig. 4·13A) undergoes **meiosis** to form four spores. In meiosis the diploid nucleus of the spore mother cell undergoes two successive divisions. The first division is reductional and the second mitotic. Both constitute meiosis. The walls between the four haploid nuclei are, however, laid simultaneously at the end of the second division. The group of four haploid daughter cells is called the **tetrad**. The cells in the tetrad are arranged tetrahedrally.

The diploid number of chromosomes in the zygote and spore mother cells in many species of *Riccia* is sixteen or $n=8$. According to Lewis (1906) the spore mother cells of *Riccia crystallina* possess 8 chromosomes ($n=4$). Roughly such a spore mother cell would undergo the following changes during meiosis :—

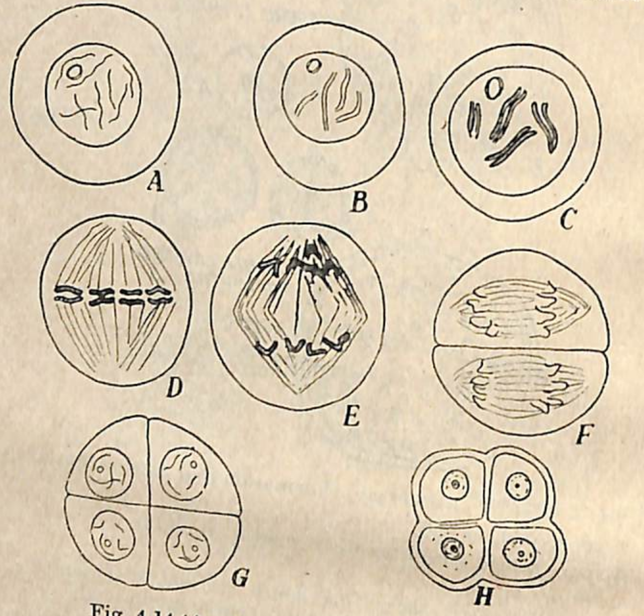


Fig. 4·14 (A—H). Stages in sporogenesis.

A. First prophase with eight chromosomes in the spore mother cell.
B. Later prophase with four bivalents.
C. Still later prophase showing double nature of the chromosomes of the bivalents.
D. First metaphase with bivalents lined up at the equator.
E. First anaphase with the chromosomes of bivalents separated and migrating to opposite poles as wholes.
F. Second Anaphase. Chromatids migrating to opposite poles.
G. Telophase.
H. Four spores of the tetrad separating. The spores in a tetrad are arranged tetrahedrally and not in the same plane as shown in Figs. F, G and H.
(Highly diagrammatic)

First Prophase. (*i*) During the early prophase of the first meiotic division the 8 chromosomes of the diploid nucleus become distinguishable (Fig. 4·14A). This is the **leptotene stage** of the first prophase. Half of these chromosomes are of male parentage and the other half of female parentage. The former are called the **paternal** chromosomes and the latter **maternal**. For every paternal chromosome there is a corresponding maternal chromosome similar in size, shape and nature of inherited characters. These are called the **homologous chromosomes**.

(*ii*) The homologous chromosomes become arranged in pairs in the next **stage** (Fig. 4·14B). This is the **zygotene stage** of the first prophase. The pairs of chromosomes are called the **bivalents**. Each bivalent has one maternal and one paternal chromosomes which are homologous. The number of bivalents is one-half of the diploid number. It is called the **haploid** number.

(*iii*) The two chromosomes of each bivalent twist about each other and become thicker and undergo knotting. Each chromosome of the pair (bivalent) exhibits a longitudinal slit which shows its double nature. Each half of the chromosome is called the **chromatid**. The bivalent thus consists of 4 chromatids. This is the **pachytene** stage of first prophase (Fig. 4·14C). Interchange of chromatin material may take place between the chromatids during this stage.

(*iv*) The modified chromosomes of each bivalent again become distinct. They separate but remain attached at the **chiasmata**. This is the **diplotene** stage of the first prophase.

(*v*) The bivalents move to the periphery of the nucleus. The nuclear membrane and the nucleoli disappear. This is the final stage of the first prophase and is called the **diakinesis**.

First Metaphase. The spindle now appears in the region of the nucleus. The four bivalents become arranged at the equator of the spindle. The double nature of the chromosomes is evident but the chromatids do not separate. This is the **metaphase** stage of the first meiotic division (Fig. 4·14D).

First Anaphase. The two chromosomes of each bivalent separate. The four whole chromosomes migrate towards each opposite pole of the spindle (Fig. 4·14 E). Each chromosome has a longitudinal split showing its double nature.

First Telophase. The chromosomal group at each pole of the spindle receives four chromosomes. This is the haploid number. The first meiotic division is thus **reductional**. Of the four chromosomes in each new daughter nucleus there is one member of each homologous pair. There is no **cytokinesis** after the first meiotic division.

(*vi*) Each of the two daughter nuclei at the telophase of the first division of meiosis receives four chromosomes (**haploid** number).

The **second division** of meiosis follows before the first is quite complete. It is **mitotic**. It starts with the **second metaphase**. Two new spindles appear in the cytoplasm of the spore mother cell (Fig. 4·14 F). The four chromosomes of each daughter nucleus arrange themselves at the equators of their respective spindles. The splits in these chromosomes which appear during the late prophase of the first meiotic division are still visible at the second metaphase. These show the double nature of each chromosome. Each half of the chromosome is called a **chromatid**. During the second metaphase the chromatids of each chromosome separate. They then move toward opposite poles. This is the **second anaphase** (Fig. 4·14 F). In this phase the four chromatids and not the whole chromosomes migrate toward opposite poles. There is thus no reduction in the number of chromosomes in the second division. Each of the four daughter nuclei at the end of the second telophase has four chromosomes. This is the haploid number. The second division of meiosis is thus mitotic. Walls are laid simultaneously between the four haploid daughter nuclei in the spore mother cell (Fig. 4·14G). A group of four daughter cells is formed. Each daughter cell matures into a haploid spore. This quartet of spores formed from a single spore mother cell is called the **spore tetrad**. The four haploid spores of the tetrad are enclosed, at first, in a common sheath. They are arranged in the form of a sphere (tetrahedral manner). In surface view only three can be seen. In the figure they are shown as if arranged in the same plane.

The four young spores are surrounded by a common sheath. As the spores mature the spore walls thicken considerably. The common sheath around each spore tetrad finally ruptures. The mature spores lie in a cavity surrounded by the outer layer of the calyptra.

Production of Meiospores. It is the concern of the sporophyte (Fig. 4·15). The sporophyte or sporogonium of *Riccia* is the simplest among the liverworts. It lacks both the **foot** and the **seta**. It is just a spore sac or capsule spherical in outline. It has a wall one cell layer thick. The capsule wall encloses a mass of spore mother cells. The two layered calyptra forms a close investment around the sporogonium. The latter never emerges out of it. Before the spore mother cells divide to form spores the single layered wall of the sporogonium disintegrates. Later the inner layer of the calyptra also break down. The mature spores lie free in a cavity or sac surrounded by the outer layer of calyptra. There are no elaters. The mature sporogonium of *Riccia* thus has no diploid or sporophytic structures (Fig. 4·15) at this stage. The meiospores which represent the future gametophyte are housed in a sac provided by the parent gametophyte.

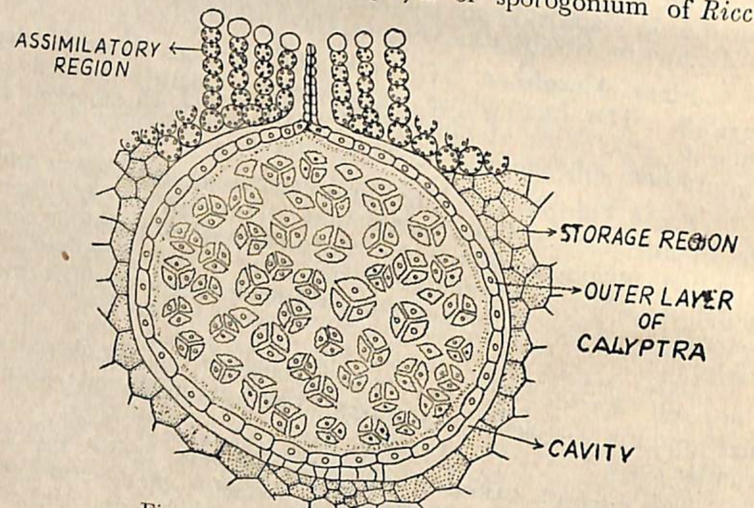


Fig. 4·15. Riccia sp. Mature sporophyte.

Nutrition. Unlike other liverworts the embryo, sporogonium and spore mother cells in *Riccia* develop no chloroplasts. Thus no starch is formed. The sporophyte remains totally dependent upon the thallus (gametophyte) for food materials, water and minerals in solution.

Comparison Between the two Generations. The sporogonium which is the sporophyte individual differs from the thallus (gametophyte plant) in structure, function and genetic constitution as well. It is radially constructed whereas the thallus is dorsiventral. It bears no appendages and is unbranched. The thallus bears appendages in the form of rhizoids and scales and is dichotomously branched. The thallus is green in colour and thus **autotrophic**. The sporogonium has no green colour and is **heterotrophic** in its nutrition. Because of the presence of air spaces the thallus is amply ventilated whereas the sporogonium, at first, is more or less a solid object. The sporogonium is the non-sexual individual which produces the **meiospores**. The thallus is responsible for **sexual reproduction**. The thallus represents the **haplophase** whereas the sporogonium represents the **diplophase**. These differences justify our stand to look upon the sporogonium of *Riccia* as a new individual in the life cycle. It is not an outgrowth of the parent gametophyte (thallus).

Dehiscence of Sporogonium. The sporogonium of *Riccia* never dehisces. The spores are liberated by the decay or shrivelling of the surrounding outer layer of the calyptra and thallus tissue. The thallus perishes in the dry season. The spores remain behind on the soil. In this condition they may be dispersed by the wind. They remain alive for some time. Finally they germinate with the onset of conditions favourable for growth.

Structure of spore (Fig. 4·13C). The liberated spore is pyramidal in shape. It consists of a tiny mass of cytoplasm containing a small haploid nucleus. The food is stored largely in the form of oil globules. The spore wall is thick, black and sculptured. It is differentiated into three layers. The outer is called the **exosporium**. The middle one is **mesosporium** and the innermost **endosporium**. The exosporium is thin, strongly cuticularized and sculptured with irregular ridges. At maturity it is black. The triradiate ridge may be present on it. The mesosporium is also cuticularised but is thick and differentiated into three concentric zones namely, an outer loosely laminated region followed by a dark zone and a densely laminated zone. The endosporium is a homogeneous layer. It is thin and composed of pectose and cellulose. These three layers of the spore wall develop in **centripetal** succession. The spore is the first structure of the future gametophyte.

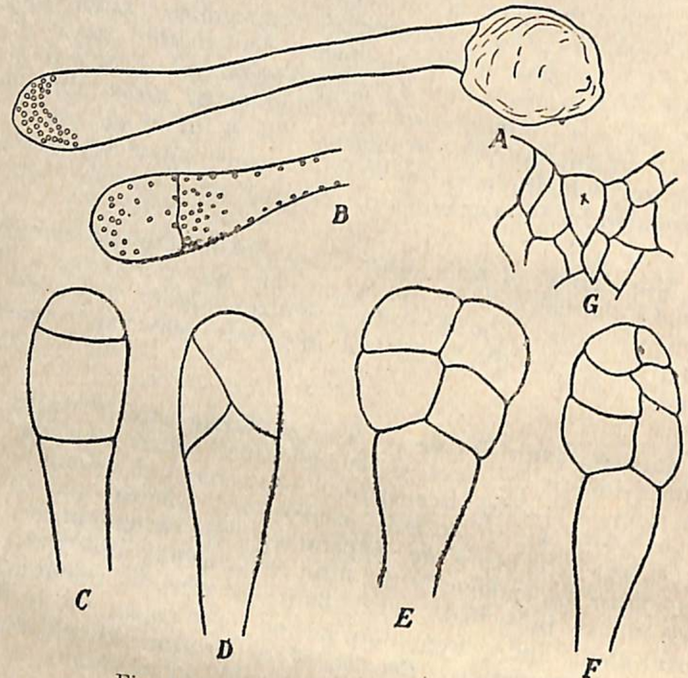


Fig. 4·16 (A—G). R. trichocarpa.
A—F. Various stages in the germination of spores.
G. Portion of the young thallus with an apical cell.
(After Campbell)

Germination of spore. Udar (1957) studied germination of spores in different species of *Riccia*. He concludes that the spores of *Riccia* enter upon no resting period. They germinate in about 6·10 days. Prior to germination the spore absorbs water and swells about 10-20 *u*. According to Campbell (1918) the black exosporium and the mesosporium rupture at the tri-radiate ridge. According to Pande (1924), Srinivasan (1940) and Udar (1957—58) the swollen spores may become more or less transparent. A prominent pore called the **germ pore** appears on the outer face opposite the tri-radiate mark. Thin colourless endosporium enclosing the contents grows out through the rupture (Campbell) or germ pore (Pande, Srinivasan and Udar) in the form of a small outgrowth. It is called the **germ tube** (Fig 4·16A). The latter may grow rapidly into a long, club-shaped structure. Often the germ tube remains short and broad. Most of the spore contents migrate to its distal, swollen end where chloroplasts appear. A transverse wall appears separating a large terminal cell at the distal end of the tube (Fig. 4·16B). Meanwhile the first rhizoid appears at its base. Udar reports that the first rhizoid makes its appearance from the base of the germ tube when it is one-celled. It is not separated by a septum. According to Campbell the first rhizoid appears relatively later. It is separated from the germ tube by a septum. A second septum parallel to the first establishes another cell at the distal end (Fig. 4·16C). Each of these two cells next divides by a vertical wall followed by a second at right angles to the first. In this way eight cells are formed at the distal end of the germ tube (Fig. 4·16E). They are arranged in two tiers of four cells each. The four cells of the proximal tier divide by transverse walls. The daughter cells elongate to form the posterior portion of the young thallus. Meanwhile one of the four cells in the distal tier begins to function as an **apical cell** with two cutting faces. It cuts off segments alternately right and left parallel to its flat cutting faces. From the segments thus cut off are derived the tissues of the new thallus (Fig. 4·17). The single apical cell of the young thallus is soon replaced by a row of apical cells.

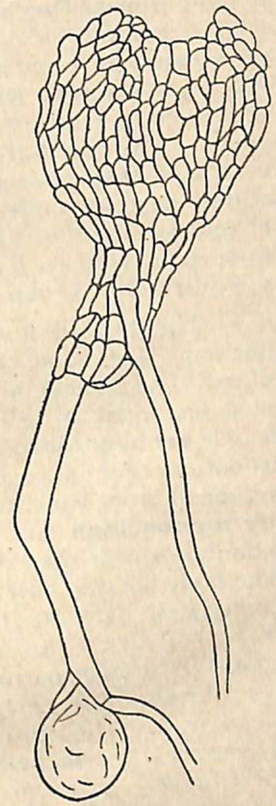


Fig. 4·17. Riccia trichocarpa. A later stage in the germination of a spore. (After Campbell)

SUMMARY OF THE LIFE CYCLE OF RICCIA (Fig. 4·18)

The life cycle of *Riccia* consists of two vegetative individuals. One of these is the parent of the other. The most conspicuous and dominant of the two individuals is the green **thallus** (Fig. 4·18, 1). It is a small, flat, green object dorsiventral in construction.

The thallus often branches repeatedly by dichotomy. It thus consists of a number of lobes. Each thallus lobe is linear to obcordate. It has a **dorsal furrow** and a depression at its apex. In the terminal depression is lodged the growing point. The thallus is fixed to the substratum by unicellular, unbranched **rhizoids**. They are of two kinds, **smooth walled** and **tuberculate**. The rhizoids absorb water and minerals from the damp soil on which *Riccia* generally grows. The dorsal green region of the thallus is spongy. It is amply ventilated as it possesses pores and intercellular spaces in the form of deep narrow canals. The latter in some species broaden into air-chambers. As the upper portion of the thallus bears chlorophyll and these green cells are bathed with air the thallus plant is capable of self-nutrition. It manufactures a large amount of food.

The thalloids green individual is concerned with sexual reproduction. It produces the gametes and is called the **gametophyte plant**. The gametes are produced in multicellular sex organs. The male sex organ is called the **antheridium** (Fig. 4·18, 2) and the female **archegonium** (Fig. 4·18, 3). They lie in the dorsal furrow at its bottom each in a separate cavity. They are developed in rows in acropetal order back from the growing apex. Some species of *Riccia* are **monoecious** and others **dioecious**. The antheridium has a globular or pear-shaped body elevated on a short, multicellular stalk. The body has an outer jacket of sterile cells enclosing a mass of androcytes. The latter produce several hundred biflagellate **sperms** (Fig. 4·18, 3). The archegonium is a flask-shaped structure. It consists of a long, narrow **neck** and an enlarged basal portion called the **venter**. Both the neck and the venter have one cell layer thick jacket wall. The venter cavity contains a single non-motile egg and a **ventral canal cell** above the latter. The neck has a row of **axial cells**. These are the **neck canal cells**. The axial row of cells excepting the egg cell disintegrate when the archegonium is mature. In this way a canal leading to the egg (Fig. 4·18) is formed.

All the structures produced by the gametophyte plant constitute the **gametophyte generation** or **phase**. The latter therefore consists of the **green thallus plant**, the **sex organs** (antheridia and archegonia) and the **gametes** (sperms and eggs). This generation starts with the spores and ends with **fertilization**. The gametes are the last structures produced during the phase. All the structures constituting the gametophyte generation have *n* number of chromosomes in their nuclei. This number is also called **haploid**. The gametophyte generation is therefore the **haplophase** in the life cycle. The sex cells (sperms and eggs) of this generation are incapable of giving rise to new individuals alone. They must fuse before they do so. This act of fusion between the sperm and the egg is called **fertilization**. The structure formed by the fusion of the two gametes is called the **zygote** (Fig. 4·18, 5).

The zygote has a diploid number of chromosomes. On germination it does not give rise to the gametophyte plant (thallus). It

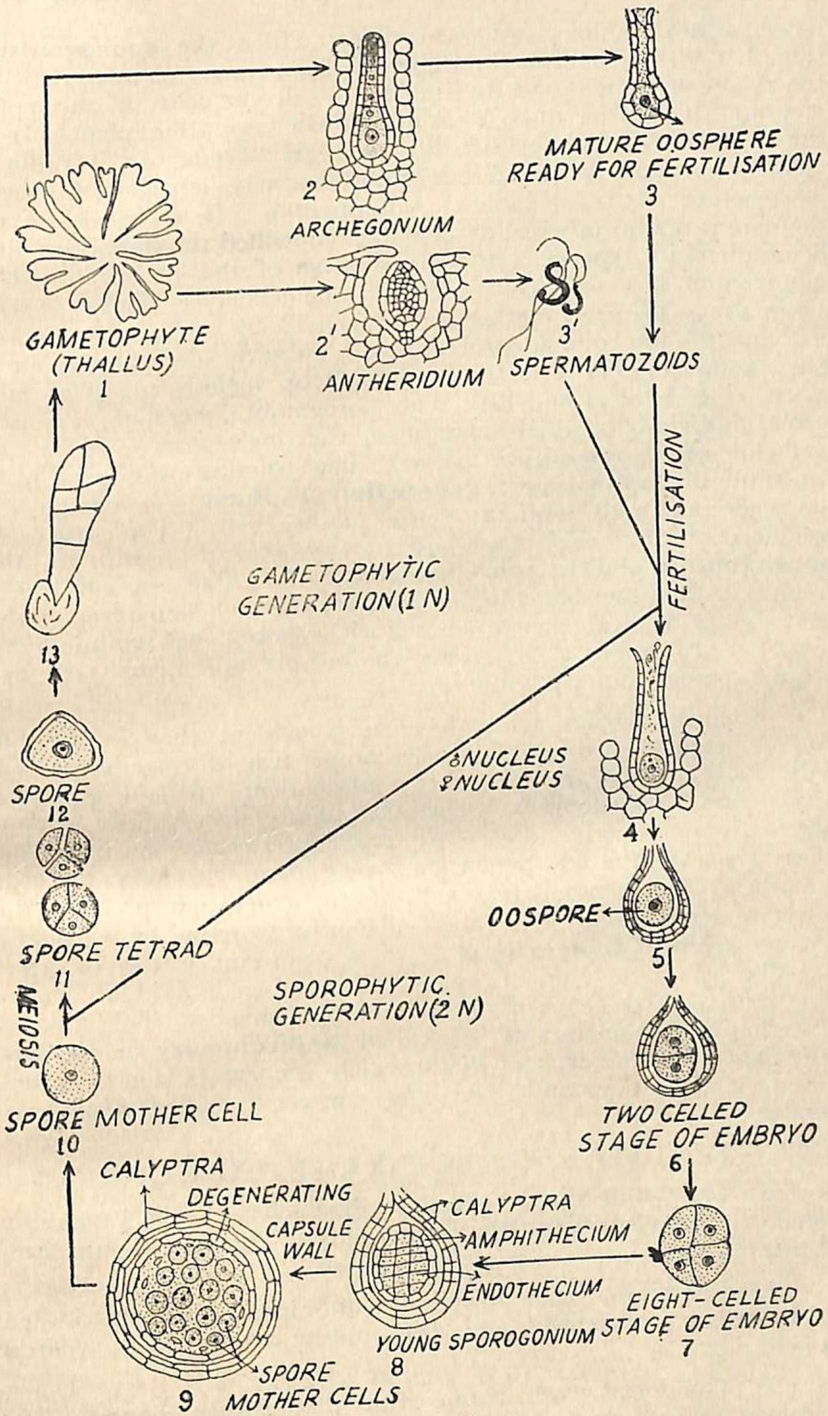


Fig. 4·18. Riccia.
Diagrammatic representation of the life cycle.

develops into a simple, spherical object called the **sporogonium** (Fig. 4·18, 8). The diploid number of chromosomes characteristic of the zygote is carried over by mitosis to all the cells of the sporogonium. The latter therefore is a **diploid** vegetative plant. It is the second individual in the life cycle of *Riccia*. It is radially constructed and is solid before reaching maturity. It is very simple in structure. It is incapable of self-nutrition. It is nourished by the parent thallus in which it remains embedded throughout its life. Being diploid it represents the **diplophase** of the life cycle. The sporogonium has a wall of sterile cells one cell layer thick. It encloses a mass of spore mother cells (Fig. 4·18, 9). The spore mother cells are the last diploid structures produced by the sporogonium. Each spore mother cell (Fig. 4·18, 10) by meiosis produces four spores, (Fig. 4·18, 11 and 12). The sporogonium, therefore, is a non-sexual individual which produces the meiospores. It is as well called the **sporophyte plant**. The structures produced by it constitute the **sporophyte generation** or **phase**. It starts with the zygote and ends with the spore mother cells. The structures produced during this phase are the **zygote**, the **embryo**, the **sporogonium** and the **spore mother cells**. The haploid spores produced from the spore mother cells are the first structures of the next gametophyte generation. Each spore, on germination, (Fig. 4·18, 13) produces the green thallus plant (gametophyte) and not the sporogonium (sporophyte).

From the account given above it is evident that in the life cycle of a single *Riccia* plant there occur two distinct vegetative individuals. They are the green independent, thalloid **gametophyte** and the colourless spherical, radially constructed **sporophyte** (sporogonium). These two individuals occur one after the other generation after generation. One plant regularly succeeds the other. The reproductive cells of one generation produce the alternate generation. This phenomenon is expressed by the phrase "**Alternation of Generations**". It is a constant feature of *Riccia* and all other bryophytes. The two alternating individuals in the life cycle of *Riccia* are dissimilar morphologically. This kind of "Alternation of Generations" is called **heterologous** or **heteromorphic**. The life cycle of *Riccia* which is characterized by alternation of generations and sporogenic meiosis is called **diplohaplontic**.

IMPORTANT FEATURES IN THE LIFE CYCLE OF RICCIA

1. Externally simple, green, ribbon-shaped, dichotomously branched, dorsiventral **thallus** is internally differentiated into several tissues.

2. The thallus bears unicellular, unbranched, smooth walled and tuberculate **rhizoids** and also minute **scales** on its ventral surface.

3. The dorsal green region of the thallus is chambered. The chambers occur as deep, narrow **air canals** or channels separated by vertical rows of green cells. They are empty and communicate with the exterior through simple, rudimentary and unspecialized pores which are simply air spaces bounded by 4 to 8 epidermal cells.

4. The ventral portion of the thallus consists of colourless, compactly arranged parenchyma cells.

5. Some species of *Riccia* are **monoecious** and others **dioecious**. The sex organs lie in the median dorsal furrow each in a separate pit.

6. The pear-shaped or ovoid body of the ripe **antheridium** has a jacket layer of sterile cells surrounding a mass of minute, somewhat coiled, biflagellate sperms.

7. The antheridial wall disintegrates at its distal end. A mucilaginous fluid containing sperms oozes through the pore of the antheridial pit at the upper surface of the thallus.

8. The typically flask-shaped **archegonium** has an outer layer of sterile jacket cells surrounding an **axial row** of cells. The basal cell of the row is called an **egg**. It lies in the venter. Above it is the **ventral canal cell**. The remainder cells of the axial row lie in the neck region and are called the **neck canal cells**.

9. Moisture is essential for the maturing of sex organs and fertilization.

10. The sperms swim to the archegonia in a thin film of water in the dorsal median furrow. They enter the open necks of the archegonia and swim down their neck canals to reach the venter where only one of them unites with the egg to accomplish fertilization.

11. The diploid zygote secretes a wall around it. It then undergoes cleavage to form a spherical, multicellular **sporophyte**.

12. The sporophyte of *Riccia* is the simplest among the liverworts. It is nothing but a **spore case**. There is neither any **seta** nor a **foot**. It is nourished by the parent thallus. The two layered venter now called the **calyptra** forms a close investment around it. The neck of the archegonium may wither by this time. By the time the spores mature the single layered sporogonium wall and the inner layer of the calyptra disintegrate. The spores lie free in the space surrounded by the outer layer of the calyptra. At this stage there is no trace of the diploid, sporophytic tissue. The spores are the first cells of the next gametophyte generation and the outer layer of the calyptra represents the parent gametophyte tissue.

13. The dispersal of spores takes place by the decay of surrounding thallus tissue.

DISCUSSION

Riccia is a very interesting genus of the Liverworts. It is rather an evolutionary riddle. The gametophyte is quite a complex structure. The sporophyte, however, is the simplest known among the liverworts. It is simply a spore case incapable of self-nutrition. It lacks both foot and seta. The capsule wall is one layer in thickness. Within the wall are the spore mother cells or spores. Some of the spore mother cells are said to degenerate. They are looked upon as the fore-runners of the sterile cells or elaters of the more advanced members of the order Marchantiales. Are we then to regard *Riccia* sporophyte as a **primitive** or a **reduced** structure ?

Bower, Campbell and Cavers hold that the simplest sporophyte of Riccia is **primitive**. The more complex sporophytes of the Liverworts when seriated illustrate a natural advance. They appear to have evolved from such a simple sporophyte as that of *Riccia* by the gradual and progressive sterilisation of its potentially fertile cells (spore mother cells). Instead of forming spores they remain sterile and are devoted to somatic functions such as nutrition, spore dispersal, etc. This resulted in the differentiation of the sporophyte into foot, seta and capsule as in *Marchantia*. Some of the potential spore mother cells become sterile to form elaters which help in spore dispersal. This hypothesis of the three eminent botanists is called the **theory of sterilisation**. It attempts to explain the evolution of the sporophyte of liverworts with *Riccia* sporophyte as the starting point. On the basis of this theory the evolution or the history of the sporophyte of the bryophytes forms an ascending series. The series begins with *Riccia* sporophyte.

The theory though appealing fails to account for the complex nature of the *Riccia* gametophyte (thallus). It is far from being the simplest among the liverworts. The primitive liverwort on the basis of this theory must be a simpler type. It should have the simplest gametophyte as well as the simplest sporophyte in its life cycle. This is not the case in *Riccia*. As a matter of fact such a combination is not known among the Liverworts.

Von Goebel, on the other hand, believes the other way. He holds that the simplest sporophyte of Riccia is **reduced** rather than **primitive**. He maintains that the simpler types like *Riccia* have resulted by reduction (also called **progressive simplification**) in both the alternative phases (gametophyte and sporophyte). His contention has been supported by Kashyap, Church and Evans. Kashyap suggested that the genus *Riccia* might have emerged from a genus like *Targionia*. This view is supported by the widespread evidence of reduction in the vegetative characters of the gametophyte of the Marchantiales. The reduction and simplification of the parts which bear and protect the sex organs runs side by side with reduction in the structure of the sporogonia which they produce. The outlines of this reduction series are :

(*i*) Loss of assimilatory filaments in the air chambers

(*ii*) Simplification of the barrel-shaped pores of the advanced Marchantiales.

(*iii*) Shifting of the terminal gametophores (antheridiophores and archegoniophores) to the dorsal position. This is accompanied by the gradual elimination of the stalk of the gametophore. The receptacles become sessile. The antheridia and archegonia actually come to lie on the upper surface of the thallus.

(*iv*) Associated with these changes is the elimination of perigynium and involucre.

All these changes are accompanied by reduction in structure of the sporophyte. The first step in reduction is the elimination of seta. This is followed by the disappearance of foot. Consequently the sporophyte becomes a mere spore case. Later the ring-like thickenings disappear from the cells of sporogonial wall. Subsequently all the endothecium cells become fertile. This step eliminates the elaters.

REVISION QUESTIONS

1. List the characteristic features of the family Ricciaceae and give the systematic position of *Riccia*.
2. With the help of a series of diagrams write an account of the life cycle of *Riccia*.
3. List in a tabulated form the differences between the gametophyte and sporophyte of *Riccia*.
4. What is an archesporium ? How does it originate and what does it give rise to in *Riccia* ?
5. List the important features in the life cycle of *Riccia*.
6. Describe the process of spore formation and mechanism of spore discharge in the sporophyte of *Riccia*.
7. Describe the various views with regard to the evolutionary position of *Riccia* sporophyte. How far is Goebel justified in assuming that forms like *Riccia* are reduced and not primitive ?
8. Analyse the mature spore case in *Riccia* ? Is it a sporophyte or a gametophyte ? Justify your answer giving cogent reasons in support.
9. Justify the truth or falsity of the following statement : "The sporogonium of *Riccia* is a new individual in the life cycle and not an outgrowth of the thallus.
10. Trace the development of antheridium and archegonium in any member of the Hepaticae you have studied.

25.11.70

CHAPTER V

MARCHANTIALES—MARCHANTIACEAE : MARCHANTIA

Marchantiaceae

General Characters. This family is represented by over 250 species. They are grouped under about 23 genera. The deep green, dorsal surface of the thallus, in most genera, is marked by rhomboidal areas (**areolae**), each with a central pore. Internally the thallus is chambered. The chambers are usually well developed with or without photosynthetic filaments. Exceptions are *Dumortiera* in which the chambers are represented only in a relic condition and *Monoselenium* in which they are lacking. The **air pores** are well developed. The sex organs are united in **receptacles**

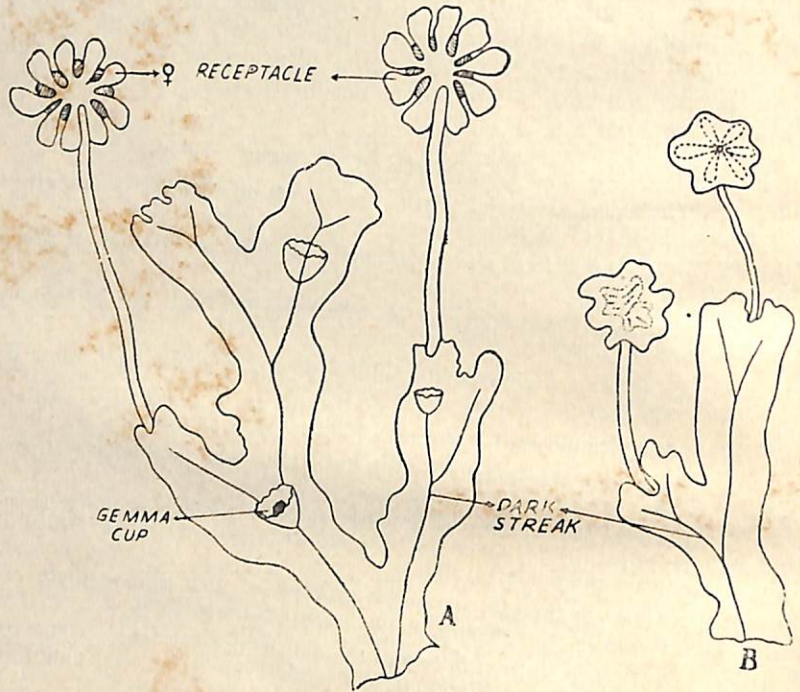


Fig. 5·1 (A—B). Marchantia palmata.
A. Female plant.
B. Male plant.

which may be sessile or stalked. The female receptacle is generally always stalked. The sporogonium is usually differentiated into the **foot**, **seta** and **capsule**. The latter produces both spores and elaters. The capsule dehisces either by the separation of a lid or by valves. The family includes a number of genera such as *Dumortiera*, *Lunularia*, *Marchantia*, *Reboulia*, *Fimbriaria*, *Targionia*, *Grimaldia*, *Plagiochasma*, etc. The most common and highly differentiated of these is *Marchantia*. We shall therefore study *Marchantia* as a type of this family.

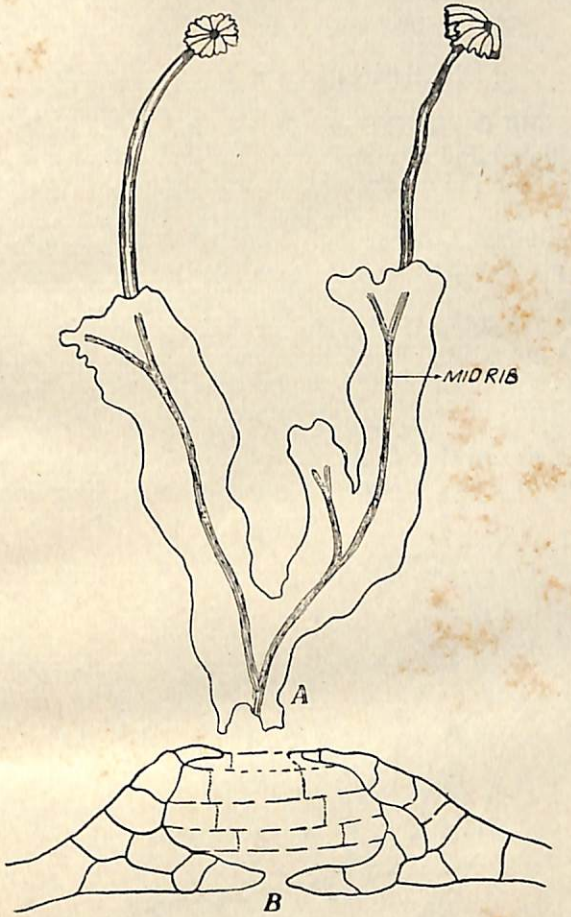


Fig. 5·2 (A—B). Marchantia nepalensis.
A. Female plant.
B. V.S. through a pore.

Systematic Position :

Bryophyta
Hepaticopsida
Marchantiales
Marchantiaceae

MARCHANTIA (March.) L.

Habitat and Distribution. *Marchantia* is the most common, highly differentiated and in many ways the most interesting genus. It is commonly found in moist, cool, shady situations and areas of burnt ground. The surface of damp soil, the sides of streams, springs, water courses, walls of wells, swamps, damp ravines and wet rocks are the places suited for the growth of this Liverwort. It grows in large mats. It has about 65 species. They are found all over the world. There are about 11 Indian species as reported by Chopra (1943). They are mostly confined to the Himalayas. The following three species of *Marchantia* have been reported by Kashyap from various parts of India, plains as well as the hills :—

1. *M. palmata* (Fig. 5·1). It is found in the plains as well as the hills. It hs been reported from Kashmir, Kumaon, Punjab

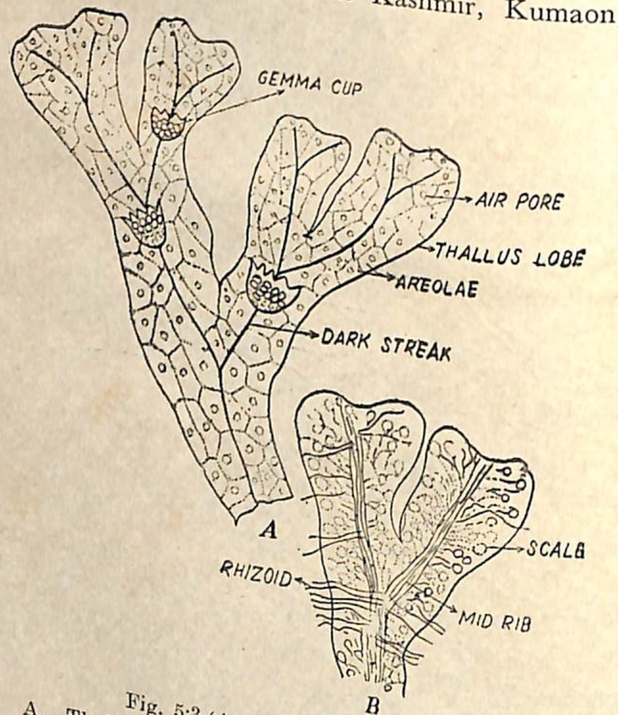


Fig. 5·3 (A—B). Marchantia sp.
A. Thallus bearing gemma cups on the dorsal surface.
B. Thallus bearing scales and rhizoids on the ventral surface.

Plains, Calcutta, Assam, South India, Lahore Sialkot, etc. It is distinguished by the presence of a median, dark streak on the dorsal surface of each lobe of the thallus. The lobes are long, narrow, margin entire and apex emarginate.

2. *M. nepalensis* (Fig. 5·2). The median dark streak is lacking. Lobes are short and broad and margin generally crisped. The apex is emarginate. It has been reported from the Outer Himalayas, Punjab Plains, Kashmir, Garhwal, Kumaon, etc.

3. *M. polymorpha* (Fig. 5·5). It has been reported from the hills such as the Outer Himalayas up to 8000 ft., Pangi, Ladakh, Leh., etc. The thallus is relatively large, broad, slightly concave or flat. The margin of the thallus lobes sinuate to lobed.

GAMETOPHYTE PHASE

It begins, as in *Riccia*, with the maturation of spores. Each spore (Fig. 5·22A), on germination, produces a green thallus (Fig. 5·22F). Externally it has the same general appearance as that of *Riccia*. However it differs in its large size, coarse nature and more prominent and pronounced elongated lobes. It is somewhat better adapted to grow on land than *Riccia*. The green thallus is the gametophyte plant.

(*a*) **External Morphology of the Thallus** (Fig. 5·3A). It is a dark, green, somewhat fleshy, flat, once or a few times dichotomously branched structure with a dorsiventral symmetry (Fig. 5·3A). Each thallus branch or lobe is traversed by a broad, thick, central **midrib**. It also has a **notch** at its apex. At the bottom of the notch is located the growing point. The upper surface of the thallus is marked by rhomoboidal to polygonal areas called the **areolae** (Fig. 5·3A). The boundaries between these areas mark the limit of the underlying **air chambers**. Each area has a tiny conspicuous hole or an **air pore** in the centre. The pore is visible on the surface as a light dot. The air pores permits aeration of the thallus with the minimum dehydration. At times little cup like structures, the **cupules** or **gemma cups** (Fig. 5·3A), are seen on the upper surface of the thallus. They arise in the **midrib** region. The margin of the cup is toothed and membranous (Fig. 5·5C). From the bottom of the cup arise numerous, green, flat, multicellular bodies called the **gemmae**. The mature gemmae get detached. The detached gemmae are washed on to the soil where each gives rise to two new gametophyte plants.

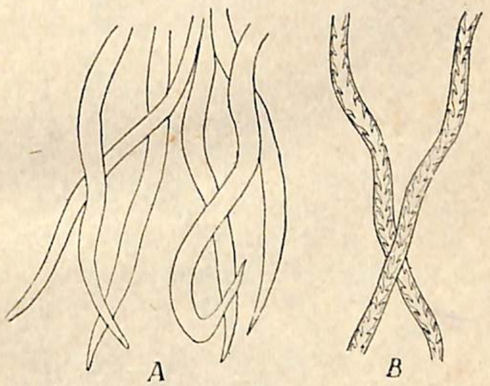


Fig. 5·4 (A—B). Marchantia sp.
A. Smooth walled rhizoids.
B. Tuberculate rhizoids.

When the thallus attains sexual maturity it bears gametangia bearing upright, stalked, umbrella-shaped structures at apices of certain lobes of the thallus. These are called the **gametophores** or **gametangiophores**. They are of two kinds, **antheridiophores** and **archegoniophores**. The former bear antheridia and the latter archegonia. The two kinds of gametophores are borne on different thalli so that *Marchantia* has male plants distinct from female plants.

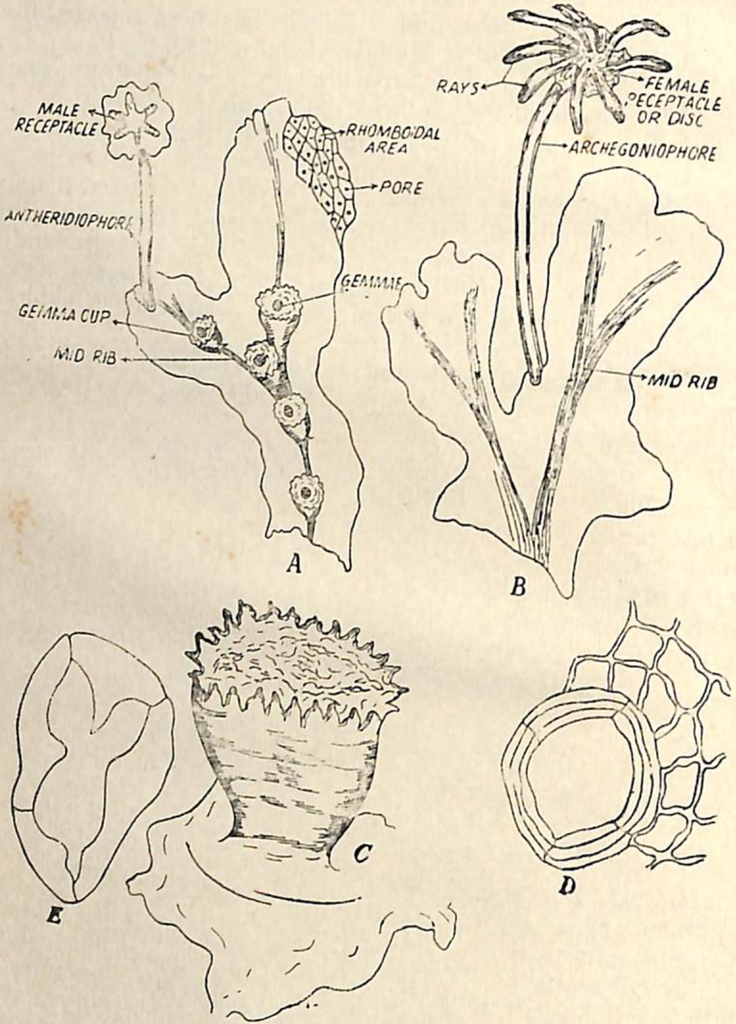


Fig. 5·5 (A—E). Marchantia polymorpha.
A. Male plant with gemmae cups.
B. Female plant.
C. A gemma cup.
D. A pore with a few epidermal cells as seen from above.
E. A pore from below with papillose cells of the lowermost tier.

From the lower or the ventral surface of the thallus arise numerous elongated, single-celled, hair-like outgrowths, the **rhizoids** (Fig. 5·6). The latter anchor the plant to the substratum. In addition they absorb water and minerals in solution. The rhizoids are of two kinds, **smooth walled** (Fig. 5·4 A) and **tuberculate** (Fig. 5·4 B). The tubercles are pronounced, peg-like invaginations of the wall. They extend across the cavity but do not form complete partitions. The tuberculate or peg rhizoids are thick-walled, narrow and appressed to the surface of the thallus. They arise from beneath the scales and function as a capillary conducting system which serves to carry water to all the absorptive parts of the thallus. The smooth-walled rhizoids stand out from the thallus and penetrate the substratum to absorb water and to fix the thallus to it. They are broad, thin-walled with colourless contents. They are the first to be formed on germination. Besides the rhizoids the ventral surface bears purplish, flattened **scales** (Fig. 5·5B). They are usually arranged in two to four rows on either side of the midrib. They are never in a single row as in *Riccia*. Each scale is a plate of cells one cell layer thick. It is attached obliquely and is divided by a narrow constriction into two parts, the **body** and the **appendage** (Fig. 3·1C and D). In some species the appendage is absent. The scales are separate from the beginning. They are not formed by the splitting of a single lamella as is the case in *Riccia*.

(*b*) **Internal Structure** (Figs. 3·2A and 5·6). There is greater internal elaboration of the thallus in *Marchantia* as compared with *Riccia*. In vertical section the thallus is many cells deep. The cells are arranged in three distinct regions (Fig 3·2A) instead of two as in *Riccia*. These are (*i*) the **epidermal** region, (*ii*) the **photosynthetic** region and (*iii*) the **storage** region.

(*i*) **Epidermal Region** (Fig. 5·6). It consists of a well-defined **upper epidermis** and **lower epidermis**. The upper epidermis forms a surface layer over the photosynthetic region. It consists of a single layer of thin-walled cells with slightly thickened outer walls. The epidermal cells contain few chloroplasts. The outer walls of the epidermal cells are practically water-proof. The epidermis is thus protective in function. It tends to check transpiration from the underlying tissues. Embedded in the epidermis are special, chimney-like or barrel-shaped **air pores** (Fig 5·6). Each pore is surrounded usually by four tiers of four or five cells each. The number of tiers, however, may go up to eight. These tiers form rings of cells one above the other. They are arranged in the form of a small chimney which encloses a wide passage (Fig. 5·6B). This passage is broad in the middle and narrow above and below. The pore wall lies half above and half below the epidermis. The opening of the pore is thus slightly raised above the surface of the thallus. The cells of the lowermost tier in some species are papillose (Fig. 5·5E). They project into the passage. However, they do not close it. A star-shaped channel remains open. Each pore leads into an underlying chamber. The presence of air pores in the epidermis facilitates gaseous exchange necessary for photosynthesis and respiration. Apparently the pores bear resemblance to the stomata of the higher plants. To them they are only **analogous.** The stomata are always absent on the gametophyte plant. The cells around the air pore do not regulate the opening as the guard cells do in the stomata. Walker and Pennington (1939) have reported that the surrounding cells by imbibitional changes in their cell walls bring about opening and closing of the air pore.

(*ii*) **Photosynthetic Region.** Beneath the upper epidermis are the **air chambers.** They are of fairly regular size, simple and distinct from one another. They are arranged in a single horizontal layer. The chambers are bounded by one cell layer thick partitions. The partitions are three or four cells in height. Each chamber communicates with the exterior through a barrel-shaped or chimney-like **pore.** From the floor of each chamber arise short, simple or branched filaments of green cells, known as the **assimilatory** or **photosynthetic filaments.** They nearly fill the cavity of the chamber. All the cells of the floor, side walls and the photosynthetic filaments contain numerous ovoid chloroplasts. Even the cells of the overlying epidermis may contain a few chloroplasts. The chambered region thus constitutes the principal centre of **photosynthesis** in the thallus. It is at its maximum rate in dim light. The arrangement of the cells in the photosynthetic region of the thallus of *Marchantia* is thus quite different from that of *Riccia.*

According to Barnes and Land (1907), the chambers in *Marchantia* originate as intercellular spaces. They are formed by the splitting of the cell walls (**Schizogenously**) and not by surface **involution.** The splitting starts usually below the epidermis. It progresses gradually inwards. For a detailed discussion of the **origin** of the **air chambers** in the Marchantiales refer to page 42 (Chapter IV).

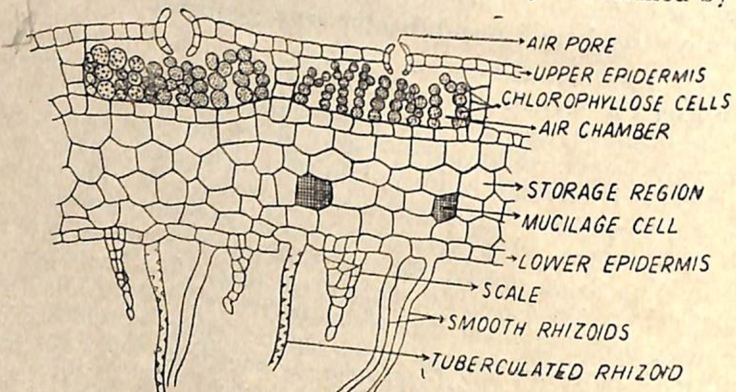


Fig. 5·6. Marchantia sp.
A vertical section through the thallus.

(*iii*) **Storage Region** (Fig. 5·6). Just below the photosynthetic region lies the ventral **storage region** of the thallus. It is thickest in the centre. Towards the margins it is reduced to 3-4 layers of cells in the thickness. It consists of a uniform tissue made up of relatively large, colourless, thin-walled polygonal, parenchymatous cells which usually lack chloroplasts and are compactly arranged. Most of them contain starch and protein grains. Isolated cells may contain a single oil body or may be filled with mucilage. The former are called the **oil cells** and the latter **mucilage cells.**

The lowermost layer of the storage region is composed of cells similar to those of the upper epidermis. It is the **lower epidermis.** From it project the **rhizoids** and the **scales.** The scales help to retain the moisture below the thallus. This enables *Marchantia* to grow in much drier places as compared with *Riccia.*

(*c*) **Comparison with Riccia.** In general form, structure and development of the thallus *Marchantia* resembles *Riccia.* Both resemble each other in the following features :—

(1) In both the green thallus is dichotomously branched, dorsiventral in construction and as a rule fleshy in texture.

(2) From its lower surface in both arise the unicellular, unbranched, smooth and tuberculate rhizoids and the multicellular scales.

(3) Internally it is differentiated in both into the upper, well ventilated, photosynthetic region and the lower compact, storage region.

(4) In both the growing point is lodged in a notch at the tip of each thallus lobe.

(5) The apical growth in both takes place by means of a group of apical cells arranged in a transverse row.

The *Marchantia* thallus, however, is more advanced and thus differs from the *Riccia* thallus in the following respects :—

(*i*) Its definitely larger size, broader, thicker and coarser lobes.

(*ii*) Better adapted to grow on land than *Riccia.*

(*iii*) Prominent expanded midrib.

(*iv*) Upper surface of the thallus marked with rhomboidal areas each with a distinct central pore.

(*v*) Internal differentiation of thallus into three distinct regions (epidermal, photosynthetic and storage) instead of two (photosynthetic and storage) as in *Riccia.*

(*vi*) A definite layer of air chambers with photosynthetic filaments arising from the floors.

(*vii*) A continuous water proof epidermis with definite barrel-shaped air pores.

(*viii*) Presence of scales in two to four rows on either side of the midrib. They help to retain moisture below the thallus. In Riccia they are arranged in two rows one near each lateral margin-

(*ix*) Presence of gemma cups containing gemmae.

These features indicate that *Marchantia* thallus is more advanced than that of *Riccia*. The presence of scales on the ventral side and not the margins as in *Riccia*. and a continuous well defined epidermal layer enable *Marchantia* to grow in drier habitats as compared with *Riccia*. The ventral scales help to retain moisture below the thallus which can be absorbed by the rhizoids. The epidermis helps to check transpiration from the underlying photosynthetic tissue. In spite of the foregoing features which make *Marchantia* better adapted to a life on land than *Riccia*, abundant moisture is still required for its active growth and fertilisation.

Apical Growth. The growing point lies at the bottom of a notch at the apex of each lobe. It has horizotal row of meristematic cells. By the activity of these the thallus grows in length.

REPRODUCTION

Marchantia reproduces **vegetatively** and by **meiospores** formed following a sexual process.

Vegetative Reproduction. The thallus plant reproduces vegetatively in the growing season by the following three methods :—

(*i*) *Fragmentation*. It is brought about by the ageing of the vegetative cells. The aged cells in the rear or basal part of the

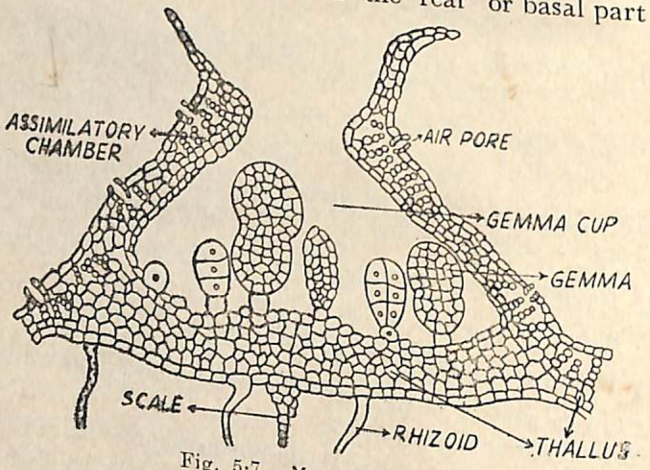


Fig. 5·7. Marchantia sp.
A vertical cross-section of the thallus passing through the gemma cup.

thallus rot and disintegrate. When this decay of cells reaches dichotomy the lobes become separated. Each of the detached lobes by apical growth and dichotomy develops into an independent plant. In this way there is a rapid increase in the number of plants in a particular area and constant invasion of the new territories.

(*ii*) *Formation of Adventitious Branches*. These may develop from any part of the thallus particularly its ventral surface. In *Marchantia palmata* development of adventitious branches from the stalk and disc of the female gametophore was reported by Kashyap. These branches when detached by the decay of the connecting tissue each develops into a new individual.

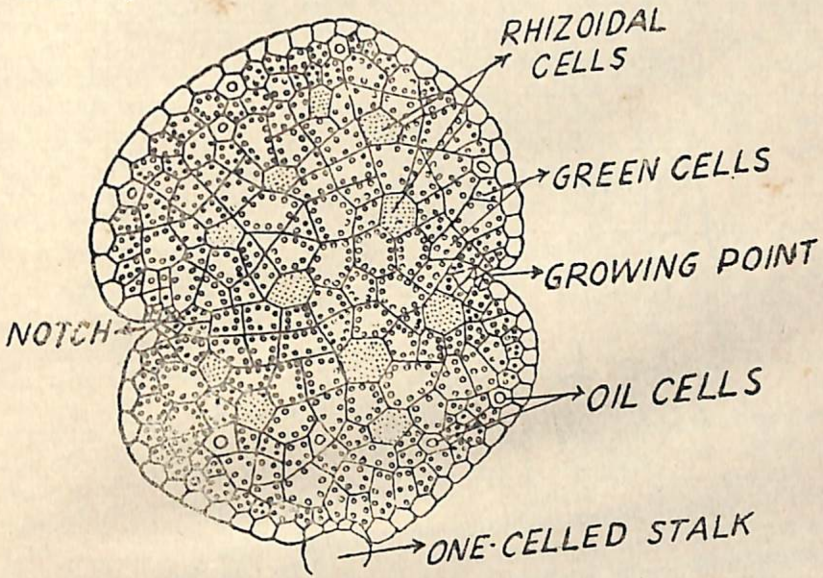


Fig. 5·8. Marchantia sp.
A single gemma.

(*iii*) *Gemmae Formation*. Another interesting and elegant method of vegetative reproduction in *Marchantia* is by the formation of multicellular bodies called the **gemmae**. The gammae develop inside little, shallow, cup-like growths with fringed margins (Fig. 5·5C). The cups are developed on the upper surface of the thallus, generally in the midrib region. The gemmae are small, green, disc-like, slightly bi-convex structures. Each gemma stands on edge on a short, delicate, single-celled stalk. The stalk attaches it to the bottom of the gemma cup (Fig. 5·7). Intermingled with the gemmae in the cup are the club-shaped **mucilage hairs** which secrete mucilage copiously. With the absorption of water provided by dew or rain the mucilage swells and causes the gemmae to get detached from their stalks rather easily. The gammae are then washed on to the soil or carried by a current of water far from the parent plant. The detached gemmae grow into new thalli on suitable soil.

(*i*) *Structure* (Fig. 5·8). The gemma at maturity is a lens-shaped multicellular structure. It is several cells thick in the median portion and deeply notched on the two opposite edges. In each marginal notch lies the growing point. There is another shallow indentation marking the point of attachment to the stalk. Majority of the cells constituting the body of the gemma are green. They contain abundant chloroplasts and are called the **green** or **chlorenchymatous cells**. Isolated cells just within the margin may contain oil bodies instead of chloroplasts. They are called the **oil cells**. The two flattened surfaces are alike and have no innate dorsiventral symmetry. Both the surfaces possess isolated, superficial colourless cells known as the **rhizoidal cells**. The dorsiventral symmetry, becomes fixed at the time of germination and is controlled by the gradients of light, temperature and other environmental factors.

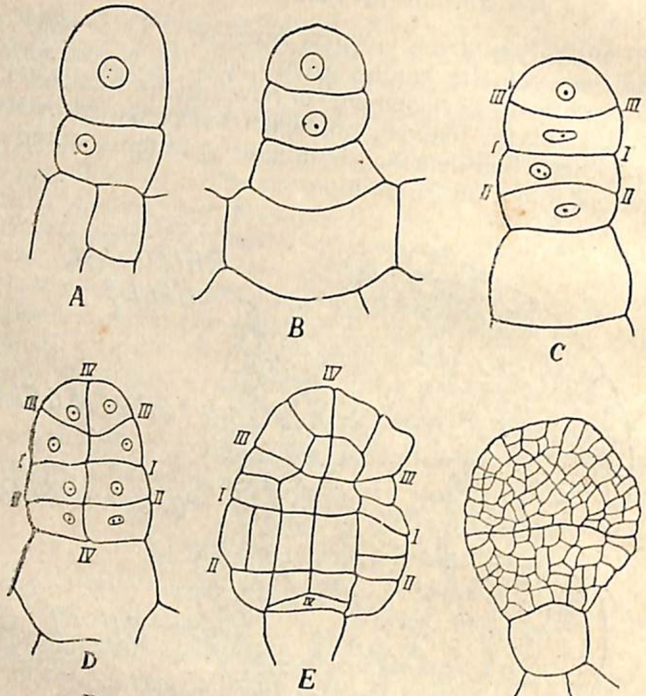


Fig. 5·9. (A—F). Marchantia polymorpha.
Stages in the development of a gemma.
(After Campbell)

(*ii*) *Germination*. When the gemmae fall on a suitable soil, the colourless rhizoidal cells of the face next to the soil develop rhizoids. The meristems or growing points in both the marginal notches begin to grow simultaneously in opposite directions. Rotting away of the central portion of the parent gemma results in the production of two separate plants. Gemmae formation is usually common during the growing season. It provides a very rapid device for multiplication and a successful means of dispersal. It has been experimentally determined by De La Rue and Narayanaswami (1957) that the germination of the gemmae *in situ* (gemma cup) is inhibited by the secretion of auxins from the growing tips of the parent thallus lobes. The auxins diffuse basipetally.

(*iii*) *Development* (Fig. 5·9 A—F). The cupules are formed a short distance back from the growing point. They arise in the form of circular ridges of cells. The gemmae originate from single superficial cells lining the floor of the cupules. Each such cell grows into a papillate outgrowth. It is the **gemma initial**. The gemma initial divides by a transverse wall into a **lower** and an **upper cell** (Fig. 5·9A). The lower cell divides no further. It forms the one-celled **stalk**. The upper cell again divides by a transverse wall (Fig. 5·9B). Each of the two resultant cells undergoes a similar division (Fig. 5·9C). A row of four cells is formed. These four cells undergo divisions both in the vertical (Fig. 5·9D) and horizontal planes (Fig. 5·9E). As a result a thin plate-like structure with a notch on the opposite sides is formed (Fig. 5·9E).

Sexual Reproduction. It is the concern of the thallus plant and is of **oogamous** type. It takes place only once during the growing season in high **humidity** when the days are long and the nitrogen content in the environment is low.

(*a*) **Position and Distribution of Sex Organs**. The sex organs in *Marchantia* are borne on the vertical branches of the thallus, highly specialised for this purpose. The sexual branches are **apical** or **terminal** in position (Fig. 5·1 A and B) as each develops from one half of a dichotomy of the apical cell. The growth in length of the thallus lobes ceases after their development. Each upright sexual branch thus a is a direct continuation of the prostrate thallus lobe from which it arises. It is called the **gametophore**. The thallus-like nature of the gametophore is shown by the presence of rhizoids in the grooves on the anterior side of the stalk and photosynthetic chambers on the posterior side.

The gametophore bearing the male sex organs (antheridia) is called **antheridiophore** (Fig. 5·5A) and the one bearing archegonia is called **archegoniophore** (Fig. 5·5B). Both the antheridiophores and the archegoniophores constitute accessory apparatus of sexual reproduction. The essential organs are the **antheridia** and the **archegonia**. Some botanists have reported the occurrence of **androgynous receptacles** in some species. In addition to the pendulous archegonia the androgynous receptacle bears antheridia in pits on the upper surface. Generally the antheridiophores and the archegoniophores are borne on different thalli. Sexual reproduction thus involves two kinds of plants—male which bear the antheridiophores and female which bear the archegoniophores. Marchantia is therefore **dioecious**.

(*b*) **Antheridiophore** (Fig. 5·5A). It consists of a stalk bearing terminally a disc or **receptacle** with a margin bearing rounded teeth. The stalk is more or less cylindrical. It is one to three centimetres long. A cross-section through the stalk reveals that there are chambers and pores on its posterior side and two grooves on its anterior side (Fig. 5·10). The grooves or furrows run longitudinally the entire length of the stalk. They contain rhizoids and scales. These tissues of the stalk correspond to those on the dorsal and ventral surfaces of the thallus lobe and prove its dorsiventral nature.

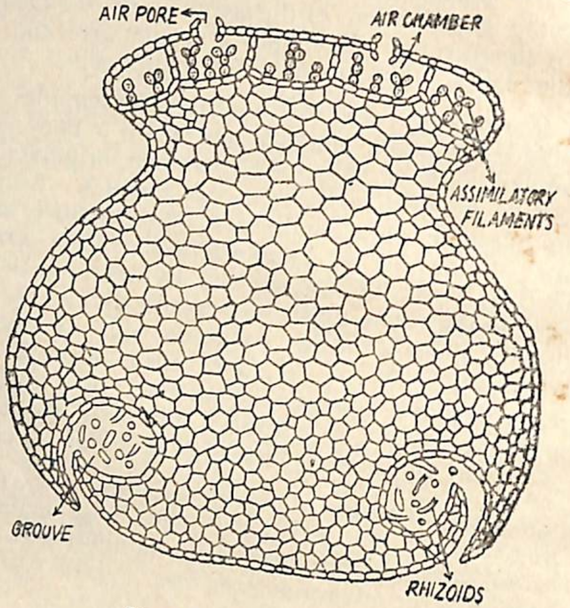


Fig. 5·10. Marchantia.
A. Cross-section through the stalk of the antheridiophore.

The terminal **male receptacle** is a flattened, lobed disc. Typically it has eight lobes occasionally four. Each lobe has its growing point lodged at its tip. The receptacle thus is a branch system. It is the result of repeated, localized dichotomy in quick succession. A vertical section of the male receptacle (Fig. 5·11) shows that it has the same tissues as are found in the thallus. There is the upper epidermis with air pores. The latter open into the underlying chambers containing the photosynthetic filaments. Beneath the chambers is the compact region of colourless parenchyma cells. The lower epidermis bears scales and rhizoids. Deeply sunk in the upper surface of each lobe are the **antheridia**. They arise in the acropetal order and are arranged in a radial row. Each antheridium lies in a flask-shaped pit (**antheridial chamber**). The latter opens by a narrow channel on the upper surface of the disc. The opening is called an **ostiole**. The antheridial cavities of chambers alternate in position with the air chambers.

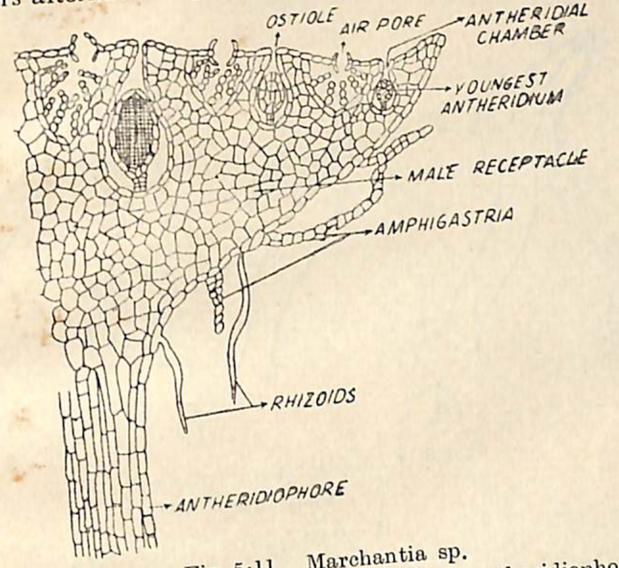


Fig. 5·11. Marchantia sp.
A vertical section through a portion of the antheridiophore.
(Diagrammatic)

(*i*) **Structure of Antheridium** (Fig. 5·13H). The mature antheridium is an ovoid object raised on a short, multicellular stalk. The stalk attaches the antheridium to the floor of the antheridial chamber (Fig. 5·11). The body of the antheridium has a jacket layer of sterile cells constituting its **wall**. The latter encloses a mass of **androcyte mother cells**. Each androcyte mother cell divides to form two **androcytes** or **sperm cells**. The protoplast of the androcyte metamorphoses into a biflagellate **sperm**.

Dehiscence. The ripe antheridium dehisces on the access of water. It is provided by rain or dew. From the concave upper surface of the male receptacle the water finds its way through the ostiole into the antheridial pit. There it comes in contact with the cells in the upper portion of the **antheridial wall** which eventually disintegrate. The antheridium thus ruptures at its distal end. A slimy mass of androcytes oozes out of the chamber at the upper surface of the receptacle into the water. Reaching the surface of water the androcytes spread out thinly as a delicate film. The sperms are now set free by the dissolution of the walls of the androcytes.

A liberated sperm (Fig. 5·12) is usually described as a small, narrowly curved structure. It is an elongated nucleus with the cytoplasm forming an extremely thin investment. From its one end project the two flagella. Sato reported the liberated sperm to be rod-like in *M. polymorpha*. While swimming it takes the form of a crawl of a snake with one flagellum lashing forward and the other backward.

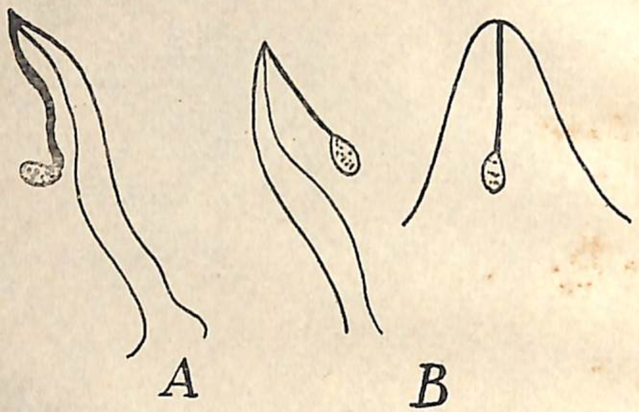


Fig. 5·12 (A—B). Marchantia sp.
A. Sperm after Ikeno.
B. Sperm after Strassburger.

(*ii*) **Development of Antheridium** (Fig. 5·13). The growth of the thallus ceases with the development of the antheridiophore. The growing apex of the very young unelongated antheridiophore divides by dichotomy. The division is repeated a number of times. The result is the formation of a disc with a wavy margin. Each lobe of the disc has a growing point situated at its apex. The antheridia arise in acropetal order behind the growing point of each lobe of the disc. The young disc or receptacle is covered by conspicuous papillae. The papillae denote the position of antheridial chambers.

Each antheridium, as in *Riccia*, arises from a single superficial cell, the **antheridial initial** (Fig. 5·13A). It lies 2 or 3 cells behind the growing point of the lobe of the male receptacle. The initial increases in size and divides by a transverse division into two cells (Fig. 5·13B). The lower cell undergoes no further development. The upper, however, divides again transversely to separate a basal **primary stalk cell** and a terminal **primary antheridial cell** (Fig. 5·13C). The former undergoes a few divisions to form the stalk of the antheridium. The primary antheridial cell divides by parallel cleavage to form a row (Fig. 5·13D) of usually two or three cells sometimes more. Each of these cells now divides by two successive vertical walls at right angles to each other (Fig. 5·13E). The body of the antheridium at this stage consists of 2, 3 or 4 tiers of four cells each. Periclinal divisions appear in all the cells of the tiers (Fig. 5·13 F). These divisions separate an outer layer of cells enclosing a mass of inner or central cells. The outer cells are called the **jacket initials** and the inner ones **primary androgonial cells** (Fig. 5·13F). During further development the jacket initials divide only by anticlinal walls to give rise to the **wall** of the antheridium (Fig. 5·13G). The primary androgonial cells undergo a considerable number of divisions. The cells of the last cell generation are called the **androcyte mother cells**. They are small, cubical and numerous in number.

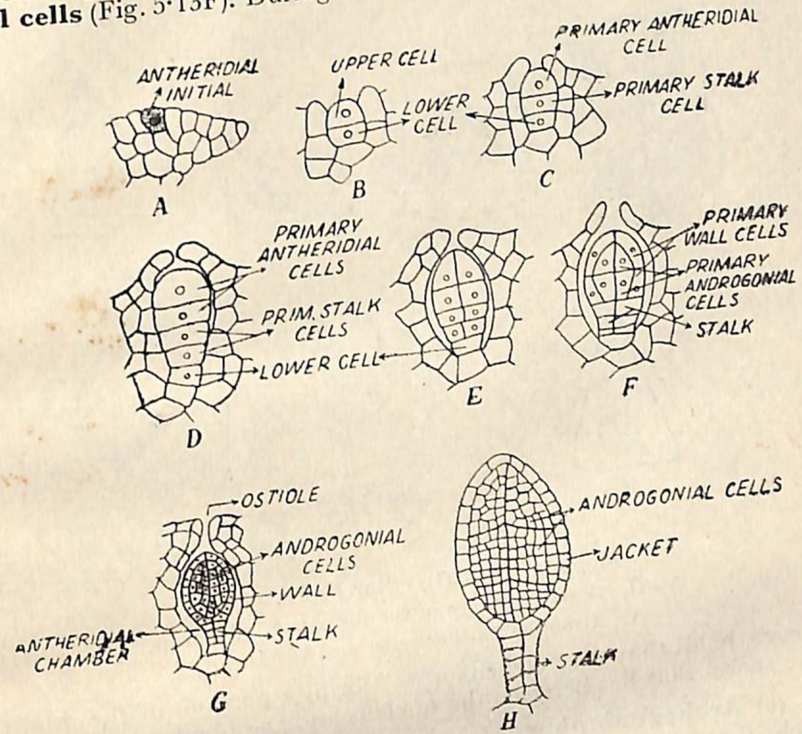


Fig. 5·13 (A—H). Marchantia sp.
A—G. Various stages in the development of antheridium.
H. Nearly mature antheridium. (Diagrammatic)

(*iii*) **Spermatogenesis** (Fig. 5·14 A—G). It is a process whereby sperms are formed from the androcyte mother cells (Fig. 5·14B). The protoplast of each androcyte mother cell divides diagonally into two. However no wall is laid between them. The two triangular daughter protoplasts are called (Fig. 5·14C) the **androcytes** or the **spermatids**. In each androcyte there develops a dot-like blepharoplast in one of its acute angles (Fig. 5·14D) which becomes the anterior end of the sperm. The blepharoplast elongates slightly and develops two flagella (Fig 5·14E). A sharply staining body appears in the cytoplasm of the androcyte at this stage

(Fig. 5·14 C and D). Ikeno calls it chromatid "Nebenkorper". He holds that it takes no part in the development of the sperm. Campbell, however, holds that the "Nebenkorper" forms a portion of the body of the sperm that lies between the nucleus and the blepharoplast.

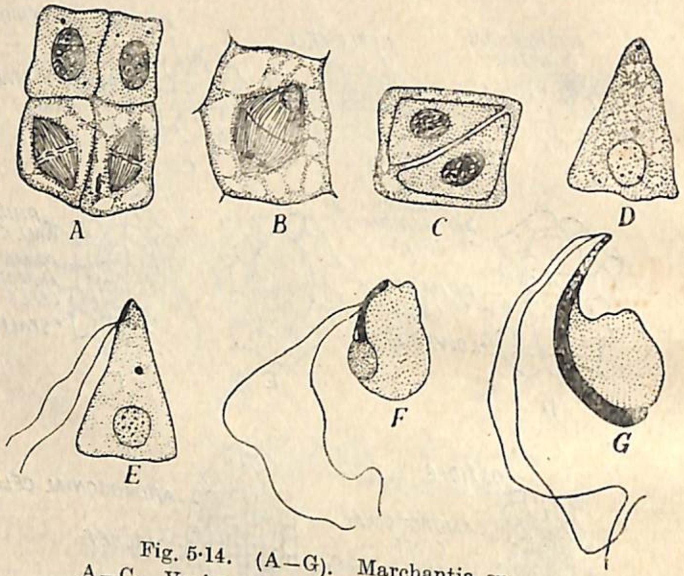


Fig. 5·14. (A—G). Marchantia sp.
A—G. Various stages in the formation of sperms.
A. Group of mother cells. (After Ikeno)

(c) **Archegoniophore** (Fig. 5·15 A and B). It is also a sexual branch that turns upwards and grows vertically. It becomes specially modified like the antheridiophore. It consists of a stalk bearing a lobed disc at its distal end. In its external and internal structure the stalk resembles that of the antheridiophore. It is however slightly longer. It may be 2 to 3 inches long. Typically the famale disc is an inconspicuously eight-lobed object. The growing apices of these lobes bend downwards and inwards towards the stalk. From the margin of the disc between the growing points grow out long cylindrical processes. These are called the **rays** (Fig. 5·15). They are usually nine in number. The rays give the mature female receptacle a **stellate form**.

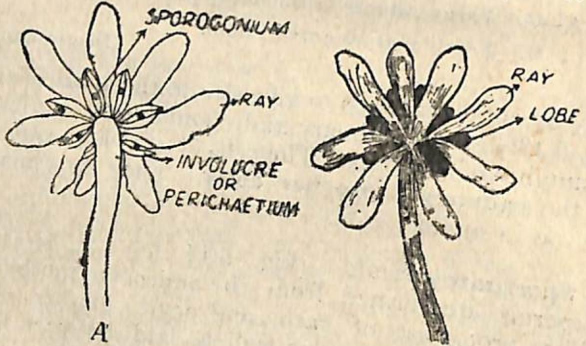


Fig. 5·15. (A—B). Marchantia sp.
A. Mature receptacle as seen from the under surface with sporogonia enclosed in involucres.
B. The same as seen from above showing rays alternating with the receptacle lobes.

(*i*) **Position of Archegonia**. The archegonia in very young receptacles are borne on the upper surface of the receptacle with their necks directed upwards (Fig. 5·16 A). They are developed in acropetal order and stand free from each other in eight radial rows. The youngest is near the growing point. There is one row to each lobe and 12-14 archegonia in each row. At this stage the stalk of archegoniophore is practically absent or very small so that the recep-

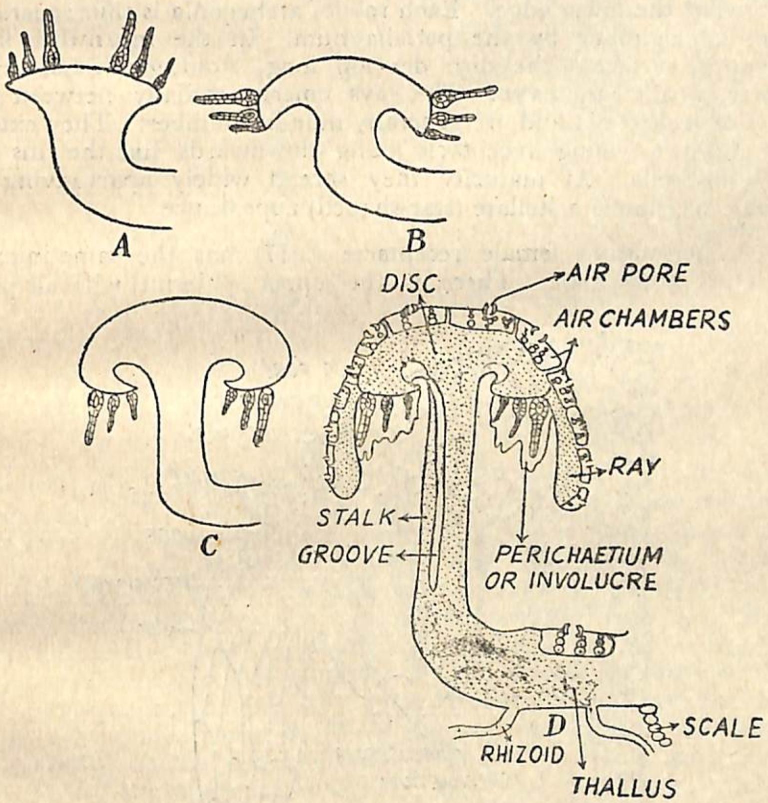


Fig. 5·16 (A—D). Marchantia sp.
Longitudinal sections of various stages of development of the archegoniophore. (Diagrammatic).

tacle appears sub-sessile. The first formed archegonia in the rows reach maturity. Fertilisation takes place at this stage. After fertilisation the stalk of the archegoniophore begins to elongate. Associated with this is a rapid growth in the central sterile region of the upper surface of the receptacle. With more growth above than below the cap, the growing points become gradually pushed downwards and inwards towards the stalk (Fig. 5·16 B and C). Consequently the archegonia become transferred to the lower surface. In a mature female receptacle they are pendulous (Fig. 5·16) and thus hang downwards from the under surface of the disc with the youngest near the stalk. The inversion of the archegonia is accompanied by the development of a plate-like tissue on either side of each row of archegonia. It is the **perichaetium** or the **involucre** (Fig. 5·16 D). The perichaetium is a two lipped, curtain-like structure. It is a single layer of cells in thickness. It grows and hangs down vertically from the under surface of the lobe and is fringed at the lower edge. Each row of archegonia is thus separated from its neighbour by the perichaetium. In the meanwhile from the upper surface of the disc develop long, stout, green cylindrical processes called the **rays**. The rays emerge radially between the rows of archegonia and are generally nine in number. They extend out and in a young receptacle hang downwards like the ribs of a tiny umbrella. At maturity they spread widely apart giving the female receptacle a stellate (star-shaped) appearance.

The mature female receptacle (5·17) has the same internal structure as the male. There is the upper epidermis with air pores

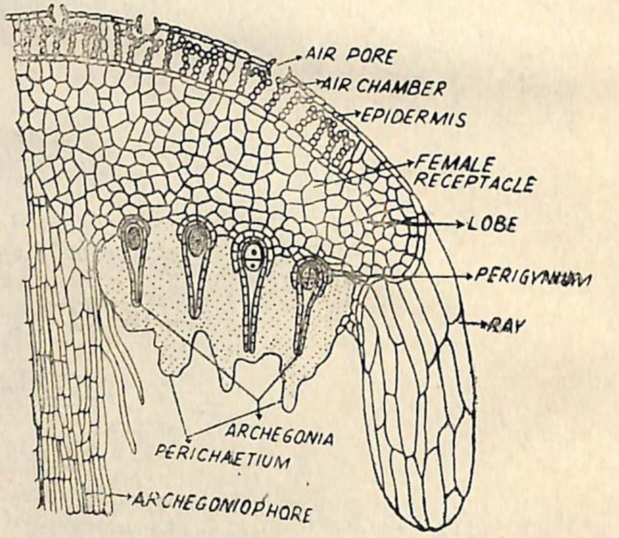


Fig. 5·17. Marchantia sp.
A vertical section through a portion of the archegoniophore after fertilisation. (Diagrammatic)

embedded in it. Beneath it are the air chambers arranged in a single layer. From the floor of the air chambers arise the assimilatory filaments. There are no pits alternating with the air chambers as are found in the male receptacle.

(*ii*) **Structure of Archegonium** (Fig. 5·18K). The archegonium of *Marchantia* is supported on a short but distinct multi-

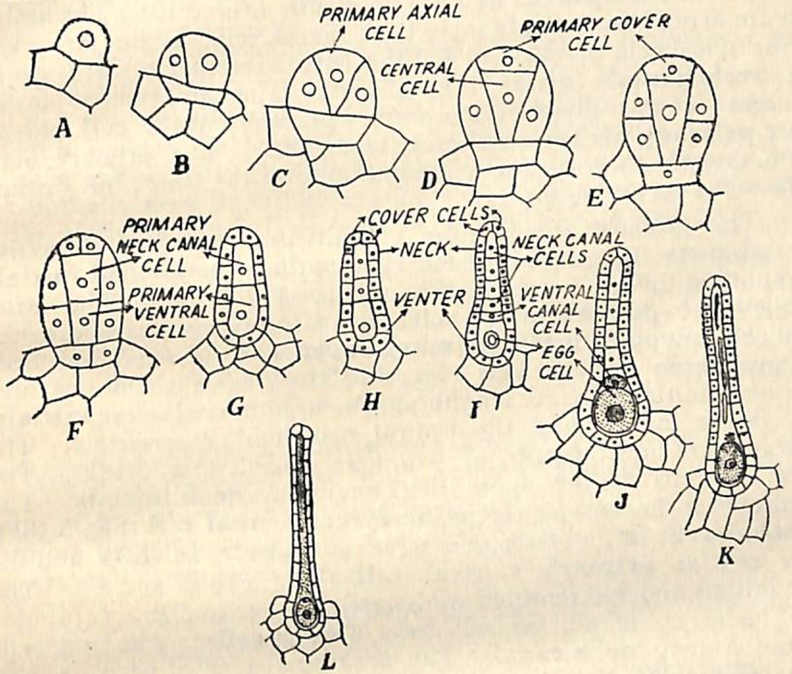


Fig. 5·18. (A—L). Marchantia sp.
A—J. Stages in the development of archegonium.
K and L. Mature archegonia. (Diagrammatic).

cellular **stalk**. The stalk attaches the archegonium to the under surface of the receptacle. The body of the archegonium consists of two parts, the **venter** and the **neck**. The venter forms the swollen, basal portion of the archegonium. It is continued into the long, slender, tubular neck. The venter consists of a **wall** of a single layer of sterile cells enclosing the **venter cavity**. The latter contains two cells. The larger **egg cell** lies at the base and when mature is surrounded by a fluid. It is surrounded by the smaller **ventral canal** *cell*. The jacket or wall of the venter is continued into the jacket of the neck which consists of six longitudinal rows of **neck cells** characteristic of the Marchantiales. The neck cells enclose a central canal called the **neck canal** which contains an axial row of about 8 **neck canal cells**. The mouth of the neck is closed by a rosette of 4 **lid** or **cover** cells. Around the base of the venter of each archegonium is developed a collar-like structure. It consists of a ring of cells and surmounts the archegonial stalk. It is called the **perigynium** or **pseudoperianth**. The formation of the perigynium is stimulated after fertilisation (Fig. 5·19 A and B). The ventral canal cell and the neck canal cells degenerate at maturity. Their products, on absorption of moisture, to give rise to a mucilage which swells and forces apart the lid cells.

(*iii*) **Development of Archegonium** (Fig. 5·18). The archegonium arises from a single superficial dorsal cell. It lies just close to the apical cell of each lobe of the female receptacle. It is called the **archegonial initial** (Fig. 5·18A). The archegonial initial enlarges. It then divides into an inner **primary stalk cell** and an outer **primary archegonial cell** (Fig. 5·18B). The primary stalk cell undergoes a few irregular divisions to form the short but distinct stalk of the archegonium.

The primary archegonium cell divides by three successive vertical intersecting walls. These separate three **peripheral initials** surrounding the fertile cell in the middle (Fig. 5·18C). The latter is called the **primary axial cell**. By a transverse cleavage in the axial cell an upper, smaller **primary cover cell** is separated from an inner large **central cell** (Fig. 5·18D). At this stage the three peripheral initials divide longitudinally to form six **jacket initials**. The jacket initials and the central cell divide transversely. The archegonium now consists of two tiers of cells (Fig. 5·18F). The outer six cells of the upper tier function as **neck initials**. The inner one is known as the **primary neck canal cell** (Fig. 5·18F). The outer cells of the lower tier serve as **venter initials** and the inner cell as **primary ventral cell** (Fig. 5·18 F and G). The neck initials undergo repeated transverse cleavage to form a tubular neck made up of six vertical rows of **neck cells**. The neck cells enclose a long **neck canal**. The neck canal is filled with a row of about eight thin-walled **neck canal cells** (Fig. 5·18I). The neck canal cells are formed by the repeated division of the primary neck canal cell. At the top of the neck is a distal rosette of four **cover** or **lid** cells formed by the divisions of the primary cover cell. Meanwhile the transverse divisions of the venter initials have produced a **venter wall**. It is one cell thick. It encloses the **venter cavity**. The latter contains a small, upper **ventral canal cell** and a lower larger **egg** or **ovum**. They are formed from the primary ventral cell (Fig. 5·18 I and J). The ripe egg has in its upper part a distinct **receptive spot**.

DISTINCTIONS BETWEEN THE MALE AND FEMALE PLANTS

The thalli of the male and the female plants of *Marchantia* are similar. The two may however be distinguished by the following characteristics of their gametophores :—

1. The antheridiophore is slender comparatively shorter than the archegoniophore.

2. The male receptacle is a flat disc with a scalloped edge whereas the female is umbrella-shaped when young and star-shaped at maturity.

3. There is no inversion of the receptacular surface of the male receptacle.

4. The antheridia in the male receptacle lie embedded on the upper surface in pits and in rows radiating from the centre. The archegonia hang from the under surface of the female receptacle.

5. The male receptacle lacks accessory structures such as rays, involucres, etc.

(*iv*) **Fertilisation**. The sex organs in *Marchantia* are developed in receptacles elevated on long stalks. Besides they are borne on different plants. These facts present difficulties in the way of fertilisation. Because of uncertainty of fertilisation reproduction by vegetative methods is very common, efficient and effective.

Fertilisation is dependent upon the presence of water and is possible when the male and female plants grow together. It takes place when the plants are wet with rain or dew. Possibly the antheridia and archegonia mature and fertilisation occurs before the elongation of the gametophores. The sperms may reach the archegonia in the following ways :

1. The sperms may be splashed by rain drops from the surface of the male on to the sessile female receptacle.

2. The sperms splashed on to the ground by the rain drops from the male receptacle may actually swim the whole way to the archegonia in wet weather.

3. The sperms may swim through the water when the male and the female thalli are actually submerged under the rain water.

The above mentioned possibilities can become realities only if the male and female plants grow near each other.

4 There is possibility of the sperms being carried by the agency of microscopic animals such as the mites.

A number of sperms may reach the female receptacle in the above mentioned ways. From the female receptacle they are attracted towards the archegonia. The source of attraction is some chemical present in the drop of mucilage that oozes through the open necks of the archegonia. A number of sperms may enter the open necks of archegonia and swim downwards in the neck canals. Normally one unites with the egg in the venter.

Post-fertilisation changes. Following fertilisation the stalks of the archegoniophores elongate. From the upper surface of the disc develop, green cylindrical processes called the **rays**. A number of archegonia may be fertilised in each receptacle. All of them, however, do not develop into sporogonia. The act of fertilisation originates the diploid condition in the nucleus of the zygote. The zygote secretes a wall around it and enters upon active segmentation to form a spherical **embryo**. The venter enlarges with the growth of embryo. A cylindrical sheath called the **perigynium** grows from the base of each archegonium and surrounds it. A two-lipped membrane with the lower edge fringed also grows downward on either side of a row archegonia.

SPOROPHYTE PHASE

With the formation of the zygote the sporophyte or the diplophase in the life cycle starts. It consists of the **zygote**, the **embryo** and the **sporogonium**. **Spore mother cells** and **elaters** are the last structures of this phase.

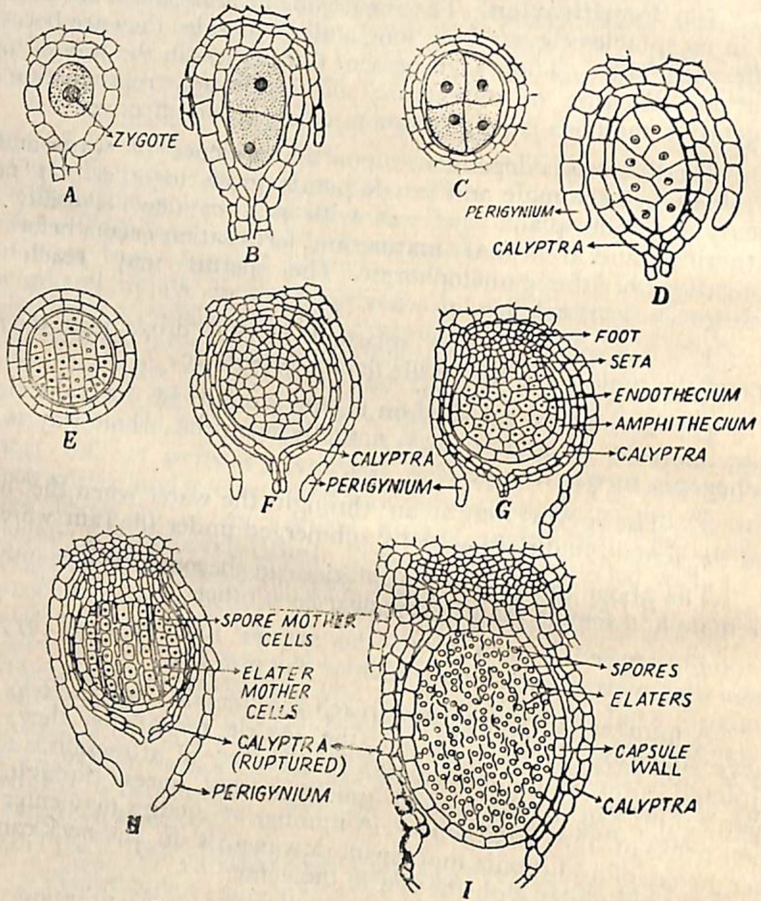


Fig. 5·19. (A—I). Marchantia sp.
A—F. Stages in the development of embryo sporophyte.
C & E are cross-sections.
G. Differentiation of foot, seta and capsule.
H. Differentiation of sporogenous tissue into spore mother cells and elater mother cells.
I. Mature sporogonium with the ruptured calyptra.
(Diagrammatic)

Development of the Sporogonium (Fig. 5·19). The zygote probably starts dividing within 48 hours of fertilisation. It divides by a horizontal wall at right angles to the long axis of the archegonium (Fig. 5·19B). This division delimits the outer or distal **epibasal** and the inner or proximal **hypobasal** regions. Since the capsule which constitutes apex of sporophyte, is formed from the outer or epibasal region embryogeny is described as **exoscopic**. The next cleavage is at right angles to the first. The globular embryo at this stage consists of four cells. It is the **quadrant stage**. There are variations in the early development of the embryo in different species. McNaught reported the formation of a three-celled filamentous embryo in *M. chenopoda*. Typically the next division produces the **octant stage** (Fig. 5·19 C). Only four cells are visible in a section. After the octant stage the embryo grows vigorously. The divisions are in an irregular sequence (Fig. 5·19 D). Associated with the changes taking place in the developing embryo the following changes take place in the surrounding gametophyte tissue :—

(*i*) The stalk of the archegoniophore elongates considerably.

(*ii*) The venter cells divide by periclinal walls to form a two to three-layered **calyptra**. The latter forms a close investment around the developing embryo sporophyte.

(*iii*) The collar-like **perigynium** eventually forms a cylindrical sheath. It is one cell in thickness and a few cells in height. The perigynium encloses both the archegonium and the sporogonium.

(*iv*) The development of a two lipped curtain-like **perichaetium** or **involucre** forming a protective covering around the whole group of archegonia.

(*v*) The development of **rays** from the margin of the female disc between the lobes. Their development is intercalary.

The four epibasal octants (nearest the neck of the archegonium) by repeated cell division accompanied by cell differentiation and continued growth give rise to the **capsule**. The four hypobasal octants form the **foot** and the **seta** (Fig 5·19 G). During further development the embryonic sporophyte elongates vertically at the expense of nutrients drawn from the gametophyte. Periclinal divisions appear in the embryonic capsule portion. These separate an outer single layered **amphithecium** from the inner mass of cells which constitutes the **endothecium** (Fig. 5·19 G). The amphithecium cells divide anticlinally to give rise to the single layered **capsule wall**. It remains one cell in thickness. At maturity the walls of these cells develop, ring-like. thickenings on their inner surface. The entire endothecium forms the **archesporium**. The archesporial cells divide and redivide mitotically to form a massive tissue. It is known as the **sporogenous tissue**. The cells of the sporogenous tissue are, at first, all alike and vertically elongated. They divide diagonally. Later they become differentiated into the following two kinds of cells (Fig. 5·19 H) :—

(*i*) **Elater Mother Cells**. Practically half of the sporogenous cells elongate still further. They become narrow and remain sterile. These are the **elater mother cells**. The latter elongate considerably to form long, slender, diploid, fusiform cells tapering at both the ends. Each of these develops two spirally thickened bands on the inner surface of its walls and lose their protoplasmic contents to become the **elaters**. The bispiral elaters are hygroscopic. They help in the dispersal of spores.

(*ii*) **Spore Mother Cells**. The other half of the sporogenous cells divide and redivide by transverse cleavage to form vertical rows of cells. These are the **spore mother cells**. There is a good deal of evidence to support the view that the elater and spore mother cells do not belong to the same cell generation. There is a difference of 3-4 or 5 successive cell generations. The diploid elaters are differentiated earlier from the sporogenous tissue. The spore mother cells are, at first, somewhat cubical. Later they grow equally in all directions to become rounded. They contain dense cytoplasm and a conspicuous diploid nucleus. Each spore mother cell undergoes **meiosis** to form four meiospores as in *Riccia*. The average output of spores per capsule in *Marchantia polymorpha* is estimated to be about 300,000.

The young sporogonia are effectively protected by three protective sheaths (Fig. 5·20 A) developed from the tissue of the female

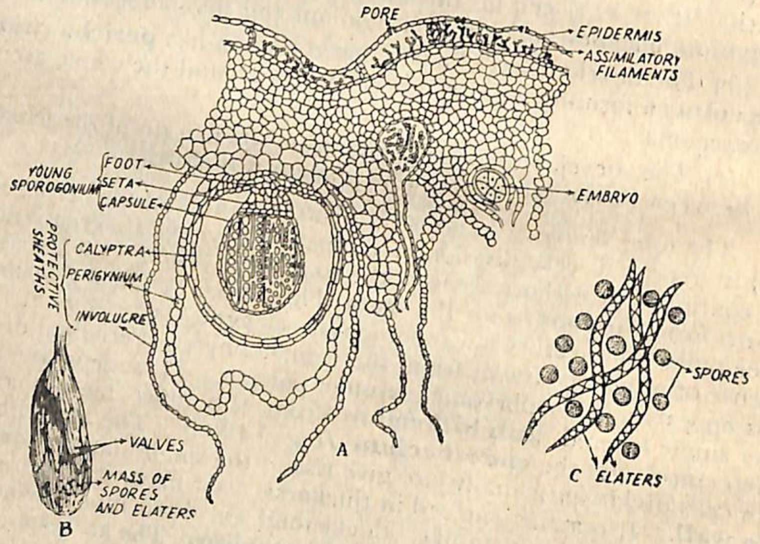


Fig. 5·20 (A – C). Marchantia palmata.
A. V. S. through a portion of the female receptacle showing two sporogonia at different stages of development.
B. Dehisced sporogonium.
C. Elaters and spores.

receptacle. These are the **perigynium**, the **calyptra** and the **perichaetium** or the **involucre**. The first and the third are absent in *Riccia*. The development of the capsule is accompanied by the growth of the foot and the seta. The absorptive foot is embedded in the tissue of the lower surface of the female disc and is differentiated early. With the differentiation and the maturation of spores in the capsule the constriction-like seta elongates slightly. *The slight elongation of the seta in Marchantia is an anatomical necessity.* The sporogonium hangs downwards. Greater elongation of the seta will carry the capsule nearer to the ground and thus hinder efficient dispersal of spores.

Production of Meiospores. It is entirely the concern of the **sporogonium** (Fig. 5·21). It is devoted to the production of spores (meiospores) and their dispersal. It hangs downwards from the under surface of the female receptacle.

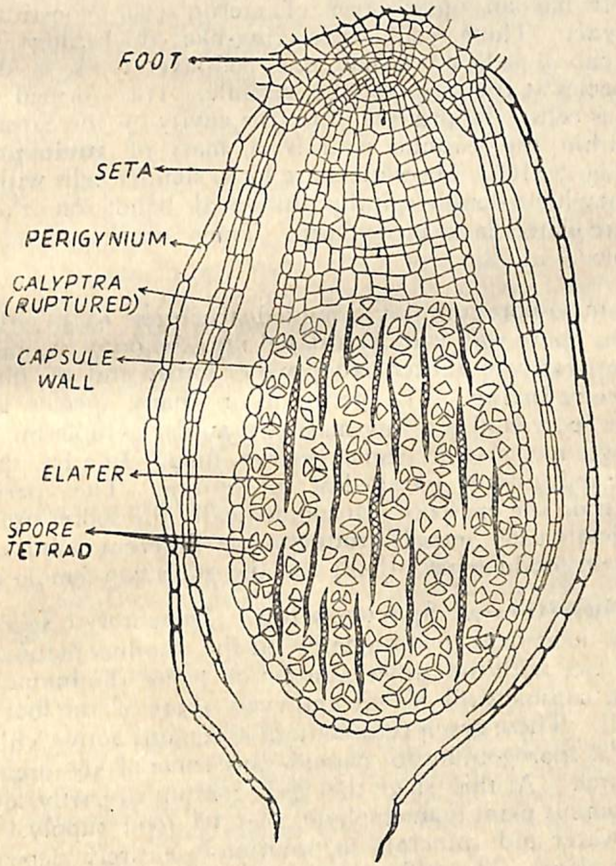


Fig. 5·21. Marchantia sp.
Longitudinal section of the mature sporogonium.

(*a*) **Structure of Sporogonium**. It is differentiated into the following three regions :—

(*i*) **Foot**. It is an absorptive and anchoring organ forming the basal broad portion of the sporogonium. It consists of parenchymatous cells and is embedded in the tissue of the female receptacle on its lower surface. It absorbs all the nourishment from the gametophyte for the developing sporogonium.

(*ii*) **Seta**. It is at first very short and constriction-like. It connects the foot and the capsule. The cells constituting it are arranged in vertical rows. With the formation of spore tetrads in the capsule the seta elongates slightly. The slight and sudden increase in the length of the seta ruptures the calyptra. It pushes the mature capsule through the sheaths enclosing the venter. These are the **perigynium** and the **perichaetium** involucre.

(*iii*) **Capsule**. It is oval in form and yellow in colour when mature. It has an outer layer of sterile cells constituting the **capsule wall**. These cells have ring-like thickenings on their walls. A cap of cells more than one cell-layer thick is developed in some species at the apex of the capsule. It is formed from the sporogenous cells. It projects into the cavity of the capsule. Enclosed within the capsule wall is a mass of **meiospores** and **elaters** (Fig. 5·21C). The elaters are long, slender cells with pointed ends. They have double spirally thickened bands on their walls. The mature elaters lack protoplasm. They are thus dead and are hygroscopic.

The meiospores are tiny, rounded structures each with a thick wall. The spore wall is differentiated into the outer smooth or reticulate comparatively thicker **exospore** or **exine** and an inner, thin **endospore** or **intine**. The perinium in many species is absent. Within the spore wall is a tiny mass of granular cytoplasm. It contains a single nucleus and some reserve food. In a few species the spores are indistinctly tetrahedral in outline. The perinium is present outside the exospore. Morphologically the spores are all alike but genetically each tetrad produces two different kinds of spores. Two of them produce male thalli and the other two female thalli.

(*b*) **Nutrition of Sporogonium**. The embryo sporophyte is completely dependent nutritionally on the thallus plant (gametophyte). Later with the differentiation of parts the immature cells of the seta, capsule wall, elaters and even those of the foot develop chlorophyll. These green cells contain abundant active chloroplasts enabling the sporogonium to manufacture some of its organic food such as starch. At this stage the sporogonium is partly dependent upon the parent plant (gametophyte) for its food supply. For the supply of water and minerals in solution it entirely depends upon the parent plant. The chloroplasts, however, disintegrate as the sporophyte reaches maturity.

(*c*) **Dehiscence of Capsule** (Fig. 5·20B). With the ripening of spores there is slight elongation of the seta. The capsule breaks through the calyptra. It projects beyond the perigynium and the perichaetium. As the exposed capsule dries the apical cap, if any, ruptures along an irregular line. The capsule wall then splits open along four to six lines. Each split starts from the apex to about the middle of the capsule. Since there are no regular lines of dehiscence on the capsule wall the latter splits in an irregular manner by four to six lobes or valves. The mass of spores and elaters is consequently exposed.

(*d*) **Dispersal of Spores**. There is ready and efficient dispersal of spores by wind in *Marchantia*. It is aided by the following two structural features.

(*i*) *Presence of Elaters*. The hygroscopic elaters help to eject the spores from the exposed spore mass. They coil and uncoil with the changes in the moisture content of the surrounding air. As they dry they coil and twist undergoing jerking movements. The latter knock the spores about and throw them into the air where they are readily caught up by the air currents and dispersed.

(*ii*) *Elevation of the hanging sporophyte on the long archegoniophore*. The elevated position of the hanging sporogonium is an additional advantage. It favours the dispersal of spores by air currents. The small spores ejected into the air by the squirming movements of the elaters are readily caught up and distributed by the air currents. The greater elongation of the seta would not have helped spore dispersal. On the other hand it would have hindered it by carrying the capsule downwards more to the ground.

COMPARISON WITH RICCIA

Sporogonium of Riccia	Sporogonium of Marchantia
1. In *Riccia* the sporogonium is the simplest known sporophyte among the bryophytes. It lacks both the **foot** and the **seta**. It is just a spore case or capsule globular in outline.	1. In *Marchantia* the sporogonium is larger and more complex. It is differentiated into the **foot, seta** and the **capsule**.
2. The globular sporogonium consists of a jacket layer of simple, sterile cells constituting the **wall** which surrounds a mass of fertile cells known as the **spore mother cells.** There are no elater mother cells.	2. The cells of the single layered capsule wall develop ring-like thickenings on their walls and surround a mass of **spore mother cells** and **elater mother cells**.
3. Excepting the single layered sporogonium wall and a few of	3. Much of the sporogonium produces the sterile tissue in the

Sporogonium of Riccia	Sporogonium of Marchantia
the **nurse cells** that undergo degeneration, major portion of the sporogonium is devoted to spore formation.	form of foot, seta and capsule wall. Half of the sporogenous tissue forms the **elater mother cells** and the rest by a few more divisions constitute the **spore mother cells**.
4. The nurse cells which eventually disintegrate to form the nutritive fluid are considered by some bryologists as the **forerunners** of the elaters of the more advanced members of the Marchantiales. The elaters are thus absent in the sporogonium of *Riccia*.	4. The elater mother cells form long, slender, fusiform cells with tapering ends and are called the **elaters**. They are hygroscopic and help in the dispersal of spores.
5. In fact at maturity it has no diploid tissue at all. The outer layer of the spore sac which houses the spores represents parent gametophyte and the spores represent the future gametophyte.	5. The mature sporogonium wholly consists of diploid tissues except the spores which represent the new gametophyte.
6. The sporogonium remain embedded in the thallus tissue and is protected and surrounded only by the two layered **calyptra.** The perigynium and perichaetium are lacking.	6. The sporogonium hangs from the undersurface of the female receptacle and is surrounded by the two layered **calyptra, perigynium** and the **perichaetium.** Later by the rapid elongation of the seta, the capsule breaks through the calyptra and projects beyond the perigynium and the perichaetium.
7. The mature spores are released simply by the disintegration of the cells of the capsule wall, calyptra and finally by the death and decay of the surrounding thallus tissue. The sporogonium never dehisces.	7. The capsule dehisces in a more regular manner by 4—6 **valves** to allow the spores to escape into the air.
8. The mature meiospores are simply left behind on the soil by the decay of the surrounding tissues and are not dispersed. In that condition they may be carried by the wind.	8. The elevation of the hanging sporogonium on a long stalk of the archegoniophore and the presence of hygroscopic elaters in the spore mass constitute an efficient provision for the distribution of meiospores by the wind.

Germination of Spores. The spores are viable for about a year. However, on falling on a suitable damp soil, they germinate immediately. On germination the spore absorbs water. Consequently it enlarges considerably (Fig. 5·22A) in size. No germinal tube is formed. Instead the contents divide immediately in one plane to form a short irregular filament (Fig. 5·22C). It consists of 6—8 cells. It may become two cells broad at the apex (Fig. 5·22D). Soon an apical cell with two lateral cutting faces is established at the apex of the filament. It cuts off segments alternately right and left parallel to its cutting faces. Five to seven segments are cut off in this way. These divide and re-divide. A green plate of several cells is formed (Fig. 5·22E). It is the young thallus (Fig. 5·22F). Now the two faced apical cell itself divides and re-divides. A group of cells is formed. A transverse row of apical initials constituting the apical meristem is soon established in this group.

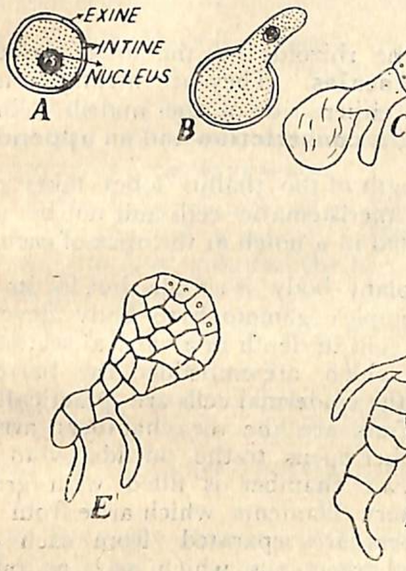


Fig. 5·22 (A—F). Marchantia sp.
A. Mature spore.
B—F. Various stages in the germination of a spore.

Important Features.

(1) The plant body is a repeatedly forking, flat, green, broad dorsiventral **thallus** with a distinct broad, central **midrib** which is more pronounced on the ventral side.

(2) Dorsally the thallus surface is marked by rhomboidal or polygonal areas called the **areolae**. Each areole has a distinct dot-like **air pore** in its centre.

(3) Small, shallow **gemma cups** with frilled, membranous margins are usually present on the upper surface of the thallus in the midrib region. The cups contain numerous, green, lens-shaped objects, the **gemmae**. When detached each gemma develops into two new thallus plants.

(4) From the ventral surface of the thallus, in the midrib region, arise unicellular, unbranched smooth-walled and tuberculate attaching filaments, the **rhizoids**. They secure the thalloid gametophyte to the substratum.

(5) Associated with the rhizoids on the lower surface of the thallus are the membranous **scales**. They are arranged in two to four alternating rows on either side of the midrib. Each scale typically consists of a **body**, a **constriction** and an **appendage**.

(6) The growth in length of the thallus lobes takes place by the activity of a group of meristematic cells and not by an apical cell. The former are situated in a notch at the apex of each lobe.

(7) Externally the plant body is simple but in its internal structure it is the most complex gametophyte body developed by any liverwort. It is many cells in depth in a vertical section. There is the upper epidermis in which are embedded the barrel-shaped pores. The outer walls of the epidermal cells are practically waterproof. Beneath the epidermis are the air chambers arranged in a single layer. Each chamber opens to the outside by an air pore. The shallow cavity of each air chamber is filled with green, frequently branched, assimilatory filaments which arise from its floor. The neighbouring chambers are separated from each other by groups of vertically arranged green cells which serve as pillars supporting the upper epidermis. The ventilated, green chambered upper portion of the thallus is called the **photosynthetic region**. The portion of the thallus below the air chambers consists of several layers of compactly arranged parenchymatous cells forming the **storage region**. Rhizoids and scales grow from the lower epidermis.

(8) Without exception sexual reproduction is of **oogamous** type. The plants are **dioecious**. The sex organs are **antheridia** and **archegonia**. They are developed in disc-shaped receptacles elevated on long stalks. They are the **gametophores**. The gametophores are terminal in position and in direct continuation of the midrib. The stalks have two furrows each running the whole length.

(9) The male receptacle is a lobed disc with a wavy margin. The antheridia are deeply sunk on the upper surface of the receptacle each in an **antheridial pit** opening to the outside by an **ostiole**. The antheridial pits alternate with the air chambers. The sperms are flagellate, curved structures. The male receptacles lack rays characteristic of the female receptacles and are usually eight lobed.

(10) The female receptacle is eight lobed. The lobes are not very conspicuous. Alternating with the lobes grow out the stout finger-like **rays** from the periphery of the disc. The rays are nine in number In young receptacles they hang downwards like the

ribs of a tiny umbrella. At maturity they spread widely apart giving the female receptacle a star-shaped appearance.

(11) The archegonia are pendulous. They hang downwards from the under surface of the lobes of the female receptacle.

(12) Fertilisation takes place in the presence of water furnished by rain or dew and when the female receptacles are sessile.

(13) The two lipped, curtain-like **perichaetium** may enclose several young sporogonia each enclosed by the **calyptra** and surrounded by the **perigynium**.

(14) The sporogonium, at maturity, is differentiated into a foot, a small seta and a capsule. The cells of the single layered capsule wall develop annular bands. Inside the wall is a mass of meiospores and elaters.

(15) The ripe capsule wall dehisces by 4-6 irregular teeth or valves.

(16) The elaters are simple, long cells pointed at both ends. Each has two spiral bands on the wall.

(17) The elaters are hygroscopic and thus help in the dispersal of spores.

(18) The ready dispersal of spores is aided by the pendulous sporogonium being elevated on a long archegoniophore.

(19) The short seta of the hanging sporogonium serves as an additional aid in the dispersal of spores.

(20) Each spore, on germination produces a tiny gametophyte which, at first, grows by an apical cell with two cutting faces. Soon the apical cell is replaced by a group of meristematic cells.

SUMMARY OF THE LIFE HISTORY OF MARCHANTIA (Fig. 5·23)

Life history of *Marchantia* is similar to that of *Riccia*. There occur two distinct vegetative individuals in the life cycle. They are the green, thalloid *Marchantia* plant (Fig 5·23, 1) and the radially constructed more or less solid sporogonium (Fig. 5·23, 6). The former is the most conspicuous of the two and is independent. It is called the **gametophyte** as it bears the gametes. The gametophyte plant is a green, dorsiventral, forking, highly developed thallus with a distinct, broad midrib. It is anchored to the ground by unicellular, unbranched, smooth and tuberculate **rhizoids**. The rhizoids absorb water and solutes for it. Associated with the rhizoids are the **scales**. They are arranged in 2 to four longitudinal rows on either side of the midrib. Internally the upper surface of the fleshy thallus has a layer of **air chambers**. They are separated from each other by vertical partitions of cells. The partitions also act as pillars supporting the single layered roof called the **upper epidermis**. The cavities of air chambers are filled with simple or branched, short, filaments of green cells. Each chamber communicates with the outside through a well defined, barrel-shaped **pore**. Beneath the air chambers is a several layered thick storage region of compactly arranged colourless parenchyma cells. Scattered in the storage region are a few **oil** and **mucilage** cells.

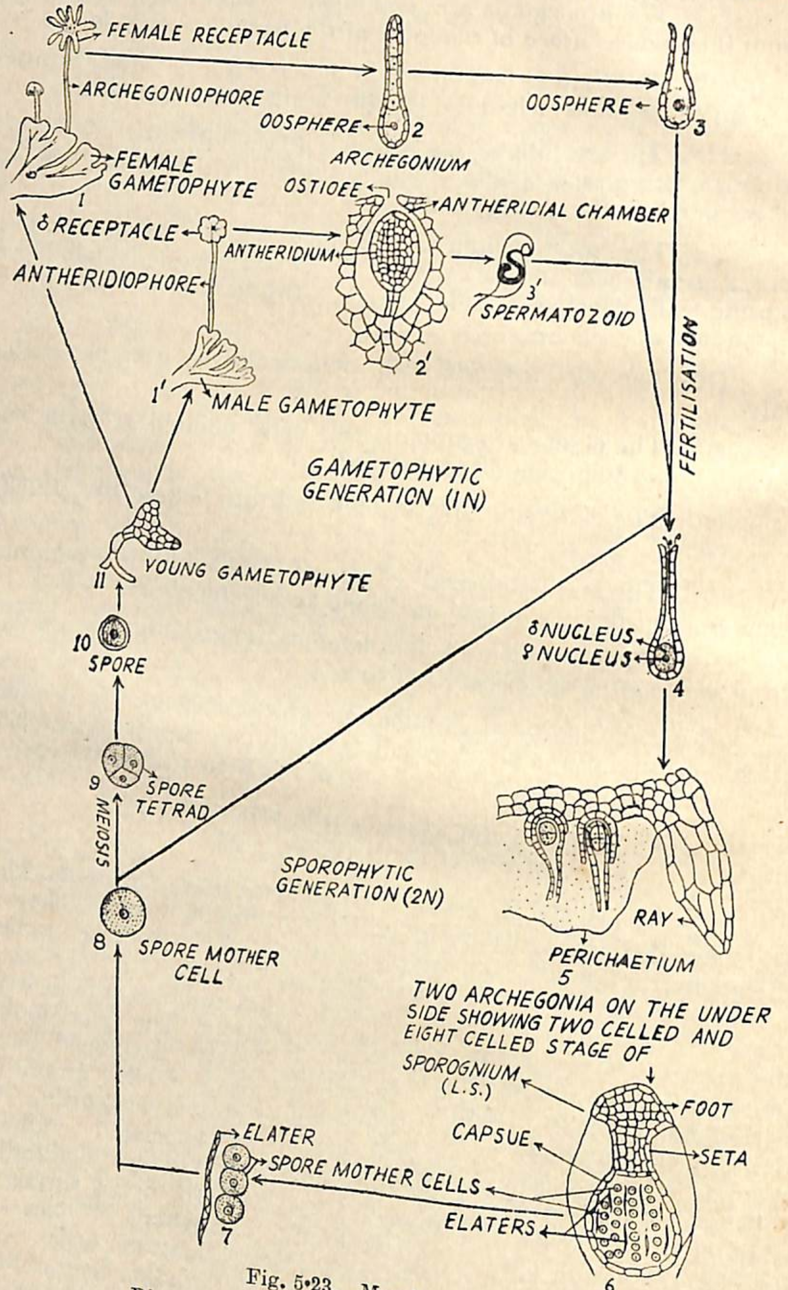


Fig. 5·23. Marchantia.
Diagrammatic representation of the life cycle.

Each thallus lobe has a growing point situated at its apex. The growing point consists of a group of meristematic cells.

The gametophyte or the sexual thallus bears the sex organs. They are borne in localised areas which are disc-shaped. These are the **receptacles**. The receptacles in *Marchantia* are invariably elevated on long stalks. The stalked receptacles are terminal in position on the thallus lobes. The antheridial (Fig. 5·23, 1) and archegonial receptacles (Fig. 5·23, 1) occur on separate plants. Together with their stalks the receptacles are called the **antheridiophores** and the **archegoniophores** respectively. *Marchantia* is thus **dioecious**. The female receptacle, at maturity, is star-shaped. The archegonia occur in the tissue between the finger shaped rays. They are pendulous with the necks directed downwards. The archegonia of each group are protected by a two-lipped involucre. The male receptacle has a lobed margin. Each lobe has a growing point at its tip. The antheridia are sunk deeply on the upper surface. Each lies in its own flask-shaped **antheridial pit** opening at the surface by an **ostiole** (Fig. 5·23, 2). All these structures produced by the thallus gametophyte constitute the **gametophyte generation** or the **haplophase**. They are the green thallus, the antheridiophores, the archegoniophores, the antheridia, the archegonia, the sperms and the eggs. The first structures of this phase are the spores and the last are the gametes. With the formation of the gametes the haplophase ends. In *Marchantia* there is provision for additional multiplication of the thallus plant. It is done by the production of gemmae in the gemma cups. The gemmae are thus the accessory means of multiplying the haplophase. They play no role in the alternation of generations.

With the act of fertilisation the life cycle of *Marchantia* switches on to the second phase. It is the **diplophase** or the **sporophyte phase**. It originates with the **zygote** (Fig. 5·23, 5). The latter undergoes cleavage to form the **embryo**. The embryo in the bryophytes is a short-lived structure. Soon by further cleavage and differentiation it forms the second vegetative individual in the life cycle. It is the **sporogonium** (Fig. 5·23, 6). All the young sporogonia in a particular group are protected by the common, two lipped **involucre**. Besides, each sporogonium is closely invested by the calyptra. External to it is the **perigynium**. The sporogonium is more or less a solid, radially symmetrical object without any appendages. It is incapable of self-nutrition. It consists of three regions, the **foot**, the **seta** and the **capsule**. The latter produces the meiospores and elaters (Fig. 5·23, 7). The elaters help in the dispersal of spores. The parasitic sporogonium of *Marchantia*, as it produces the spores, is called the **sporophyte**. It is concerned with reproduction. The structures produced after fertilisation such as the **zygote**, the **embryo** and the **sporogonium** with its foot, seta and capsule constitute the **sporophyte phase** or the **diplophase**. It ends with the **spore mother cells** and **elaters**. The spore mother cells by meiosis produce meiospores which are the first structures of the future gametophyte generation.

From the account of the life cycle of *Marchantia* given above it is clear that the gametophyte and the sporophyte phases are very closely connected. In the single life cycle they alternate with each other. The reproductive cells of one generation, on germination, produce the alternate plant. The two critical points in the life cycle are **fertilisation** and **meiosis**. With the former starts the diplophase or the sporophyte generation. The meiosis originates the gametophyte phase or the haplophase. The regular alternation in a single life cycle of one phase with the other is expressed by a biological phase, 'Alternation of Generations'. Since the alternating plants in the life cycle are dissimilar the alternation of generations is of **heterologous type**.

DISCUSSION

The gametophyte plant of *Marchantia* is independent and photosynthetic. It is simple externally being a dorsiventral thallus. The elaboration is internal rather than external. Internally it has reached the highest level of differentiation achieved by a thalloid gametophyte. The sex organs are borne on stalked receptacles. The sporophyte is complex being differentiated into foot, seta and capsule. The question arises which of the two is primitive, *Marchantia* or *Riccia* ?

There are two opposite hypothesis with regard to the evolutionary position of *Marchantia*. Some bryologists consider *Marchantia* as the most advanced member of the group. They hold that it has evolved from *Riccia* which is simple and thus primitive as shown by the following characteristics :—

(*a*) Thallus much smaller in size and relatively simple both externally as well as internally.

(*b*) Photosynthetic region less elaborate and less water conserving than the photosynthetic system in the form of air chambers as in *Marchantia*.

(*c*) Absence of well defined upper epidermis and definite air pores.

(*d*) Absence of stalked gametophores, the sex organs developing in pits on the upper surface of the thallus.

(*e*) Sporophyte completely dependent on the gametophyte for its nutrition.

(*f*) Simple sporophyte consisting of little more than a capsule without foot and seta.

(*g*) At maturity it is simply a spore case with no diploid tissue.

(*h*) Absence of any mechanism for dispersal of spores which must thus await the decay of surrounding gametophyte tissues.

The changes involved are :

(*a*) Gradual and progressive widening of the air canals till they form well developed **air chambers**.

(*b*) Associated with the above change are the development of **assimilatory filaments** from the floor of each chamber and the elaboration of **air pores** into well defined barrel-shaped structures.

(*c*) Development of sex organs in restricted areas of the thallus called the **receptacles**.

(*d*) Elevation of receptacles on long stalks.

(*e*) Cessation of apical growth of the thallus lobes after the development of sex organs so that the gametophores become **terminal** in position.

(*f*) Gradual and progressive sterilisation of the potentially fertile cells of the sporogenous tissue in the sporophyte.

This theory of **progressive sterilisation** was first proposed by Bower and later elaborated by Cavers. On the basis of this theory the fertile cells devoted to spore formation become gradually progressively diverted to vegetative functions such as protection, nutrition and spore dispersal. This resulted in the differentiation of the sporophyte into the **foot**, **seta** and the **capsule**. Some of the potential spore mother cells become sterile to form narrow, pointed, hygroscopic **elaters** which help in spore dispersal.

The supporters of this hypothesis consider *Riccia* as primitive and *Marchantia* as a highly evolved or advanced genus. The other genera of the order form a complete ascending series of intergrading forms. So seriated they say the series forms an excellent example of **progressive evolution** or natural advance. Smith is another ardent supporter of this hypothesis.

There is another school of thought led by Goebel. They hold that the genera of Marchantiales seriated as above illustrate a case of **retrogressive evolution** and form the descending series. According to them *Marchantia* is primitive. They consider *Marchantia* to have given rise to *Riccia* by progressive simplification or reduction. The changes involved are :

(*a*) The air chambers become progressively reduced in width till they become deep, narrow canals. This change is accompanied by the disappearance of assimilatory filaments from the air chambers and simplification of air pores.

(*b*) Loss of stalks and receptacles of the gametophores. With this the growth of the growing points is continued forward. Consequently the sex organs become scattered on the upper surface of the thallus.

(*c*) Elimination of protective sheaths (involucre and perigynium) around the sporogonium. This is accompanied by reduction in the complexity of the structure of the sporophyte. The evolutionary trend has been the gradual and progressive simplification of the sporophyte. First the seta and later the foot also disappears. The sporogonium becomes simply a spore case. The ring-like thickenings disappear from the walls of the cells of the capsule wall. All the inner (endothecium) cells become fertile so that the elaters are eliminated. The nutrition to the numerous developing spore tetrads is supplied by the degeneration of some of the potential spore mother cells, capsule wall and inner layer of the calyptra.

All the changes enumerated above finally resulted in the origin of forms like *Riccia* from primitive ancestors like *Marchantia*.

The hypothesis of progressive evolution as advocated by Bower, Cavers and others appears plausible but the breeding experiments carried out by Bergeff (1943) with *Marchantia* support the theory of progressive simplification or reduction. In his cultures of *Marchantia* he observed a number of mutants which he hybridized in various ways and obtained a *Marchantia* thallus of var *riccioides*. It resembles *Riccia* in having narrow thallus lobes and immersion of sex organs in the thallus tissue.

The striking results of these breeding experiments suggest the way forms like *Marchantia* may have yielded genera like *Riccia* by a process of simplification. On the basis of this *Riccia* would be considered an advanced but a reduced form and *Marchantia*—a primitive genus.

REVISION QUESTIONS

1. List the important features of the family Marchantiaceae and name some important genera of the family.

2. Describe the habit, habitat and distribution of *Marchantia*. Name at least three species of the genus.

3. Describe the external features and internal structure of the thallus of *Marchantia*. List the points in which it differs from *Riccia*.

4. Name the various types of reproduction met with in *Marchantia*. Give an account of any one of them in detail.

5. Describe sexual reproduction in detail in *Marchantia*. How does fertilisation take place in this genus ?

6. Give an illustrated account of the development of antheridium and spermatogenesis in *Marchantia*.

7. Describe the development of archegonium of *Marchantia*.

8. Give an illustrated account of the development of sporogonium of *Marchantia*. Compare it with that of *Riccia*.

9. Describe the structure of mature sporogonium of *Marchantia* and compare it with that of *Riccia*.

10. What do you know about the dehiscence of capsule and dispersal of spores in *Marchantia*.

11. List the important features in the life cycle of *Marchantia*.

12. With the help of a series of diagrams describe the life history of *Marchantia*. (*Agra University 1954, 56*)

13. Justify the truth or falsity of the following statements giving reasons :—

(*a*) The air pores on the thallus of *Marchantia* are homologous to the stomata of higher plants.

(*b*) The short seta of *Marchantia* sporogonium is an anatomical necessity.

(*c*) The gemmae of *Marchantia* are reproductive structures which do not play any role in the phenomenon of alternation of generations.

14. Describe the main structural features of the gametophyte of *Marhantia*. (*Agra Univ. 1954*)

15. Compare the gametophyte of *Marchantia* with that of *Riccia*. Draw suitable sketches. (*Agra Univ. 1957*)

CHAPTER VI

HEPATICOPSIDA (HEPATICAE)—JUNGERMANNIALES

The jungermanniales, like other hepatics, are prostrate in habit and dorsiventral in configuration. The only exceptions are *Haplomitrium* and *Calobryum*. In both these the plant body is erect. For this and other reasons Campbell places them in the order Calobryales.

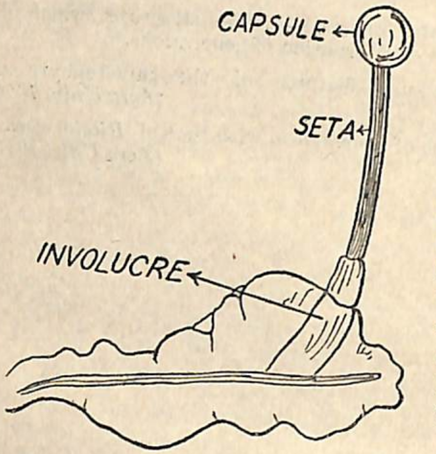


Fig. 6·1. Pellia neesiana.
A female plant bearing a sporogonium.

Thallus. In a few species the gametophyte is a simple, dorsiventral, flat, green, dichotomously branched thallus (Fig. 6·1). It resembles that of *Riccia* or *Marchantia* in external appearance or even simpler. A few species show foliar development of a rudimentary type (*Fossombronia*). In genera higher in organisation the thallus is **leafy** (**foliose**). The leafy forms are about 84% of all liverworts. The thallus in the foliose forms consists of a central branched or unbranched axis bearing leaf-like expansions (Fig. 6·2A). The leaves are generally closely set on the stem and its branches. Consequently they overlap somewhat. The leaf arrangement is said to be **incubous** if the anterior edge of the leaf is above the posterior margin of the leaf in front (Fig. 6·2A). It is **succubous** if reverse. In the latter case the anterior margin of the leaf is covered by the posterior margin of the one in front. The simpler foliose forms have the leaves arranged in two lateral rows. The leaves in the advanced foliose forms are frequently arranged in three rows. Two of these are **dorsal** and one **ventral**. Each dorsal leaf is usually **bilobed**. The lobes are dorsal and ventral in position. The dorsal lobe of the leaf is larger than the ventral. The smaller ventral lobe is called the **lobule** and the larger dorsal as the **lobe**. The leaf is invariably without a **midrib**. Most of the advanced foliose forms are **epiphytic**.

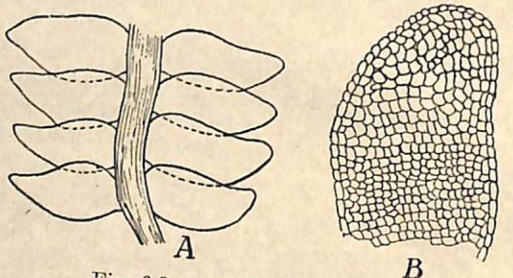


Fig. 6·2. (A—B). Porella Sp.
A. Portion of the leafy gametophyte from above showing incubous arrangement of leaves.
B. A leaf seen from above.

The external elaboration of the thallus in the Jungermanniales is accompanied by little or no internal differentiation of tissues. The whole thallus consists of similar parenchyma cells. The air chambers and air pores are absent.

The thallus is usually secured to the substratum by the **rhizoids**. They are unicellular and always of simple, smooth, thin-walled type. The scales are lacking. Notwithstanding the external elaboration of the advanced leafy forms the Jungermanniales form the most natural group. There is a striking series of transitional forms which connect the simplest thallose forms with the most specialised leafy ones.

Distribution and Habitat. The order includes about 244 genera with 9,000 species. The leafy forms are by far the richest in species. The jungermanniales are widespread in their distribution occurring both in the cold climates and in the tropics. They are, however, abundant in the tropics but extend north and south up to the polar regions. Himalayas particularly the eastern part and South India are the treasure houses of the leafy Jungermanniales. Mussoorie, Darjeeling, Almora, Garhwal, etc., are some of the places rich in these hepatics.

Combination of shade and abundant moisture is a pre-condition for their successful growth. A few species are aquatic but the majority are hygrophytic or mesophytic. They grow on damp soil, moist rocks, logs of wood, bark of trees and their leaves in the damp tropical forests.

Vegetative Reproduction. Vegetatively the Jungermannials reproduce by the following methods :—

1. **Gemmae**. Many jungermanniales reproduce by gemmae. These are bud-like structures variable in form and size. In *Riccardia* (*Aneura*) the gemmae are small, two-celled structures. They are produced endogenously in the superficial cells of the thallus. The gemmae of *Blasia pusilla* are multicellular and star-shaped. They are usually produced behind the apex on the thallus and rarely in flask-shaped gemma receptacles. They are readily detached and

The latter may serve as nutritive cells but more often get metamorphosed into **elaters**. The spore mother cells usually become four lobed before further division. The ripe capsule, as a rule, dehisces in a regular manner. It splits by four **valves** (Fig. 7·11). The valves become reflexed. The elaters radiate out and by their hygroscopic movements aid in the dispersal of spores.

Germination of Spores. The liberated spores germinate under suitable conditions. Each may either directly develop into a thallus or form a distinct protonematal stage. The latter in some species is short-lived and ephemeral. Protonema stage is characteristic of the foliose forms Sometimes it is long-lived.

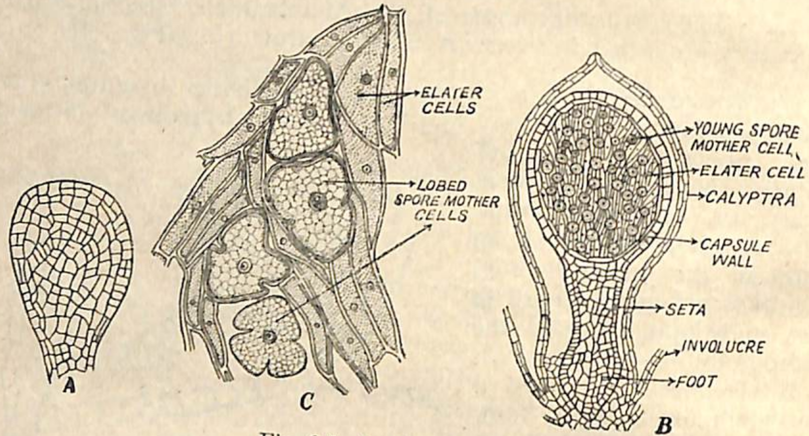


Fig. 6·6 (A—C). Porella sp.
A. Advanced embryo.
B. L S. young sporogonium.
C. Lobed spore mother cells and elaters. (After Campbell).

Classification. Evans and Buch divide the Jungermanniales into the following three sub-groups giving each the rank of a sub-order :—

1. **Haplomitrineae** which includes the erect forms like *Haplomitrium* and *Calobryum*.
2. **Metzgerineae** or Anacrogynous Jungermanniales.
3. **Jungermannineae** or Acrogynous Jungermanniales.

Campbell separates the Haplomitrineae from the Jungermanniales and gives it the rank of an order—Calobryales coordinate with the Marchantiales, Sphaerocarpales and Jungermanniales.

The consensus of opinion favours Campbell's suggestion. The order Jungermanniales, therefore, *on the basis of the position of the archegonia*, is divided into the following two sub-orders :—

1. **Anacrogynae** or **Metzgerineoe**. The plant body is generally of a **thalloid** construction. It is, however, not characteristic of the sub-order as a whole. Some species are **foliose**. Transitional forms between the foliose and the thalloid forms are also present. They show rudimentary foliose development. The archegonia usually occur in clusters. The archegonial cluster is never terminal. It is borne on the upper surface some distance back from the growing apex. The apical cell is thus never used up in the formation of an archegonium. This sub-order comprises about 23 genera and more than 550 species. The modern trend is to allot them to six or seven families such as the Riccardiaceae, Pelliaceae, Treubiaceae, Fossombroniaceae, Blasiaceae, Pallaviciniaceae, and Metzgeriaceae. Of these family *Pelliaceae* is considered in this text.

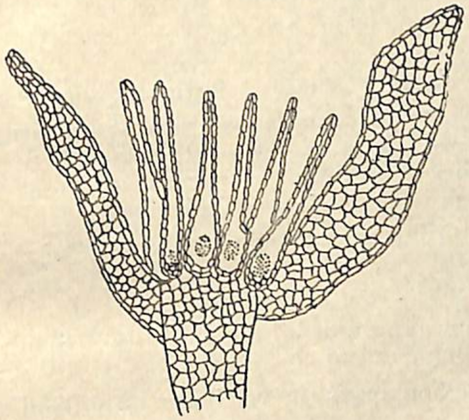


Fig. 6·7. Porella sp.
Terminal archegonial cluster.

2. **Acrogynae** or **Jungermannineae** It includes the advanced foliose forms which are by far the richest in species and according to Muller constitute about 84% of all liverworts. The leaves on the axis are usually arranged in three lateral rows. Two of these are dorsal and one ventral. The dorsal leaves are bilobed and larger. The thallus grows by means of a three-sided apical cell having the form of an inverted pyramid. The apical cell itself is used up in the formation of an archegonium in the terminal cluster (Fig. 6·7). The growth of the axis is thus arrested. The sporophytes are therefore terminal in position. This sub-order includes about 220 genera with 8,500 species. They are placed under 17 families. Of the numerous families included in this sub-order *Madothecaceae* or *Porellaceae* is taken up here.

SALIENT FEATURES

1. The haplophase or the gametophyte in the lowest Jungermanniales is a simple, flat thallus. The advanced forms show foliar

development. In the latter the thallus is differentiated into the so-called **stem** and the **leaves**.

2. In either case the thallus shows little or no internal histological differentiation. The whole plant consists of similar parenchyma cells.

3. Even the leafy forms are distinctly dorsiventral.

4. The leaves in the foliose forms are arranged in two or three lateral rows. The leaves of the dorsal rows are closely set on the axis. They slightly overlap each other in a succubous or incubous manner. The leaf has no midrib.

5. The rhizoids are unicellular but always of simple. smooth, thin-walled type.

6. The scales are usually absent.

7. The apical growth in all the Jungermanniales takes place by means of a single apical cell.

8. The sex organs are never borne on stalked receptacles.

9. The archegonia usually occur in groups and are distinctly stalked. The venter is almost as broad as the neck or only slightly broader than the neck. The neck consists of only five vertical rows of neck cells.

10. The antheridia are oval or globular in outline. They are usually superficial, occasionally seated in cavities. They may be sessile but usually elevated on long, slender stalks. In the advanced foliose forms the antheridia are lateral and axillary in position.

11. The sperms are biflagellate but larger and show more numerous coils than those of the Marchantiales.

12. The zygote invariably divides by a transverse or approximately transverse wall to give rise to an upper epibasal cell and a lower hypobasal cell.

13. The hypobasal cell takes no further part in the development of the sporogonium. The entire sporogonium develops from the epibasal cell. It is differentiated into foot, seta and the capsule. The seta is much elongated at maturity.

14. The capsule wall is two or more cell layers in thickness. The cells of the jacket layer are always sclerified.

15. The sporogenous cells are differentiated into spore mother cells and the sterile cells.

16. The spore mother cells become four-lobed before further division.

17. The sterile cells in most genera develop into elaters. Rarely they function as nutritive cells.

18. The ripe capsule usually dehisces in a regular and a definite manner along lines of dehiscence. It splits into four valves which become reflexed.

19. The elaters after dehiscence radiate out and by their hygroscopic movements help in scattering the spores.

20. Formation of a protonema stage is characteristic of the foliose forms. It is generally short-lived and ephemeral but sometimes long lived.

COMPARISON BETWEEN THE JUNGERMANNIALES AND THE MARCHANTIALES

The general life history is the same in both the *Jungermanniales* and the *Marchantiales*. There are differences in detail. The **Jungermanniales differ** from the **Marchantiales** in the following respects :

1. Greater external elaboration of the gametophyte in the foliose Jungermanniales.

2. No or little histological differentiation so that there are neither any air chambers nor any air pores. The entire thallus usually consists of similar parenchyma cells.

3. Absence of tuberculate rhizoids.

4. Absence of scales. Evans, however, likens the scales of Marchantiales to the ventral leaves of the foliose Jungermanniales. This view is supported by the fact that both are one cell thick and are attached by a broad base. Besides, scales of the Marchantiales, in many members of the order, contain chloroplasts, at least, in early stages of development.

5. Growth always by means of a single apical cell.

6. Sex organs never borne on stalked receptacles.

7. Archegonia usually in groups and distinctly stalked.

8. Venter nearly as broad as the neck or only slightly broader than the neck.

9. Neck of five vertical rows of neck cells.

10. Antheridia frequently superficial. They are lateral and axillary in position in the advanced foliose forms.

11. Larger sperms with more numerous coils.

12. Development, in most genera, of the entire sporogonium from the epibasal cell.

13. Greater internal elaboration of the sporogonium.

14. The capsule wall two or more cell thick with the cells of the jacket layer always sclerified.

15. Presence of perfect elaters in most if not all the Jungermanniales.

16. Dehiscence of the ripe capsule in a definite and regular manner along four lines of dehiscene.

17. Presence of a protonematal stage in all the foliose forms.

The **Jungermanniales resemble** the **Marchantiales** in the following features :–

1. The simple thalloid plant body of the lower Jungermanniales is a constant feature of Marchantiales.
2. Prostrate habit and dorsiventral configuration.
3. Presence of unicellular, simple, smooth-walled rhizoids.
4. Sex organs similar in essential respects in both, differing only in details.
5. Presence of perianth in both. It is widespread in the Jungermanniales and is represented in some of the Marchantiales.
6. The same basic chromosome complex of $n=9$ chromosomes (Mehra).
7. Similar radial and general plan of construction of the sporogonium into foot, seta and capsule in both. The elaboration in the Jungermanniales is internal rather than external.
8. Similar type of elaters.
9. Presence of intercalary growth in the sporophytes of both.
10. Absence of ventilated photosynthetic tissue in both so that the sporophyte is physiologically dependent on the gametophyte.

REVISION QUESTIONS

1. Give a brief account of the habitat, distribution and external features of the gametophyte of Jungermanniales.
2. In what respects do the Jungermanniales (*a*) differ from and (*b*) resemble the Marchantiales ?
3. Give a brief account of the vegetative reproduction in the Jungermanniales.
4. List the salient features in the life cycle of Jungermanniales.
5. In what respects do the archegonia of Jungermanniales differ from those of the Marchantiales ?

CHAPTER VII

JUNGERMANNIALES—METZGERINEAE : PELLIACEAE

General Characteristics. This family includes two or three genera with a thallose gametophyte. The thallus is prostrate and dorsiventral often lobed by irregular incisions. It is secured to the ground by means of simple, unseptate, smooth and thin-walled rhizoids. The scales are absent. The sex organs are either scattered or in groups on the upper surface of the thallus. The archegonial cluster is always surrounded by an involucre which is an outgrowth of the thallus. The capsule is usually spherical or oval in outline and elevated on a long, slender stalk, the **seta**. The capsule wall is generally two to four layers in thickness. There is a coherent mass of elaters attached to the floor of the cavity of the capsule. It constitutes the **basal elaterophore**. The elaters are free. Each elater has two to four spirals bands. The spore mother cells become four lobed before entering upon meiosis. The lobes are arranged tetrahedrally. The important genera included in this family are *Pellia* and *Noteroclada*. Evans (1939) added a third to the list. It is *Calycularia*. Of these *Pellia* is taken as a type.

Systematic Position :

Bryophyta
  Hepaticopsida
    Jungermanniales
      Anacrogynae or Metzgerineae
        Pelliaceae
          Pellia Raddi

Habitat. It occurs in diverse situations commonly on damp soil. Generally it occurs by the sides of streams, springs, wells, and in damp woods, sometimes, actually under water. Rarely it is found on moist rocks. The aquatic forms usually remain sterile. The form and texture of the thallus varies according to the habitat. The individuals growing on damp soil have a robust thallus with broad, elongated lobes. When growing submerged or in very humid, damp, shady places the thallus is delicate, long, narrow, ribbon-shaped with a distinct midrib and thin margin. Three species of this genus are found in India. They are *P. epiphylla*, *P. neesiana* and *P. calycina* (Fig. 7·1).

Distribution. *Pellia calycina* (*P. fabbroniana*) has been reported by Kashyap from Kumaon, Western Himalayas, Mussoorie, Kulu, Simla, Dalhousie, etc. It occurs between 5000 to 8000 ft. on moist soil or actually under water. *P. epiphylla* (Fig. 7·3) is common in Sikkim and eastern Himalayas. *P. neesiana* (Fig. 7·7) is not commonly found. All the three species of *Pellia* are commonly found in the North Temperate Zone.

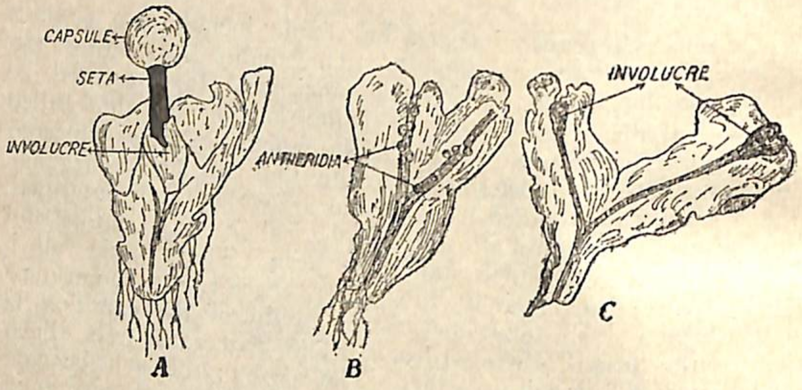


Fig. 7·1 (A—C). Pellia calycina (dioecious).

A. A plant bearing a nearly mature sporogonium.

B. Male plant.

C. Female plant.

External Characters. The plant body is a small, simple, dorsiventral thallus. It grows dichotomously as *Marchantia* but differs in its external form. The thallus is thin, flat, green and lobed (Fig. 7·1B). The margin is sinuous and irregularly lobed. The lobes often overlap one another. The branching is dichotomous. The upper surface of the thallus is smooth without areolae. It appears deep green and translucent and not light green and opaque as that of *Marchantia*. Since many plants grow together it is difficult to distinguish the individuals in the patch. The central portion of each lobe is thicker than the margins. It constitutes the **midrib**. The broad poorly defined midrib extends to the apex of each lobe and slightly projects below. From the ventral side of midrib arise numerous smooth walled **rhizoids**. They attach the plant to the substratum. Scales and tuberculate rhizoids are absent. Each lobe of the thallus has a terminal notch. At the bottom of this notch lies the growing point.

Structure of the Thallus (Fig. 7·2). Internally the thallus is simple but several cell layers deep. However there is no differentiation between different cells. The entire thallus is thus composed of thin, polyhedral, parenchyma cells. The cells are joined together in a honey-comb-like manner. The thallus is several layers of cells thick along the median line or midrib region. In some species (*R. epiphylla* and *P. neesiana*), the cells in the midrib region are elongated in the direction of the long axis of the thallus lobes. The cell walls of these elongated cells are thickened by brown or yellow layers of thickening bands forming a kind of network. The thallus gradually thins out towards the margins where it may be one cell layer thick. The cells near the surface contain abundant chloroplasts. The starch grains, however, occur in all the cells. A few cells may, sometimes, contain oil. The single layer of regularly arranged cells which covers the upper and the lower surface of the thallus are sometimes referred to as the **epidermis**. The air pores and air chambers characteristic of *Marchantia* are absent. The unicellular rhizoids grow out as tubular outgrowths from the cells of the under surface in the midrib region.

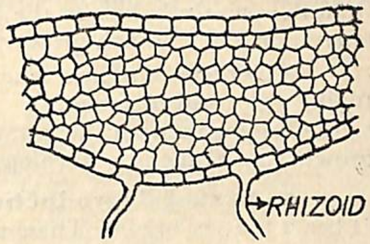


Fig. 7·2. Pellia sp. V.S. thallus.

Apical Growth. It takes place by means of a single, large, apical cell. It lies in a depression at the anterior end of each thallus lobe. In *P. epiphylla* the apical cell is lenticular and cylindric. It cuts off segments parallel to its two sides and the posterior convex base. The former by repeated divisions give rise to the wings of the thallus. The latter build up the broad, thickened median portion. Owing to more rapid growth of the marginal cells the growing apex becomes sunk in a depression. There it is protected from damage. Near the growing point certain cells of the lower surface grow into grandular hairs. They secrete mucilage which protects the growing point from drying. At the time of dichotomy the apical cell divides by a longitudinal wall into two equal cells. Each of the latter functions as an apical cell of a branch.

REPRODUCTION

The **thallus** or the **gametophyte** of *Pellia* reproduces by two methods, **vegetative** and **sexual**. The second individual in the life cycle, which is called the **sporogonium** is concerned with the production of meiospores.

1. **Vegetative Reproduction**. Vegetatively *Pellia* reproduces by two methods, *adventitious branches* and *fragmentation*.

(*i*) *Adventitious branches.* They arise from the upper surface of the thallus or the margin. Eventually these branches separate from the parent thallus by the decay of the connecting tissues. On separation each branch grows as an independent plant.

(*ii*) *Fragmentation.* The cells in the basal, older regions of the thallus die and disintegrate leading to the separation of the lobes or the fragments from the parent thallus. Each fragment by apical growth and branching develops into an independent individual.

2. **Sexual Reproduction**. The thallus is the sexual plant. It bears the sex organs. These are **antheridia** and **archegonia**. Some species of *Pellia* are **dioecious**, others **monoecious.** Examples of dioecious species are *P. calycina* (Fig. 7·1 B and C) and *P. neesiana.* The third *P. epiphylla* is monoecious (Fig. 7·3). The monoecious species are **protandrous.**

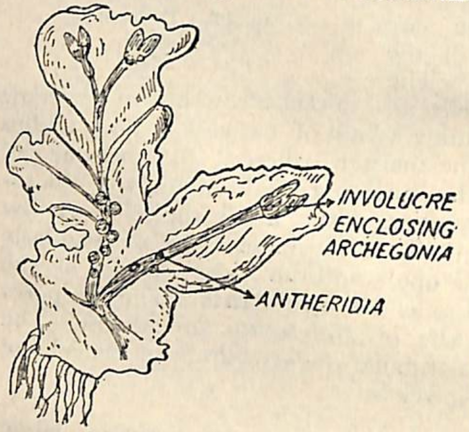


Fig. 7·3. Pellia epiphylla (Monoecious).

(*a*) ANTHERIDIA

(*i*) **Position and Structure**. Mature antheridia are seen as circular spots on the upper surface of the thallus (Fig. 7·3). They occur singly and lie irregularly scattered in two or more rows in the broad midrib region. Each antheridium is immersed in the thallus. It lies in a cavity called the **antheridial chamber** (Fig. 7·5A). The latter opens on the upper surface of the thallus by means of a small opening, the **ostiole**.

The antheridium is a stalked, globular structure (Fig. 7·4 K). The stalk is short, slender and multicellular. The globular body of the antheridium has an outer wall. It is one cell-layer thick and surrounds a central mass of **androcyte mother cells** Each androcyte mother cell divides diagonally into two **androcyte** or **spermatids**. The protoplast of the androcyte metamorphosis into a biflagellate sperm. The liberated sperm is an elongated, spirally coiled biflagellate structure (Fig. 7·4 L). The two flagella are inserted at different points at the anterior thin end. The tapering coiled body of the sperm is entirely nuclear in origin.

(*ii*) **Development** (Fig. 7·4). Each antheridium arises as a single superficial cell. It is called an **antheridial initial** (Fig 7 4 A). It lies on the upper surface of the thallus close to the growing apex. The antheridial initial increases in size and projects above the surface of the thallus. It then divides by a transverse wall into two (Fig. 7·4 B). Of these the lower or basal cell remains embedded in the thallus. The outer cell, which projects above the

thallus, functions as an **antheridial mother cell**. It divides transversely into a lower **primary stalk cell** and an upper **primary anheridial cell** (Fig. 7·4 C). The former undergoes a few divisions to form the short, multicellular stalk.

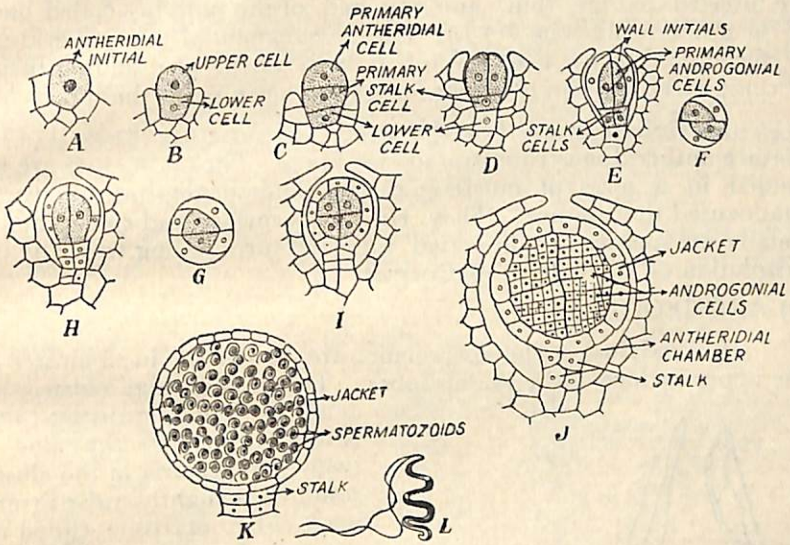


Fig. 7·4(A—L). Pellia sp.
Development of antheridium.

A—J. Various stages in the development of an antheridium. (Explanation in the text)

K. Mature antheridium.

L. A sperm. (Diagrammatic]

The primary antheridial cell develops into the body of the antheridium. It first divides by a longitudinal wall into two daughter cells (Fig. 7·4 D). They are of equal size. The next wall in each daughter cell is in a plane diagonal to the first division. It is nearly periclinal (Fig. 7·4 E). It divides each daughter cell into a pair of unequal cells (Fig. 7·4 F). The smaller cell of the pair constitutes the **jacket** or **wall initial**. The larger sister cell again divides periclinally into an outer and an inner cell (Fig. 7·4 G). The outer cell is the **second jacket** or **wall initial**. The inner cell functions as the **primary androgonial cell**. These divisions can best be seen in transverse sections. At this stage the body of the young antheridium consists of four wall initials. They enclose the two primary androgonial cells. The jacket or wall initials divide only by anticlinal walls to form the one cell thick wall of the antheridium (Fig. 7·4 I). The primary androgonial cells divide and redivide several times. The cells of the last cell generation constitute the **spermatocytes** or the **androcyte mother cells** (Fig. 7·4 J). Each androcyte mother cell divides diagonally into two **androcytes** or **spermatids**. Each androcyte produces a single antherozoid (Fig. 7·4 K). It is formed mainly from its nuclear material. It is furnished with two long flagella. They are inserted at the thin, anterior end of the tapering coiled body of the antherozoid (Fig. 7·4 L). The development of the antheridium is accompanied by the upward growth of the surrounding tissue. It completely encloses it except for a small opening at the top.

(*ii*) **Dehiscence**. On the access of moisture the wall of the mature antheridium ruptures at its apex. The androcytes are extruded in a mass of mucilage through the opening into the water that caused the rupture. They rise to its surface and spread apart. Finally the sperms are liberated into the surrounding water by the dissolution of the walls of androcytes.

(*b*) ARCHEGONIA

(*i*) **Position**. The archegonia are produced in a cluster on the upper surface of the thallus lobes. The archegonial cluster lies close to the growing apex (Fig. 7·5 B). All the four to twelve archegonia in the cluster stand on a slightly raised transverse ridge of tissue called the **receptacle**. The latter faces the growing apex. The archegonia of the cluster are surrounded by a complete or incomplete tubular sheath, the **involucre** (Fig. 7·3). The involucre is protective in function. It is tubular in *P. calycina*, short and cylindrical in *P. neesiana* and reduced to a pouch open in front in *P. epiphylla*. Amidst the archegonia in the cluster occur the mucilage hairs.

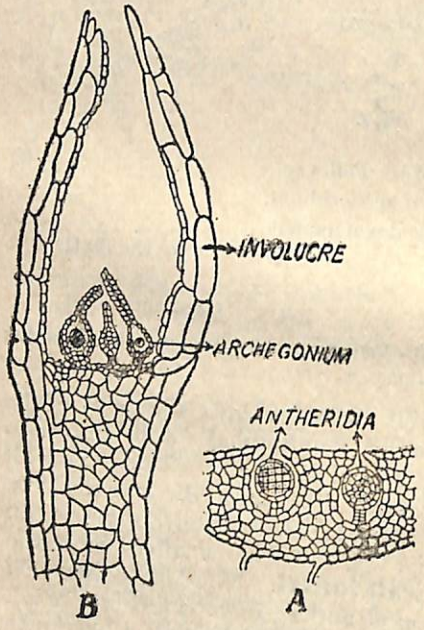


Fig. 7·5 (A–B). Pellia calycina. (Dioecious)

A. V. S. through the male thallus showing antheridia.
B. Section through the female thallus bearing archegonia.

(*ii*) **Structure**. The archegonium is typically a flask-shaped structure (Fig. 7·6 I). It is essentially the same as the corresponding organ in the Marchantiales but usually more massive. The differences are only in detail. It is seated on a short but stout and a massive **stalk**. The venter consists of two layers of cells. The venter cavity contains the **egg** and a small **ventral canal cell**. The elongated neck is not sharply marked off from the venter. It consists of five

longitudinal rows of cells. They enclose a canal containing a row of usually 6-9 **neck canal cells**. A rosette of four rather large **cover** or **cap cells** are located at the top of the neck. Sometimes the lower portion of the neck also becomes two cell layers thick.

(*iii*) **Development** (Fig. 7·6). The archegonia arise from a group of cells on the upper side of the thallus lobes. These are the surface cells of the younger segments of the apical cell. The apical cell itself is not directly concerned in their development. A variable number of cells in this group function as **archegonial initials**. The result is that the archegonia stand in a group on the upper surface of the thallus lobes near the growing point.

Any surface cell in the group may function as an **archegonial initial** (Fig. 7·6 A). It enlarges into a papilla-like outgrowth.

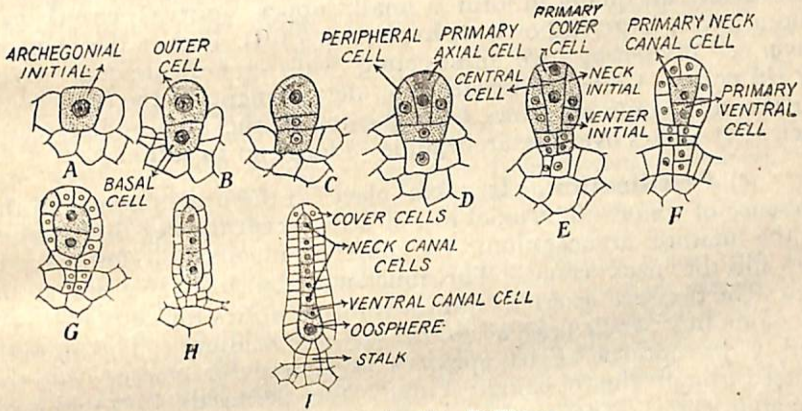


Fig. 7·6 (A—I). Pellia sp.

Development of the archegonium.

(A—H). Earlier stages. (Explanation in the text).

I. Nearly mature archegonium. (Diagrammatic).

The papillate archegonial initial divides horizontally into a basal **pedicel cell** and an upper or outer **archegonium mother cell** (Fig. 7·6 B). The latter undergoes the usual divisions to produce an archegonium. The basal pedicel cell divides to form the short, multicellular stalk.

The archegonium mother cell divides by three intersecting vertical walls so as to cut off three lateral or **pheripheral cells** (Fig. 7 6 D). Of these one is the smallest. They surround an internal, middle cell called the **primary axial cell**. The latter slightly overtops the peripheral cells. The axial cell divides transversely to form a small, outer **primary cap** or **cover cell** and a lower, larger **central cell** (Fig. 7 6 E). The two larger, lateral or peripheral cells divide by vertical walls. The smallest peripheral cell does not divide. The central cell now becomes enclosed in a ring of five cells. They are the **envelope cells** or the **jacket initials**. All the cells constituting the young archegonium including the central cell divide transversely. The young archegonium is now divided into two halves (Fig. 7·6 F). Each half consists of five envelope cells and one central cell. The five envelope cells of the upper half constitute the **neck initials**. Its central is the **primary canal cell**. The five envelope cells of the lower half constitute the **venter initials**. Its central cell functions as the **primary ventral cell**.

The neck initials divide repeatedly by transverse walls to form the archegonial neck. It consists of five vertical rows of **neck cells**. In the meanwhile the primary neck canal cell divides to form a row of six to nine or more **neck canal cells**. They fill the neck canal. The venter initials divide to form the venter wall. It encloses a **venter cavity** (Fig. 7·6 H). Before fertilisation the venter wall becomes two or three cell layers thick. The primary ventral cell divides unequally to form a small, upper **ventral canal cell** and a lower, large **egg** or **oosphere** (Fig. 7·6 I). Finally the primary cover cell divides by two intersecting walls to form the four **cover** or **lid cells**. Coincident with the development of the archegonia a delicate membrane grows from the top of the archegonial receptacle. It arches over the archegonia to form an **involucre**.

(*c*) **Fertilisation**. It takes place in the usual manner in the presence of water. The axial row of cells except the egg disorganises in the mature archegonium. A mass of mucilage is formed. It now fills the neck canal. The mucilage absorbs water and swells up. The pressure exerted from within separates the cap cell. At the same time water finds access to the antheridium. The antheridial wall ruptures at its apex. The androcytes emerge into the water through the opening. Finally the sperms are liberated from the androcytes. They swim to the archegonia and enter the open archegonial necks and swim down the canals to reach the egg. One of them probably the first to reach there loses its flagella and penetrates the egg to fuse with the female nucleus to accomplish fertilisation. The fertilised egg secretes a wall around it and is now called the **zygote** or the **oospore**.

Production of Meiospores. It is the concern of the non-sexual individual in the life cycle. It is called the **sporogonium**. It produces the **meiospores** commonly called the spores and also helps in their dispersal by wind.

(*a*) **Sporogonium** (Fig. 7·8). It is formed from the zygote by cell division and cell differentiation.

(*i*) **Structure**. At maturity the sporogonium consists of the **foot**, the **seta** and the **capsule** (Fig. 7·7). The foot forms the basal, absorbing region of the sporogonium. It is distinct and conical in form. Its edges project upwards (Fig. 7·8) forming a collar-like structure around the base of the seta. The seta is of pure white colour. It is almost transparent and terminates in a dark green or black capsule.

The capsule is globular in outline. The capsule wall is two or more cell layers thick. The outer layer of the capsule wall consists of polygonal cells (Fig. 7·8). Their radial walls possess rod-like thickening bands. The cells of the second layer are flattened. They are, somewhat, reticulately thickened. Within the capsule wall is a central tuft of 50—100 erect, elater-like cells. It is styled as an **elaterophore** (Fig. 7·8). The lower ends of the cells of the elaterophore are attached to the floor of the capsule cavity. The upper free ends radiate into the cavity intermingling with the spores and the free elaters. The spores are large. They begin to germinate before they are shed. The elaters have two or three bands of spiral thickening each. Smith holds that the basal elaterophore helps in bringing about a gradual shedding of the spores. Others believe that it functions as a primitive sort of vascular system. The capsule wall has on its surface four vertical strips of thin-walled cells. These are called the **lines of dehiscence**. The mature capsule splits as a rule into four sectors along the lines of dehiscence. The split starts at the top and extends right up to the base. The four valves spread and become everted. This regular method of dehiscence is also a feature in sharp contrast to the capsule of Marchantiales which opens irregularly.

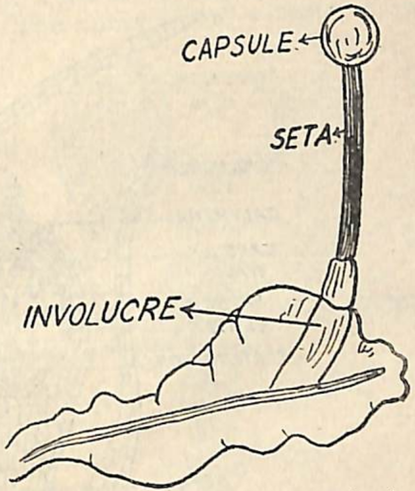


Fig. 7·7. Pellia neesiana (Dioecious). The female plant bearing a sporogonium.

The capsule of *Pellia* contains more sterile tissue as compared with that of *Marchantia*. It consists of the foot, the long seta. more than one cell-layer thick capsule wall, basal elaterophore and the elaters. In short the sporophyte of *Pellia* is a more elaborate object. It has a more complex structure as compared with that of *Marchantia*. Of course the elaboration is internal rather than external. The sterilisation of potentially fertile tissue (sporogenous tissue) has advanced. The fertile tract is partially decentralised by the substitution of a sterile, basal elaterophore. Some people look upon the elaterophore as the forerunner of the columella. This view is disputed by others.

Nutrition and Protection. Like that of *Marchantia* the mature sporophyte lacks photosynthetic tissue. The foot which is housed in the thalloid gametophyte absorbs adequate nutrition from the latter for the entire sporogonium. Protection to the developing sporophyte is provided by the calyptra and involucre. Usually only a single sporogonium is developed within each involucre.

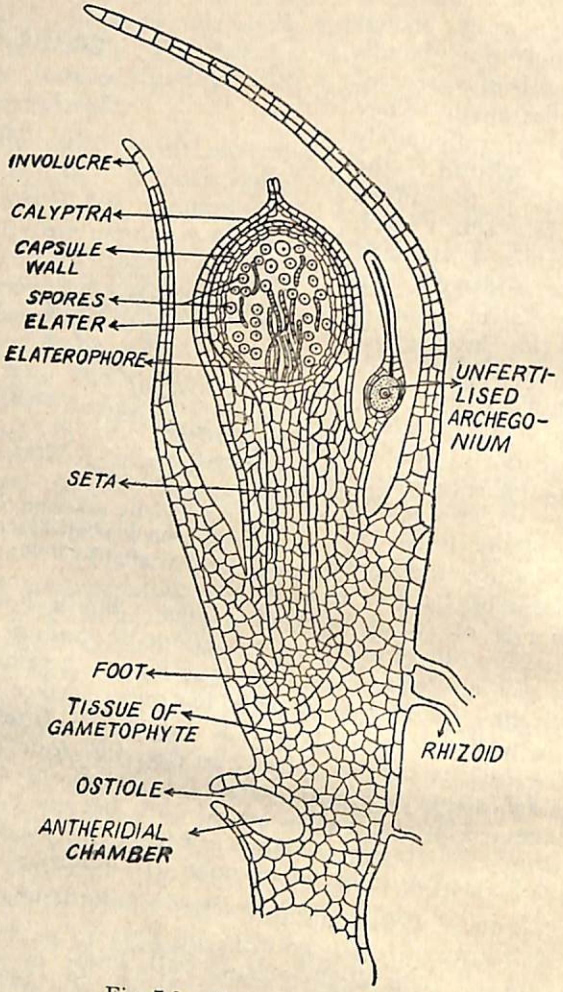


Fig. 7·8. Pellia epiphylla.
A section through the thallus bearing a sporogonium.
(Diagrammatic)

(*ii*) **Development of Sporogonium.** Five or six days after fertilisation the oospore or the zygote (Fig. 7·9A) undergoes segmentation. The first division wall is transverse (Fig. 7·9B). It separates an upper **epibasal cell** from a lower **hypobasal cell**. The hypobasal cell undergoes no further division. It usually remains as a one-celled appendage called the **haustorium**. Some people called it **suspensor** (Fig. 7·9C). It helps the growing embryo to go deeper into the tissue of the receptacle. The entire sporophyte (seta and capsule) is derived from the epibasal cell.

The latter divides first by a vertical wall and then by a transverse wall (Fig. 7·9C). The transverse division is at right angles to the first. The embryo at this stage consists of four cells. Each of these divides by a vertical wall. The embryo now consists of two

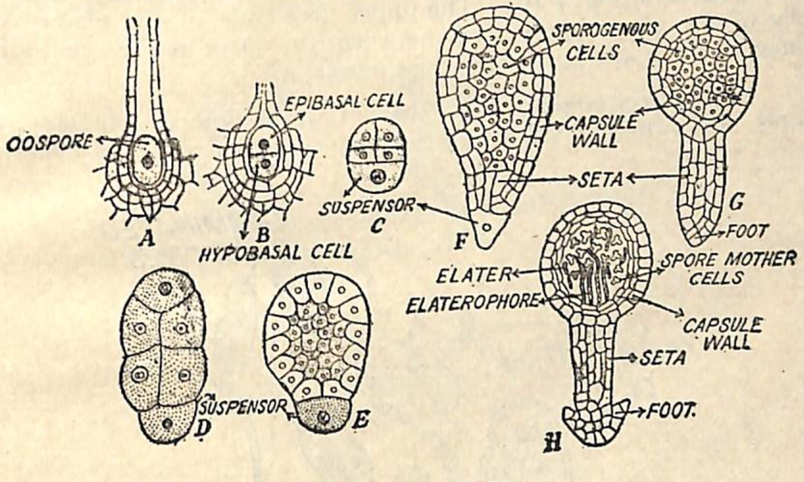


Fig. 7·9 (A—H). Pellia sp.
Various stages in the development of the sporogonium.
Explanation in the text. (Diagrammatic)

tiers of four cells each (Fig. 7·9C). The cells of both the tiers divide and redivide. The derivatives of the upper tier form the capsule (Fig. 7·9 F). The lower tier develops into the stalk or the seta. The seta at its lower end differentiates into a distinct, conical absorbing organ, the **foot** (Fig. 7·9G). The foot attaches the seta to and is embedded in the tissue of the thallus. The conical foot has its edges projecting upwards forming a collar-like structure at the base of the seta. In outline it looks like a barbed arrow head. The seta consists of uniform, small-celled parenchyma.

Each of the four cells of the upper tier of the octant stage divides periclinally separating a single layered **amphithecium**. The latter surrounds an inner mass of cells constituting the **endothecium** (Fig. 7·9E). The endothecium functions as the **archesporium** or the **primary sporogenous tissue**. As the capsule advances towards maturity the amphithecium divides by anticlinal walls to form the **capsule wall** (Fig. 7·9 F and G). Later the wall becomes two or more cell layers thick by further periclinal divisions (Fig. 7·9H). The archesporium cells divide and redivide to give rise to a mass of **sporogenous cells** (Fig. 7·9 F and G). Quite early a central mass of sporogenous cells at the base of the capsule becomes differentiated into sterile cells. These sterile cells elongate considerably and develop spiral thickening on their walls. These elater-like cells radiate from the base upwards and outwards. This basal structure is called an **elaterophore** (Fig. 7·9H). In the meanwhile the remaining sporogenous cells which surround the elaterophore become differentiated into the **spore mother cells** and the sterile **elater cells**. The latter elongate considerably. The elongated cells develop into long, thin, doubly pointed tubular structures with a double spiral thickening on their walls. These are the **elaters** (Fig. 7·10). The upper free ends of the elater-like cells of the elaterophore pass between the spore mother cells and elaters in the upper part of the capsular cavity.

(*iii*) **Sporogenesis** (Fig. 7·10). It is the process whereby the spores are differentiated from the spore mother cells by meiosis.

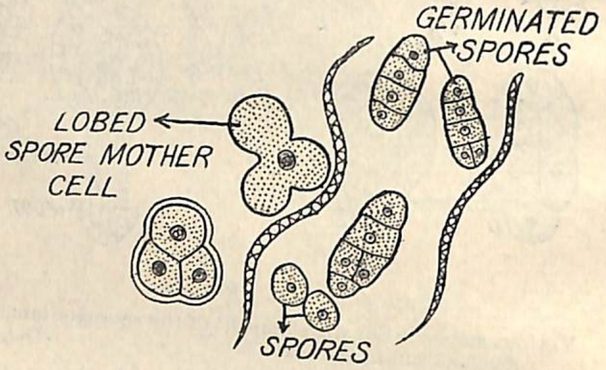


Fig. 7·10. Pellia sp.

Lobed spore-mother cells, spores, germinating spores and elaters.

The spore mother cells eventually become deeply, four-lobed structures. The lobes are tetrahedrally arranged. They are connected in the middle by a narrow neck. The latter contains the **diploid** nucleus. The nucleus divides twice by **meiosis** into four haploid nuclei. One of these migrates into each of the lobes. The lobes finally separate by cell walls laid simultaneously between them. A tetrad of haploid spores is formed. It is surrounded by a common sheath. The latter ruptures and the ripe spores are separated. They contain chlorophyll. The exospore is poorly developed The spores are unicellular and haploid structures. They later develop into multicellular structures before they are shed. Towards maturity most of the wall cells in the two layered capsule wall become thickened. There is, however, no thickening of the wall cells in the four vertical apical strips. These constitute the **lines of dehiscence**. They extend right from the apex down to the middle or the base of the capsule.

All the above-mentioned developmental changes take place within the venter. The latter in the meantime has enlarged keeping pace with the growth of the sporophyte inside. It forms a complete envelope, the **calyptra** around the young sporogonium. The seta at this stage is quite short. It remains so until the spores are ripe. With the ripening of the spores the seta elongates rapidly.

The calyptra ruptures and remains around the base of the seta as a torn membrane.

(*iv*) **Dehiscence of the capsule** (Fig. 7·11A and B). The dehiscence of the capsule is attained by the elongation of the

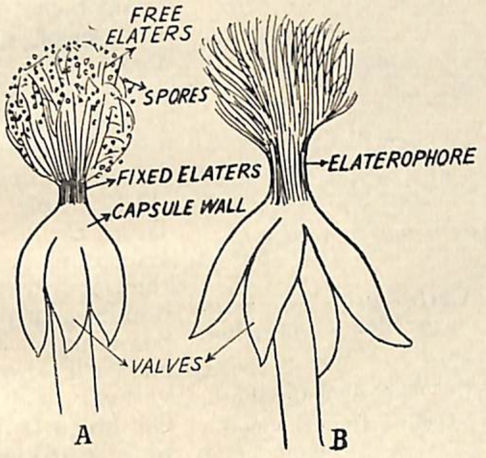


Fig. 7·11 (A—B). Pellia sp.

Two stages in the dehiscence and dispersal of spores.

A. Dehisced capsule showing recurved valves, elaterophore, free elaters and spores.

B. The same with the spores shed and only elaterophore left behind.

seta. The calyptra is ruptured and the capsule is carried above the surrounding involucre. It is now exposed to the drying effect of the surrounding air. Drying out of the capsule initiates the hygroscopic movements in the thickened cells of the capsule wall. This opens the capsule by crossed cleavages from the apex along the lines of dehiscence into four parts or valves. The four segments or valves bend back upon themselves. This exposes the mass of spores and the free elaters held round the basal elaterophore.

(*v*) **Dispersal of Spores**. The separation of the spores from the exposed mass is assisted by the hygroscopic movements of the elaters. They coil and uncoil with the changes in the moisture content of the air. The loss of moisture stretches out the elaters. This stirs up and separates the spores from the exposed spore mass. The flicking to and fro of the elaterophore helps in the gradual shedding of the loosened spores. When all the spores are shed the elaterophore persists. It stands like a column in the centre of the four spreading valves (Fig. 7·11B).

Germination of Spores (Fig. 7·12 A—G). The spores of *Pellia* begin to germinate before they are shed. This precocious germination of spores is an exceptional feature. Each spore divides by two successive transverse divisions. An oval object consisting of a number of tiers of cells is formed (Fig. 7·12C). It may be called a **sporeling**. Each cell of the sporeling contains chloroplasts, a nucleus and abundant protoplast. The whole structure, in fact, is a minute thallus. Excepting the basal and the end cells the others divide vertically (Fig. 7·12D). Sometimes the apical or end cell also divides by a vertical wall (Fig. 7·12E). On liberation the so-called multicellular spores or the sporelings rather the young gametophytes are six to nine-celled ovoid masses. On falling on moist soil they begin to grow at once. The basal cell grows into a small rhizoid (Fig. 7·12F). The central cells undergo longitudinal divisions. A cell at the apex starts functioning as an **apical cell**. It cuts off segments which divide and redivide to build up the tissue of the thallus (Fig. 7·12G)

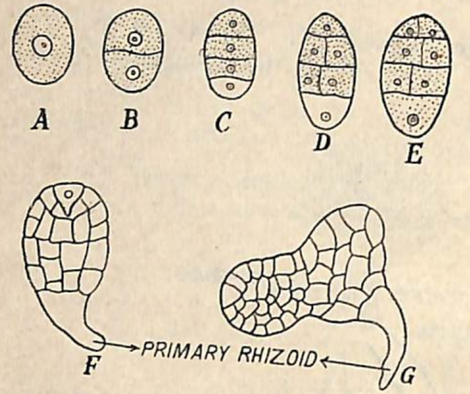


Fig. 7·12 (A—G). Pellia sp.
Various stages in the germination of spores.
A—E. Earlier stages.
F. Formation of a rhizoid and an apical cell.
G. Formation of a thallus from the germling F.
(Diagrammatic)

SALIENT FEATURES

1. The flat, deep green, translucent dorsiventral **thallus** of *Pellia* grows dichotomously as *Marchantia* but differs in external appearance. It is thinner and simpler than the light green and opaque thallus of *Marchantia* and shows no differentiation beyond a poorly defined mid-rib and a crop of rhizoids on the lower surface.

2. The upper surface of the thallus is **smooth**. There are no hexagonal areas (**areolae**) marked by dot-like central **air pores** characteristic of *Marchantia*.

3. There are no **scales** on the lower surface of the thallus.

4. The rhizoids that arise from the lower side of the broad, poorly defined slightly projecting midrib are unicellular, simple and of **smooth thin-walled** type. Tuberculate rhizoids are absent.

5. Internally the thallus of *Pellia* is much simpler than that of *Marchantia*. There is no or little differentiation of tissues. The **air chambers** and **air pores** characteristic of *Marchantia* are absent. The epidermal layers are not well-defined. There is lack of differentiation between the different cells except that the superficial cells of dorsal and ventral surface contain abundant chloroplasts.

6. The apical growth is by means of a single **apical cell.**

7. Some species of *Pellia* are **monoecious** and others **dioecious.** The former are markedly **protandrous**.

8 The sex organs are never borne on **stalked receptacles**.

9. The shortly stalked, globular antheridia are immersed singly in **antheridial chambers** on the upper surface of the thallus. They are either scattered or arranged in two or more rows in the broad **midrib** region.

10. The body of the antheridium has a usual structure. It consists of a single layered **antheridial wall** enclosing a mass of **androcytes**.

11. The **biflagellate sperms** are larger in size than those of most of the Marchantiales. They have more coils. The two flagella are inserted at different points of the thin, enterior end.

12. The early stages of development of the antheridium differ from those of the Marchantiales. The primary antheridial cell divides by a **vertical** instead of a transverse division. The succeeding divisions are **diagonally vertical**.

13. The archegonia occur in a **cluster** on the upper surface of the thallus just back of the growing point. They are stalked. The stalk though short is distinct. The archegonial neck consists of **five** vertical rows of neck cells instead of six characteristics of the Marchantiales. Before fertilisation the venter wall consists of two layers of cells. In other respects the archegonia are similar to those of the Marchantiales.

14. Of the three lateral or **peripheral cells** surrounding the primary axial cell only **two** divide by vertical walls to give rise to five jacket initials instead of six as in the Marchantiales.

15. The early development of embryo in *Pellia* differs from that of the Marchantiaceae. The **hypbasal cell** formed as a result of the first transverse division of the zygote takes no further part in the development of the sporogonium. It remains as a single-celled appendage at the base of the sporogonium. The sporogonium is entirely developed from the **epibasal region** of the two-celled embryo.

16. The capsule is raised on a long, slender stalk, the **seta**.

17. The capsule of *Pellia* shows greater **internal elaboration** than that of the Marchantiales. The capsule wall is two or more cell layers thick. The cells of the two layers of the capsule wall develop **strengthening bands**. The mature capsule dehisces in a regular and definite manner along the four **lines of dehiscence** into four **valves** which become reflexed. The sporogenous tissue is differentiated into spore mother cells, the elaters and the elatero-

phore. The spore mother cells become **four lobed** before entering upon meiosis. The presence of a **basal elaterophore** is a distinctive feature.

18. The germination of the spores before being discharged is another exceptional feature.

19. The absence of a protonema stage is a feature in which *Pellia* differs from most of the advanced foliose forms.

SUMMARY OF THE LIFE CYCLE (Fig. 7·13)

In general the life cycle of *Pellia* is similar to that of the other liverworts. There are differences in the details of the sex organs and sporogonium. As in other liverworts the life cycle consists of two generations, the **sexual** (gametophyte) and the **asexual** (sporophyte). The two are closely connected. As a matter of fact the **asexual individual** (sporogonium) remains organically connected with the **sexual plant** throughout its life and is dependent upon it for its nutrition.

The sexual plant (**gametophyte**) is independent (Fig. 7·13, 1). It is a thin, flat, green, dichotomously branched **thallus**. Each thallus lobe has a broad slightly thickened, median portion, the **midrib**. The latter gradually thins out to a thin layer at the margins which are **sinuous**. The upper surface of the thallus is **smooth**. The ventral surface has no **scales**. The thallus is secured to the moist substratum by numerous, **smooth walled rhizoids**. The latter spring from its lower surface in the midrib region. Internally the thallus shows no differentiation into the upper photosynthetic and the lower, compact, storage region. It entirely consists of similar cells except that the superficial layers of cells of the dorsal and ventral surfaces are rich in chloroplasts. There are no air chambers and no air pores.

The thallus bears the **sex organs**. It may be **monoecious** or **dioecious**. The male sex organs or the **antheridia** (Fig. 7·13, 2) are borne on the upper surface of the thallus either scattered or in two or more rows. Each antheridium lies in a pit. It is shortly stalked and has a globular body. The body consists of a single layered antheridial wall enclosing a mass of androcytes. The latter get metamorphosed into biflagellate **spermatozoids** or **sperms** (Fig. 7·13, 3). The body of the sperm is entirely made up of nuclear material. It is tapering and spirally coiled. The coils are more numerous. The two flagella are inserted at the thin, anterior end. The **archegonia** occur in a cluster on the upper surface of the thallus just back of the growing apex. They are typically flask-shaped structures (Fig. 7·13, 2). The archegonial neck consists of **five** vertical rows of neck cells. The neck canal is filled with 6 to 9 or even more neck canal cells. The venter is two layers thick even before fertilisation. The cavity of the venter is occupied by a large egg or oosphere (Fig. 7·13, 3′) and a smaller ventral canal cell. The sperms and the eggs are the last structures of **the gametophyte**

generation. The latter comprises the *meio spores*, the *green thallus*, the *antheridia*, the *archegonia*, the *sperms* and the *eggs*. It starts with meiosis and ends with fertilisation in the life cycle. The sexual generation is characterised by the haploid number of chromosomes in the nuclei of its cells.

The fertilised egg secretes a wall around it (Fig. 7·13, 5). It is the first structure of the sporophyte or asexual generation in the

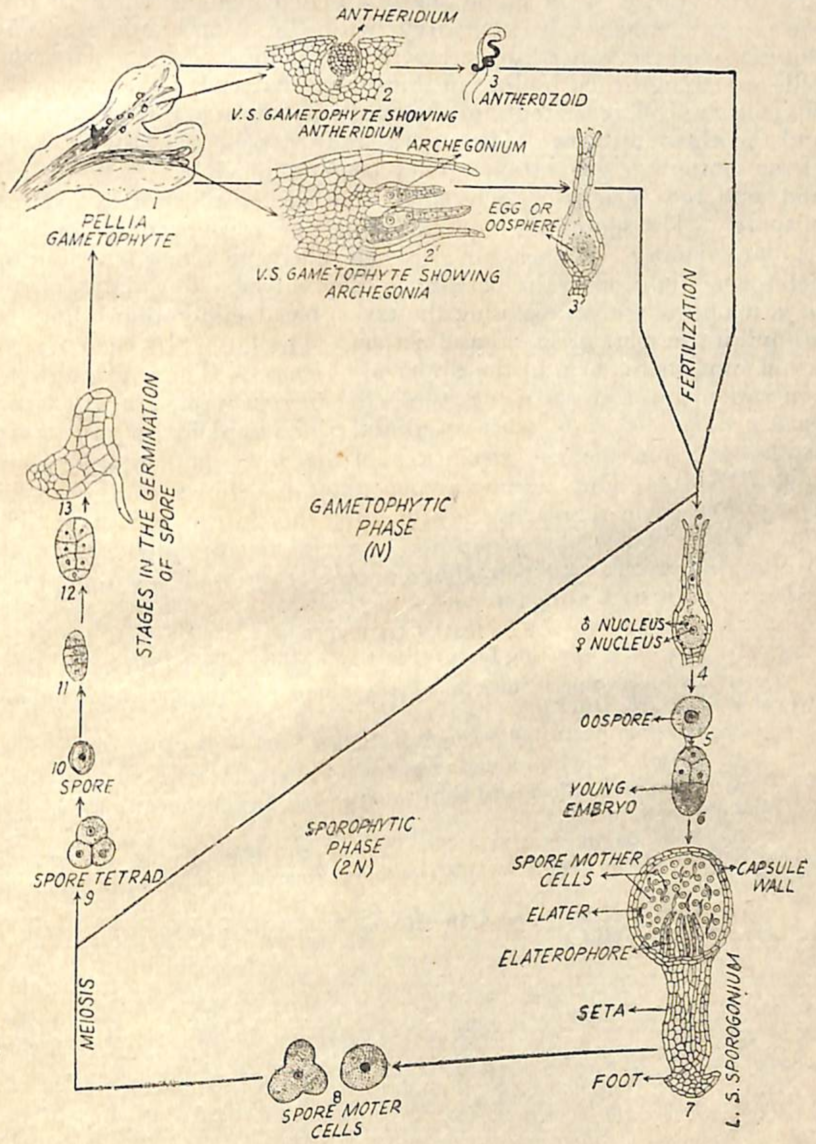


Fig. 7·13. Pellia.
Diagrammatic representation of the life cycle.

life cycle. Lodged in the venter it soon enters upon segmentation. By repeated mitotic divisions and differentiation it forms the **asexual plant** also called the **sporogonium** or the **sporophyte** (Fig. 7·13,7). It is characterised by the presence of **diploid** number of chromosomes in the nuclei of its cells. The asexual plant is differentiated into a **foot**, a long **seta** and a spherical **capsule**. The capsule shows greater **sterilisation** of the potentially fertile tissue. Associated with this is a corresponding more efficient mechanism for dispersal of meiospores as compared with the Marchantiales. The capsule wall is two or more layers of cells in thickness. The wall cells are strengthened by bars of thickening material. The sporogenous cells are differentiated into the **spore mother cells**, the **elaters** and the **elaterophore**. The spore mother cells are the last cells of the sporophyte generation. They become four-lobed (Fig. 7·13, 8) and undergo meiosis. Each spore mother cell thus forms a tetrad of spores. The spores are haploid. The ripe capsule dehisces in a regular manner. It opens by crossed cleavage along four lines of dehiscence right up to the base into four valves. The latter bend back upon themselves exposing the erect, basal elaterophore holding around it the mass of spores and elaters. The latter by their hygroscopic movements help in the dispersal of spores. The **sporophyte** generation thus consists of the *zygote*, the *sporogonium*, and the *spore mother cells*. It ends with **meiosis**. The haploid spores (meiospores) are the pioneer structures of the next gametophyte phase (Fig. 7·13, 10). The accompanying diagram shows that the two generations occur regularly one after the other in the life cycle. The reproductive cells of one generation give rise to the alternate plant in the life cycle. This phenomenon is expressed by the phrase '**Alternation of Generations**'.

REVISION QUESTIONS

1. List the interesting features in the life history of *Pellia*.
2. In what respects does the sporogonium of *Pellia* shows an advance over that of *Marchantia* ?
3. Give an illustrated account of the life history of *Pellia*.
4. Describe the reproductive phase of *Pellia*.
5. Compare and contrast the structure and development of sex organs in *Pellia* and *Marchantia*.
6. Describe in detail the structure of the sporogonium of *Pellia*. In what respects do you consider it to be more advanced than that of *Riccia* and *Marchantia*.
7. Compare the stages in the development of sporogonium of *Pellia*, *Riccia* and *Marchantia*.

23.11.70

CHAPTER VIII

JUNGERMANNIALES—JUNGERMANNINEAE : PORELLACEAE (MADOTHECACEAE)

General Characteristics. The family Porellaceae includes advanced **foliose** forms with leaves arranged in three rows. The ventral leaves are well developed and usually deccrrent at the base. The dorsal leaves are **incubous** and **bilobed**. The ventral lobe lies more or less parallel to the axis. The rhizoids are scarce and spring from the lower side of the stem in tufts generally near the base of the ventral leaves. The antheridia are **solitary**. The archegonia arise in a **terminal cluster** on small lateral branches. All the archegonia in the cluster are surrounded by a common **perianth** with a bilabiate and dorsiventrally compressed mouth. The globose capsule dehisces by four valves separating only halfway down to the base. The seta is short. The elaters are short, each with two or three spiral bands. The family is represented by a single genus *Porella* (*Madotheca*).

Systematic Position :

- **Bryophyta**
  - **Hepaticopsida**
    - **Jungermanniales**
      - **Acrogynae or Jungermannineae**
        - **Porellaceae (Madothecaceae)**
          - **Porella L.** (**Madotheca Dum.**)

GAMETOPHYTIC PHASE

Distribution. It is the best known and widely distributed genus of the advanced Jungermanniales with more than 180 species. They flourish the most in the tropics. Many species, however, are found in the cold temperate regions also. *Porella platyphylla* appears to be cosmopolitan in its distribution. It has been reported from Europe, America, Asia, and India. About 34 species of *Porella* have been found in India. They mostly occur at various places in the Himalayas such as simla, Dalhousie, Mussoorie, Garhwal, Sikkim, Chamba, Tirhi Garhwal, Kulu valley and Kumaon. Chopra (1943) recorded a few species from South India.

Habit and Habitat. *Porella* (*Madotheca*) is generally found in the moist, shady places growing flat on logs, trunks of trees and rocks over which water trickles. It grows in dense layers forming large mats closely covering the substratum.

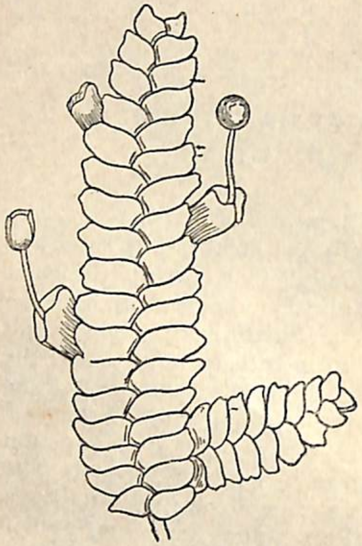


Fig. 8·1. Porella or Madotheca. Portion of the female plant bearing sporogonia.

External Characters (Fig. 8·1). The plant body is greenish, **leafy** and fairly large, up to 15 cm. or even more long. It grows flat on the substratum and is thus **dorsiventral** in configuration. It consists of a branched **central axis** bearing **leaf-like expansions**. The axis or the **stem** is thin and cylindrical. It is always branched in a bi-or tripinnate manner. The branching is **monopodial**. The branch primordium lies close to the apical cell. It takes the place of the ventral lobe of a dorsal leaf. The stem and the branches bear two kinds of leaves, large **dorsal** (Fig. 8·2 B) and small **ventral**. They are arranged in three rows (Fig. 8·3 A).

The dorsal leaves are closely set in two lateral rows (Fig. 8·1). They cover the stem from above and overlap each other. The anterior edge of each leaf covers the posterior edge of the leaf in front.

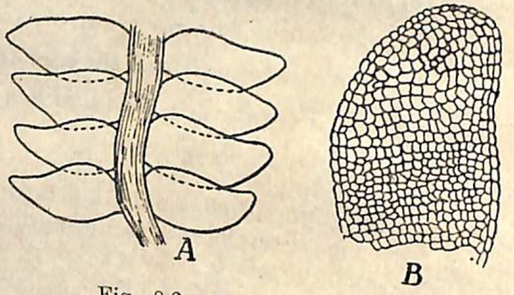


Fig. 8·2 (A—B). Porella sp.

A. Portion of a shoot from above showing incubous arrangement of leaves.

B. A dorsal view of a leaf.

Such an overlapping arrangement of the leaves is described as **incubous** (Fig. 8·2 A). Each dorsal leaf is **bilobed** (Fig. 8·3 B). Of the two lobes the upper or dorsal is large and usually oval in outline. It has a rounded apex and is also called the **antical lobe**. The ventral smaller lobe is called the **postical lobe** or the **lobule**. It is folded back and has an acute apex. It is closely appressed to the lower surface of the dorsal lobe and runs more or less parallel to the stem so as to appear like an extra leaf. The small ventral leaves which are usually decurrent at the base are also called the **amphigastria** (Fig. 8·3A). They are simple and are arranged in a single row on the ventral side of the stem. Together with the postical lobes to which they resemble in form and size they appear to form three rows on the lower surface of the stem (Fig. 8·3A). The leaves of *Porella* like other foliose liverworts regularly lack nerves. Even the midrib is absent. Each consists of a single layer of cells (Fig. 8·2B).

The rhizoids arise from the lower surface of the stem near the bases of the ventral leaves. They are few in number and are thin-walled. Their chief function is to fix the plant to the substratum. Absorption is believed to take place directly through the leaves.

Internal Structure. The young stem consists of a perfectly uniform tissue of green parenchyma cells. Even the epidermal layer is not well defined. The central strand also cannot be made out. The stem of *Porella,* therefore, is very simple in its internal structure as it shows no differentiation of tissues. In the older portions of the stem there is differentiation of tissues. It consists of an outer **cortical** and an inner **medullary region**. The cortex is made up of small cells with slightly thickened walls. The medulla is composed of comparatively larger cells with thinner walls.

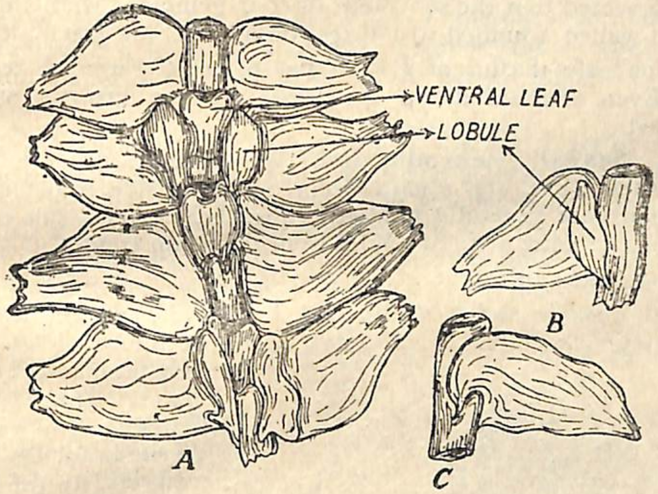


Fig. 8·3 (A—C). Porella (Madotheca sp.)

A. Shoot from the ventral side showing ventral leaves and lobules of dorsal leaves.

B. A leaf with its lobule attached to the stem seen from below.

C. A leaf attached to the stem seen from above.

The leaf consists of a thin plate of uniform cells, one cell layer in thickness. The cells contain abundant chloroplasts and are polygonal in outline. There is no midrib.

Growth. Increase in size takes place by means of an apical cell. It is pyramidal in shape with three cutting faces. One of these is towards the ventral side and the other two towards the dorsal side.

REPRODUCTION

Reproduction. *Porella* reproduces **vegetatively** and by **meiospores** formed following a sexual process. In fact meiospore formation is considered a stage in sexual reproduction. The thallus reproduces by vegetative methods and is concerned with the sexual process. Meiospores are produced by the non-sexual individual in the life cycle called the **sporogonium**.

1. **Vegetative Reproduction**. The species growing under the humid conditions propagate by **fragmentation**. Vegetative reproduction by the formation of discoid gemmae developed on the lower surface of the leaves of *Porella rotundifolia* was recorded by Schiffner from Brazil. This was denied by Degenkolbe in 1938 who discovered that the so-called discoid gemmae, were in reality the thin-walled, rounded structures containing blue green algae.

The leafy thallus of *Porella* has a great power of regeneration. Even the dried up specimens resume growth on being moistened.

2. **Sexual Reproduction**. All species of *Porella* are **dioecious**. The sex organs occur on short, side branches. The male plants are generally smaller. They bear special, side branches apparently arising at right angles from the main stem.

(*a*) **Antheridia**.

(*i*) *Position and Structure* (Fig. 8·4). The antheridia usually occur singly in the axils of small leaves or bracts of the special side branches of the male plant. The antheridial branches differ from the sterile branches in two respects. In the first instance the special male branches stand approximately at right angles to the main stem. Secondly they bear light-green leaves or bracts which are closely imbricated and bear antheridia singly in their axils. These two features make them conspicuous and different from the sterile vegetative branches.

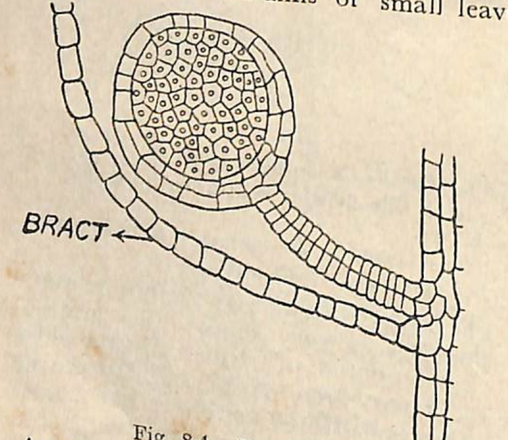


Fig. 8·4. Porella sp.
A mature antheridium arising in the axil of a bract.

The antheridia are long stalked. The stalk bears the nearly spherical body. It consists of two rows of cells. The globular body has a **jacket** or **wall** one cell thick in the upper part and two to three cells thick towards the base. The wall cells contain numerous chloroplasts. Inside the wall is a mass of colourless **androcytes** or **spermatids**. Each androcyte gives rise to a spirally coiled, biflagellate **sperm** (Fig. 8·5 C).

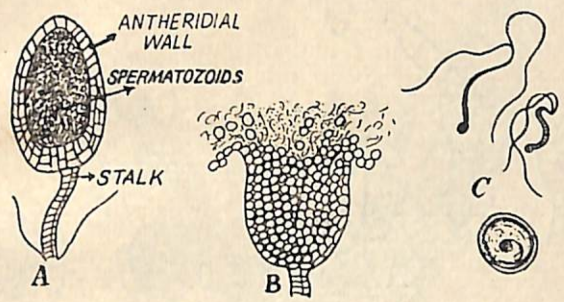


Fig. 8·5 (A—C). Porella sp.
A. L.S. Mature antheridium.
B. Dehisced Antheridium.
C. Sperms. (After Campbell)

(*ii*) *Dehiscence* (Fig. 8·5 A and B). On the access of water the mature antheridium dehisces in a very characteristic manner. The cells of the wall absorb water. The thinner upper part bursts open into a number of irregular lobes (Fig. 8·5 B). The latter curl back to allow the androcytes to escape enmass into the water that causes the rupture. With the dissolution of the walls of the androcytes the sperms are set free.

(*iii*) *Development of Antheridia* (Fig. 8·6). Each antheridium arises from one of the surface cells close to the growing apex of the male branch. It is called an **antheridial initial**. It lies at the base of the leaf and enlarges to become **papillate**. The papillate antheridial initial divides transversely into an outer and inner (basal) cell. The inner cell remains embedded. The outer cell projects above the surrounding tissue. It is called the **anthridial mother cell**. The latter divides by a horizontal wall into two cells (Fig. 8·6 A). Of these the upper one functions as a **primary antheridial** cell and the lower as a **primary stalk cell**. The latter undergoes segmentation (Fig. 8·6 B) to give rise to a stalk two cells in width and several cells in height.

The primary antheridial cell develops into the body of the antheridium. It undergoes a vertical division to produce two equal sister cells (Fig. 8·6 B). Each sister cell divides by two intersecting walls. These divisions can best be seen in cross-sections of the antheridium. They separate a **central androgonial cell** from the

two outer **jacket** or **wall initials** (Fig. 8·6 C). The former is **tetrahedral** in form. The first jacket initial in each half has by now

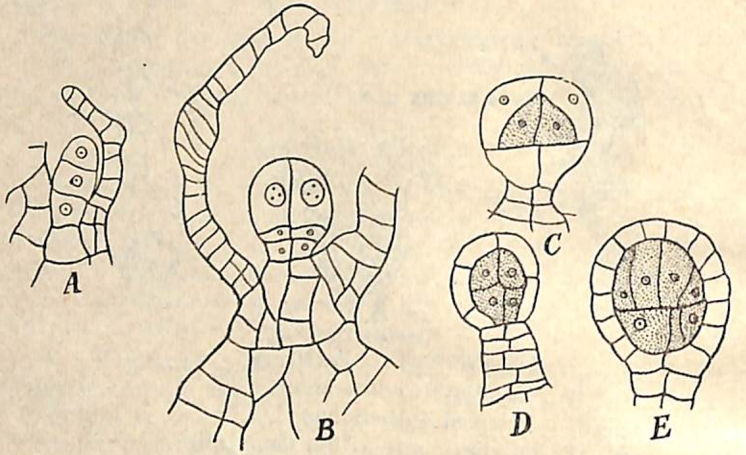


Fig. 8·6 (A—E). Porella (Madotheca) sp.
Development of antheridium.
A—E. Earlier stages. (Explanation in the text).
(After Campbell)

divided by an anticlinal wall into two. The body of the antheridium in a cross-section, at this stage, shows two **androgonial cells** surrounded by six **jacket** or **wall initials.** The latter divide and redivide by anticlinal divisions to produce a single layered **antheridial wall** (Fig. 8·6 E). Later on periclinal divisions appear in the cells of the lower part of the antheridial wall. The latter thus becomes 2 to 3 layers thick at the base (Fig. 8·5 A). The androgonial cells in the meantime divide and re-divide to produce a mass of **androcyte mother cells**. Each androcyte mother cell divides by a diagonal wall to form two **androcytes**. The protoplast of each androcyte metamorphosis into a biflagellate **sperm**. The sperm (Fig. 8·5 C) has a slender, spirally coiled body. It shows two complete coils. The flagella are somewhat longer than the body. They are inserted at the anterior thin end. A small vesicle is attached to the posterior end of the spirally coiled body.

(*b*) **Archegonia.**

(*i*) *Position and structure*. The archegonia are produced on the lateral branches of plants other than the males. These **female plants** are larger than the males. The side branches bearing archegonia are exceptionally short. Each archegonial branch usually bears a few usually four or five leaves. After these the segments cut off by the apical cell of the archegonial branch produce archegonia. The latter arise in acropetal order. Eventually the apical cell itself is used up. It is transformed into an archegonium. The archegonia thus occur in a terminal cluster (Fig. 8·7).

The further growth of the archegonial branch is arrested after the formation of the terminal archegonium in the cluster. Later the

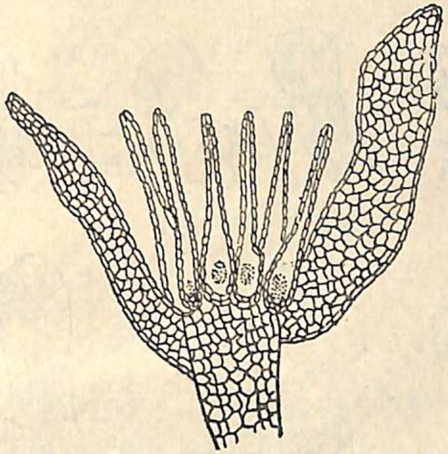


Fig. 8·7. Porella sp.
A female branch bearing a terminal cluster of archegonia.

whole cluster of archegonia is surrounded by a common protective envelope, the **perianth**.

The mature archegonium is stalked (Fig. 8·8 H). It is more or less a cylindrical object. The neck consists of five vertical rows of **neck cells**. They enclose the **neck canal**. The neck canal is usually filled with 8 broad, **neck canal cells**. The basal portion of the archegonium is called the **venter**. It is but little enlarged. It has a two cell-thick wall surrounding the **venter cavity**. The latter contains a small **egg** with the **ventral canal cell** above it.

(*ii*) *Development* (Fig. 8·8). The first three to four segments cut off by the apical cell of the female branch develop into leaves. Thereafter the derivatives of the apical cell function as **archegonium initials**. They thus lie very close to the growing apex. Each archegonium initial (Fig. 8 8 A) enlarges into a papillate outgrowth. The latter divides horizontally into a **basal cell** and a **distal cell**. The former is called the **pedicel cell** (Fig. 8·8 B). It undergoes repeated segmentation to form the **stalk** of the archegonium. The distal cell functions as the **archegonium mother cell**. It undergoes segmentation on the lines usual for the other Jungermanniales (*Pellia*) to produce the archegonium.

The archegonium mother cell divides by three eccentric vertical walls (Fig 8·8 C). Of these the last division wall is the shortest. In this way three **lateral** or **peripheral cells** are separated from the **primary axial cell** surrounded by them. Two of the peripheral cells are large and the third is the smallest. Each of the former two again divides by a vertical wall. The smaller cell remains undivided.

A ring of five peripheral cells is formed. They are the **jacket initials**. They surround the middle **primary axial cell**. The latter overtops the jacket initials and divides transversely to produce an outer cell and an inner cell (Fig. 8·8 D). The former is called the **primary cap cell** and the latter **central cell**. The central cell is enclosed by the five jacket initials. From this stage onward the development is exactly similar to that of *Pellia* and other hepatics. It is described on pages 119-120.

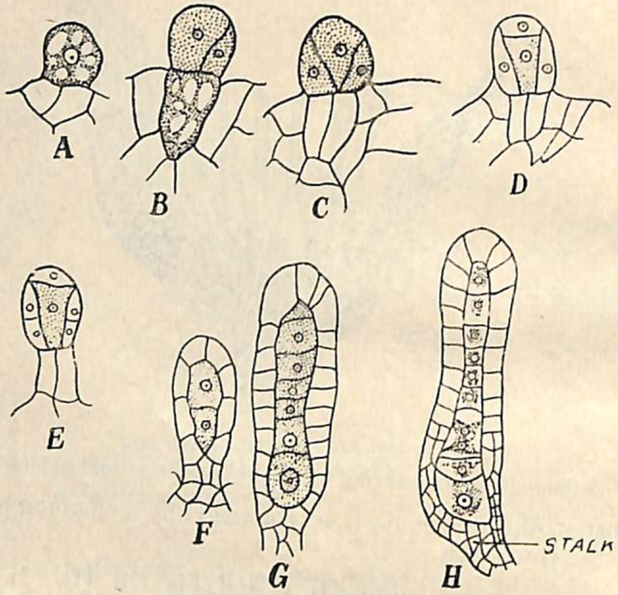


Fig. 8·8 (A—A). Porella (Madotheca) sp.
Development of archegonium.
A—F. Earlier stages.
G. Young archegonium.
H. Nearly mature archegonium. (After Campbell).

(*iii*) *Dehiscence*. On the access of water the mature archegonium opens at its tip. The cover cells are separated from each other and folded back. All this is brought by the hydrostatic pressure set up within the archegonium by the mucilage mass resulting from the disintegration of the axial row of cells except the egg.

(*c*) **Fertilisation**. It takes place in the presence of water as in the other liverworts. It is provided by the rain or dew. The transportation of the sperms is facilitated by the fact that the male and the female plants grow in company in dense patches closely covering the substratum. The sperms from the dehisced antheridia swim in thin films of water covering the male and the female plants and reach the archegonia to bring about fertilisation in the usual way.

SPOROPHYTIC PHASE

This phase in the life cycle is concerned with the production and efficient scattering of meiospores. It is the function of the non-sexual individual in the life cycle called the **sporogonium** or the **sporophyte** (Fig. 8·9). The sporogonium is developed from the diploid zygote by repeated mitotic divisions, differentiation of cells and their growth. For its nutrition the adult sporogonium depends entirely upon the archegonial branch (sexual plant) to the top of which it remains organically attached throughout its life.

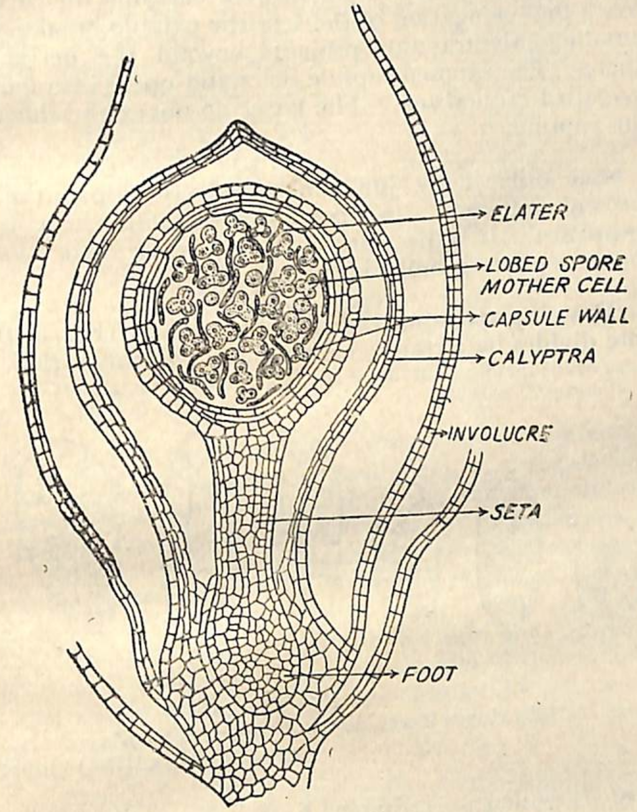


Fig. 8·9. Porella sp.
Longitudinal section of a nearly mature sporogonium.

3. (*a*). **Production of Meiospores**. It is the concern of the **sporogonium**. The sporogonium at maturity, is differentiated into the **foot, seta** and **capsule**.

Foot. It is merely a somewhat enlarged base of the seta. It is indistinct.

Seta. It is short. It carries at its top the spherical capsule.

Capsule. The spherical capsule at maturity, has two to four cells thick wall. Within the capsule wall are the spores and elaters. The elaters are short, each with one to three spiral bands. The elaterophore is absent. With the maturing of the spores within the capsule the seta suddenly elongates carrying the capsule upward. With the elongation of the seta the capsule breaks through the surrounding calyptra and projects beyond the perianth and the involucre. The exposed capsule dries and opens into four spreading lobes called the **valves**. The latter do not extend down to the base of the capsule.

In some other leafy jungermanniales the tip of the female branch becomes enlarged into a pouch-like structure. It is called the **marsupium**. It is the store-house of water and food. The foot of the sporophyte is embedded in it.

(*b*) **Development of the Sporogonium** (Fig. 8·10 A—F). The zygote divides by a transverse wall into two halves (Fig. 8·10A).

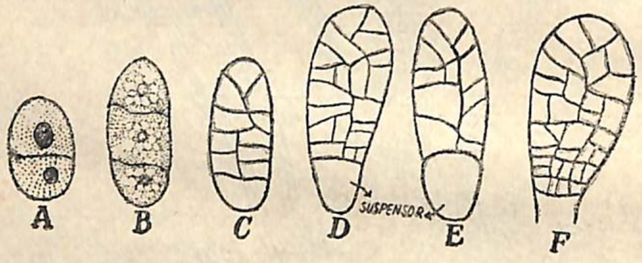


Fig. 8·10 (A—F). Porella sp.
Various stages in the development of the embryo.
(After Campbell)

The upper is called an **epibasal half** and the lower **hypobasal**. The former enters upon active segmentation and divides by a transverse wall into two cells (Fig. 8·10 B). The young embryo, at this stage, consists of a row of three superimposed cells. The basal cell of the row is the hypobasal cell. It takes no further part in the development of the embryo. It remains as a small appendage at the base of the developing sporophyte and is called the **haustorium**. Some writers call it **suspensor** (Fig. 8·10 D and E). The upper two cells of the row derived from the epibasal half develop into the entire sporogonium. They divide by transverse and longitudinal divisions (Fig. 8·10 C—F). These divisions however, are in an irregular sequence. It becomes difficult to make out the number of segments which form the capsule. As a matter of fact the distinction into the seta and the capsule regions is obscure. The embryo consists of a mass of undifferentiated cells (Fig. 8·11A). The cells show a good deal of irregularity in their arrangement. Campbell reports that the first periclinals in the cells of the upper part of the embryo appear at different distances from the surface. The differentiation into the **amphithecium** and **endothecium** regions is therefore not established by the first periclinals. At a subsequent stage these regions are well defined. The single layered amphithecium, at first, divides by anticlinal walls and later by periclinal walls to give rise to the capsule wall two or more cells in thickness. The entire endothecium mass becomes the **archesporium**. The latter by divisions forms the **sporogenous tissue**.

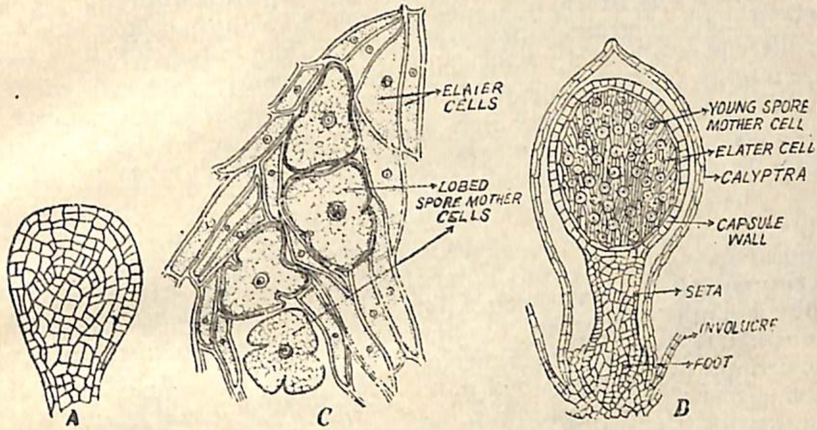


Fig. 8·11 (A—C). Porella sp.

A. L.S. embryo (advanced stage)
B. L.S. Young sporogonium still enclosed within the calyptra.
C. Portion of capsule enlarged to show the lobed spore mother cells and elater cells. (After Campbell)

At a later stage many of the cells of the sporogenous tissue cease to divide. They function as **spore mother cells**. They grow in all directions. The remaining cells of the sporogenous tissue divide and become elongated. They are the **elater cells**. The spore mother cells and the elater cells are intermingled. They are not arranged in any regular order. Prior to meiosis the spore mother cells become deeply four-lobed structures. The elongated elater cells lie in between them with their thin tapering ends fitting into the spaces between the lobed spore mother cells (Fig. 8·11C).

(*c*) **Sporogenesis**. The inner layer of the wall of the spore mother cell projects into its cavity to make it a four-lobed structure. The lobes are tetrahedrally arranged and mark the position of the four spores (Fig. 8·11C). They are connected in the middle by a narrow neck which contains the **diploid nucleus**. The latter divides by **meiosis** to produce four haploid daughter nuclei. One of these migrates into each of the four lobes. The lobes finally separate by cell walls laid simultaneously between them. A tetrad of spores is formed. It is surrounded by a common sheath. The latter ruptures and the ripe spores are separated. Each spore has a poorly developed exospore. The elater cells develop 1 to 3 spiral bands of thickening material on their wall.

The seta which is developed from the lower portion of the embryo remains short. It projects a little beyond the surrounding protective envelopes. The latter in *Porella* are the **calyptra**, the **perianth** and the **involucre**. The calyptra is many layers thick. The perianth is formed by the fusion of the two distal bracts immediately below the archegonial cluster. The bracts around the perianth become enlarged to form the involucre. The inconspicuous foot is developed from the base of the seta. It is, in fact, the enlarged base of the seta.

(*d*) **Dehiscence of the capsule**. As soon as the spores are mature the seta elongates. By this the calyptra is ruptured. The capsule is raised above the surrounding protective envelopes which are the perianth and involucre. Drying out of the exposed capsule opens it at the apex by crossed cleavages into four spreading valves. The valves do not extend down to the base. The hygroscopic movements of the elaters help in flicking away the spores to some distance.

Germination of Spores. The spores begin to germinate immediately after liberation. Precocious division of the spores in *Porella* has also been reported. The development proceeds within the exospore. Neither the exospore ruptures nor the germ tube is formed. With the division of the protoplast the endospore expands. The expanding endospore stretches the exospore considerably. Eventually the latter no longer remains visible. The repeated division of the protoplast produces a mass of cells which is circular and disc-like. It is the **protonema**. It develops one or more rhizoids which anchor it to the substratum. Subsequently a large apical cell is established at the edge of the protonema. The apical cell functions as the growing point of the future gametophyte.

SALIENT FEATURES :

1. The plant body is a **leafy thallus** which is an elaborate, delicate object. It has the appearance of leaf-like expansions arising from the central axis.

2. The slender, central axis or the stem is branched in a bi- or tripinnate manner. The branching is always **monopodial**. Dichotomous branching which is so characteristic of other liverworts is absent in the acrogynous Jungermanniales.

3. The leaf-like expansions arising from the stem are of two kinds, large **dorsal** and small **ventral**.

4. The large dorsal leaves are arranged in two lateral rows on the main axis and its branches. Being compactly arranged they cover the axis from above and overlap each other **incubously**.

5. Each dorsal leaf is a **bilobed** structure. The upper larger lobe is oval. The smaller ventral lobe is closely appressed to its lower surface. It lies more or less parallel to the stem.

6. The ventral leaves are small, simple and reduced. They are arranged in a single row on the ventral side of the axis. Together with the ventral lobes of the dorsal leaves they present the appearance of three rows of leaves on the lower surface of the axis.

7. Each leaf generally consists of a single layer of cells and has no **midrib**.

8. Simple, **smooth-walled** rhizoids spring from the ventral side of the axis near the bases of the ventral leaves and fix the plant to the substratum. They are unicellular.

9. The elaborate leafy external form is correlated with the simple internal structure. There is slight or no differentiation of tissues. The mature stems are differentiated into outer cortex and central medulla.

10. The **scales** and **tuberculate rhizoids** are absent.

11. Apical growth takes place by means of a single, large **apical cell** pyramidal in shape.

12. All species of *Porella* (*Madotheca*) are **dioecious**. The female plants are distinctly large than the males. The sex organs are borne on special side branches.

13. The **antheridia** occur singly in the axils of leaves on the **antheridial branches** which spring approximately at right angles from the central axis and bear closely imbricated light green leaves which are often called the **bracts**.

14. The spherical **body** of an antheridium is elevated on a long, slender **stalk**.

15. The spirally coiled body of the biflagellate **sperm** shows, at least, two complete coils.

16. The **archegonia** occur in a cluster at the apex of a very short **archegonial branch**. The latter bears only two to four leaves.

17. The growth of archegonial branch is arrested by the formation of the terminal archegonium of the cluster.

18. The mature archegonium more or less is a cylindrical object with the **neck** as broad as the **venter**.

19. The neck consists of five vertical rows of **neck cells** enclosing a **neck canal** containing usually 8 broad, **neck canal cells**.

20. The venter wall is two cell layers thick before fertilization. The venter cavity contains a small egg and a ventral canal cell above the former.

21. The mature sporogonium is differentiated into an indistinct **foot**, a short **seta** and a spherical **capsule**. It is developed from the epibasal half of the embryo.

22. The capsule wall is two to four cell layers thick. It encloses the spores and elaters. The elaters are short, each with 1 to 3 spirals. The elaterophore is absent. The spore mother cells become deeply four-lobed structures before meioses.

23. The mature capsule dehisces by four spreading lobes or **valves** which extend only half way down to its base.

24. The spore, on germination, produces a distinct **protonema stage.**

SUMMARY OF THE LIFE CYCLE (Fig. 8·12)

The life cycle of *Porella* may be summarized with the help of the accompanying diagram (Fig. 8·12). It is comprised, as usual, of two generations, the **gametophyte** and the **sporophyte**.

1. **Gametophyte generation.** The conspicuous structure of this phase is the **sexual** or the **gametophyte** plant (Fig. 8·12, 1). It is produced by the germination of a haploid spore (meiospore). The spore, on falling on a suitable substratum, undergoes segmentation to produce a multicellular, disc-like **protonema**. On the edge of the protonema is established **an apical cell**. The latter by active segmentation produces the sexual or gametophyte plant (Fig. 8·12, 12). It loves to grow on rocks over which water trickles and the bark of trees. It is the most conspicuous and independent plant in the life cycle. It is chiefly concerned with sexual reproduction. The sexual plant grows dorsiventrally upon the substratum and consists of a central axis (the so-called stem) bearing leaf-like expansions (Fig. 8·12, 1). The long, slender stem is branched in a bi- or tri-pinnate manner. The so-called leaves that it bears are of two kinds, **dorsal** and **ventral**. The dorsal leaves are large and nearly oval. They are closely set in two lateral rows on the stem which they completely cover from above. They overlap each other **incubously**. Each dorsal leaf is divided into two lobes. The ventral smaller lobe is closely appressed to the lower surface of the larger lobe. It runs more or less parallel to the stem.

The ventral leaves are small, simple and reduced. They are arranged in a single row on the lower side of the stem. Both kinds of leaves of *Porella* consist of a single layer of cells. There is no **midrib**. The external elaborate appearance of the gametophyte plant is not correlated with histological differentiation. There is slight or no differentiation of tissues.

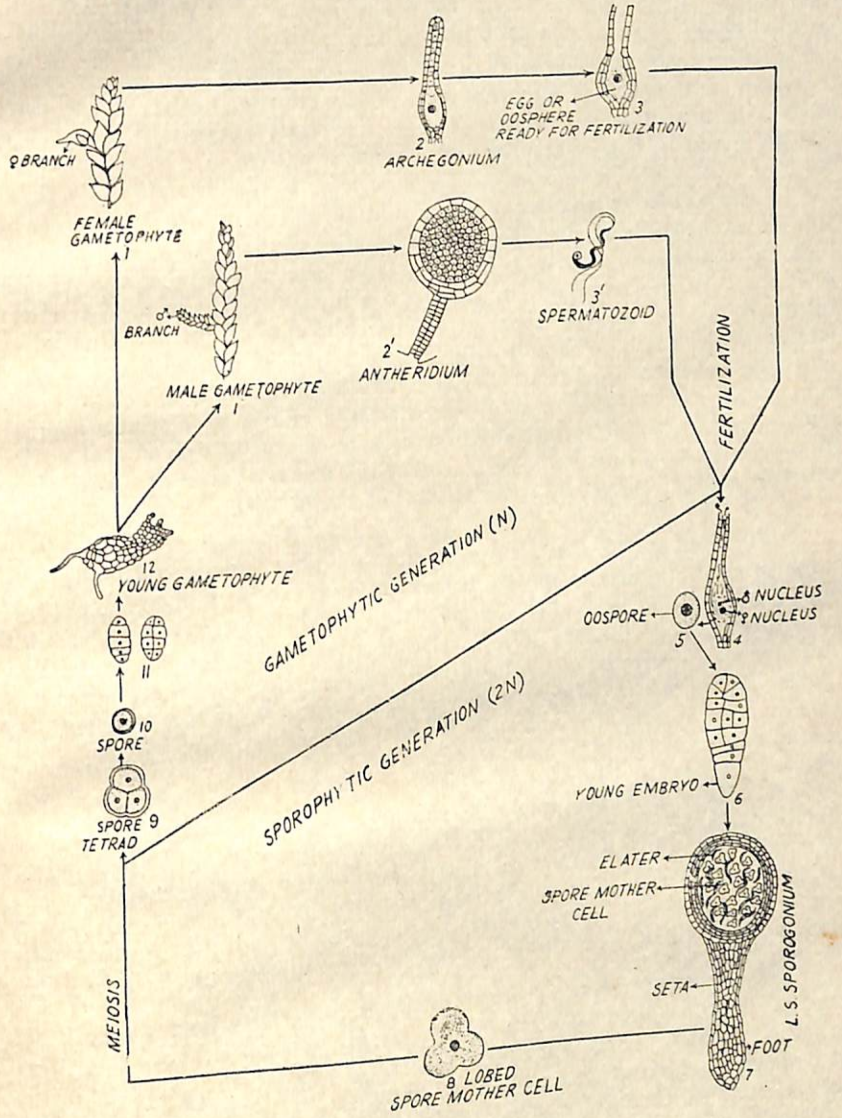


Fig. 8·12. Porella or Madotheca.
Diagrammatic representation of the life cycle.

The sexual plants are **dioecious**. The male plants are markedly smaller than the females. The male plant bears **antheridia** singly in the axils of leaves on special side branches which spring nearly at right angles from the main stem. The long, stalked antheridium has a globular **body** (Fig. 8·12, 2). The wall of the antheridium is single layered in the upper part but 2 to 3 cell layers thick in its basal part. On the access of water the thinner apical part of the antheridium ruptures. The biflagellate sperms (Fig. 8·12, 3) are liberated in the water that causes the rupture.

The **archegonia** occur in a cluster at the apex of a very small side branch arising from the female plant. The archegonial branch bears only 2 or 3 leaves. The apical cell of the female branch is also involved in the formation of the terminal archegonium in the cluster. The growth of the female branch thereafter is arrested. Each archegonium is more or less a cylindrical object with the **venter** as broad as the **neck** (Fig. 8·12, 2). The neck consists of five vertical rows of **neck cells**. They enclose the narrow neck canal. The latter contains usually a row of 8 **neck canal cells**. The venter contains an **egg** and the **ventral canal cell**. The **venter wall** is two cell layers thick before fertilization.

The sexual plant along with the structures produced on it constitutes the **gametophyte generation** in the life cycle. It starts with meiosis and ends with fertilisation. Meiospores are the first structures of this phase. The last structures are the gametes (eggs and sperms). The gametophyte generation therefore comprises the *spores*, *protonema*, *leafy plant*, *antheridia*, *archegonia*, *sperms* and *eggs*. They all are characterised by a haploid number of chromosomes.

2. **Sporophyte phase**. It starts with the **diploid zygote** which is formed as a result of fertilisation (Fig. 8·12, 5). The zygote, by active segmentation, gives rise to a mass of undifferentiated cells called the **embryo** (Fig. 8·12, 6). The latter by further segmentation, differentiation and growth develops into a radially constructed **sporophyte plant**. It is also called the **sporogonium** (Fig. 8·12, 7).

The sporogonium is differentiated into a short **seta** terminating in a globular **capsule**. The basal portion of seta forms an indistinct **foot**. The sporogonium is incapable of self-nutrition. It lives parasitically upon the parent gametophyte. In fact it is specialised to receive nutrition from the parent gametophyte to which it remains organically connected throughout its life. The capsule region of the sporogonium is devoted to the production and the dispersal of meiospores. It consists of a wall two to four cell layers thick. Within the capsule wall is the solid sporogenous tissue. The latter gets differentiated into spore mother cells and elater cells.

The sporogonium and the structures produced by it constitute the **sporophyte generation**. All these structures have a **diploid** number of chromosomes. The sporophytic generation starts with fertilisation and ends with meiosis. So the first structure of this phase is the **zygote** and the last **spore mother cells**. The sporophytic generation therefore consists of the *zygote*, the *embryo*, the *sporogonium*, the *spore mother* and *elater cells*. The spore mother cells (Fig. 8·12, 8) which are the last structures of this phase become deeply four lobed and each undergoes **meiosis** to produce four haploid spores. With meiosis the sporophyte generation ends.

From the account given above it is clear that the reproductive structures of one phase, on germination, do not produce the same phase. On the other hand they give rise to the alternate plant in the life cycle. This results in the regular alternation of the sexually reproducing generation with the asexually reproducing one. This phenomenon is called "**Alternation of Generations**".

JUNGERMANNIALES AND MARCHANTIALES COMPARED

Jungermanniales (*Pellia and Porella*)	**Marchantiales** (*Riccia and Marchantia*)
1. The plant body shows a great diversity in form ranging from a flat, green, dichotomously branched thallus (*Pellia*) apparently resembling that of *Riccia* or *Marchantia* to the elaborate foliose type (*Porella*).	1. The plant body is invariably a simple, flat, green, branched thallus with no external differentiation into leaves and stem.
2. The elaborate leafy habit is not correlated with histological differentiation. There is no distinction into the upper photosynthetic and the lower storage regions. There are neither any air chambers nor air pores.	2. The externally simple thallus shows considerably complex internal structure. There is the upper photosynthetic region and lower storage region. The photosynthetic region has characteristic air chambers and air pores.
3. The thallus is fixed to the substratum by only simple, thin, smooth-walled rhizoids which arise from its lower surface.	3. The thallus is anchored to the substratum by both smooth-walled and tuberculate rhizoids.
4. Both the tuberculate rhizoids and scales are absent.	4. Both tuberculate rhizoids and scales are generally present.
5. The branching in the Anacrogynous Jungermanniales is dichotomous but monopodial in the Acrogynous forms.	5. Branching is always dichotomous.
6. The sex organs are never borne on stalked receptacles.	6. The sex organs in *Marchantia* and many other genera are borne on stalked receptacles.

Jungermanniales	Marchantiales
7. The antheridia in the thalloid forms develop on the upper surface in the midrib region. They may be superficial or each immersed in a pit and are sessile or shortly stalked. In the foliose forms they are axillary in position and occur singly or in groups. They may be small or long stalked.	7. The antheridia in *Riccia* occur sunk in the tissue on the upper surface of the thallus whereas in *Marchantia* they are developed in rows, each in a flask-shaped pit on the upper surface of the male receptacle which is elevated on a long stalk.
8. The primary antheridial cell divides by a vertical wall. The succeeding ones are also nearly vertical.	8. The primary antheridial cell divides by horizontal divisions varying in number in different species before the vertical walls appear.
9. The sperms are biflagellate, elongated, spirally coiled structures. They have more coils and are larger than those of the Marchantiales.	9. The sperms are biflagellate, narrowly curved structures.
10. The archegonia are developed in a cluster on the dorsal surface of the thallus in *Pellia* and terminally on a special side branch in *Porella*.	10. The archegonia in *Riccia* are sunk in the tissue on the dorsal surface of the thallus whereas in *Marchantia* they are arranged in rows on the under surface of the lobed receptacle which is elevated on a long stalk.
11. The cylindrical archegonium is a stalked structure. It has a neck consisting of five vertical rows of neck cells and a venter wall two or more cell layers in thickness.	11. The flask-shaped archegonium has a neck consisting of six vertical rows of neck cells and the venter wall one cell layer in thickness.
12. The first wall in the zygote is horizontal. It separates the lower hypobasal region from the upper epibasal half. The sporogonium is entirely developed from the epibasal half of the embryo. The hypobasal region takes no further part in the development of the sporogonium.	12. The first wall in the zygote is transverse. Soon it is followed by vertical walls in both the halves. The quadrants are then bisected by the octant walls. The quadrant and the octant stages in the embryo are absent in the Jungermanniales. The sporogonium is formed from the entire embryo in the Marchantiales.
13. The sporogonium is an elaborate structure. The elaboration is internal. It consists of a foot, a well developed seta and a globular capsule. The latter consists of a capsule wall 2-4 cell layers thick. There are four vertical strips of thin-walled cells on it. These are called the **lines of dehiscence.**	13. The sporogonium is simple in the lower forms in which it lacks both the foot and the seta whereas in the higher Marchantiales it is differentiated into a foot, a seta and a capsule. The capsule wall is one cell layer thick. There are no **lines of dehiscence.**
14. Within the capsule wall is a mass of spores and perfect elaters.	14. The elaters are not always present.
15. The spore mother cells become deeply four lobed before meiosis.	15. The spore mother cells do not become lobed.
16. Sterilisation of the potentially fertile tissue in the Jungermanniales has advanced. Besides the elaters there is a basal elaterophore in *Pellia* and apical in many others though absent in *Porella.*	16. A structure like elaterophore is entirely absent.
17. The capsule dehisces in a regular and a definite manner along the lines of dehiscence into four valves.	17. The dehiscence of the capsule is variable. It opens by several irregular teeth or by the separation of a lid.

REVISION QUESTIONS

1. List the characteristic features of the family Porellaceae (Madothecaceae).
2. Describe the vegetative phase of any foliose Jungermanniales.
3. Give a brief account of the structure and development of the sex organs of *Porella* (*Madotheca*).
4. Describe in detail the sporophyte phase of *Porella.*
5. Enumerate the salient features you come across in the life cycle of *Porella* (*Madotheca*).
6. With the help of a sketch give the life cycle of *Porella.*
7. Compare the Jungermanniales and the Marchantiales.
8. Compare the structure and development of the sporogonium of *Marchantia* and *Pellia* or *Porella.* Which of the two is advanced and why ?
9. Taking examples from the types studied, form an idea of the arrangement and distribution of sex organs in the Marchantiales and the Jungermanniales.
10. List the points of resemblance between *Porella* and *Pellia.*

CHAPTER IX

ANTHOCEROTOPSIDA (ANTHOCEROTAE)— ANTHOCEROTALES

General Characteristics. The class Anthocerotopsida (Anthocerotae) embraces a small group of plants which prefer to grow in moist, shady places. They are mostly found in the tropical and warm temperate regions. They all have a lobed, thallose gametophyte, simple in form and without regular dichotomous growth. It is either with or without a midrib. The dorsiventral thallus shows very little internal differentiation of vegetative tissues apart from internal cavities which contain mucilage and open by slit-like openings on the lower surface of the thallus. Occasionally the cavities contain a blue green alga *Nostoc*. There are neither any air chambers nor air pores. Most of the species have a single chloroplast in each cell. It contains a central pyrenoid—a feature unknown in other bryophytes and higher plants but common in algae. The thallus is fixed to the substratum by simple, unicellular, smooth-walled rhizhoids. The tuberculate rhizoids and the ventral scales are absent. The sex organs are sunken in the thallus. The archegonium is developed from the superficial and antheridium from the hypodermal cell on the upper surface of the thallus. The antheridia are thus endogenous in origin and lie in roofed pits. The sporophyte is comparatively a long-lived object and is unique for its continued growth throughout the growing season from a basal meristem. It is differentiated into foot and capsule with a constriction-like meristematic region in between. There is no seta. The archesporium is amphithecial in origin. It is a dome-shaped cylinder parallel with the elongated axis of the sporogonium arching over the central columella at the top. The capsule dehisces basipetally from the top downwards by two valves which being hygroscopic curl back exposing the central column of spores and pseudoelaters. The class includes a single order **Anthocerotales**.

ANTHOCEROTALES

It has the same characteristics as the class. Formerly five genera namely *Anthoceros*, *Notothylas*, *Megaceros*, *Aspiromitus* and *Dendroceros* with more than 300 species were included in the order Anthocerotales. Campbell in 1940 questioned the status of *Aspiromitus* as a genus based as it is on a single character, presence of long, simple, thick-walled elaters in *Aspiromitus* and their absence in *Anthoceros*. His contention has been supported by Proskauer (1948), and Mehra and Handoo (1953). The order thus is represented at present by four universally accepted genera. These are *Anthoceros*, *Notothylas*, *Megaceros* and *Dendroceros*. Of these *Anthoceros* alone comprises more than 200 species. Lately Proskauer (1951) has suggested to split the Anthoceros complex into two genera, *Phaeoceros* and *Anthoceros*. The former includes species which are characterised by :—

(*i*) Absence of large intercellular cavities in the gametophyte.

(*ii*) Antheridial jacket consisting of numerous small cells not regularly arranged in four tiers.

(*iii*) Spores yellow and translucent.

In *Anthoceros* are included species in which large intercellular cavities are present in the gametophyte. The antheridial jacket consists of elongated and rectangular cells regularly arranged in four vertical tiers. The spores are dark brown or black in colour.

Proskauer's suggestion has not received enthusiastic support from other bryologists. *Anthoceros* and *Notothylas* are cosmopolitan in their distribution. They are ground dwellers and are found in the tropics, subtropics, and moist temperate regions. *Dendroceros* and *Megaceros* chiefly inhabit the tropics and subtropics. They grow usually as epiphytes on the bark of trees, damp litter and other suitable substrates. The order contains a single family **Anthocerotaceae**. Modern bryologists (Muller, 1940, Proskauer and Reimers 1954) recognise two, **Anthocerotaceae** and **Notothylaceae**. The latter includes a single genus *Notothylas*.

1 ANTHOCEROTACEAE

General Characteristics. The sporogonium is generally a long, upright, uniformly cylindrical object arising from the dorsal surface of the thallus. At the base it is surrounded by a tubular sheath called the **involucre**. It is differentiated into a bulbous *foot*, a median *meristematic zone* above the foot and a long *capsule*. The ripe capsule dehisces from the apex downwards. The capsule wall is several cell layers thick. Typical stomata are found in the epidermis and the subepidermal cells of the capsule wall contain chloroplasts. The central, solid core of columella is endothecial in origin. It is over-arched by the archesporium. The latter differentiates into the spores and the simple or branched **pseudo-elaters**. The family includes four genera *Anthoceros*, *Phæoceros*, *Megaceros*, and *Dendroceros*. Of these *Anthoceros* is the best known. It is taken as a type. *Notothylas* is placed in the family Notothylaceae.

ANTHOCEROS L

Habitat and Distribution. *Anthoceros* is a cosmopolitan genus with about 200 species. They occur both in the tropical and temperate regions of the world. In India alone 25 species have been reported The three common Indian species which occur in the Himalayas are *Anthoceros himalayensis* (Fig. 9·1), *A. erectus* (Fig. 9·2) and *A. chambensis*. They usually occur at an altitude ranging from 5,000 to 8,000 ft. They have been reported by Kashyap from Mussourie, Kulu, Manali, outer Himalayas, and Kumaon, Chamba Valley, Punjab, S. India, Madras, and Travancore. Mehra and Handoo collected the first two species from Simla, Nainital and Dalhousie also. All the species grow on moist, clay soil or wet rocks in very moist, shady places, usually in dense patches. Sides of moist slopes along the hill side roads, ditches, along claybanks of streams and moist hollows among rocks are the usual habitats where they are commonly found. *A. himalayensis* is perennial but *A. erectus* is annual.

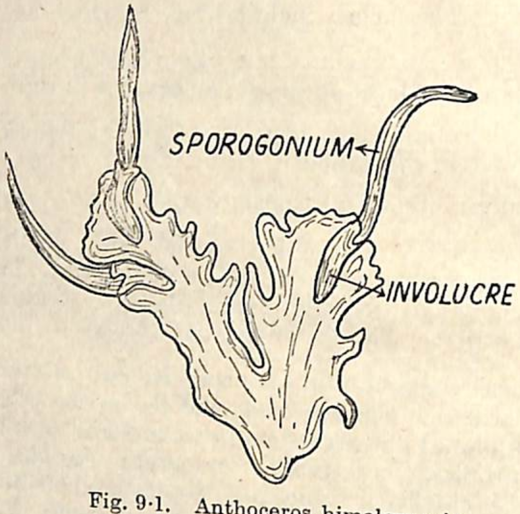


Fig. 9·1. Anthoceros himalayensis.

External Features. The plant, as in the other bryophytes, is the gametophyte. It is a small, yellowish green or dark green without any gloss, dorsiventral, lobed thallus. The lobes with divided margins overlap. The thallus in some species is suborbicular in outline and variously lobed. The lobes are thick and fleshy generally more or less divided to form an irregularly lobed and folded margin. There is no distinct midrib. The upper surface of the thallus is smooth in some species and rough in others due to the presence of ridges. The ventral surface lacks scales, tuberculate rhizoids and mucilage hairs. However it bears numerous, unicellular, smooth-walled rhizoids. These anchor the prostrate thallus to the substratum. In addition small, rounded, bluish green thickened areas can be spotted on the ventral surface of the thallus. These thickened spots are called the **nostoc colonies** as each is inhabited by a blue-green alga *Nostoc*.

Anthoceros erectus has generally a different habit. The thick, fleshy thallus of this species is often raised on a thick, upright or

ascending, stalk-like structure (Fig. 9·2 A and B). The latter expands above into a cup-like structure. Sometimes the thallus is prostrate and fan-shaped. It is deeply lobed with a toothed margin.

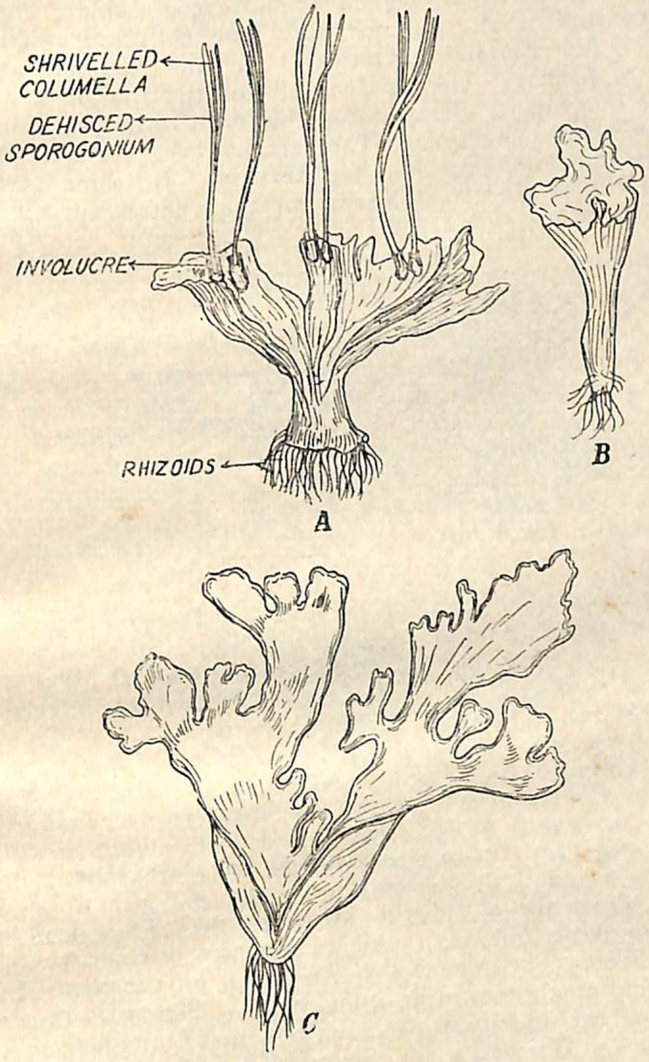


Fig. 9·2 (A—C). Anthoceros erectus
A. A fertile plant bearing sporogonia.
B and C. Sterile plants.

In the months of September and October the *Anthoceros* thallus fruits. It usually bears long, cylindrical, delicate objects. These are the **sporogonia**. They arise in clusters from the dorsal surface of the thallus. Each sporogonium has a tubular sheath around it at its base. It is the **involucre** (Fig. 9·1).

Internal Structure of Thallus (Fig. 9·3). Internally the thallus is several layers of cells thick but without a midrib. There is, however, little differentiation of vegetative tissues. Thus the assimilatory and storage regions are not recognisable. The entire thallus consists of soft parenchyma. The cells are uniform and compact. Air containing **channels** or air chambers and **air pores** are lacking. The surface cells of the thallus show more regular arrangement. They are smaller, each with a comparatively large, lens-shaped chloroplast. They are, however, not cuticularized. There is thus no organised **epidermis**. In some species of *Anthoceros* there are stoma-like slits on the ventral surface of the thallus. These are called the **slime pores.** They lead inwards, often into large rounded intercellular spaces or cavities which contain mucilage. The mucilage cavities open on the ventral surface of the thallus through the slime pores. The latter thus serve as outlets for the mucilage. Very often these mucilage cavities are inhabited by *Nostoc*—a blue green alga. The cavities containing *Nostoc colonies* appear as small, dark, blue green specks. The association of this alga may benefit the gametophyte of *Anthoceros*. However, Pierce (1906) was able to raise healthy plants without the alga. In some species such as (*A. himalayensis*) the mucilage cavities are absent. So Proskauer places it in the genus *Phaeoceros* as *P. himalayensis*. The mucilage is stored in specially enlarged cells in the older portions of the thallus. They are called the **mucilage cells**.

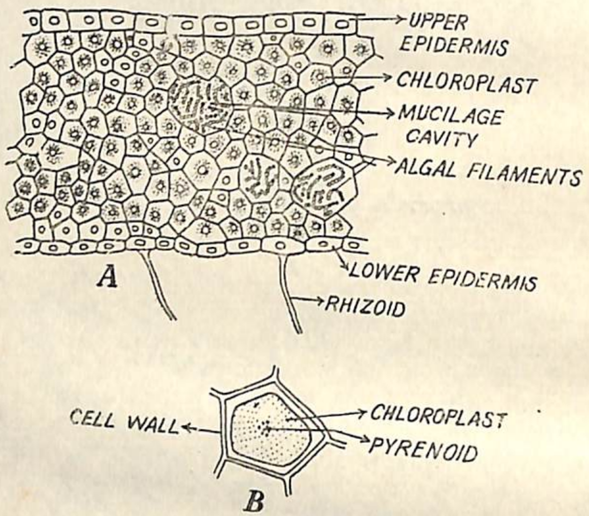


Fig. 9·3 (A—B). Anthoceros sp.
A. V.S. Thallus.
B. A single cell containing a chloroplast.

Every thallus cell usually contains one large **chloroplast**. It is usually oval or flattened and has a large **pyrenoid** in the centre. The presence of a pyrenoid is an unusual feature because pyrenoids are characteristic of algal cells only. They are unknown elsewhere in the plant kingdom. The only exceptions are *Anthoceros thallus*, *Isoetes* and *Selaginella*. The pyrenoids of *Anthoceros* are, however, different from those of Algae. According to McAllister each pyrenoid consists of a mass of 25 to 300 discoid to fusiform bodies. Each of the latter may become a rudimentary starch grain without any change in form and position. Some species of *Anthoceros* have more than one chloroplast particularly in the deeper cells of the thallus. Their number varies from two (*A. pearsoni*) to four (*A. hallii*). Each of these encloses a pyrenoid. The single nucleus of the cell lies in the cytoplasm in close apposition to the chloroplast.

The thallus of *Anthoceros* in its simple external form and little differentiation of vegetative tissues recalls that of *Pellia* as it does in the complete absence of ventral scales and tuberculate rhizoids. There is no well organised epidermis and neither any air chambers nor air pores in both. The two, however, differ in the absence of regular dichotomous growth and mid-rib, presence of internal cavities containing mucilage or occasionally a blue green alga *Nostoc* and a single chloroplast with a pyrenoid in each cell in the thallus of *Anthoceros*.

Apical Growth. According to Campbell, Bower and Smith apical growth in *Anthoceros* takes place by means of a single **apical cell**. It is pyramidal in shape and has four cutting faces. It is located in the deeply emarginate growing point of each thallus lobe. The segments cut off right and left add to the width of the thallus. The others which are cut off parallel to the upper and lower surfaces increase its thickness. Mehra and Handoo, however, support Leitgeb who found several cells of equal rank constituting the growing point. They report that in *A. erectus* and *A. himalayensis* the growing point consists of a group of **initials**. They lie protected in a shallow depression filled with mucilage at the anterior end of each thallus lobe.

REPRODUCTION

Anthoceros reproduces vegetatively and by meiospores formed following sexual reproduction. The **thallus**, however, is concerned with vegetative reproduction and the sexual process. Meiospore formation is the concern of the **sporogonium** or **sporophyte**,

1. **Vegetative Reproduction**. Vegetatively the thallus of *Anthoceros* is propagated by the following methods :–

(*i*) *Fragmentation*. The cells in the basal older portions of the thallus die and disorganise. When the progressive decay and death of cells reaches the branching region the thallus lobes become separated. Each separated lobe by continuous apical growth grows into a new thallus. However propagation by this method is not so common in *Anthoceros*.

(*i*) *Gemmae*. Some writers report the formation of gemmae on short stalks on the upper surface and along the margin of the thallus in *A. glandulosus*, *A. formosae* and *A. propaguliferus*. The detached gemma grows into a new thallus.

(*iii*) *Tubers*. Certain species of *Anthoceros* exposed to drought regularly develop rounded, marginal thickenings called the **tubers**. The cells of 2 or 3 surface layers of the tuber develop corky walls. The corky surface layers protect the inner cells that store starch, oil globules and protein. With the approach of dry season the thallus dies leaving behind the tubers. In this state *Anthoceros* tides over the adverse conditions. With the onset of conditions favourable for growth each tuber develops into a new thallus. According to Mehra and Handoo (1953) the growth is apical and by a row of apical cells as in the thallus. The tubers thus primarily function as organs of **perennation** and secondarily serve as means of vegetative propagation. The sterile thalli of *A. himalayensis* (Fig. 9·4) usually bear stalked tubers. They are developed at the apex, along the margin and on the ventral surface of the thallus. The stalks are long and cylindrical. Rhizoids develop both on the tubers and stalks. Occasionally the fertile plants of this species also bear tubers. They are, however, sessile and borne ventrally or along the margin of the thallus. Tuber formation has also been reported in other species such as *A. tuberosus*, *A. pearsoni* and *A. hallii*. They are developed on the margin of the thallus.

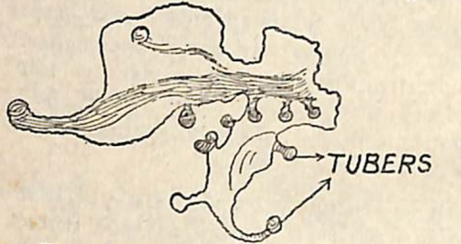


Fig. 9·4. Anthoceros himalayensis. A. Sterile plant bearing tubers.

(*iv*) *Persistent Growing Apices*. Campbell reports that the two perennial Californian species, *A. pearsoni* and *A. fusiformis* grow in regions with dry summer. With the approach of summer these plants dry up. Only the growing points of the thallus lobes with a little of adjacent tissue survive. The apices persist through the long summer drought and resume growth with the return of conditions favourable for growth. Probably the growing apices become modified in some way to resist drought or the lot of mucilage in the thallus cells prevents the loss of water.

(*v*) **Apospory**. Schwarzenbach (1926) and Lang (1901) reported that *Anthoceros* thallus may arise from the unspecialised cells of the various parts of the sporogonium particularly the intercalary meristematic zone, sub-epidermal and sporogenous regions of the capsule. In this way the life cycle is shortened by cutting the spore stage. The thallus (gametophyte) is produced directly from the vegetative cells of the sporogonium. This phenomenon

is called **apospory**. Genetically the aposporously produced thalli are **diploid**. They are however normal in appearance.

2. **Sexual Reproduction**. Many species of *Anthoceros* are **monoecious**, others **dioecious**. Examples of the former category are *A. gollani*, *A. longii*, *A. fusiformis* and *A. punctatus*. The common dioecious species are *A. erectus*, *A. chambensis*, *A hallii* *A. pearsoni* and *A. leavis*. According to Kashyap *A. himalayensis* is dioecious. Mehra and Handoo report that *A. himalayensis* is monoecious but markedly **protandrous**. The antheridia appear a good deal earlier than the archegonia. The sex organs develop within the surface tissues and not above them and thus are immersed in the thallus tissue on the upper surface. They are not borne on special sexual branches. However Kashyap reported the male plants in *A. himalayensis* to be smaller than the female. According to Bell and Woodcock (1968) the formation of sex organs in *Anthoceros* depends upon photoperiod. The formation of gametes is initiated by diminishing day length. Fertilisation thus occurs in winter.

(*a*) **Antheridia**.

(*i*) *Position and Structure* (Fig. 9·5 J & K). The antheridia of *Anthoceros* are unique in being normally **endogenous**. They occur singly or in groups on the upper surface of the thallus within closed cavities called the **antheridial chambers**. Each antheridial cavity has a two-layered **roof** The ripe antheridia are bright orange in colour.

Each antheridium has an ovoid or pouch-like **body**. It is raised on a multicellular, short or long, slender **stalk**. The latter usually consists of four vertical rows of cells. In *A. laevis* it is thicker. The body of the antheridium, as in the liverworts, consists of a **jacket layer** or an **antheridial wall** enclosing a mass of **androcytes**. Each androcyte forms a single sperm. The cells of the jacket layer, in the dark spored species (*A. erectus*), are elongated and rectangular. They are regularly arranged in four superimposed tiers. In others (yellow spored species) the wall consists of a larger number of irregularly arranged small cells (*A. himalayensis*). The wall cells contain plastids, one each. The plastids change colour. When the antheridia are young the plastids are colourless. Later on they become green. In the mature antheridium the green plastids become bright orange or red (chromoplasts).

(*ii*) *Dehiscence* (Fig. 9·5 L). When the antheridia reach maturity the roof of the antheridial chamber bursts open irregularly. The antheridia now lie in cup-shaped depressions or antheridial 'craters' with their orange coloured contents obvious. On the access of water either the cells of the upper tier of the jacket layer separate (*A. punctatus*) or there is irregular separation of the cells of the wall (*A. laevis*). An aperture is thus formed at the distal end of the antheridium. The androcytes *enmass* get out of the aperture. Finally the sperms are discharged in the water that causes the rupture by dissolution of the walls of the androcytes.

The liberated sperm (Fig. 9·5M) is a tiny, biflagellate structure. The two flagella are equal and almost of the same length as the body. They are inserted at the slightly broader, anterior end of the slender body which is slightly curved. The unused portion of the cytoplasm of the androcyte remains attached for some time to the swollen posterior portion.

(*iii*) *Development* (Fig. 9·5). The antheridia in *Anthoceros* develop **endogenously**. They lie in roofed chambers sometimes singly, sometimes in groups. In either case the antheridium or the antheridial cluster in the antheridial chamber together with the latter's two layered roof is traceable to a single **surface cell**. This surface cell lies close to the growing apex on the upper surface of the thallus. It has denser cytoplasm and a conspicuous nucleus (Fig. 9·5 A). It divides periclinally into an **inner segment** and an **outer segment** (Fig. 9·5 B). The former functions as an **antheridial initial** and develops into an antheridium or an antheridial cluster. The outer segment is the **roof initial**. It forms two layers of cells over roofing the chamber.

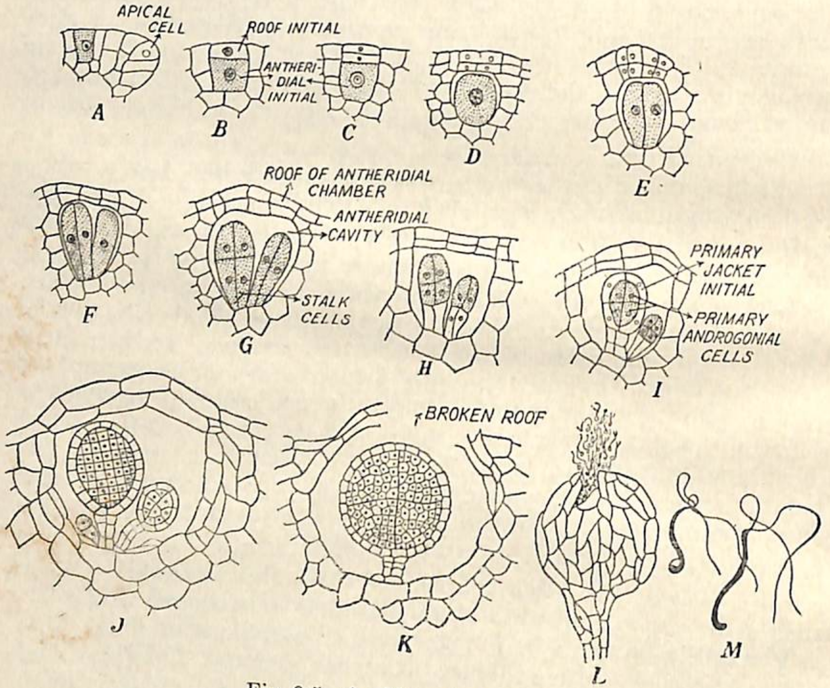


Fig. 9·5 (A—M). Anthoceros sp. Development of antheridium.

A—J. Earlier stages. (Explanation in the text).
K. Mature antheridium with the overlying roof broken off.
L. Antheridium ruptured to liberate the sperms.
M. Liberated sperms.

Soon after, the *antheridial* and the *roof initials* separate from each other. The space formed between them is filled with mucilage (Fig. 9·5 D). The other cells surrounding the antheridial initial gradually shrink away. The mucilage space finally enlarges into a definite cavity called the **antheridial chamber**. The roof initial first divides by a periclinal wall (Fig. 9·5 C). Later the two resultant daughter cells divide and redivide by anticlinal walls to form the two-layered roof of the antheridial chamber (Fig. 9·5 D). The antheridial initial before segmentation nearly rounds off (Fig. 9·5D). It then either directly develops into a single antheridium (*A. pearsoni*) or it may divide vertically into two (Fig. 93 E), four or sometimes into more daughter cells (*A. erectus*). Each of the latter functions as a antheridial initial so that there is a group of two, four or more antheridia in the chamber.

In either event the antheridial initial divides by two vertical divisions at right angles to each other to form four cells (Fig. 9·5 F). Each of these cells again divides by a transverse wall. The young antheridium at this stage consists of eight cells (Fig. 9·5 G). They are arranged in two tiers (upper and lower) of four cells each. The four cells of the lower tier are the **stalk cells**. They divide and redivide transversely to form the stalk composed of four vertical rows of cells. The four cells of the upper tier again divide transversely (Fig. 9·5 H). The octant of cells thus formed gives rise to the body of the antheridium. Each cell of the octant divides by a curved wall (periclinally). In this way eight inner **primary androgonial cells** are separated from the eight outer **primary jacket cells** (Fig. 9·5 I). The latter divide only by anticlinal walls to form the single layered **antheridial wall**. Repeated divisions of the primary androgonial cells result in the formation of a central mass of fertile **androgonial cells**. The cells of the last cell generation of the central fertile mass are called the **androcyte mother cells**. Each androcyte mother cell divides to give rise to two **androcytes**. The protoplast of each androcyte metamorphoses into a biflagellate **sperm**.

In some species of *Anthoceros* (*A. erectus*) secondary antheridia may arise by budding from the stalks of the older ones (Fig. 9·5 J).

(*b*) Archegonia

(*i*) *Position and Structure* (Fig. 9·6 F). The archegonia of *Anthoceros* are remarkable in certain respects. They are sunk deep in the fleshy thallus on its upper surface. They lie close to the growing point in regular rows and are developed in **acropetal order**. In the monoecious species the archegonia appear later, on the same thallus which produced antheridia.

Each archegonium (Fig. 9·6 F) consists only of **an axial row** of usually four to six **neck canal cells**, a **ventral canal cell** and an **egg**. There is no sterile **jacket layer** except the distal rosette of **cover cells** forming its tip. The cover cells slightly project above the general, upper surface of the thallus where it is usually surrounded by a somewhat funnel-shaped mass of mucilage called the **mucilage mound**. The surrounding vegetative cells of the thallus offer protection to the cells of the axial row. The archegonium of *Anthoceros* immersed in the thallus and in direct contact with the surrounding vegetative cells differs from that of all other bryophytes and resembles certain of the pteridophytes.

(ii) *Development* (Fig. 9·6). Each archegonium originates from a dorsal segment of the apical cell just close to it. It is called the **archegonium initial** (Fig. 9·6 A). According to Mehra and Handoo the archegonium initial directly functions as the **primary archegonial cell**. It does not project above the general surface of the thallus nor does it undergo the usual horizontal division. The absence of this division accounts for the sunken nature of the archegonium and its histological continuation with the adjacent cells of

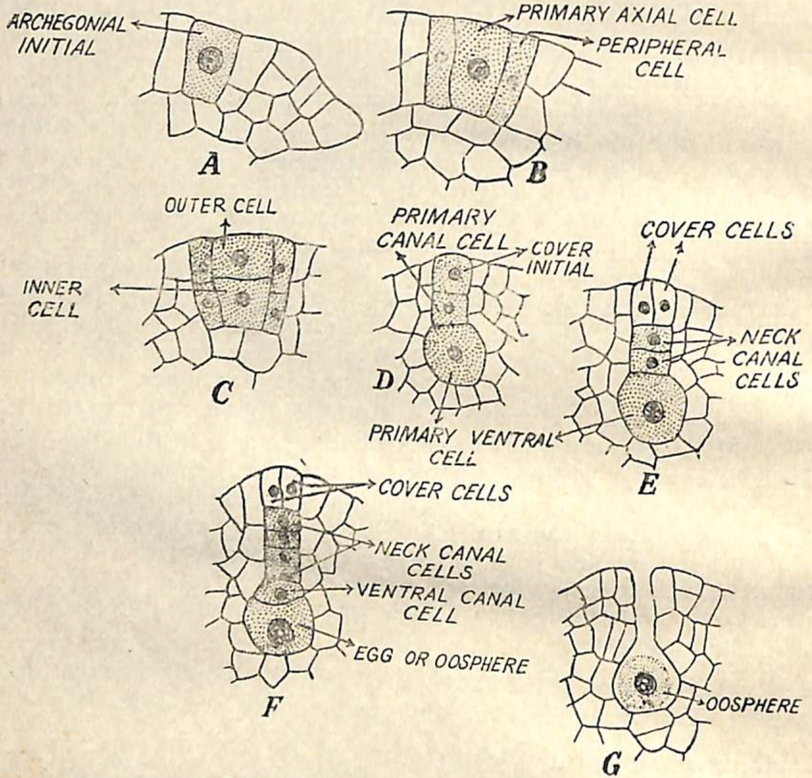


Fig. 9·6 (A–G). Anthoceros sp. Development of Archegonium.
A-E. Earlier stages (Explanation in the text).
F. Mature archegonium.
G. Mature archegonium with egg ready for fertilisation.

the thallus. Some writers such as Campbell, Bower and others, however, hold that the archegonium initial divides by a transverse or periclinal wall to form an outer **primary archegonial cell** and an inner **primary stalk cell**. The consensus of opinion favours the first view.

The primary archegonial cell divides by three vertical intersecting walls. This separates the three **jacket initials** from the central **primary axial cell** which they enclose (Fig. 9·6 B). The archegonium rudiment which now consists of four cells is completely embedded in the tissue of the thallus. The primary axial cell divides transversely into an **outer cell** and an inner **central cell** (Fig. 9·6, C) The latter (central cell) functions directly as a **primary ventral cell**. It enlarges and finally divides to give rise to the **ventral canal cell** and the **oosphere** or **ovum** (Fig. 9·6 F). The outer cell which corresponds to the primary cover cell of the liverworts undergoes a transverse division to separate a terminal **cover initial** from the inner **primary neck canal cell** (Fig. 9·6 D). The cover initial divides by two intersecting walls to form the distal rosette of four **cover** or **lid cells** forming the apex of the archegonium (Fig. 9·6 E). The primary neck canal cell undergoes a series of transverse divisions to form a chain of four to six **neck canal cells** (Fig. 9·6 E and F).

Smith gives a different account. He describes that the primary **axial cell** divides transversely into a **primary cover cell** and a **central cell**. The central cell further divides into a **primary canal cell** and a **primary ventral cell** as is the case in the liverworts.

Meanwhile the three jacket initials have divided transversely into two tiers of 3 cells each. The three cells of the upper tier destined to form the sunken neck divide by vertical walls. The resultant six jacket cells divide repeatedly by transverse divisions to form the six vertical rows of **neck cells**. They form a single layered jacket of sterile cells (neck) around the neck canal cells. However the archegonia of *Anthoceros* being completely sunk in the thallus tissue, the development of the jacket layer of the archegonium is difficult to follow. It is indistinguishable from the adjacent cells of the gametophyte. In any case the egg towards its lower face is protected by the adjacent vegetative cells of the thallus.

(c) *Fertilisation*. With the archegonia immersed in the thallus, fertilisation presents no difficulties. On the access of water the cells of the axial row excepting the ovum gelatinize. The neck canal is now filled with mucilage and the remains of the canal cells. The mucilage absorbs water and swells. Consequently the cover cells are thrown off. An open passage down to the egg is formed. A biflagellate sperm swims down the canal and fuses with the egg to form a **zygote**. The latter swells to fill the venter cavity completely. Thereafter the zygote secretes a cellulose wall around it. A number of zygotes are formed on a single thullus.

SPOROPHYTIC PHASE

The zygote is the pioneer structure of this phase. By repeated segmentation it develops into an elongated **embryo.** The latter by further cell division, cell differentiation and continued growth rapidly grows into an elongated, spindle-shaped object with a bulbous base. It is the **sporogonium** or the **sporophyte** (Fig. 9·7.) The sporophytes usually grow in clusters from the upper surface of the thallus each surrounded at its base by a tubular **involucre**.

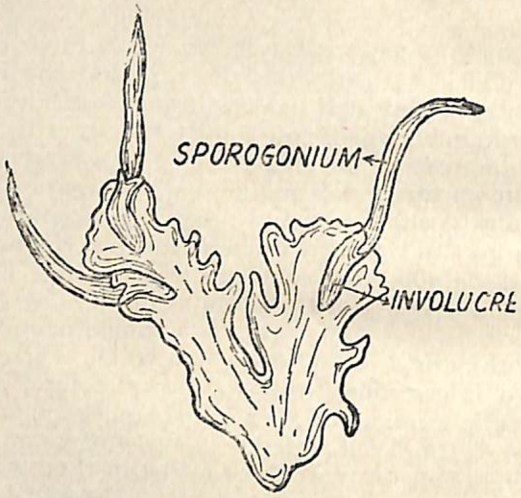


Fig. 9·7. Anthoceros himalayensis.
Thallus bearing sporogonia.

3. **Production of Meiospores.** It is the concern of the diploid individual which is the **sporogonium.** The sporogonium produces the spores and brings about their efficient dispersal. For this reason the sporogonium is also called the **sporophyte**.

(*a*) **Structure of Sporogonium**. It (Fig. 9·9 A) is differentiated into three regions ; (*i*) the **capsule**, (*ii*) the **intercalary** or **intermediate zone** and (*iii*) the **foot**. The **seta** is absent. Its place is taken up by the intercalary zone which is **meristematic**. The sporogonium ranges from one to several centimetres in length. At the base it is surrounded by a tubular sheath, the **involucre**. The latter is an outgrowth from the thallus and thus is a gametophytic structure. It is protective in function and also gives support to the weak intercalary zone.

(*i*) **Capsule** (Fig. 9·9 A). It forms the major and conspicuous part of the sporophyte. In form it is long, slender, smooth, upright and cylindrical. It is nearly of uniform thickness throughout its length except towards the apex where it slightly tapers. Usually it is 2 to 3 cms. or in some species up to 15 cms. long. It is light green at first but turns grey or brown towards maturity. It has relatively a small proportion of fertile tissue.

Internally the capsule shows great elaboration and complexity of structure. In the centre of the capsule is a solid core of sterile tissue. It is the **columella** (Fig. 9·8 A and B). The cells constituting it are narrow, elongated with somewhat uniformly thickened walls. They are arranged in sixteen vertical rows. In a cross-section they form a solid square. In the young capsule, however, the columella consists of four vertical rows of cells only. It is **endothecial** in origin. The columella extends from the base right through the capsule and ends a little behind its distal end. The chief function of columella is to give support to the long, delicate capsule. To some extent it helps in the dispersal of spores. Some writers look upon it as a primitive type of vascular cylinder.

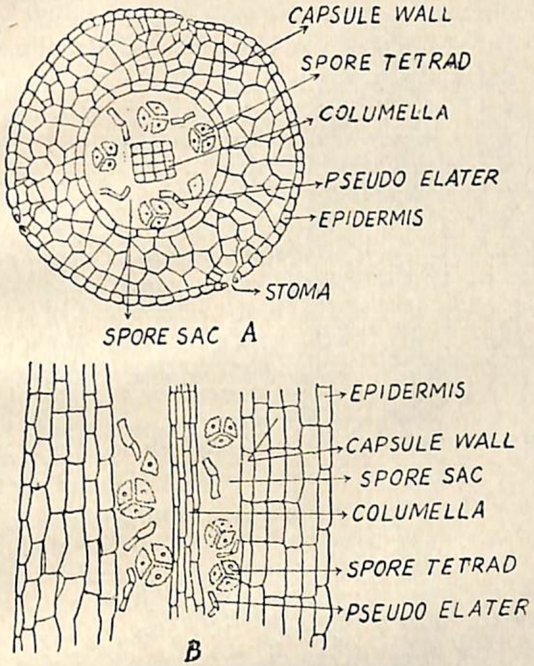


Fig. 9·8. (A—B). Anthoceros sp.
A. Transverse section of capsule.
B. Longitudinal section of capsule,

Around the columella is a double layer of elongate but domed **sporogenous tissue**. Sometimes it is one cell layer thick throughout (Fig. 9·9 A). It is differentiated from the inner layer of the **amphithecium**. It extends over the top of the columella like a dome—a feature in sharp contrast to the liverworts. In this respect *Anthoceros* sporophyte resembles *Sphagnum* moss. The sporogenous tissue originates in the meristematic zone where it is single layered and is called the **archesporium**. Higher up it becomes a two-layered sporogenous tissue (*A. himalayensis*), rarely 3 or 4 cells in thickness. In *A. erectus* the archesporium remains single layered throughout.

The archesporial cells have denser cytoplasm. At successive higher levels **spore mother cells**, **spore tetrads** and **meiospores** are

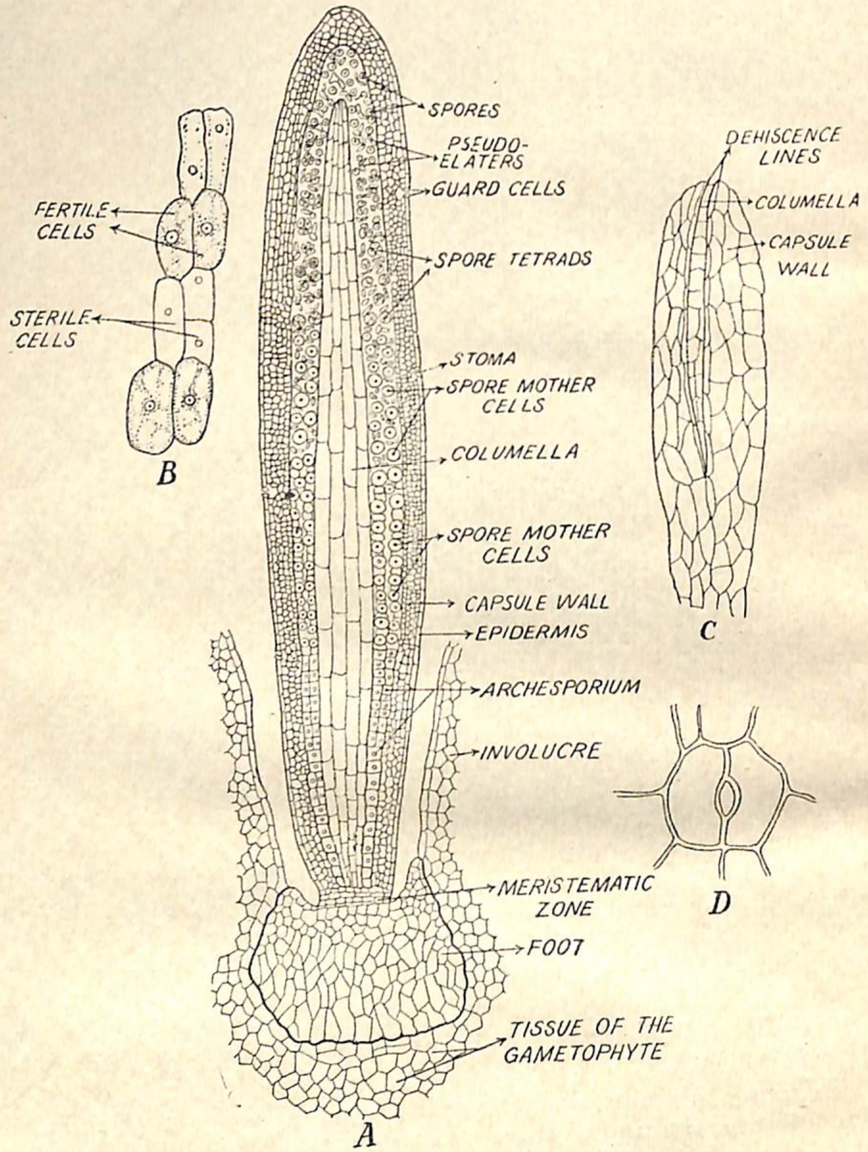


Fig. 9·9 (A—D). Anthoceros sp.
A. L. S. mature but undehisced sporogonium. (Diagrammatic).
B. A portion of the archesporium differentiated into alternate bands of sterile (elater) cells and sporogenous (fertile) cells.
C. A portion of the capsule showing lines of dehiscence.
D. A stoma from the surface of the capsule.

formed. Among the spore tetrads and mature spores are found the **pseudoelaters** (Fig. 9·8 A and B). They form chains of one to four

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elongated, thick-walled, sterile cells of irregular shape. The pseudoelaters are smooth-walled and are nutritive in function. They lack spiral thickenings and are pluricellular, sometimes unicellular. According to Pande the pseudoelaters in *A. physocladus* are long and have thick walls with an extremely reduced lumen.

External to the fertile zone is the **capsule wall**. It is several layers (usually 4 to 6) of cells in thickness. The outermost layer of the wall is the **epidermis**. It consists of narrow, vertically elongated cells with their outer walls cutinized. Here and there the epidermal layer is punctured by **stomata** similar to those of the higher plants. Each stoma consists of a **pore** surrounded by two **guard cells**. The cells of the capsule wall within the epidermis are **chlorenchymatous**. They have intercellular spaces between them. Each cell contains double the number of chloroplasts characteristic of the gametophytic tissue. As a rule there are two large chloroplasts per cell. They are similar to those of the thallus. The capsule wall is thus actively **photosynthetic** in function. The intercellular spaces between the chlorenchymatous cells communicate with the exterior through the stomata to form a typically **ventilated photosynthetic tissue**.

(*ii*) **Intermediate** or **intercalary zone**. It is a narrow zone of **meristematic cells** located at the base of the capsule just above the foot. The meristem constantly adds new cells to the capsule at its base. They become progressively differentiated into columella, archesporium and capsule wall. The presence of a basal intercalary meristem enables the capsule to grow for a long period and form spores.

(*iii*) **Foot**. It is a rounded, bulbous structure deeply embedded in the tissue of the thallus. By means of the foot *Anthoceros* capsule is well anchored upon and attached to the thallus. The region of contact between the foot and the thallus tissue is well marked in many species. It is called the **placenta**. The foot mainly consists of a mass of parenchymatous cells. The surface cells of the foot, however, often grow out into short, tubular, **rhizoid-like** outgrowths. The latter serve to increase the absorptive surface of the foot and penetrate the tissue of the thallus. The foot of *Anthoceros* sporogonium is thus specialised to function as a **haustorium**. It absorbs food and water from the parent thallus for the sporophyte.

(*b*) **Nutrition of Sporophyte**. The wall of *Anthoceros* capsule has a well developed, typically ventilated, photosynthetic tissue. It enables the sporogonium to become at least partially, if not fully, self-sufficient so far as supply of carbohydrates is concerned. It has been observed that a young sporophyte covered with a tin-foil cap still grows and reaches maturity. This is a positive proof of the fact that it still receives a considerable amount of its food supply normally from the gametophyte. For water and minerals in solution it entirely depends upon the parent gametophyte to which it is attached by the foot. The sporogonium of *Anthoceros* thus is a **semi-parasite**.

(*c*) **Development of Sporophyte** (Fig. 9·10). The fertilized egg enlarges until it fills the venter cavity. It then secretes a wall around it. After this the zygote enters upon active segmentation. The first wall is vertical (Fig. 9·10 A). It divides the embryo into two equal daughter cells. The next division is transverse (Fig. 9·10B). The embryo now consists of four cells. Of these the upper two cells are usually larger than the lower ones. Bhardwaj, however, reports that the first division is transverse and the second vertical. In either event each of the resultant four cells divides by a vertical wall at right angles to the first. The embryo now consists of eight cells arranged in two tiers of four cells each (Fig. 9·10 B). This is the **octant stage** of the embryo. The four cells of the upper tier are larger than the lower ones. According to Mehra and Handoo the upper tier (*A. erectus*) forms the capsule and the intermediate zone. The lower tier gives rise to the foot.

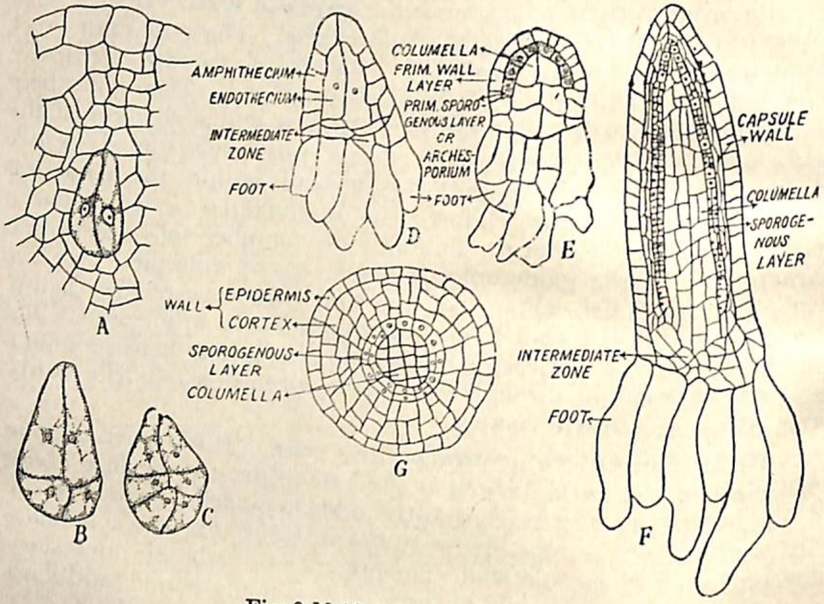

Fig. 9·10 (A—G). Anthoceros sp.
Development of sporogonium.
A—E. Early stages in the development of embryo.
(Explanation in the text).
F. L.S. of an advanced stage.
G. T.S. of the above. (After Campbell)

In the majority of the species, however, the four larger cells of the upper tier undergo another transverse division (Fig. 9·10 C). The embryo now consists of three tiers of four cells each. The cells of the uppermost tier are still larger. The four cells of the lowest tier (formed from the hypobasal half of the zygote) form the foot, whole of it or at any rate a major part of it. The uppermost tier develops into the capsule. The median tier gives rise mainly to the intermediate zone and in part to the foot. The cells of the intermediate zone remain **meristematic**. They establish an intercalary meristem at the base of the capsule. According to Mclean and Cook these early divisions in *A. laevis* result in an embryo composed of four tiers of four cells each. The highest tier forms the capsule and the intermediate zone while the lower three give rise to the foot.

The cells of the foot tier (Fig. 9·10 D and E) divide and redivide in all directions to form a rounded mass of parenchymatous cells. It is broad, massive and shaped like an inverted cap. This structure is called the **foot**. The surface cells of the foot, in some species, grow out into short, tubular rhizoid-like processes. The latter penetrate the tissue of the gemetophyte. They are **haustorial** in function.

The four cells of the uppermost tier which are destined to form the capsule, divide by periclinal walls. This separates a central group of four cells from the surrounding peripheral ones (Fig. 9·10 D). The former constitute the **endothecium** and the latter **amphithecium**. Some bryologists hold that the four top cells undergo one or two transverse divisions before the periclinal walls are laid in them. From the entire endothecium originates the sterile **columella**. The latter in the young capsule is made up of four vertical rows of cells (Fig. 9·10 E). In the older capsule it consists of sixteen vertical rows. The corresponding tissue in the liverworts forms the **archesporium**. The **archesporium** in *Anthoceros* is formed from the inner cells resulting from the periclinal division of the amphithecium cells (Fig. 9·10 D). The outer cells of the series function as **jacket** or **wall initials**. The jacket or wall initials undergo repeated divisions by anticlinal and periclinal walls to form the **capsule wall**. It is four to six layers of cells in thickness (Fig. 9·10 F). The outermost layer of the capsule wall is **epidermis**. It develops **stomata** (Fig. 9·9A and D). The epidermal cells are cutinised. The wall cells within the epidermis are photosynthetic. They, as a rule, have two large chloroplasts per cell, sometimes one, rarely as many as four. There are intercellular spaces between them. The photosynthetic tissue communicates with the exterior through the stomata.

The single-layered **archesporium** is parallel to the elongated axis of the capsule and is dome-shaped. It over-arches the rounded apex of the columella (Fig. 9·10 E and F) and extends nearly to its base. The cells of the archesporium can easily be distinguished from the sterile cells of the columella by their denser protoplasm. In some species the archesporium remains single layered throughout (*A. erectus*) and functions as the primary sporogenous layer. In other species it becomes two-layered (Fig. 9·10 F) above the base of the capsule (*A. himalayensis*). In still others it becomes 2 to 4 cell layers thick by periclinal divisions and forms the sporogenous tissue. The **sporogenous tissue** differentiates into the following two kinds (Fig. 9·9B) of cells :—

(*i*) *Fertile spore mother cells.* These are large cells, oval to spherical in form. Each contains granular, denser cytoplasm, a distinct nucleus and a chloroplast.

(*ii*) *Sterile pseudo-elater mother cells.* These are slender, sterile cells with smaller nuclei. They give rise to pluricellular **pseudo-elaters.**

These two kinds of cells may arise in regularly alternating layers or bands. As the spore mother cells separate from each other,

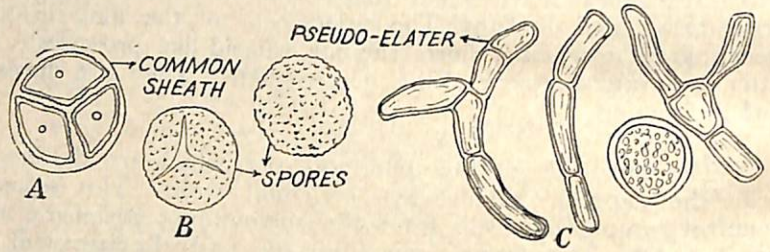

Fig. 9·11 (A—C). Anthoceros.
A. Spore tetrad.
B. Spores.
C. Pseudo-elaters.

the sterile cells become joined into simple or branched chains of 3 or 4 cells (Fig. 9·11C). These are the **pseudo-elaters**. They lack the spiral thickening characteristic of elaters. The pseudo-elaters form a sort of a network. In their interstices lie the spore mother cells. The latter undergo the meiotic division, each resulting in a spore tetrad (Fig. 9·11A).

The apical growth of the capsule ceases with the establish-ment of the archesporium, columella and the wall regions. Further growth is by the activity of the basal intercalary meristem in the median zone. It continually adds new cells at the base of the capsule. They become progressively differentiated into the columella, the archesporium and the capsule wall. Consequently the growth and the dehiscence of the capsule extends over long periods. The sporophyte of *Anthoceros* continues to live as long as the thallus lives. It is a feature in sharp contrast to the short-lived sporophytes of the liverworts.

Early growth of the sporophyte is correlated with the enlarge-ment and growth of the venter of the archegonium called the **calyptra** and equal upward growth of **involucre**. Later the sporophyte grows faster. Consequently the sporophyte ruptures the calyptra and pushes up through the involucre. The latter forms a tubular sheath at the base of the mature sporophyte.

(*d*) **Dehiscence of Capsule** (Fig. 9·9 C). The spores ripen basipetally from the top downwards. As they ripen the mature portion of the capsule turns grey, brown or black depending upon the species. It loses water, shrinks and consequently ruptures longitudinally along the lines of dehiscence. The longitudinal slits extend basipetally downwards. According to Mehra and Handoo there are two such lines of dehiscence on the capsule wall in *A. erectus* and *A. himalayensis*. They lie on the opposite sides each in a shallow depression. Each line of dehiscence consists of two rows of thick-walled epidermal cells with their adjacent walls remaining thin along which the slit occurs. Thus the ripe *Anthoceros* capsule usually dehisces basipetally along two longitudinal slits which extend downwards from near the apex. The portions of the capsule wall between the slits are commonly called the **valves**. The two valves separate progressively downwards and curl back a little bit at a time. The continuous, downwards reflexing of the valves exposes the underlying mass of spores and pseudoelaters of more and more recent origin. With further drying the valves become spirally twisted owing to reversible hygroscopic reaction. This results in the shedding of spores. The spore dispersal is further assisted by drying of the columella and the intermixed pseudo-elater s which in spite of the absence of spiral thickenings on their walls execute some hygroscopic movements. The spores thus loosened in the exposed spore mass on the central column may be scattered by the air currents.

According to Proskauer (1948) the slit first appears at a level where the shrinking capsule wall meets resistance from the under-lying solid mass of spores and pseudo-elaters. It occurs along the thin adjacent walls of the two rows of cells and extends progressively downwards and gradually widens. The underlying spore mass is exposed. The pseudo-elaters in the exposed fertile mass are hygro-scopic. They exhibit twisting movements with the changes in the moisture content of the air. These movements cause active back pressure of the exposed fertile mass on the shrinking capsule wall. This results in more slits appearing along other lines of dehiscence. The *Anthoceros* capsule according to Proskauer dehisces by a varying number of slits. The number varies from 1—4 according to the species.

Spores. The mature spores are usually tetrahedral in shape and thick-walled. The thick spore wall is differentiated into two coats. The outer exospore is thick, opaque and beset with small spines or tubercles. It varies in colour from dark, brown, black or yellow according to the species. It is black and warted in *A. erectus*. In *A. himalayensis* it is yellow and beset with numerous, blunt papillae. The inner endospore is thin. Within the spore wall is the tiny protoplast. It contains a single nucleus, a colourless plastid and reserve food materials.

Germination of Spore (Fig. 9·12). According to Campbell (1928) the liberated spore in *A. fusiformis* usually enters upon a resting period. Mehra and Kachroo (1962) who studied germination in *A. erectus* and *A. punctatus* report that obligatory resting period is not necessary before germination. At the time of germination the spore absorbs water and swells. The exospore ruptures along the triradiate ridge. The endospore protrudes through the cleft in the form of a tube of varying lengths. It is called the **germinal tube** (Fig. 9·12 A). The contents of the endospore migrate

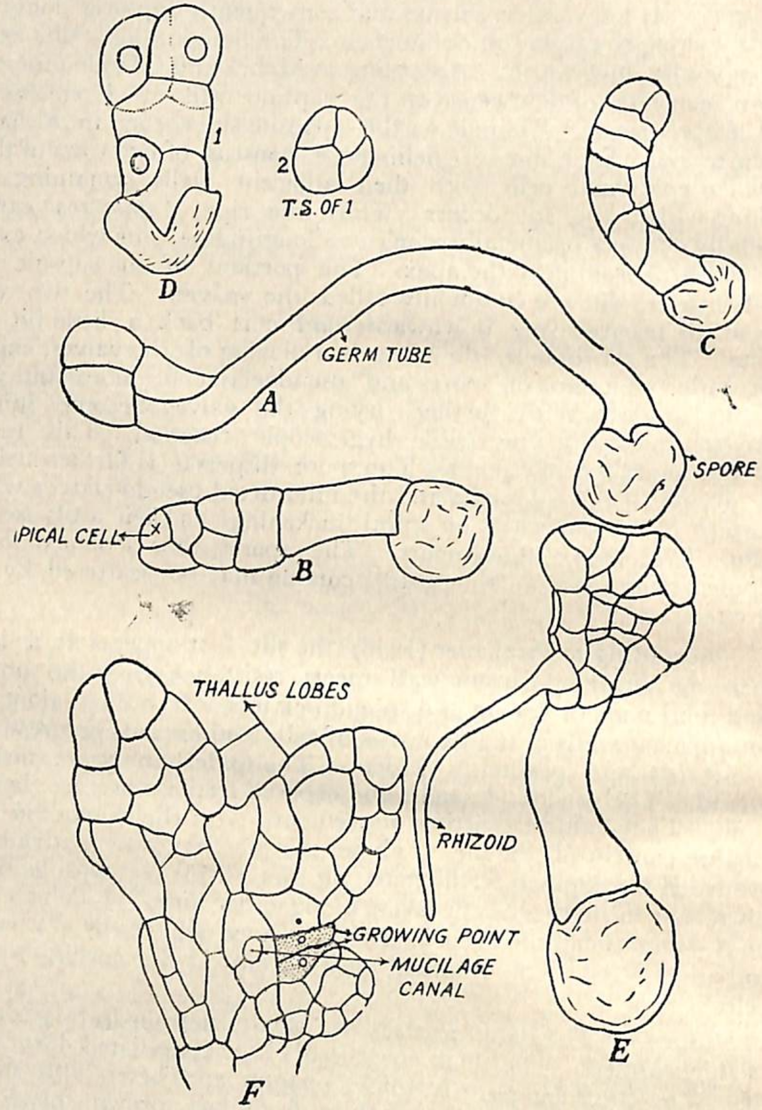

Fig. 9·12 (A—F). Anthoceros fusiformis. Germination of spores, (After Campbell).

into the tube where the single plastid present turns green. Two successive transverse walls are laid at the distal end of the germinal tube. These separate two cells at its apex. The terminal cell divides by a vertical wall. A similar division takes place in the lower cell. A group of four cells is formed. Vertical walls at right angles to the first divide the four celled structure into an octant. The four apical octants constitute the growing region of the sporeling. No apical cell with two cutting faces is established. First rhizoid appears as an elongation of any cell of the young thallus. On its ventral surface appears the first mucilage slit close to the growing point. Development of rhizoids and more mucilage slits then follows and finally *Nostoc* infection as the growth proceeds.

SALIENT FEATURES

(*a*) **Gametophyte**. 1. The gametophyte is a simple thallus usually without a midrib.

2. Except for smooth-walled rhizoids the ventral surface of the thallus bears no appendages. The scales, the mucilage hairs and the tuberculate rhizoids are all absent.

3. Internally the thallus is very simple in structure. It shows no differentiation into photosynthetic and storage tissues. There are no air containing channels nor any air pores. The entire thallus consists of parenchyma composed of chlorenchymatous cells.

4. A striking feature of the gametophyte is the presence of usually a single chloroplast with a pyrenoid, in each cell—an unusual feature not known elsewhere in the bryophytes and higher plants. In the latter the chloroplasts are discoid and occur in large numbers in each cell and have no pyrenoids.

5. Another peculiar feature is the presence of mucilage clefts on the lower surface of the thallus. These lead inwards and open into larger cavities filled with mucilage.

6. Very often the mucilage cavities are inhabited by *Nostoc*. The cavities containing *Nostoc* appear as small, dark, blue-green specks.

7. Apical growth according to Campbell takes place by means of a single, four-sided **apical cell**. It is pyramidal in shape. According to Mehra and Handoo it is initiated by a group of cells of equal rank.

8. The sex organs are not borne on any special sexual branches. The remarkable feature, however, is that they are immersed in the thallus tissue. They actually develop within rather than above the surface of the thallus.

9. The antheridia are **endogenous** in origin. They occur singly or in a cluster on the floor of a roofed antheridial chamber.

10. The antheridium or the antheridial cluster in the closed chamber together with the latter's two layered roof is traceable to a single **surface cell**. It means that the antheridial cluster in the chamber and the overlying two-layered roof are homologous to the single antheridium of liverworts.

11. The archegonia are fully immersed with their venters and necks confluent with the adjacent vegetative cells. The distal rosette of cover cells only slightly projects above the general surface of the thallus. Each young archegonium according to Proskauer, and Mehra and Handoo is surrounded by a mound of mucilage.

12. The usual **archegonial jacket** of sterile cells enclosing the axial row of cells is not recognizable. Protection to them is probably afforded by the adjacent cells of the thallus.

13. Unlike the liverworts the **archegonial initial** directly functions as the primary archegonial cell. There is no division of the former into the primary stalk cell and the primary archegonial cell by a horizontal wall. The absence of this division explains the sunken condition of the archegonium and its lateral contact with the adjacent cells of the thallus.

14. The **neck canal cells** in *Anthoceros* are derived from that segment of the primary axial cell which corresponds to the **primary cover cell** of the liverworts and not from the central cell.

(*b*) **Sporophyte**. 15. The sporophyte of *Anthoceros* is a long, upright, slender, cylindrical object surrounded at its base by a tubular sheath, the **involucre**.

16. It is differentiated into a bulbous **foot**, an **intermediate zone** composed of intercalary meristem and an unusually long, upright, cylindrical **capsule**. **There is no seta**.

17. The foot becomes specialised to function as a **haustorium**. It is furnished with rhizoid-like processes which penetrate deep down into the thallus tissue to absorb water and mineral salts in solution.

18. As soon as the apical growth of the capsule ceases the intercalary meristem of the median zone becomes active. It adds new cells at the base. These cells progressively become differentiated into the tissues of the columella, archesporium and the capsule wall. Thus the *Anthoceros* sporophyte continues to grow for a long period from a basal intercalary meristem and yields spores over a considerable period. In both these features *Anthoceros* stands alone in the bryophytes.

19. The **capsule wall** is several cell layers thick. The surface layer of the wall (epidermis) is punctured with true stomata and the component epidermal cells are cuticularised. Within the epidermis is the assimilatory tissue with intercellular spaces between the cells. The stomata lead into the air containing channels ventilating the sub-epidermal, assimilatory tissue. The sporophyte of *Anthoceros* thus carries on photosynthesis actively.

20. The archesporium which is devoted to spore formation forms only a small part of the sporophyte. The sterilisation of potentially fertile tissue in *Anthoceros*, therefore, shows further advance.

21. The archesporium is **amphithecial** in origin. The function of spore formation has thus been transferred from the central to the more superficial tissue. The sporogenous tissue forms the **spores** and the **pseudo-elaters**.

22. The columella, which forms a central solid core of sterile cells, is formed from the entire **endothecium**. The latter in the liverworts gives rise to the archesporium. There is thus transformation of the entire endothecium from the fertile to the sterile condition in *Anthoceros*. The sporogonium of *Anthoceros* thus reaches a high degree of complexity and elaboration. The latter is internal rather than external.

23. The capsule dehisces basipetally usually by two valves which curl back exposing the mass of spores intermixed with pseudo-elaters on the central column.

SUMMARY OF LIFE CYCLE

The life cycle of *Anthoceros* (Fig. 9·13) consists of two regularly alternating generations with fertilisation and meiosis as its two critical points. With either of these the life cycle switches on from one alternating generation to the other. One of these generations is the **haplophase** and the other **diplophase**.

1. **Haplophase (gametophyte generation)**. The haplophase starts with the formation of **spores** (Fig. 9·13, 11). The spores are differentiated from the spore mother cells by **meiosis** (Fig. 9·13, 10). They germinate under suitable conditions each forming a simple, green fleshy **gametophyte** plant (Fig. 9·13, 12). It loves to grow in moist, shady places. It grows, according to Campbell, by means of a four-sided **apical cell** which is pyramidal in shape. Mehra and Handoo's contention is that the growing point is constituted by a **group of initials** of equal rank.

The thallus never attains any great size. It is simple in its internal structure. Internally the gametophyte (thallus) is made up of uniform parenchyma cells, each usually with one sometimes more chloroplasts of a large size. Each **chloroplast** encloses a **pyrenoid**. The gametophyte plant is thus green and independent throughout its existence (Fig. 9·13, 1). It has neither any air **containing channels** nor **air pores**. Very often it develops mucilage clefts on its under surface. These open into large rounded, mucilage cavities which may be inhabited by *Nostoc*. There are no **scales** and **mucilage hairs**. Nor are the **tuberculate** rhizoids present. The thallus is fixed to the substratum by **smooth-walled rhizoids only**.

The gametophyte at a certain stage bears the **sex organs**. They are deeply sunk in the fleshy thallus. Normally the

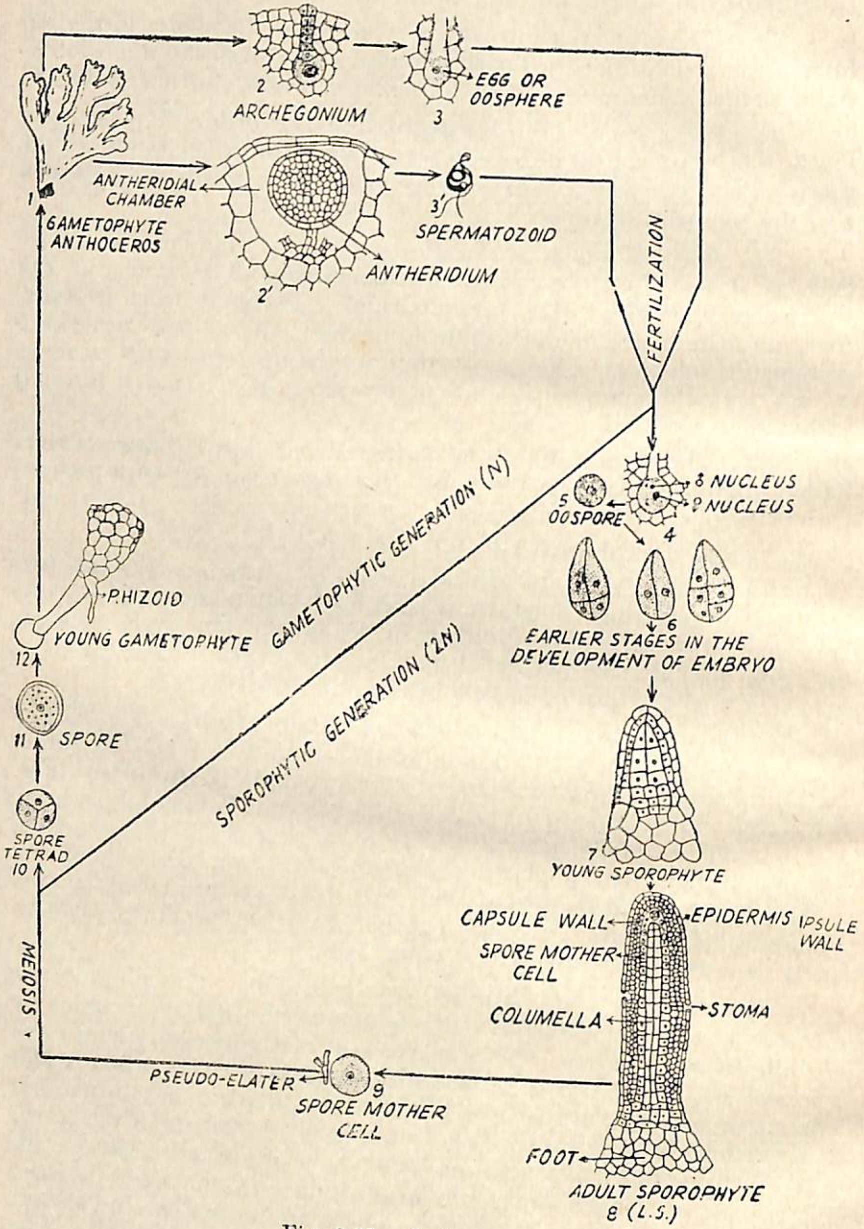

Fig. 9·13. Anthoceros sp.
Diagrammatic representation of the life cycle.

antheridia are **endogenous** (Fig. 9·13, 2). They occur singly or in a cluster inside closed cavities called the **antheridial chambers**.

The antheridia produce biflagellate **sperms** (Fig. 9·13, 3'). The archegonia also are embedded in the thallus (Fig. 9·13, 2). They are thus histologically continuous with the cells of the thallus lateral to them. Only a distal rosette of **cover cells** projects above the surface of the thallus. The axial row of cells consisting of 4 to six **neck canal cells** and a **ventral canal cell** except the egg gelatinize at maturity (Fig. 9·13, 3). The cover cells are thrown off to form an open passage for the sperms to reach the egg.

All the structures produced by and connected with the gametophyte plant constitute the **haplophase** or gametophyte generation. They are all characterized by a **haploid** (N) number of chromosomes. These structures are the *spores*, the *fleshy*, dorsiventrally flattened *green thallus*, the *antheridia*, the *archegonia* and the *gametes* (sperms and eggs). Fertilisation or syngamy is the end of this phase. Sperms and eggs are therefore the last structures of the haplophase.

2. **Diplophase** (**sporophyte generation**). The diplophase starts with the fertilized egg or the **zygote** (Fig. 9·13, 5). It has a **diploid** number of chromosomes. By active segmentation the zygote forms an **embryo** (Fig. 9·13, 6). The latter by differentiation of cells and continued growth develops into the alternate vegetative individual in the life cycle. It is the **sporogonium** (Fig. 9·13, 7 and 8). It is also called the **sporophyte** as it produces meiospores and aids in their efficient dispersal. The sporophyte of *Anthoceros* is a structure unique among the bryophytes in many respects. It is a long, slender, upright, green, more or less a cylindrical object surrounded at its base by a tubular **involucre**. It is differentiated into three regions, the **foot**, the **narrow intermediate zone** and the **capsule**. The foot is specialized as a **haustorium**. It gives out tubular, rhizoid-like outgrowths from its surface. These penetrate deep into the tissue of the gametophyte and absorb water and minerals in solution for the sporophyte. The intermediate zone is **meristematic**. The capsule is shaped like a long spindle. It consists of several cell layers thick **capsule wall**. The superficial layer of the wall functions as an **epidermis**. It is punctured with true **stomata**. The sub-epidermal tissue consists of chlorenchymatous cells with intercellular spaces between them. The chloroplasts are large in size and two in number per cell as a rule. Each chloroplast encloses a pyrenoid. The stomata communicate with the intercellular spaces to form a typical **assimilatory system**. It makes the sporophyte partially self-supporting. Within the capsule wall is the **archesporium**. It forms only a small part of the capsule and is shaped like a dome. It arches over the rounded apex of the central solid core of a sterile tissue, the **columella**. The archesporium is **amphithecial** in origin and later differentiates into alternate bands of spore mother cells and enlongated, sterile cells (Fig. 9·13, 9). The latter mature into **pseudo-elaters**. The spore mother cells by **meiosis** produce the haploid spores which are the first structures of the next haplophase. The diplophase thus ends with the formation of meiospores. It comprises the *zygote*, the

embryo and the *sporophyte*. The **spore mother cells** are the last structures of this phase. Another unusual feature of *Anthoceros* sporophyte is the presence of the basal intercalary **meristem** in the median zone of the sporogonium. As soon as the apical growth of the capsule ceases (with the differentiation of the capsule wall, the archesporium and the columella), the intercalary meristem becomes active. It adds new cells at the base of the capsule to the columella, the archesporium and the capsule wall. As a result, the capsule continues to grow and produces a continued succession of new spores. The sporogonium of *Anthoceros* is therefore a **long-lived** structure. It continues to grow as long as the thallus remains alive.

The top of the green capsule turns grey, brown or black according to the species at the time of dehiscence. The capsule wall at maturity dries and shrinks. Consequently longitudinal slits appear along the two opposite lines of dehiscence. The slits extend downwards. The two segments or valves of the capsule wall curl back and separate from the underlying spore mass. The valves thus separated diverge and twist hygroscopically. The twisting of the valves and the hygroscopic movements of the pseudo-elaters in the exposed spore mass assist in the shedding of spores. The free spores may probably be scattered by the air currents. The dried up thread-like columella protrudes between the two valves.

The two phases or generations constituting the single life cycle of *Anthoceros* regularly occur one after the other. The life cycle of this type which is characterised by **alternation of generations** and **sporogenic meiosis** is termed **diplohaplontic**.

2. NOTOTHYLACEAE

General Characteristics. The gametophyte shows strong resemblance with the Anthocerotaceae. The sporophyte, however, is slightly different. It is short, compact, marginal and grows out horizontally from the fertile lobes of the rosette-like thallus. The photosynthetic tissue, in the capsule wall, is absent and the stomata are lacking. The columella varies from species to species. It is well developed and central in position in some or entirely lacking in others. The pseudo-elaters are simple, equal in size or longer than the spores, with spiral or oblique bands. The family includes a single genus *Notothylas*.

NOTOTHYLAS

Distribution and Habitat. The genus comprises a number of species which are widely distributed both in the tropics and temperate zones. Of these four namely, *N. indica*, *N. levieri*, *N. chaudhurii* and *N. javanicus* have been recorded in India. They are found on moist rocks and damp earth in humid, shady localities.

Thallus (Fig. 9·14A and B).

(*a*) **External Features**. The delicate, thin thallus is dorsiventral and grows flat on the substratum. Usually it is orbicular or suborbicular in form, yellowish or light green in colour and very much lobed. Each lobe may be entire or toothed or beset with blunt, irregular processes. From the under surface of the thallus arise the unicellular, smooth-walled rhizoids which anchor it to the substratum. As in *Anthoceros*, the scales and tuberculate rhizoids are absent.

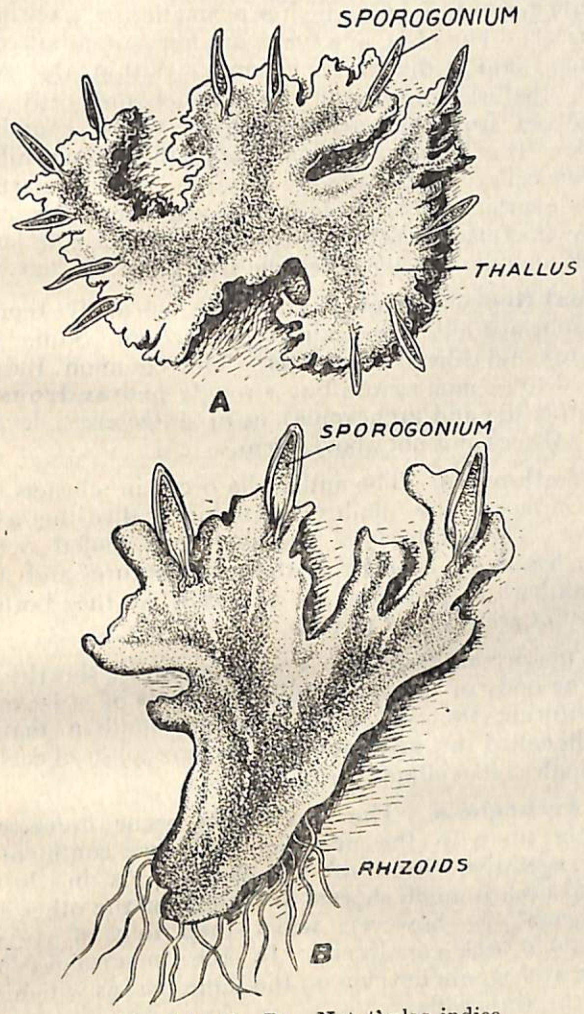

Fig. 9·14 (A—B). Notothylas indica.
A. Thallus bearing sporogonia.
B. A portion of the same slightly enlarged.

(*b*) **Internal structure**. A vertical section of the thallus lobe reveals that it is 6 to 8 layers of cells thick in the middle portion which forms the midrib. Gradually it thins out in the expanded portion of the thallus to a single layer at the margin. The superficial limiting layer at the upper and lower surfaces shows a more regular arrangement of cells which are smaller in size than the cells in the interior. The cells, however, are not cuticularised and thus not organised into a distinct epidermis. Within the two limiting layers the thallus consists of soft parenchyma cells of uniform pattern. Apart from the internal cavities which contain mucilage and occasionally a blue green alga *Nostoc*, there is no differentiation of vegetative cells. The mucilage cavities open by narrow slits at the ventral surface. In *N. javanicus* the mucilage cavities are absent. As in *Anthoceros* the cells contain only a single large chloroplast which includes a body called the **pyrenoid**.

Sexual Reproduction. *Notothylas* normally reproduces by meiospores formed following sexual reproduction. Some species are **monoecious** and others **dioecious**. The common Indian species are reported to be monoecious but strongly **protandrous**. The sex organs (antheridia and archegonia), as in *Anthoceros*, develop within the surface tissues and not above them.

1. **Antheridia**. The antheridia occur in clusters of 2—6 on the dorsal surface of the thallus in cavities called the **antheridial chambers**. The antheridial chambers are roofed over at first. With the ripening of antheridia the roof ruptures and the orange coloured antheridia standing in a cluster at the bottom of the antheridial pit are exposed to view.

The mature antheridium is a large, oval, shortly pedicellate object. The body of the antheridium consists of a jacket of sterile cells constituting the wall. The latter surrounds a mass of small, cubical cells called the **androcytes**. The protoplast of each androcyte forms a single, biflagellate sperm.

2. **Archegonia**. The archegonia occur immersed close to the growing tip with the necks and venters confluent with the adjacent vegetative tissue of the thallus. As in *Anthoceros* the archegonial neck is much shorter than those of the other bryophytes. The neck canal is, however, wider than that of *Anthoceros*. It contains 3—5 neck canal cells. In the monoecious protandrous species the archegonia develop on the same thallus which had earlier produced the antheridia.

The development and structure of sex organs and the method of fertilisation are the same as in *Anthoceros*.

Sporophyte

1. **Development**. The zygote formed as a result of fertilisation, enlarges in the venter. It then secretes a wall around it and starts dividing. The first division is either transverse or vertical. To the first category belong *N. indica* and *N. orbicularis* and to the second *N. levieri* and *N. javanicus*. In case the first division is vertical, the second is transverse or *vice versa*. The embryo after the

second division in any case, consists of four cells. It is the quadrant stage. Each quadrant divides by a vertical wall at right angles to the first. The embryo now consists of eight cells, arranged in two tiers of four cells each. It is the **octant** stage. The cells of the upper tier undergo another transverse division. The embryo now consists of three tiers of 4 cells each. The cells of the uppermost tier by repeated divisions, differentiation and continued growth form the **capsule** and the **intermediate narrow zone**. The cells of the lower two tiers form the **foot**.

Periclinal divisions appear in the cells of the uppermost tier which is destined to form the capsule. This division separates the inner **endothecium** from the outer **amphithecium**. The fate of the endothecium varies in different species. Depending on the fate of the endothecium the different species of *Notothylas* are divided into two categories namely **columellate** species and **non-columellate** species.

(*a*) **Columellate species**. In *N. indica* and *N. orbicularis* the entire endothecium forms the columella. It is central in position.

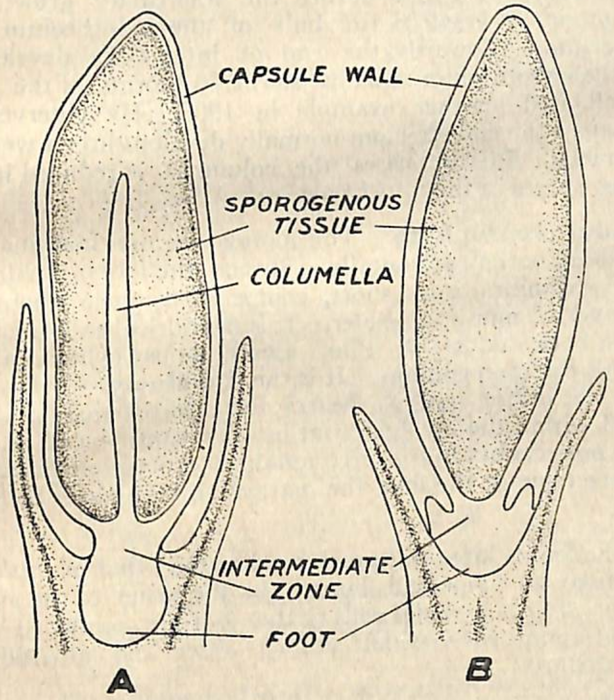

Fig. 9·15 (A—B). Notothylas.

A. V.S. columellate sporogonium of N. indica.

B. V.S. Non-columellate sporogonium of Notothylas levieri.

The amphithecium cells divide by a periclinal wall into **outer** and **inner** cells. The cells of the outer layer form the **capsule wall** and the cells of the inner layer function as the **archesporium** which is dome-shaped and arches over the columella. The archesporium when fully formed consists of 4 layers of cells. During further development the archesporium differentiates into alternate bands of fertile spore mother cells and sterile cells. They extend from the columella to the capsule wall.

(*b*) **Non-columellate species**. In these the columella is entirely absent. *N. chaudhurii* and *N. levieri* are the examples of this group. The entire endothecium is fertile and forms the archesporium. The amphithecium forms the capsule wall. The archesporium becomes differentiated into alternate bands of spore mother cells and sterile cells. They extend across the cavity of the capsule. The spore mother cells, as usual, undergo meiosis to form the meiospores.

There are a few species of *Notothylas* which belong to neither of the above mentioned two groups. They form a connecting link between the columellate and non-columellate species. Lang in 1907, observed that during the intercalary growth of the sporophyte in *N. breutelii* the bulk of the endothecium forms the archesporium. Towards the end of intercalary development the rest of the endothecium remains sterile and forms of the columella. Campbell cited another example in 1908. He observed that in *N. javanicus* the endothecium normally develops into a well developed columella. In rare cases the columella is reduced in size and produces spores in the upper part.

Adult sporophyte. The sporogonia are marginal in position and are borne horizontally between the lobes usually in pairs. Each sporogonium is a short, compact structure about 3 mm in length and 0·5 mm in diameter. It is cylindrical in form but tapers towards both ends. A thin, membranous cylindrical envelope surrounds the sporogonium. It is the **involucre**. In some species such as *N. indica* and *N. levieri* the sporogonium is completely enclosed within the involucre but in *N. javanicus* and *N. breutelii* it slightly projects beyond it. The mature sporophyte is differentiated into three regions, the foot, the narrow intermediate zone and the capsule.

The foot is large but much smaller than that of *Anthoceros*. It is triangular in shape and housed in the tissue of the gametophyte (thallus). The superficial cells of the foot are produced into small, rhizoidal outgrowths which absorb water and nutrition from the parent thallus.

The narrow intermediate zone is short and slender. It shows little meristematic activity and thus plays no significant role.

The capsule has a wall which is four layers of cells in thickness. The outermost layer is the **epidermis**. It consists of brown cells with thick walls. The stomata are absent. The sub-epidermal cells either lack chlorophyll or develop very little of it.

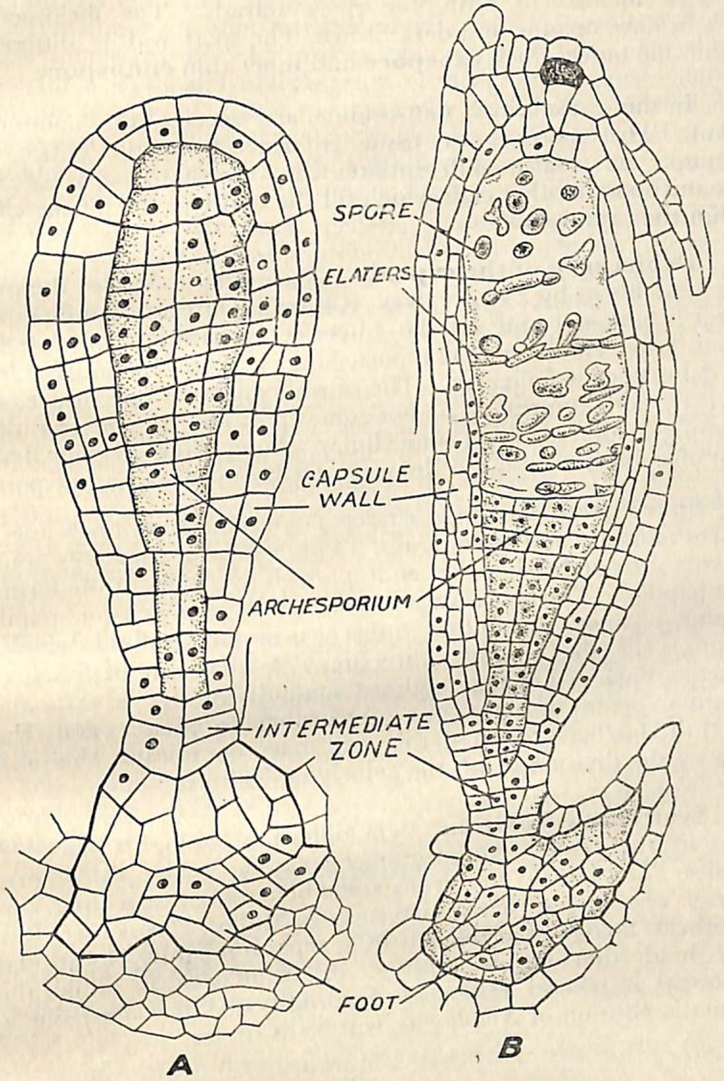

Fig. 9·16 (A—B). Notothylas levieri

A. L.S. young sporogonium.

B. L.S. Adult sporogonium.

After Pande,

Within the capsule wall is the **sporogenous tissue**. It surrounds the central columella in the columellate species. The sporogenous tissue in a mature capsule differentiates into alternate bands of unicellular sterile cells and spore mother cells. The former give rise to the short, simple, unicellular elaters. They are irregular in form and have rudimentary spirals on their walls in the form of short, curved, thin or thick oblique bands. The spore mother cells undergo meiosis to form the spore tetrads. The meiospores in *N. indica* are opaque and dark brown. The spore wall is differentiated into the outer, thick **exospore** and inner thin **endospore**.

In the capsule of non-columellate species the columella is absent. The sporogenous tissue is formed from the entire endothecium. As usual it differentiates into alternate bands of sterile cells and spore mother cells which fill the entire cavity of the capsule within the capsule wall.

Dehiscence of the capsule. According to Muller the mature capsule dehisces by 2 to 4 valves. Kashyap, Dutt and Pande reported that it is basipetal and by the imperfect separation of two broad valves. Later Pande in 1932 reported that in *N. indica* and *N. levieri*, the dehiscence is follicular. The capsule opens by one suture, sometimes, by both sutures. The horizontal position of the capsule, the enclosing involucre, small unicellular elaters, lack or poor development of columella stand in the way of efficient dispersal of spores.

Spore germination. Under favourable conditions the spore absorbs moisture and germinates. The exospore ruptures and the contents surrounded by the endospore bulge out in the form of a short papilla. The first division in the short germ cell or papilla is variable. It may divide by a transverse or longitudinal wall. The second is in the opposite direction. A quadrant of four cells is formed. Each cell of the quadrant again divides by a vertical wall to form an octant of eight cells. According to Mehra and Handoo (1962) the further growth of this cell mass or minute thallus takes place by the division of all the cells lying in front.

Systematic Position. The older morphologists place *Notothylas* in the family Anthocerotaceae along with *Anthoceros* and its allies. The basis is the strong resemblances between their gametophytes. The modern bryologists such as Muller, Proskauer, Reimers and others favour its inclusion in a separate family Notothylaceae. They hold that the sporophyte of *Notothylas* is unlike that of *Anthoceros* in several respects. According to the latest view the systematic position of *Notothylas* will be as under :—

Kingdom	**Plantae**
Division	**Bryophyta**
Class	**Anthocerotopsida**
Order	**Anthocerotales**
Family	**Notothylaceae**
Genus	**Notothylas**
Species	*levieri*

Evolutionary Position. The evolutionary position of *Notothylas* is controvertial. The bryologists hold two opposite views on this point. Lang in 1907 put forward the view that *Notothylas* is a reduced member of the Anthocerotales. It has evolved from forms like *Anthoceros* by the process of simplification. He thus considers *Anthoceros* a **primitive** genus of this group because many of the unique features of *Anthoceros* sporophyte are either absent or present in a modified form in the *Notothylas* sporophyte. It has lost its columella. There is no photosynthetic tissue in the capsule wall and the stomata in the epidermis are lacking. The basal meristem is little active. He reads genetic relationship between the Anthocerotales and the liverworts in a downward direction through forms like *Notothylas*. The supporter's of Lang's hypothesis thus consider *Anthoceros* as a **primitive** genus and *Notothylas* as an **advanced** but a **reduced** genus. It has evolved from *Anthoceros* by a process of simplification.

Cavers in 1911 advanced a view diametrically opposed to that of Lang. He considers *Notothylas* as a link between the liverworts and Anthocerotales but reads genetic relationship in the upward direction. The supporters of this hypothesis consider *Notothylas* as a **primitive** genus and *Anthoceros* as a highly **evolved** or **advanced** genus which has evolved from *Notothylas* by the process of progressive evolution or natural advance.

CONCLUSION AND DISCUSSION

Affinities of Anthoceros. The life history of types like *Anthoceros* deserves special attention. The reason is that there are certain features in its life cycle which it shares with the Mosses. There are others in which it resembles the liverworts. In a few others it shows a remote resemblance with the simplest vascular plants. Some common features also exist between *Anthoceros* and the Chlorophyceae. This led the bryologists to regard *Anthoceros* as a **synthetic** type.

(*a*) **The features which Anthoceros shares with the Chlorophyceae are** :

(*i*) Smaller number per cell (one to four) but larger size and definite shape of the **chloroplasts**.

(*ii*) Presence of **pyrenoids**. The pyrenoids are characteristic of algal cells only.

(*iii*) Simple, green dorsiventrally flattened **thallus-like** plant body and its branching.

(*iv*) Biflagellate sperms with both flagella of whiplash type.

The above mentioned features of *Anthoceros* which recall those of the algae are considered by some to indicate that *Anthoceros* stands close to the line of evolution leading from the algae to land plants. Others however hold that these similarities are of general nature. They are so few and not so consistent as to denote any near alliance between *Anthoceros* and the *Green Algae*.

(*b*) **Features common with the Liverworts are** :

(*i*) A simple, thallus-like gametophyte without any differentiation of tissues and absence of any appendages, except the smooth-walled rhizoids, are the features which *Anthoceros* shares with the thallose Jungermanniales such as *Pellia*.

(*ii*) Similar apical growth of the thallus lobes.

(*iii*) Sex organs differ in essential details but are constructed on the hepatic plan.

(*iv*) The biflagellate sperms similar to those of the Hepaticae.

(*v*) The construction of the deeply emarginate growing point as in the Marchantiaceae.

(*vi*) Separation of the amphithecium and endothecium by periclinal walls in the same way as in the Hepaticae.

(*vii*) Differentiation of archesporium into spore mother cells and the elongated sterile cells which develop into pseudo-elaters. In the related genus *Megaceros* the walls of the sterile cells are spirally thickened to form elaters as in the Hepaticae.

(*c*) **Features common with the Mosses are :**

(*i*) Development of a typically **ventilated assimilatory system** in the capsule wall.

(*ii*) Presence of a central solid core of sterile cells, the **columella** which is entirely endothecial in origin. In this respect *Anthoceros* resembles *Sphagnum*.

(*iii*) Archesporium greatly reduced forming a small part of the capsule.

(*iv*) Archesporium differentiated from the inner side of the amphithecium and shaped like a dome covering the top of the columella as in the *Sphagnum* moss.

(*d*) **The features in which Anthoceros resembles the Pteridophytes are :**

(*i*) General similarity in the structure of the thallus of *Anthoceros* and the fern prothallus.

(*ii*) Sex organs as in the pteridophytes are deeply sunk in the gametophyte.

(*iii*) Similarity in the structure of the mature archegonia.

(*iv*) Campbell holds that the elaborate semi-parasitic sporophyte of *Anthoceros* with its typically ventilated assimilatory system and continued growth denotes the nearest alliance to the independent rootless, leafless, dichotomously branched sporophyte of the primitive fossil vascular plants, *Psilophytales*.

The account given above justifies the contention that *Anthoceros* is a **synthetic** type. It forms a connecting link between the Liverworts and the Mosses on one hand and links the bryophytes with the primitive pteridophytes on the other. A remote connection with the Chlorophyceae is also indicated.

SYSTEMATIC POSITION OF ANTHOCEROS (Anthocerotales)

It is still a debatable question. The conventional treatment is to consider the Anthocerotales as one of the three orders of the class Hepaticae. The other two are the Marchantiales and the Jungermanniales. Many eminent scientists still follow this taxon. The chief among them are Bower, Leitgeb, Kashyap, Cavers, Goebel, Maclean and Cook, etc. On the basis of this classification the systematic position of *Anthoceros* is given below :

Kingdom	**Plantae**
Division	**Bryophyta**
Class	**Hepaticae**
Order	**Anthocerotales**
Family	**Anthocerotaceae**
Genus	*Anthoceros*
Species	*himalayensis*

Hope, Campbell, Smith and Thakhtajan are of a different opinion. They point to the following fundamental differences in which the Anthocerotales differ from the Hepaticae :—

1. Presence, as a rule, of a single chloroplast per cell as against numerous in the Hepaticae.
2. Nature of chloroplasts each of which contains a pyrenoid.
3. Sex organs deeply sunken in the thallus as against their superficial nature in the Hepaticae.
4. Mode of development of sex organs.
5. Mode of development of the sporogonium.
6. Presence of a narrow meristematic zone between the foot and the capsule as against its complete absence in the Hepaticae.
7. Presence of a thin, slender core of sterile tissue, the **columella** in the capsule as against its absence in the Hepaticae.
8. Differentiation of the domed archesporium from the amphithecium as against its endothecial nature in the Hepaticae.
9. Presence of amply ventilated photosynthetic system in the capsule wall as against its absence in the Hepaticae.
10. Basipetal dehiscence of the ripe capsule from the tip downwards along two longitudinal lines of dehiscence, which separate the capsule wall usually into two values, is unique.
11. The long, narrow, cylindrical, upright capsule with stomata and simple or branched pseudo-elaters without spiral thickenings have no parallel in liverworts.
12. Number of chromosomes which is usually 5 or 6 as against 8 or 9 in the other liverworts.

In view of these differences they separate the Anthocerotales from the class Hepaticae and instead assign them a position parallel in rank with the latter.

Leitgeb vehemently opposes this step pointing to the several features which the Anthocerotales share with the Hepaticae, particularly the Jungermanniales (refer to pages 183-184). He maintains that these common features between the two indicate that the Anthocerotales are sufficiently near to the Jungermanniales. He thus advocates the retention of the Anthocerotales in a series with that order opposed to the Marchantiales.

Cavers also attaches no importance to the above mentioned differences between the Anthocerotales and the Hepaticae. He explains them away as follows :

The number of chloroplasts per cell varies considerably in the order Anthocerotales. The endogenous origin of antheridia is a secondary character derived from the exogenous origin. The sunken archegonia are also found in the order Hepaticae as in *Aneura* though the neck is free in the latter. The meristematic zone might have arisen through the persistence of meristematic activity of repeated transverse divisions in the cells between the foot and the capsule in *Pellia*. Presence of stomata in the epidermis may be in response to the many layered capsule wall consisting of assimilatory parenchyma.

Bower considers the sunken condition of sex organs of the Anthocerotales as probably a special and secondary condition to provide biologic protection. He considers the amphithecial origin of the archesporium of the Anthocerotales as of secondary origin due to the general tendency of decentralisation of the central tract in the Hepaticae.

Recently Watson (1964) sounded a mild note of caution saying "such a step is not necessary, although *Anthoceros* remains a remarkable plant." He further adds that the long, narrow, cylindrical shape, a degree of radial symmetry and upright position of *Anthoceros capsule* with its long-lived basal meristem, well ventilated photosynthetic tissue in the capsule wall, thin slender columella, one to three celled pseudo-elaters, basipetal mode of dehiscence of the capsule and the amphithecial origin of the sporogenous tissue are features which accord *Anthoceros* a unique status but for the intermediaries like *Notothylas*. The gametophyte of the latter strongly resemble that of *Anthoceros*. The capsule however is short and compact. It grows out horizontally from the thallus lobes. The epiderms lacks stomata and the subepidermal tissue in the capsule wall has no chlorophyll. The columella, in some species, is entirely absent.

In *Notothylas levieri* (Anthocerotales), for example, the archesporium is endothecial in origin. The entire endothecium remains fertile. On the basis of this Pande favours the retention of the Anthocerotales in the Hepaticae. He holds that forms like *N. levieri* serve to link the Anthocerotales and the Hepaticae.

Recently Mehra and Handoo added another point—perhaps a decisive one to the list of differences between the Anthocerotales and the other Hepaticae. It is the difference in the basic chromosome complex. The Anthocerotales have the basic number as five or six whereas the other Hepaticae (Marchantiales and Jungermanniales) have eight or nine. In the Sphaerocarpales it is ten.

It follows from the above discussion that the Anthocerotales possess certain characteristics in common with the Hepaticae yet they cannot be grouped with the latter on account of the fundamental differences enlisted above. Similarly the Anthocerotales possess certain features which they share with the Mosses particularly *Sphagnum* (refer to page 186) differing totally from them, at the same time, in others. Consequently the growing tendency among the present day bryologists is to consider the Anthocerotales as a separate group named *Anthocerotae* or *Anthocerotopsida* equal in rank to the other two classes of the bryophytes. Since the Anthocerotae form a connecting link between the other two classes they are placed in between the Hepaticae or Hepaticopsida on one hand, and the Musci or Bryopsida on the other.

The consensus of opinion at present favours this view. So according to the latest view the systematic position of *Anthoceros* will be as under : –

Kingdom	**Plantae**
Division	**Bryophyta**
Class	**Anthocerotopsida**
Order	**Anthocerotales**
Family	**Anthocerotaceae**
Genus	*Anthoceros*
Species	*himalayensis*

Biological Importance of Anthoceros Sporophyte. *Anthoceros* has a remarkable sporophyte. It is distinctly different from the sporophytes of the other bryophytes and is considered a unique and an advanced type. The advanced features which also indicate evolutionary trends or the probable lines of biological progress in *Anthoceros* sporophyte are :—

1. *Amply ventilated photosynthetic system in the capsule wall.* The capsule wall consists of several layers of **green cells** with **intercellular spaces** between them. External to these is the protective surface layer forming the **epidermis** which is cuticularised. It is punctured with **stomata** similar to those of the higher plants. The development of the **ventilated photosynthetic tissue** is the first step towards the beginning of physiological independence of *Anthoceros sporophyte*. It makes much of its own food. However it never becomes entirely independent of the parent gametophyte at any stage.

2. *Decentralisation and complete sterilisation of the central fertile tract, the* **endothecium**. This evolutionary tendency resulted in the following two events :—

(*i*) *Development of a central core of sterile tissue forming the columella.* It consists of narrow, vertically elongated, conducting cells with uniformly thickened walls. The presence of a central columella is suggestive of the demarcation of a region in *Anthoceros* sporophyte for the location and the origin of the vascular tissue. Although columella never develops any vascular elements even in exceptional cases in the entire group yet some scientists consider that its central position corresponds to the initial vascular cells of the early tracheophytes. They believe that it plays a definite role in conduction and affords mechanical support. For these reasons it is considered the forerunner of a protostele in some evolutionary concepts.

(*ii*) *Archesporium becoming amphithecial in origin.* The complete sterilisation of the central endothecium to form a columella resulted in the office of spore production being shifted from a central to a more superficial position, *i.e.*, the inner layer of the amphithecium. This superficial origin of the generative tissue (archesporium) promotes easy dispersal of spores and its position on the surface of columella ensures easy and ready supply of nourishment.

3. *Differentiation of amphithecial archesporium into alternate bands of fertile and sterile tracts.* This evolutionary tendency is believed by some scientists to have great potentialities. It is considered the first step towards the origin of sporangia and sporophylls. In fact a noted British botanist Bower made the arrangement of fertile and sterile tissue into alternate bands in *Anthoceros* capsule as the basis for the origin and evolution of leaves and sporangia of the pteridophytes. It is called theory of the origin of the *strobilus*. The separated sterile and fertile masses become more and more superficial on account of their amphithecial origin. Eventually the sterile, superficial tracts turn green. The green tissue develops into membranous expansions, the **sporophylls** with each of the sporogenous masses becoming enclosed by a sporangial wall to form **sporangia**. Of course all these suggested changes are hypothetical.

4. *Presence of a basal intercalary meristem.* It equips the capsule, at least, theoretically with unlimited power of growth. The meristem continually adds new cells at the base which get differentiated into the columella, the generative region and the photosynthetic capsule wall. This unique feature prolongs the period of spore production. The sporophyte of *Anthoceros* is thus a long-lived object as compared with the other bryophytes. It continues to live, as long as the parent gametophyte, producing and distributing spores.

5. *The upright, cylindrical body* (*capsule*) *and large bulbous foot.* The upright body helps in the efficient dispersal of spores and its cylindrical form is considered more suitable for a branched habit. The massive foot embedded in the thallus produces short, rhizoid-like processes. The latter penetrate the thallus tissue to absorb nutriment. The development of these rhizoidal processes

from the actively growing foot was for some time a subject of interesting speculation. The probability of *Anthoceros* sporophyte becoming independent with the foot penetrating the thallus tissue to become a root in the soil was thus suggested.

The above suggestion, in fact, became a conviction with some of the bryologists. Campbell was one of them. He formulated a theory known as the *anthocerotean origin of pteridophytes.* On the basis of this theory the sporophyte of *Anthoceros* and its allies was considered to be on the line of evolution leading to the simplest and the primitive independent sporophyte of the pteridophytes. The discussion about the origin of the Pteridophytes from ancestors like *Anthoceros* entirely centred around the sporophytic generation only. It was argued that the upright. *Anthoceros* sporophyte with its simply ventilated photosynthetic system and long continued growth is nearly equipped for independent existence. It lacks only a vascular tissue and a root with its foot-hold in the soil otherwise it approaches the simplest and the most primitive, free living sporophyte of the pteridophytes. To support his contention Campbell cited the example of certain large, bulky specimens of the sporophyte of *Anthoceros fusiformis* collected in California by Pierce. They were about 6 inches tall and had been growing in unusually favourable habitats for about 9 months or more. These specimens were characterized by :—

(*i*) Suppression of sporogenous tissue near the base of the capsule.

(*ii*) Ventilated photosynthetic tissue highly developed at least twice that in the normal sporophyte.

(*iii*) Columella nearly double in diameter than that in the normal type and differentiated in its basal portion into a conducting "strand of elongated cells highly suggestive of a simple vascular bundle."

(*iv*) Foot large and bulky than usual and more or less in direct contact with the soil due to the disorganisation of the adjacent thallus tissue.

Campbell opined that these sporophytes of *Anthoceros* have "reached a condition comparable to that of the young pteridophyte after it has established its first root." This theory of Campbell received but little support from the other bryologists. They pointed out the wide gap between the rootless, leafless, non-vascular, dependent sporophyte of *Anthoceros* and the rooted, leafy, vascular, independent sporophyte typical of the simplest pteridophytes.

Origin of Anthocerotales. It is a difficult problem. The genetic relationship of Anthocerotae with any other existing forms of bryophytes including even the Hepaticae appears to be very remote. Campbell opined that in its thallus and sporophyte the Anthocerotae have their nearest affinities with certain Pteridophytes. Kashyap was an ardent supporter of this view. So impressed was he with the structural similarities between the radially organised prothallus of *Equisetum debile* and thallus of *Anthoceros erectus* that he suggested the possibility of the origin of the Anthocerotae by reduction from this Pteridophyte. Mehra and Handoo do not subscribe to this view. They consider it untenable for a variety of reasons. The chief among them are :

(*i*) There is nothing in common between the sporophytes of the two.

(*ii*) Absence of any relic of the lost vascular system even in exceptional and abnormal cases in the entire class Anthocerotae.

(*iii*) The difference in the basic chromosome complex of the two is very wide and thus irreconcilable. The Anthocerotae have the basic number as five (5) whereas in *E. debile* it is 10.

Campbell, Smith and others, on the other hand, emphasized phylogenetic relationship between the Anthocerotae and the Psilophytales (Pteridophytes). The latter were a small group of the oldest and most primitive of all known vascular plants. All of these were the fossils of the Devonian age. The two most important of these were *Rhynia* and *Horneophyton*. They were placed in the family Rhyniaceae of the order Psilophytales. The Rhyniaceae were small, herbaceous sporophytes about 2 feet in height. They were rootless. The simplest of them were even leafless. The plant-body consisted of a rhizome bearing slender, erect, dichotomously branched shoots. The rhizome was anchored to the substratum by rhizoids. The vascular cylinder was of the nature of a protostele. There was no secondary growth. The reproductive organs were the sporangia which resembled the sporophyte of the Anthocerotae. They were borne singly and terminally. Each sporangium produced many spores. It possessed a central columella and had distal dehiscence.

Smith was so struck with the remarkable resemblance between the sporophytes of the Anthocerotae and the sporangia of this ancient group (Rhyniaceae) that he suggested *affinities between them by descent in an upward direction*. The opponents of this view point out that *Anthoceros* sporophyte not only has any roots but also no vascular tissue. It exhibits no branching. To crown all the meristem in *Anthoceros* is at the base and not at the apex.

There is, however, another school of thought. They read *genetic relationship between the Anthocerotae and the Rhyniaceae by descent in a downward direction*. According to them the Anthocerotae are a retrograde group derived from the Rhyniaceae by simplification or reduction. Mehra and Handoo find it difficult to reconcile themselves to the view. They argue, "It is difficult to visualize so complete a loss of the vascular system that it would not be present in any exceptional or abnormal cases in the entire Anthocerotales. Moreover the structure of the columella shows no differentiation in any of the members.

Mehra and Handoo feel that the Anthocerotales and the Rhyniaceae have sprung up from the same ancestral stock in the pre-Devonian. They call it the Antho-rhyniaceae. The latter evolved from a still earlier hypothetical pro-liverwort stock from which have also arisen the Marchantiales, the Jungermanniales and the Sphaerocarpales. The origin of this pro-liverwort stock according to them must be sought in some of the Chlorophyceae that migrated to land.

REVISION QUESTIONS

1. Describe the external features and internal structure of the thallus of *Anthoceros*.
2. Give an illustrated account of the structure and development of the sex organs of *Anthoceros*.
3. Give a concise account of the life history of *Anthoceros*.
4. "*Anthoceros* is a **synthetic** type." Justify the truth or falsity of this statement.
5. Discuss the biological importance of the sporogonium *Anthoceros*.
6. Give an account of the structure and development of the sporophyte of *Anthoceros*.
7. Discuss the systematic position of the Anthocerotales.
8. Discuss the affinities of forms like *Anthoceros*.
9. With annotated sketches trace the life history of *Anthoceros*. (*A.U. 1958*)
10. Discuss the origin of Anthocerotae.
11. How would you justify the separation of *Anthoceros* from the Hepaticae ?
12. In what respects does the sporogonium of *Anthoceros* differ from *Riccia* or *Marchantia* ?
13. Describe with the help of a labelled sketch the structure of the sporophyte of *Notothylas*.
14. Which of the two is primitive, *Anthoceros* or *Notothylas* ?

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CHAPTER X

BRYOPSIDA (MUSCI OR MOSSES)

The mosses are the higher bryophytes. They number about 14,500 species which are placed under 660 genera. The plant body is differentiated into the **stem** and **leaves**. Koch (1956) prefers to call the moss stem as **cauloid** and moss leaves **phylloids**. The leafy plant body is better adapted for a life on land than the thallus of the liverworts. Mosses often are gregarious in habit. Different species grow in diverse habitats such as on the roofs, wall tops, rocks, fallen trees, bark of living trees, actually submerged in flowing water or at the bottom of lakes. Many are swamp growers. Majority grow in damp situations forming extensive mats. Some, however, are able to endure drought. In summer they curl up and apparently look dry or dead. With the first shower they absorb water, uncurl and resume growth. The predominant stage in the life cycle is the **gametophyte**. It generally consists of the following two **growth stages**.

(1) **Protonema Stage**. It is creeping, green, branched and frequently filamentous. In rare cases it is plate-like. It develops directly from a spore. The chief role of this juvenile stage is vegetative. It bears no sex organs.

(2) **Leafy Stage**. It consists of an upright, slender axis bearing spirally arranged leaves. This stage finally produces sex organs. It is the so-called **moss plant** comparable to the gametophores of *Marchantia*. It arises as a lateral bud from the protonema Many moss plants may arise from a protonema derived from a single spore.

The protonema in the majority of mosses dies and disappears. This makes the leafy gametophore independent and the sole representative of the gametophyte stage. In a few mosses the protonema persists as long as the gametophyte phase lasts (Phascaceae). It may turn brown and contribute to the mass of rhizoids. In such cases the leafy gametophore (moss plant) is undoubtedly a secondary structure. It is developed for a special purpose which is the production of sex organs.

Vegetative Reproduction. The mosses have developed several methods of vegetatively propagating the leafy gametophyte and thus enabling the individual plant to form dense mats extending over considerable areas. Entire leaves, portions thereof, short specialized branches, in fact any undamaged living cell of the plant or the protonema may act as a vegetative reproductive structure. Excepting a few in most of these methods the **juvenile stage** (protonema) regularly heralds the formation of the leafy moss plant. Only a few important examples of these methods are described below :

1. *Progressive Growth and Death.* Some genera of mosses have a creeping main stem. It bears upright branches. The older portions of the creeping stem which are more or less cut off from light and air, die and decay. This leads eventually to the separation of the upright branches as separate entities. The result is the rapid increase in the number of leafy individuals.

2. *Branching of the leafy stem.* In many mosses the leafy axis develops buds at its base. The buds grow into branches which finally get detached by the decay of their basal connecting parts. Each detached branch develops into an independent plant.

3. *Formation of stolons.* Some mosses develop stoloniferous branches from the base of the stem. The stolons may be naked or bear small scaly leaves and creep on or just beneath the surface of soil. Eventually the tip of each stolon grows upward as an upright, leafy axis.

4. *Preliminary Protonemal Stage.* Moss plants arise as lateral buds from the extensively branched **primary protonema**. The protonema originating from a single spore may bear several such buds. The latter develop into leafy shoots. This is accompanied by the decay of the connecting portions of the protonema. This results in the separation of the leafy shoots as separate individuals.

5. *Multiplication of the Protonemal Stage.* The primary protonema by death and decay of cells here and there may break into short, detachable segments (*Funaria*). Each segment grows into a protonema. The latter produces a fresh crop of leafy gametophores. The multiplication of the protonema stage thus provides a very efficient method of increase in numbers of the moss plants.

6. *Secondary Protonema* (Plural—protonemata). The Mosses have a great power of regeneration. Any undamaged cell of a detached or injured portion of almost any part of the moss plant (such as stem, leaf or protonema) under suitable conditions (when surrounded by moist air) develops into a green, branched, alga-like filament. It is called the **secondary protonema**. A crop of moss plants will spring from the secondary protonema as small buds. The latter grow into independent individuals by the decay of the connecting threads. Secondary protonemata may also spring from the rhizoids when the latter grow in light and are surrounded by moist air. The formation of secondary protonemata is an important and more effective method of vegetative propagation than the original protonema.

7. *Tubers.* The formation of small, underground resting, bud-like structures called the **tubers** has also been reported.

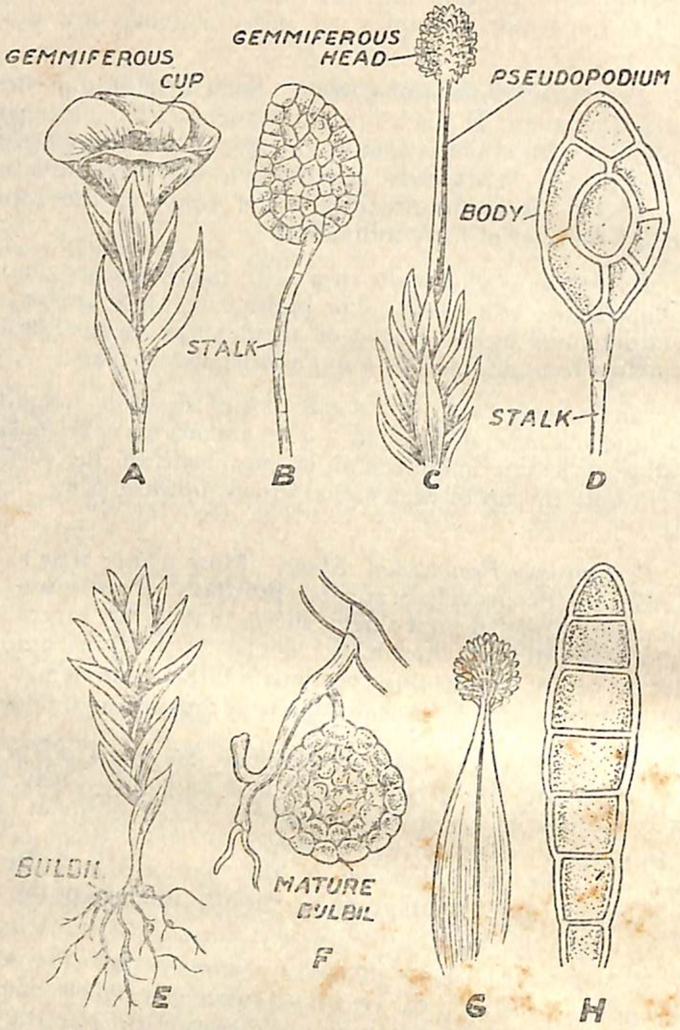


Fig. 10·1. (A—H) Vegetative Reproduction in mosses.

A. Tetraphis pellucida with a terminal gemmiferous cup.
B. Gemma with a stalk.
C. Aulacomnium androgynum with a pseudopodium ending in a gemmiferous head.
D. A stalked gemma of the same.
E. Bryum erythrocarpum bearing bulbils or tubers on the rhizoids.
F. A mature globose tuber or bulbil.
G. Ulota phyllantha, upper part of the leaf with an apical cluster of gemmae.
H. A single gemma.

Formerly they were called the **bulbils**. The tubers develop singly on the protonema or the rhizoids as small, spherical storage organs containing starch. They serve as means of **perennation** and enable the plant to tide over periods unfavourable for vegetative growth. They are found in *Funaria* and *Trematoden*. On germination in the growing season each tuber produces a protonema. It bears the buds which grow up into a new crop of leafy aerial shoots. *Bryum erythrocarpum* bears spherical tubers on the rhizoid system. They are bright red in colour when mature. *Leptobryum pyriforme* is another example. It bears ovoid tubers.

8. *Gemmae.* Frequently small, green, oval, multicellular buds are produced on short stalks in many mosses. They are the **gemmae**. The gemmae are produced in groups in the axils of leaves in *Webra prolifera* In *Tetraphis pellucida* they are long stalked and lens shaped. These gemmae are produced in a peculiar, cup-like structure called the **gemmiferous receptacle**. The latter is constituted by the enlarged spreading leaves at the summit of the erect shoot. The gammae are easily detachable. On falling on a moist soil any cell of the gemma may produce a green protonema. The gemmae in *Aulacomnium androgynum are* borne in a terminal cluster or gemiferous head on a leafless stalk or pseudopodium arising from the tip of the leafy shoot. Another interesting example is that of *Ulota phyllantha* in which the gemmae are produced in a cluster at the tip of the leaf. *Grimmia* bears gemmae on the leaves at the tips or along the midrib. Each gemma is a mass of embryonic cells. It invariably produces a protonemal stage. The latter bears the new leafy plants.

9. *Persistent Apices.* In some mosses with the creeping stems the entire plant dries up in the dry season except the growing apices. The cells of the surviving apices secrete a mucilage sheath around them and persist. With the return of favourable conditions the surviving apices resume growth.

10. *Apospory.* The mosses have an extraordinary power of regeneration. Any undamaged cell of the sporophyte besides the gametophyte, can grow out into a protonema. The wounding of the unspecialised cells of the various parts of the sporophyte, induces the production of the green protonemal filament. The latter bears a new crop of leafy gametophytes. The formation of the gametophytes directly from the cells of the sporophyte other than a spore is called **apospory**. The phenomenon of apospory cuts out the spore stage in the life cycle. In other words the moss plant is produced directly from the sporophyte without the intervention of spores. The aposporously produced moss plants have a **diploid** chromosome number. They tend to be larger but otherwise normal in appearance. They bear diploid fertile gametes. Fusion between two diploid gametes or between a diploid and a normal gamete results in a **tetraploid** (having four sets of chromosomes) or **triploid** sporophyte.

Gametic Reproduction. The sex organs containing the gametes are borne in clusters. Generally the cluster is developed at the apex of the main stem or the branches. Intermixed with the sex organs in the cluster are the sterile green filaments. They are called the **paraphysis**. Some mosses are **monoecious**, others **dioecious**. On the basis of the distribution of the **sex organs** the **monoecious mosses** are placed under the following three categories :—

1. **Paroicous mosses** in which the two kinds of sex organs are borne in the same head in separate groups. The antheridial and archegonial groups are demarcated from one another by **perichaetial** bracts.

2. **Autoicous mosses** in which the two kinds of sex organs are borne on separate branches of the same plant.

3. **Synoicous mosses**. The antheridia and archegonia occur in the same head intermingled with each other. The leaves below the sex organs usually lie close to one another forming a distinct sheath or a rosette called the **perichaetium**.

The mature moss antheridium is an orange coloured club-shaped structure. It is borne on a **stalk** of variable length. The single layered **antheridial wall** encloses biflagellate **sperms**. The archegonia are essentially similar to those of the liverworts. The fertilized egg or the zygote develops into a sporophyte or sporogonium. Ordinarily only a single sporophyte develops in each cluster.

The mature sporophyte consists of a **foot**, a **seta** and a **capsule**. It is more elaborate and complex than that of the Liverworts. It reaches a high degree of specialization and has a great amount of sterile tissue.

To sum up, the mosses in general differ from the liverworts in possessing two conspicuous morphological stages of the gametophyte, the **Juvenile stage** (protonema) and the **gametophore** or **leafy stage**. The leafy moss gametophyte is upright and radially symmetrical. The rhizoids are multicellular and branched. The capsule is more elaborate and has a more complex mechanism of dehiscence and spore dispersal. The elaters are absent.

DISTINCTIVE FEATURES

1. The moss plant is **radially** symmetrical and differentiated into **stem** and **leaves**.

2. Internally the stem shows a certain amount of tissue differentiation into the **cortex** and the **conducting strand**. There is however no true vascular system.

3. The gametophyte invariably consists of two growth stages. These are the **protonema stage** and the **leafy gametophore stage**. They are more conspicuous in the mosses than in the liverworts.

4. The upright leafy gametophore (**moss plant**) is not dichotomously branched. The branching is invariably **monopodial**. The lateral branches are never **axillary**. Each arises from below a leaf.

5. The gametophore usually grows by means of a single **apical cell** which is pyramidal in shape.

6. With the exception of *Sphagnum* the moss leaf usually has a **midrib**.

7. The cell walls are reported to consist mainly of **hemicelluloses** and **pentosanes**. Cellulose is rarely found.

8. The rhizoids which anchor the moss plant to the substratum are **multicellular** and **branched**. The septa between the cells are **oblique**.

9. The sex organs are **stalked** and the stalks are longer than those of other bryophytes.

10. Early growth of the sex organs is by means of an **apical cell**.

11. The venter of the archegonium is much more **massive** than in the Liverworts.

12. The sporophyte is more elaborate and complex and shows high degree of **specialization** and **sterilisation**.

13. With the exception of *Sphagnum* early growth of the sporophyte is by means of an **apical cell**.

14. The entire **archesporium** differentiates into spores. There are no **elaters**.

15. The capsule usually dehisces by the separation of a **lid**.

Classification. Smith divides the class Bryopsida or Musci into three groups giving each the status of a sub-class. These are the (*i*) Sphagnobrya, (*ii*) Andreaeobrya and (*iii*) Eubrya.

The older bryologists such as Bower, Campbell, Wettestein, and others divide the class into three groups but they give each of these groups the rank of an order as follows :

(*i*) Sphagnales.
(*ii*) Andreales.
(*iii*) Bryales.

The modern bryologists recognize five sub-classes as follows :

1. Sub-class Sphagnidae comprising a single order *sphagnales* with one family.

2. Sub-class Andreaeidae. It includes one order *Andreales* with a single family.

3. Sub-class Bryidae. It comprises twelve orders.

4. Sub-class Buxbaumidae with a single order *Buxbaumiales* with two families.

5. Sub-class Polytrichidae comprising two orders (*Polytrichales* and *Dawsoniales*) each with a single family.

Some bryologists including Parihar divide the class Bryopsida into the following three sub-classes :

Sub-class I. Sphagnidae.
Sub-class II. Andreaeidae.
Sub-class III. Bryidae equivalent to Bryales of the older bryologists and Eubrya of Smith.

This system has been followed in the present edition of this text.

REVISION QUESTIONS

1. List the distinctive features of the class Bryopsida (Musci or the Mosses).
2. Give a concise account of the various vegetative methods of multiplication met with in the Mosses.
3. What is apospory ? Does this phenomenon throw any light on the nature of the two generations in the life cycle of a moss plant ?
4. In what respects do the Mosses differ from the other Bryophytes ?
5. Write an essay on vegetative reproduction in the Bryophytes.

CHAPTER XI

SPHAGNIDAE—SPHAGNALES : SPHAGNUM

General Characteristics :

The sub-class Sphagnidae includes the *peat* or the *bog* mosses. They grow in extensive masses on boggy and peaty soils and also as submerged aquatics in peaty pools. The sub-class sphagnidae is characterised by the following distinctive features :—

1. A simple, flat, plate-like thallose **protonema** fixed to the substratum by numerous **rhizoids**.
2. The rhizoids are multicellular. The septa between the cells are oblique.
3. The origin of an upright, **leafy branch** from a single protonemal cell. It grows by means of a three-sided **apical cell** into the adult or mature plant, also called the **gametophore.**
4. Usually a single gametophore develops from one protonema.
5. The unique structure of the leaf of the adult bog moss. It consists of two kinds of cells, the narrow, living, green **assimilatory cells** and the large, colourless, dead **capillary cells.**
6. The absence of a **midrib** in the leaves.
7. The development of antheridia on special **side branches.** The antheridial branches are relatively stronger than the vegetative shoots.
8. The antheridia occur singly and are **axillary** in position.
9. The archegonia are **terminal** in position. They occur in clusters of three usually at the apices of short **female branches** from among a crown at the top of the plant.
10. The mature sporogonium is differentiated into an enlarged **foot**, a rudimentary **constriction-like seta** and a large, rounded **capsule** which is globular in form.
11. The capsule is not invested by calyptra.
12. The presence of a leafless, stalk-like **pseudopodium** carrying the ripe sporogonium at its top.
13. The development of columella from the entire **endothecium**. It occupies the major part of the cavity of the capsule.
14. The development of the **sporogenous tissue** as an inner layer from the **amphithecium**.

15. The central, hemispherical columella capped by the dome-shaped spore sac.

16. The dehiscence of the ripe capsule by the separation of a disc-shaped **lid** or **operculum** at its top.

17. The absence of peristome teeth.

The sub-class Sphagnidae includes a single order, Sphagnales. The latter comprises a single family **Sphagnaceae** which is represented by a single genus *Sphagnum*. The order and the family characteristics are the same as those of the sub-class.

Systematic Position :

Bryophyta
  Bryopsida or Musci
    Sphagnidae
      Sphagnales
        Sphagnaceae

SPHAGNUM (Dill). Hedwig

Habitat. The genus includes more than 336 species. Of these ten (Bruhl, 1931) to seventeen (Sharma, 1949) have been reported from India. All love to grow in very wet places as semi-aquatics and also as submerged aquatics. They thrive best in cold bogs and marshes of higher latitudes. The individual *Sphagnum* plants grow closely matted together forming extensive masses. The latter form a complete vegetative cover over the surface of water in acid pools, ponds and lakes converting them to quaking bogs of peat lands. It is dangerous to traverse the quaking bog. *Sphagnum* is intolerant of lime. The growth of *Sphagnum* increases the acidity of its fluid environment. Skene (1915) attributed it to the process of selective ionic absorption. Rose (1953) reported that the pH in the interior of tufts is usually lower as compared with the surrounding water. The bog water is antiseptic. Owing to its germicidal properties and deficiency of oxygen it acts as a preservative. Plants, animals, logs of wood and even human bodies entrapped beneath the surface in the quaking bogs have been recovered well preserved after centuries.

Distribution. *Sphagnum* has a world-wide distribution. It occurs in all parts of the world except the Arctic region. It thrives in the tropics and extends through the temperate zone to the sub-arctic and the subantarctic regions. In India it occurs in the Himalayas on the wet dripping rocks and on the sides of furrows cut by the fast flowing streams.

Habit. The *Sphagnum* plant generally is an erect **perennial** (Fig. 11·1) with various shades of green, pale green or yellow. Some species are of bright colours such as deep red (*S. rebellum*), orange brown, rose-pink (*S. plumulosum*), orange-pink, etc. *Sphagnum* is

counted among the largest mosses in point of size. As the plant grows its basal, older parts die : The dead portions accumulate from year to year as partially decomposed material which gradually fills the pond or the lake. These deposits may as well contain the remains of other plants growing there such as the sledges, heathers, cotton grass, etc. The water in which *Sphagnum* grows is often so acidic that the decay of the accumulated plant tissue is very slow. These deposits of dead, partially decomposed tissues are slowly compressed and hardened by the weight of fresh deposits above it. These compacted, partially decomposed and hardened dead plant deposits are called the **peat**. The peat is a brown or dark-coloured spongy substance. It is rich in carbon. When air dried it is used as fuel. Since *Sphagnum* is the chief peat former it is often called the **peat moss**.

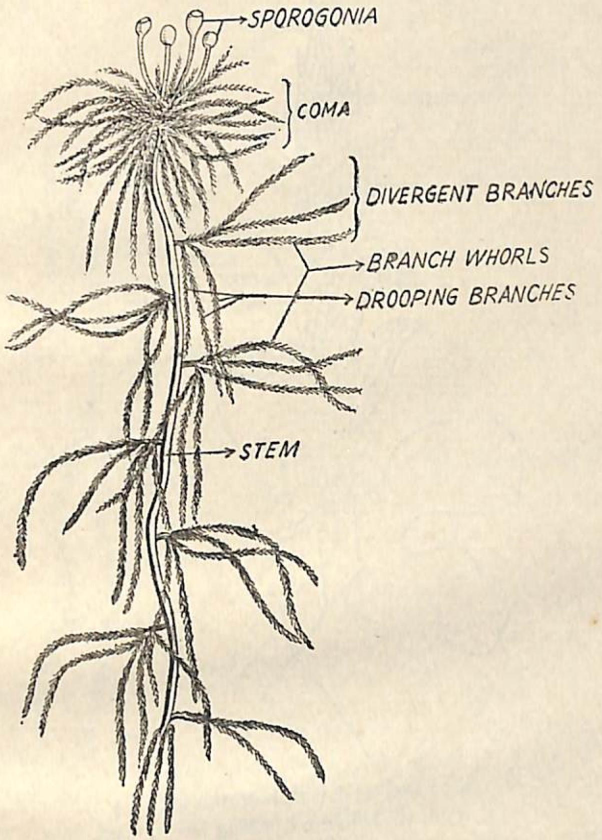


Fig. 11·1. *Sphagnum* sp.
Gametophyte bearing sporogonia each at the end of a pseudopodium.

The life cycle of *Sphagnum* includes two distinct, alternating phases or generations, the *gametophyte* and the *sporophyte*.

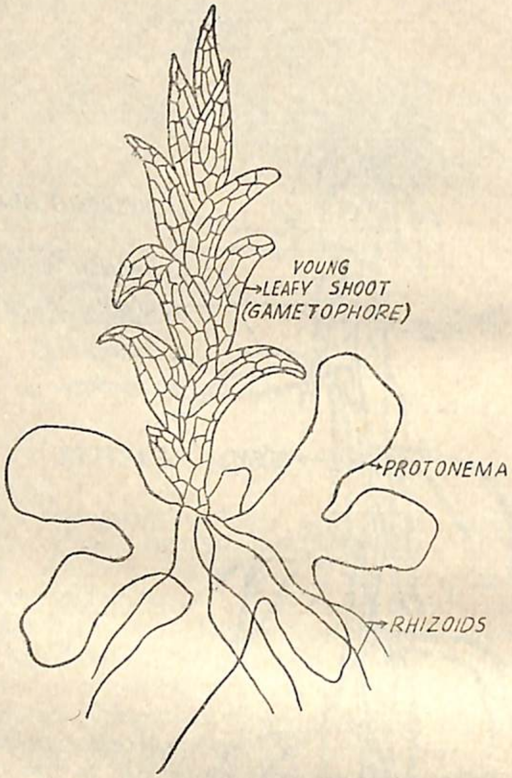


Fig. 11·2. Sphagnum sp.
Old, protonema bearing the young, leafy gametophore.

GAMETOPHYTE PHASE

It starts with the spore and consists of two stages, the **juvenile** stage and the **leafy gametophyte** *stage*.

1. **Juvenile Stage**. It is also called the **protonema** (Fig. 11·2) and is formed by the germination of the spore. When young the protonema is a short filament of a few cells. By further growth and cell division the filament becomes a flat, green plate of cells. It is an irregularly lobed **thallus-like** structure one cell in thickness. It is fixed to the substratum by multicellular rhizoids. The thallus-like protonema of *Sphagnum* moss recalls the thallose protonema of the leafy Jungermanniales and thus points out the relationship of *Sphagnum* to a liverwort ancestor. From the margin of the lobed protonema arises the erect, **leafy** gametophyte called the *Sphagnum* plant (Fig. 11·2). It is also called the **gametophore**. The stem of the young gametophore bears a few colourless rhizoids at its base. The rhizoids are delicate, multicellular, hair-like processes. The septa between the cells are oblique. As the gametophore grows the rhizoids soon disappear. The mature gametophytes of *Sphagnum* thus do not possess rhizoids.

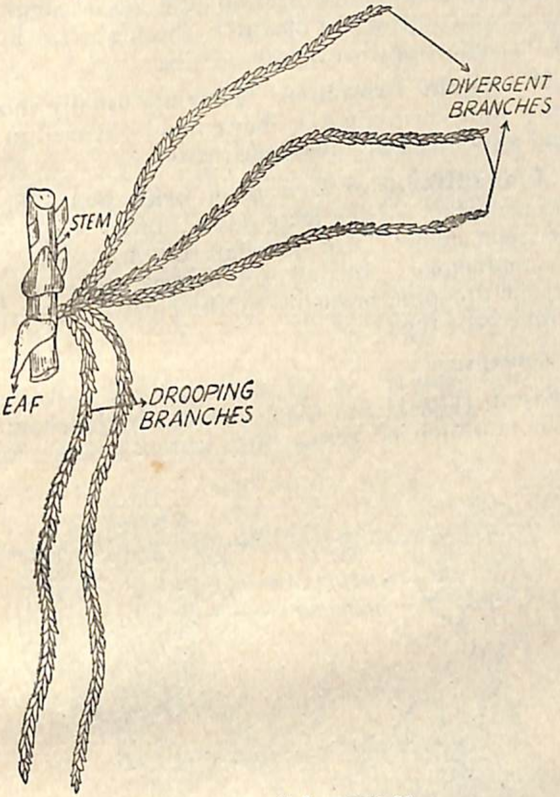


Fig. 11·3. Sphagnum sp.
A portion of the stem bearing a tuft of branches (enlarged).

2. **Leafy Gametophyte**.

(*a*) **External Characters**. The leafy gametophyte is a perennial plant (Fig. 11·1). It has an upright stem. Individually the erect stem is weak and fragile. It gets support to grow upright from the neighbouring dense clumps of stems. The stem often grows to a considerable length—a foot or more. It lacks the rhizoids but branches freely. The branching is usually lateral. Both the stem and the branches are clothed with small leaves. At the apex of the stem is a dense cluster of short, stout branches. They are of limited growth. This terminal cluster of closely set branches protects the apical bud and forms a conspicuous compact head of the plant. It is called the **coma** or **comal tuft**.

Lower down on the stem are borne additional elongated branches. They usually occur in tufts or fascicles of 3 to 8 commonly five in the axil of every fourth leaf on the main stem (Fig. 11·3). In the species which grow out of water the branches in these clusters are of the following two types :

(*i*) **Divergent branches**. They are usually short and stout. As they grow from the main axis they extend outward in a horizontal position and sometimes slightly upward.

(*ii*) **Flagelliform or Drooping branches**. They are long, slender and drooping. They hang down, often very close to and around the main stem. These pendent or decurrent branches act as water conductors. In the submerged species of *Sphagnum* (*S. obesum*) the drooping branches in the cluster are rare. They are all of the divergent type.

(*b*) **Anatomy**

(*i*) **Stem** (Fig. 11·4 A—C). Internally the stem shows well marked differentiation of tissues into three zones. From without inwards they are the **cortex** or the **hyalodermis**, the **hadrome** and the **medulla**.

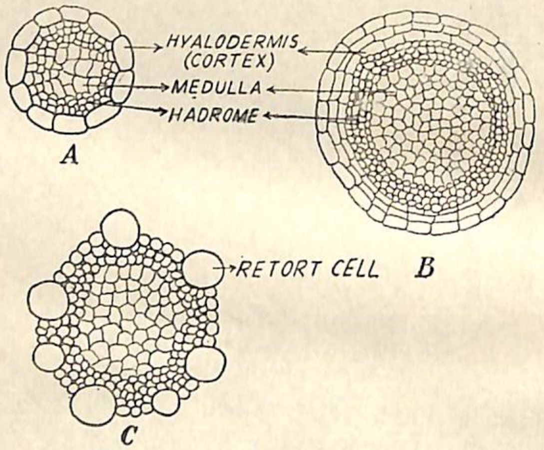


Fig. 11·4 (A—C). Sphagnum sp.
Cross-section of stem.

A. Cross-section of a young stem with a single layered cortex.
B. Cross-section of an old stem.
C. Cross-section of a branch of S. molluscum with retort cells.

(After Cavers)

The **cortex** or **hyalodermis** forms the outermost region of the stem. It varies in thickness. In young stems and branches it is only one cell thick (Fig. 11·4 A). It consists of small compactly arranged cells. In older stems the cortex becomes 3 to 6 layers of cells thick (Fig. 11·4 B). Gradually the cortical cells lose their protoplasmic contents and increase in size. In the mature stems they are thus dead, empty, colourless and large in size. In many species (*S. palustre*) the cortical cells develop large oval pores on their walls and sometimes spiral thickenings also. The cortex of older stems consequently becomes spongy or porous in nature. The cortical cells store water. Like velamen in the Orchid roots, the cortex of the stem absorbs water by capillary action. It thus compensates for the absence of rhizoids in the adult gametophyte plant.

The cortex of the side branches remains one cell thick. The cortical cells of the side branches in certain species such as *S. tenellum* and *S. molluscum* develop peculiar absorptive cells at the points of insertion of leaves. These are elongated and flask-shaped. Some people call them the **retort** cells (Fig. 11·4 C). The neck of each retort cell is turned outward away from the axis. It opens at its distal end by an aperture. The retort cells are inhabited by small microscopic animals.

The **hadrome** lies next to the cortex. It surrounds the medulla and consists of elongated thick-walled, prosenchymatous cells. The hadrome functions as a supporting tissue.

The **medulla** forms the core of the stem. It is composed of colourless, collenchymatous cells with thin walls. The cells are somewhat elongated. The medulla thus forms a tissue corresponding,

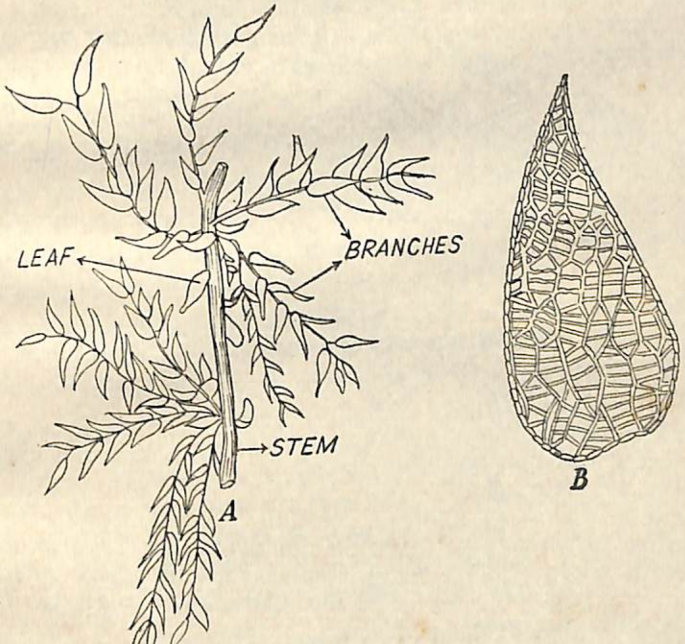


Fig. 11·5 (A—B). Sphagnum sp.

A. Portion of an older part of the gametophyte.
B. A single leaf as seen under low power.

somewhat, to the pith of the higher plants and functions as a storage region.

(*ii*) **Leaves**. The leaves occur on the main stem as well as the branches. On the branches they are closely set and thus overlapping. On the main stem they are a little apart (Fig. 11·5 A). Besides, the leaves on the stem differ in size, shape and details of cell structure from those on the branches. In general the leaves are small, thin and scale like. They are sessile and are arranged spirally on the stem. The midrib is lacking. The margin is entire and the apex acute. *Sphagnum* has a unique type of leaf. It is a single layer of cells in thickness (Fig. 11·5 B). The cells constituting it are much elongated. They are of two kinds, the **hyaline cells** and the **photosynthetic** or the **assimilatory cells**. The two kinds of cells alternate with each other to form a net-like pattern. When viewed under the microscope the narrow, elongate assimilatory cells are seen to form the network with large and wide capillary cells occupying the meshes.

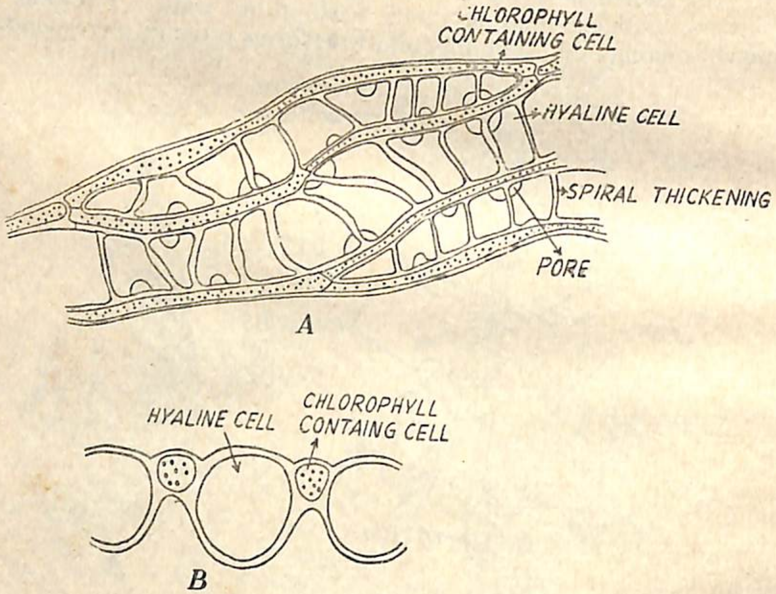


Fig. 11·6 (A—B). Sphagnum sp.
A. Surface view of cells from a mature leaf.
B. The same as seen in cross-section.

The hyaline cells (Fig. 11·6 A) have no protoplasmic contents and thus are dead and somewhat rhomboidal in shape. They are colourless, wide and filled with water. They frequently have circular or oval pores on either the upper or lower surface of their walls. The inner surface of the walls of the hyaline cells is frequently strengthened by spiral or ring-shaped thickening bands of wall material. The strengthening bands help the empty dead cells from collapsing. The pores enable the leaf to absorb water readily and retain it much like a sponge. Because of this property the hyaline cells are also called the **capillary cells**.

The assimilatory cells (Fig. 11·6 A) are alive and photosynthetic in function. They contain chloroplasts and are thus green in colour. They are very narrow and lie between the dead hyaline cells forming a network. The meshes are thus occupied by the dead hyaline cells—one dead cell per mesh. Owing to the presence of dead capillary cells the *Sphagnum* leaves play an important role in the absorption and retention of water.

The cross-section of a mature leaf has a bead-like appearance (Fig. 11·6 B). The bead consists of two kinds of cells. They are the large **capillary cells** and the small, green, **assimilatory cells**. The two kinds of cells alternate with each other. The assimilatory cells are variable in form and position according to the species. In *S. acutifolium* the assimilatory cells have their bases directed towards the upper surface of the leaf and the apices towards the lower surface. They are in flush with the upper surface of the leaf. The large bead-like capillary cells bulge towards the lower surface. The leaves of *S. tenellum* have the position of these two kinds of cells reversed. The large capillary cells bulge towards the upper surface. The basis of triangular assimilatory cells face the lower surface. *S. squarrosum* has fusiform assimilatory cells. They are hemmed inbetween the capillary cells. Their ends reach neither the upper nor the lower surface of the leaf.

Physiology of Water Absorption, Retention and Conduction

The adult *Sphagnum* plant lacks rhizoids. Their function of water absorption is taken up by :—

(*i*) The **spongy cortex** of the stem and branches which consists of dead, water filled cells with porous walls.

(*ii*) The large, hyaline **capillary cells** of leaves with entrance pores. These cells have no protoplasmic contents. Instead they are filled with water.

The capillary cells of both the stem and the leaves account for the remarkable water absorbing and water retaining capacity possessed by *Sphagnum*. It absorbs water directly through its leaves and stem by the capillary action of these cells. The latter as well hold a large amount of water like a sponge. These porous elements of the cortex of the stem also serve as a capillary apparatus for raising the water to the top of the plant and to other places where needed.

In species which lack the porous elements in the cortex of the stem the upward movement of water is facilitated by the **drooping branches**. They hang down and around the main stem clothing it thickly and acting as water conductors. The spaces in the thick, loose covering of the pendent branches serve as a **capillary apparatus**. They draw up water by capillary action.

Apical Growth. The stem grows by means of a three sided **apical cell**. It has three cutting faces. Each segment, cut off parallel to its flat face, divides by a periclinal wall into an outer cell and inner cell. The outer cell undergoes divisions to form the stem cortex and a single leaf. The inner cell gives rise to the central tissue of the stem. In this way each segment derived from the apical cell forms a leaf and the subtending portion of the stem. This explains the three ranked arrangement in the younger portions of the stem. This arrangement is, however, soon replaced by more complex phyllotaxy.

The leaf when young grows by means of an **apical cell**. It has two cutting faces. Segments are cut off alternately right and left parallel to its flat faces. This results in a young leaf consisting of a single layer of cells. It is made up of only one kind of cells. They are all green and contain protoplasm and chloroplasts. Later the apical growth ceases. The further growth of the leaf is entirely **basal**. At this stage striking differentiation of leaf cells takes place. Certain of the leaf cells increase in size. They lose their protoplasmic contents and chloroplasts to become hyaline and empty. These empty cells develop entrance pores on their walls and spiral thickenings on the inner surface of the walls only.

REPRODUCTION

Sphagnum gametophyte reproduces by two methods usual for all the bryophytes. They are **vegetative** and **sexual reproduction**. Following fertilisation is produced the non-sexual individual which is the **sporogonium**. The latter produces the meiospores.

1. **Vegetative Reproduction**. *Sphagnum* lacks special structures for vegetative propagation. The stem progressively disintegrates from the basal, older parts upwards. Consequently the adjacent branches become separated and develop into independent plants.

Occasionally one of the branches in the axillary cluster may turn upward. It grows more vigorously than the others and continues its upward growth. This long, upright branch takes on all the characteristics of the main axis. It is called an **innovation**. Sooner or later the innovations become separated from the main stem by progressive dying of their basal, older part. The detached innovation establishes itself as an independent individual. Vegetative propagation by this method is a very effective means of multiplication in *Sphagnum*. It is mainly responsible for its occurrence in extensive masses.

According to Woesler (1934) the leafy gametophyte of *S. palustre* reproduces vegetatively by several methods. Buds and even plates of cells from the young growing apices of stems and

young leaves grow into new leafy individuals. Even old leaves and short branches under exceptionally humid conditions and moderate light function as vegetative reproductive structures.

Sphagnum has great power of regeneration. Even dried up specimens when put under normal conditions resume growth and become green.

Vegetative reproduction also takes place by multiplication of the protonemal stage. Any marginal cell of the thallose, primary protonema may become **meristematic**. By division and growth it forms a green cellular **filament**. The apical portion of the filament grows into a flat, thallus-like green **secondary protonema**. From one of its marginal cells arises the erect leafy gametophore.

2. **Sexual Reproduction**. *Sphagnum* normally reproduces by the formation of **antheridia** and **archegonia**. They are formed

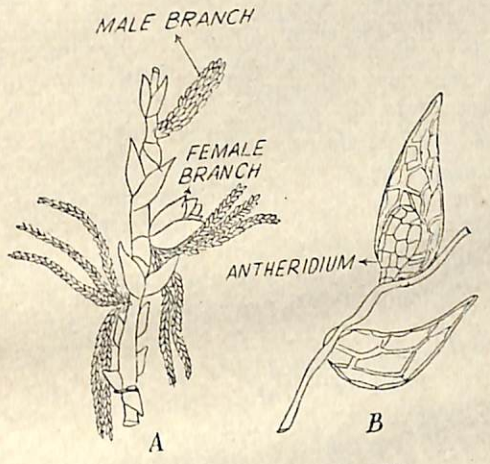


Fig. 11·7 (A—B). Sphagnum sp.
A. Portion of an adult gametophyte bearing male and female branches.
B. Portion of the male branch bearing two leaves and an antheridium (Enlarged).

in autumn on special, short, densely leafy and slightly modified branches. The **sexual branches** either occur in the terminal branch cluster, the **coma** (Fig. 11·1) or lower down on the stem (Fig. 11·7 A). In some species the antheridial and archegonial branches are borne on the same plant and in others on separate plants. The former are called **monoecious** (Fig. 11·7 A) and the latter **dioecious**. Even in the monoecious species the two kinds of sex organs never occur on the same branch. The antheridial branches appear first. The sex organs are formed in abundance. Paraphyses are always absent.

(*a*) **Antheridial Branches**. The antheridial branches are usually shorter but stouter than the vegetative branches. They are spindle-shaped and resemble small catkins. They are strongly pigmented and often densely clothed with red, purple, brown or yellow leaves generally smaller than the foliage leaves.

Antheridia

(*i*) *Position and Structure*. The antheridia occur singly in the axils of leaves on the antheridial branches (Fig. 11·7 B). They take the position of axillary buds and are homologous to them. The mature antheridium (Fig. 11·8 I) consists of a **globular body** elevated on a long, slender **stalk**. The stalk may be as long as the body of the antheridium. It is usually 2 cells broad and consists of 2-4 vertical rows of cells. The body of the antheridium has a jacket layer of sterile cells. It is known as the **antheridial wall**. It is one cell thick and surrounds a mass of **androcytes**. The androcytes metamorphose into **sperms**. Each sperm (Fig. 11·8 K) is an elongated, spirally coiled structure furnished with two **flagella**. The number of coils is 2 to 3. The flagella are inserted at the anterior end which is cytoplasmic in origin and called the **flagellophore**. The greater part of the body of the sperm is nuclear in origin. To its posterior end is attached a vesicle-like structure consisting of a cytoplasmic matrix.

(*ii*) *Dehiscence* (Fig. 11·8 J). On the access of water the mature antheridium dehisces at its apex. It opens by a number of irregular lobes. The lobes turn backwards ejecting the androcyte mass. With the dissolution of the androcytes the sperms are liberated. They swim about actively in the water that causes the rupture.

(*iii*) *Development* (Fig. 11·8). Each antheridium develops from a single superficial cell of the stem. It is the modified initial cell of the axillary bud. It grows into a papilla-like outgrowth (Fig. 11·8 A). The papilla is then cut off by a transverse wall at the base (Fig. 11·8 B). The protruding papillate cell now functions as an **antheridial initial** (Fig. 11·8 B). It divides a number of times by transverse walls to produce a row of few cells (Fig. 11·8 C). The terminal cell of the row functions as an **apical cell** (Fig. 11·8 E). It has two cutting faces. The segments are cut off alternately right and left parallel to its two faces (Fig. 11·8 F). When the young antheridium is 12-15 cells in height each of the last 2 to 5 segments derived from the apical cell undergoes two successive vertical divisions (Fig. 11·8 G). The first division is asymmetrical. It cuts off a small **jacket initial** from a larger **sister cell** (Fig. 11·8 F′). The second vertical division divides the sister cell into a **second jacket initial** and a **primary androgonial cell** (Fig. 11·8 G′). The young antheridium at this stage has 2 to 5 primary androgonial cells (Fig. 11·8 G.) They are surrounded by a wall of a few jacket initials. The old apical cell of the antheridium also contributes to one of the jacket cells. The jacket initials divide

by anticlinal walls to form the single layered wall of the antheridium (Fig. 11·8 I). The primary androgonial cells undergo repeated divisions. The cells of the last cell generation are called the **androcytes**.

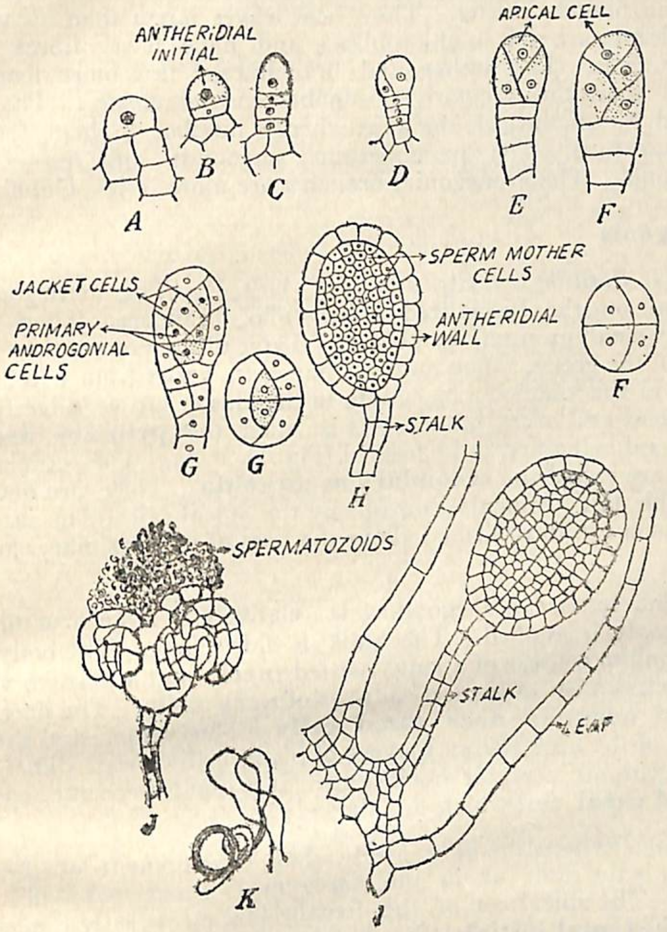


Fig. 11·8 (A—J). Sphagnum sp.

A—H. Stages showing the development of the antheridium. F′, G′ are transverse sections of the young antheridium. The rest are longitudinal sections. (After Mellin).

I. A portion of male branch with an antheridium.

J. Dehisced antheridium.

K. A liberated sperm. (J and K, after Schimper).

Meanwhile the lower cells of the row which do not take part in the formation of the body of the antheridium undergo divisions. They divide by vertical and transverse walls to form the stalk of the antheridium.

(*b*) **Archegonial Branches** (Fig. 11·7 A). The female branches are very short. They are green and bud-like in appearance. In many species they occur just below the apex of the stem within the terminal branch cluster. They bear leaves larger than the normal. These leaves are rich in chloroplasts and have fewer fibres in the hyaline cells. The archegonial branches are thus more deeply pigmented than the vegetative branches in the cluster. The leaves diminish in size towards the apex where a number of them form the **perichaetium**. The perichaetium surrounds and protects the archegonia. The archegonial branches are more or less globular.

Archegonia

(*i*) *Position and Structure* (Fig. 11·9 I). The archegonia are terminal on the specialized archegonial branches. They usually occur in small groups (Fig. 11·9, I). Typically there are three archegonia in the group. The number, however, varies from 1 to 5. The central or the middle archegonium in the cluster grows directly from the **apical cell** of the branch. It is called the **primary archegonium** and is the first to be formed (Fig. 11·9 A). The others in the cluster are called the **secondary archegonia**. They are developed from the last segments cut off by the apical cell. The secondary archegonia are thus formed about the base of the primary archegonium.

The mature archegonium is relatively a large structure (Fig. 11·9 I). It is stalked. The stalk is fairly long. The body of the archegonium consists of a long, twisted **neck** and a massive **venter**. The neck consists of six vertical rows of **neck cells**. The neck canal contains numerous **neck canal cells**. The venter and the lower portion of the neck is 2 to 3 layers of cells in thickness. The venter cavity contains a small ovoid **egg**. It is about the same size as the **ventral canal cell** which lies above it.

(*ii*) *Development* (Fig. 11·9). The development of the archegonium is the same as in the Acrogynous Jungermanniales (liverworts). The apical cell of the female branch directly functions as an **archegonial initial** (Fig. 11·9A). It forms the primary archegonium of the cluster and is reported to undergo a succession of transverse divisions. In some cases it functions as an **apical cell** of the archegonium with two cutting faces. There is thus some irregularity in the early segmentation. However in either case a short filament of cells is formed (Fig. 11·9B).

The development of the secondary archegonia of the cluster is brought about by the segments of the apical cell functioning as archegonium initials. The initial of the secondary archegonium invariably undergoes a series of transverse divisions to form a short filament of 4 to 5 cells. The first step in the development of the archegonium in both cases is the formation of a filament of a few cells.

During further development the terminal cell of the filament increases in size. It then divides by three oblique vertical walls (Fig. 11·9C). This results in the separation of three peripheral cells, the **jacket initials**. They surround a single central cell called the **primary axial cell**. It has the form of an inverted pyramid. The primary axial cell divides by a transverse wall into an **outer** and an **inner cell** (Fig. 11·9D). The former is called the **cover initial** and the latter **central cell**. The cover

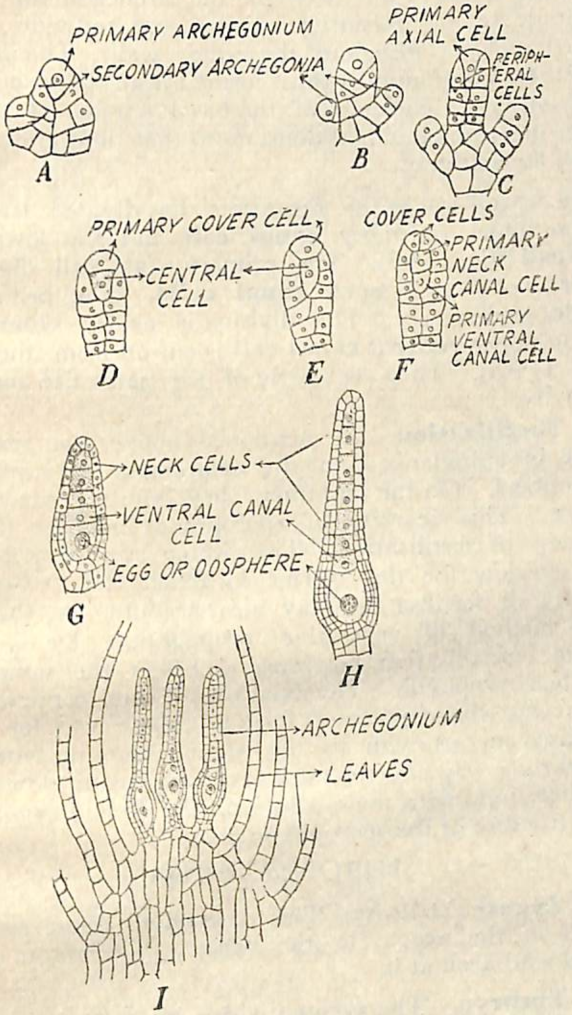


Fig. 11·9 (A—I). Sphagnum sp.

A—G. Stages showing the development of Archegonium.
H. Mature archegonium.
I. V. S. through the tip of female branch showing a cluster of archegonia.

initial divides by a series of vertical walls to form a group of cells. These by further divisions in other directions form the terminal portion of the jacket of the neck of the archegonium. The three jacket initials in the meantime divide and redivide to form the lower portion of the neck and the venter wall. The jacket portion (wall) of the archegonium is thus formed from the cover initial and the jacket initials. The cells of the basal portion of the neck and the venter undergo periclinal divisions so that these portions become 2 to 3 cell layers thick.

The central cell in the meantime has divided transversely to produce an upper **primary canal cell** and the lower **primary ventral cell** (Fig. 11·9F). The primary canal cell divides to give rise to a row of 8 to 9 **neck canal cells**. The primary ventral cell divides transversely. The division is nearly symmetrical. As a result an upper **ventral canal cell** is cut off from the lower **egg cell** (Fig. 11·9G). They are nearly of the same size and lie in the venter cavity.

(6) **Fertilization**. As mentioned above the sex organs are produced in abundance but the sporogonia are rarely found in large numbers. On the contrary they are regarded as of rare occurrence. This scarcity of sporophytes may be the result of infrequency of fertilisation. The water level may be either too high or too low for the sperms to reach the archegonia. The uncertainty of fertilisation may also account for the rapid and effective method of vegetative propagation by *innovations* in *Sphagnum*. Fertilisation, however, occurs in the same manner as in the other bryophytes. The axial row of cells in the archegonium, except the egg, disintegrates to form a passage way for the sperms. The released sperms swim to the archegonium in water. Some of them find their way into the neck canal and swim down to the egg. One of them fuses with the egg to form the diploid zygote. It is the pioneer structure of the sporophytic phase.

SPOROPHYTE PHASE

(*a*) **Zygote** (11·10 A). The sporophyte phase starts with the formation of the zygote in the venter. The zygote enlarges and secretes a wall around it.

(*b*) **Embryo**. The zygote divides by a transverse wall. The division is nearly symmetrical. The accounts of the segmentation of the basal cell vary. According to Waldner it undergoes a few irregular divisions to form the **foot**. Bryan holds that it functions as a **boring organ**. However it is evident that there is some irregularity in the segmentation of the basal cell. Hence its fate is difficult to follow.

The upper cell divides by a series of horizontal walls. Consequently a filament of 6—12 cells is formed (Fig. 11·10 C and D). The early growth of the embryo (young sporogonium) is thus by a succession of transverse walls. The upper three to four cells of

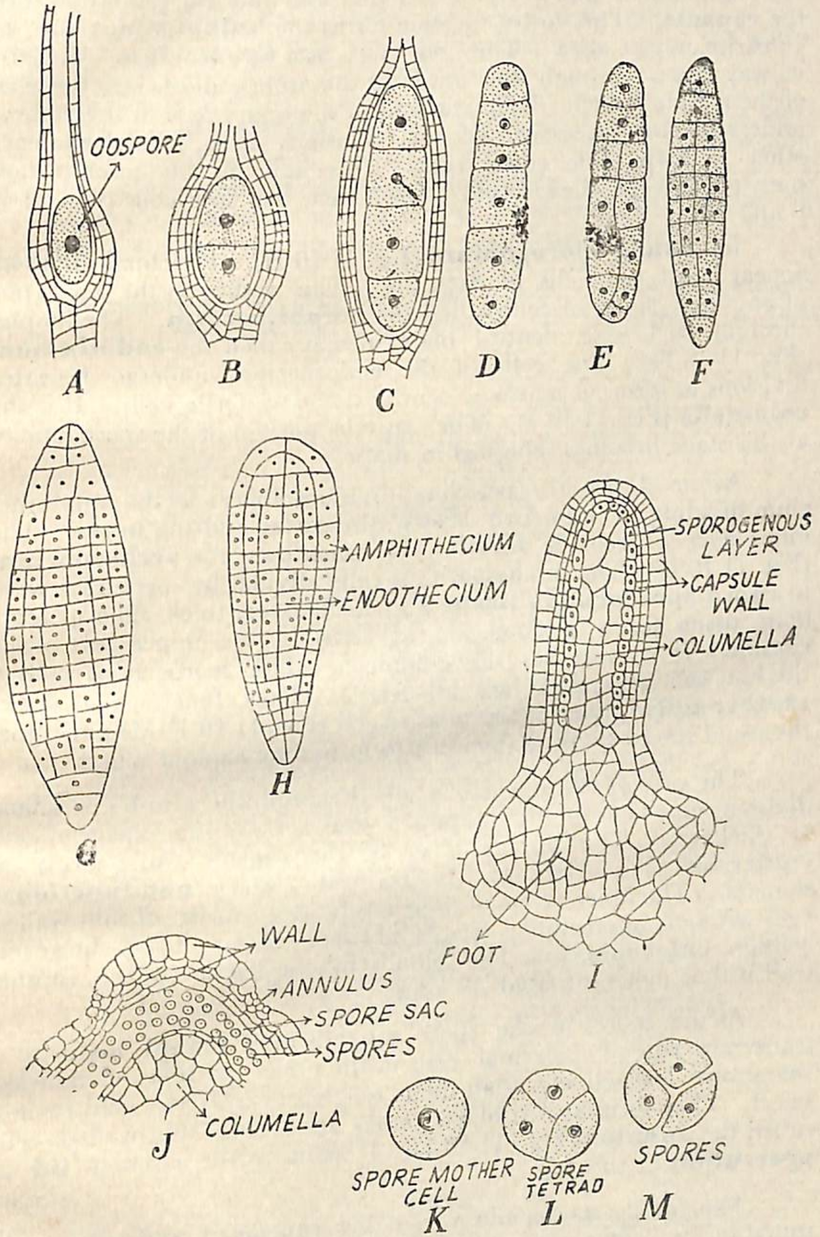


Fig. 11·10 (A—M). Sphagnum sp.

(A—I). Various stages in the development of embryo. (B—G. after Bryan, H—I, after Waldner). Explanation in the text.

I. Median longitudinal section of a young sporogonium.

J. Portion of the upper region of the capsule in longitudinal section.

the filamentous embryo by further divisions and differentiation form the **capsule**. The lower portion forms the **bulbous foot** and the constriction-like **seta**. The foot acts as a **haustorium**. It bores its way down through the stalk of the archegonium into the apex of the female branch. Each segment of the upper part of the embryo undergoes two successive vertical divisions at right angles to each other to form four equal cells. This half of the embryo now consists of several tiers of cells. Each tier has four cells (Fig. 11·10 F and G).

(*c*) **Young Sporogonium** (Fig. 11·10 H). Periclinal divisions appear in all the cells of each tire. This results in the separation of an outer layer of cells called the **amphithecium**. The amphithecium encloses a central mass of cells called the **endothecium** (Fig. 11·10 H). The cells of the endothecium undergo repeated divisions to form a massive, central dome of sterile cells. It is the **columella** (Fig. 11·10 I). The capsule portion of the sporogonium at this stage becomes spherical in shape.

As in *Anthoceros* periclinal divisions appear in the amphithecium dividing it into two layers, the **outer** and the **inner**. The inner layer of cells is **fertile**. It constitutes the **archesporium** (Fig. 11·10 I). The archesporium cells divide by periclinal walls to form a **sporogenous tissue** 2 to 4 cell layers thick. The sporogenous tissue forms a dome-shaped zone in the upper part of the capsule. It over-arches the columella. The sporogenous cells of the last cell generation are all fertile. They functions as **spore mother cells**. Each spore mother cell (Fig. 11·10 K-M) undergoes the usual tetrad division (meiosis) to form four haploid spores.

The cells of the outer layer of the amphithecium by periclinal divisions give rise to the **capsule wall**. It is 4 to 6 layer of cells in thickness. The surface layer of the capsule wall forms an **epidermis** (Fig. 11·10 I). It has rudimentary **non-functional** stomata. The inner layers of the capsule wall consist of thin-walled cells without intercellular spaces between them. They, however, contain **chloroplasts**. The photosynthetic tissue in the capsule wall is thus not ventilated.

As the spores in the spore sac advance toward maturity a transverse ring of epidermal cells in the upper portion of the capsule grows less actively than their neighbours. These cells remain small. They form a sort of a circular groove of thin-walled cells called the **annulus** (Fig 11·10 J). It delimits the circular **lid** or **operculum** at the top.

The young sporogonium remains enveloped and thus protected in the venter now called the **calyptra**. The latter in the early stages of development of the young sporogonium keeps pace with its growth. The neck of the archegonium however dries up. As the capsule enlarges and advances towards maturity, the delicate calyptra ruptures irregularly. A cup-like sheath remains at the

base surrounding the foot. The seta in the sporogonium of *Sphagnum* remains suppressed. It is very short and constriction-like. Its function is taken up by a peculiar leafless stalk called the **pseudopodium**.

The **pseudopodium** (Fig. 11·11) is an outgrowth of the apex of the archegonial branch. It develops by the rapid elongation of the tip of the archegonial branch when the capsule is ripe. It is thus a gametophytic structure. As it elongates it carries the ripe sporogonium at its top beyond the perichaetial leaves.

Production of Meiospores. The mature sporogonium (Fig. 11·11) produces the meiospores. It consists of a **foot**

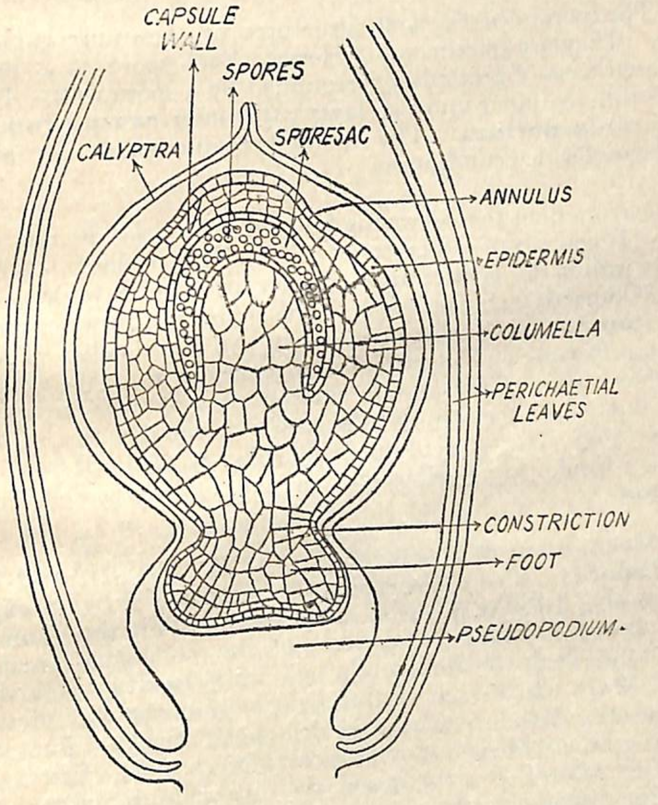


Fig. 11·11. Sphagnum sp.
Median longitudinal section of a nearly mature sporophyte.

and a **capsule**. The two are separated by a constriction. The constriction represents the **seta region**. The foot is an enlarged, bulbous structure. It is embedded in the tissue of the dilated apex of the leafless, stalk-like structure, the **pseudopodium** which develops after fertilisation. The pseudopodium is about 12 mm. or a little more in length. It elevates the capsule far above the perichaetial leaves and the terminal branch cluster. The pseudopodium compensates for the poor development of the seta region and thus, aids in spore dispersal. It is liable to be mistaken as seta. In reality it is a part of the parent gametophyte.

The capsule is a small, spherical, dark brown or black object. It mainly consists of a massive, central hemispherical **columella** of sterile cells. The columella is over arched by a relatively thin, dome-shaped **spore sac**. The spore sac thus extends over the top of the columella. It contains the **haploid spores**. There are no elaters. With the formation of spores the sporophyte phase ends. The spore mother cells are the last structures of this phase.

The spores are the first structures of the future gametophyte phase. They are tetrahedral in form. Each spore is a tiny, uninucleated mass of protoplast surrounded by a spore wall. The spore wall is differentiated into two layers, the outer **exosporium** and the inner **endosporium**. The spores remain viable for about six months under dry conditions.

Surrounding the columella and the spore sac is the **capsule wall**. It consists of 4-6 layers of cells. The surface layer of the capsule wall is the **epidermis**. It consists of thick-walled, cuticularized, compactly arranged cells. The epidermis possesses **rudimentary stomata**. Each stoma consists of two guard cells. There is no stomatal aperture. The cells of the inner layers of the capsule wall have thin walls. They contain chloroplasts but have no spaces between them. At the top of the capsule is the disc-shaped **operculum** or **lid**. The operculum is sharply marked off from the rest of the capsule by a ring-like groove of thin-walled cells, the **annulus**.

Mechanism of Dehiscence (Fig. 11·12 A—D) **and Dispersal of Spores**. The dehiscence of the capsule is by an **explosive** mechanism. It takes place on sunny days. With the formation of spore tetrads in the spore sac, cells of the columella break down. This results in the formation of a large **air cavity** below the spore sac (11·12 A). Under the influence of the sun the wall of the exposed, mature, dark brown capsule dries and shrinks. The spherical capsule gradually becomes cylindrical (Fig. 11·12 B). The imprisoned air in the capsule is compressed and thus held under considerable pressure. It cannot escape. As the capsule wall shrinks the thickened lid cells resist shrinkage. A difference in tension is thus set up. This puts a strain on the thin-walled annulus cells which finally rupture under the mounting pressure of air within. This loosens the small, convex lid which is literally blown off. The imprisoned air is suddenly released and with it the spores in a cloud. Ingold (1939) described the method of spore discharge in *Sphagnum*

as 'air gun' mechanism. The spores discharged upward into the air (Fig. 11·12D) are readily taken up by the wind and dispersed.

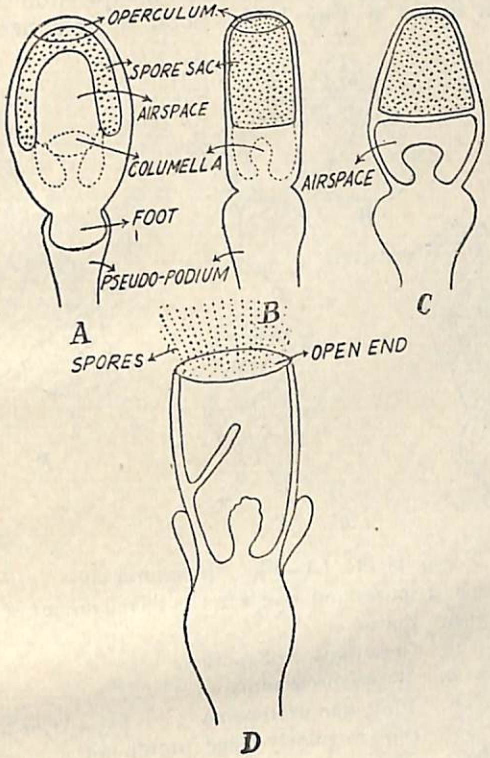


Fig. 11·12 (A—D). Sphagnum sp.
Various stages in the dehiscence of the capsule.
A. Undehisced capsule.
B—C. After drying just before dehiscence.
D. Dehiscing capsule. (After Nawaschin).

Germination of Spores (Fig. 11·13 A—F). Under suitable conditions the spore germinates within a week's time. It absorbs water and swells up slightly. The exosporium ruptures (Fig. 11·13 B). The endosporium grows through the split into a short, green filament of 2 to 4 cells (Fig. 11·13C). At this stage the terminal cell of the filament begins to function as an apical cell. It has two cutting faces (Fig. 11·13D). Segments are cut off parallel to these alternately right and left. Consequently a flat, green protonema is formed (Fig. 11·13E). It consists of photosynthetic cells. They are arranged in the form of a plate, one cell thick. During further growth the apical cell becomes inactive and indistinguishable. Certain marginal cells of the plate-like protonema undergo anticlinal and periclinal divisions. As a result the primary protonema becomes an irregularly lobed, green plate, one cell in thickness (Fig. 11·13F). It is fixed to the substratum by colourless, multicellular rhizoids. From one of the marginal cells near the base of the primary protonema arises the erect, leafy gametophore. The cell in question by growth and segmentation forms a tiny bud. Soon a tetrahedral apical cell becomes established in the bud. It cuts off segments like the apical cell of the adult gametophore. As a result an upright, apically growing shoot of *Sphagnum* is formed. Normally one leafy shoot is developed from a single protonema (Fig. 11·2). The protonema itself soon disappears after the establishment of the leafy gametophore.

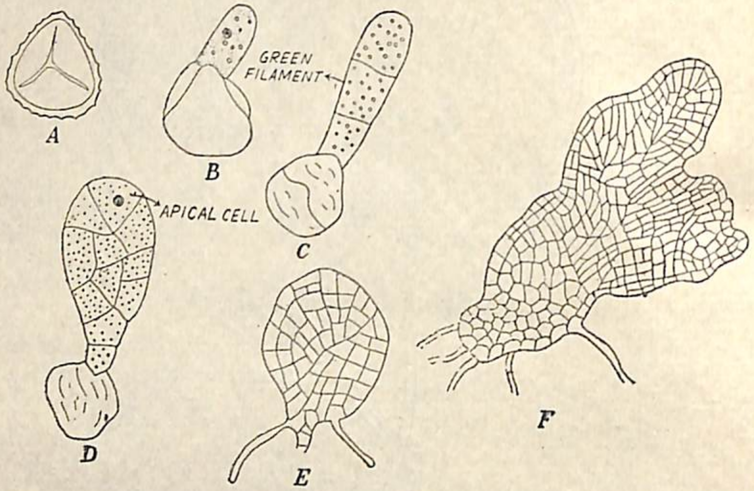
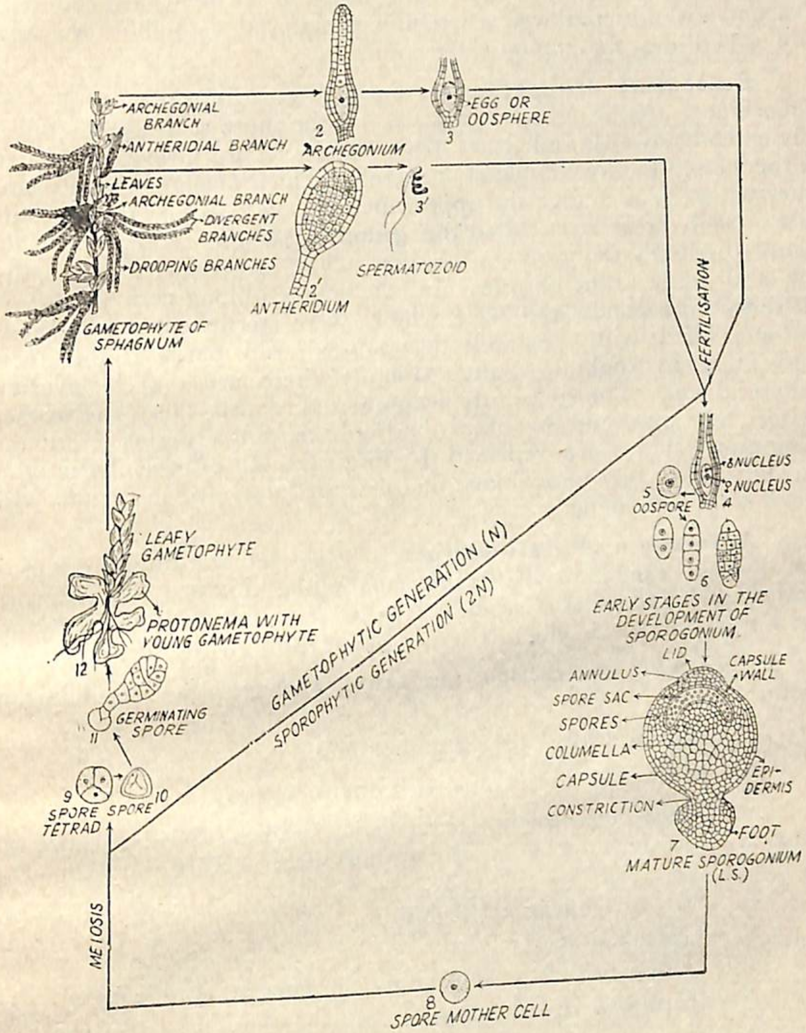


Fig. 11·13 (A—F). Sphagnum sp.
Germination of spores and stages in the development of protonema.
A. Sporo.
B. Germinating of spore.
C—D. Young protonema.
E. Plate-like protonema.
F. Old irregularly lobed protonema.
(After Muller).

The protonema stage may be propagated vegetatively. Any marginal cell of the thallose primary protonema may become meristematic. By growth and segmentation it grows into a green cellular filament. The apical portion of the filament in turn may grow into a new, green, flat thallus-like structure. It is called the **secondary protonema**.

Economic Importance. It is the only genus of the bryophytes which is of real worth. The peat deposits are cut into blocks, dried and used as fuel. Because of its superior absorptive powers and antiseptic properties carefully dried, cleaned and sterilized *Sphagnum* has been employed for gauze to dress wounds and is used for other surgical dressings in hospitals. For its ability to hold water tenaciously, dried *Sphagnum* is remoistened and used for packing live plants and cut flowers which are to be shipped and thus are to be protected from drying. Peat is also of great use in horticulture. It is added to heavy (clayey) soils to improve their texture as it keeps them porous and prevents caking. When added to dry, sandy soils or other humus poor soils it improves their water holding capacity. It is employed by gardeners as a substratum in which seeds are germinated and other plants are grown. It is as well used as a packing for grafting scions to protect them against drying influence of the surrounding air.



11·14. Sphagnum sp.
Diagrammatic representation of the life cycle.

Some of the by-products of peat such as peat tar, ammonia, and paraffin are of industrial use. By filling ponds, pools and lakes with its extensive growth and debris these areas are converted into solid earth. Hence this moss is considered a great soil builder. *Sphagnum* is also employed as a stuffing material in upholstery and also as bedding for domesticated animals.

Ecological Importance. *Sphagnum* is of great ecological importance. As it establishes itself on the shore of a lake it gradually extends inwards and grows over water. The surface of water in the lake is finally completely covered. The *Sphagnum* plants are intertwined so as to give the appearance of solid soil from the surface. Such areas are called the **quacking bogs**. Sometimes seed plants (hydrophytic) grow on the bog. The moss plants gradually die and settle to the bottom. In the course of long periods of time these swamps, ponds, and lakes, which were sterile sheets of water, become filled with partially decomposed, old parts of this moss and other hydrophytic plants. Finally these areas are converted into solid soil. The constantly accumulated debris raises the surface level. The moss and the other hydrophytic angiosperms gradually disappear. They are replaced by forest growth of mesophytic type. In this way *Sphagnum* moss modifies the landscape in regions with small lakes and ponds.

Affinities or Relationships. *Sphagnum* is a unique genus of the Mosses. One is struck by the remarkable mixture of liverwort, anthocerote and moss characters it possesses. In addition it possesses certain characters in which it stands apart from all the three.

Sphagnum **resembles** the **true Mosses** in the following features :—

1. Radial, leafy, upright gametophore.
2. Multicellular rhizoids with oblique septa.
3. Apical growth of stem, leaves and antheridia as in the mosses. The development of the antheridium is after the manner of of the mosses.
4. Structure of the archegonium.
5. Absence of elaters.
6. Dehiscence of the capsule by the separation of a lid.
7. Rupturing of the calyptra.

In view of the above mentioned characteristics which *Sphagnum* shares with the true mosses it is rightly placed in the class Musci or Bryopsida.

Sphagnum **differs** from the **higher mosses** in its peculiar gross morphology, leaf anatomy and certain features of the sporophyte. These are enumerated as follows :

1. Broadly thallose protonema.
2. Absence of rhizoids in the adult gametophyte.

3. Origin of branches in clusters in the axils of leaves.
4. The spongy cortex of the mature stem consisting of dead, empty cells with pores on their walls.
5. Presence of two kinds of cells in the leaves ; larger, dead, **hyaline** perforate cells and living **green** cells.
6. Development of archesporium from the amphithecium.
7. Archesporium over-arching the columella.
8. Origin of the columella from the entire endothecium.
9. Early development of the embryo by a succession of transverse walls.
10. Presence of pseudopodium and absence of seta.
11. Absence of peristome teeth.

From among the **Liverworts** *Sphagnum* **resembles** the **Jungermanniales** in the following respects :

1. Flat, disc-like protonema resembles the juvenile stage of some Acrogynous Jungermanniales.
2. Axillary position of antheridia, and their dehiscence like Acrogynous Jungermanniales.
3. Position and development of archegonia like Acrogynous Jungermanniales.
4. Presence of rudimentary stomata scattered over the capsule wall is, another feature in which it resembles the Jungermanniales.

These similarities between the Jungermanniales and *Sphagnum* point to the intermediate position which the latter occupies between the **Liverworts** and the **Mosses**.

Features **common** with the **Anthocerotae** (**Anthocerotopsida**) are :—

1. Absence of apical growth in the embryo sporophyte.
2. Origin of the archesporium from the amphithecium.
3. Dome-shaped amphithecium over-arching the columella.
4. Entire endothecium forming the columella.
5. Presence of assimilatory tissue in the capsule wall which of course is not ventilated.
6. Presence of massive foot and constriction-like seta.

These features serve to link *Sphagnum* to the **Anthocerotae** rather than to the true Mosses.

However, in its spherical form, absence of basal meristem, absence of any type of elaters and dehiscence of the capsule by the separation of a lid, the sporophyte of *Sphagnum* differs from that of *Anthoceros*.

From the foregoing account it is evident that *Sphagnum* combines the characters of all the three classes of the bryophytes.

It serves to link them together. Such forms are called the **synthetic types**.

Characters peculiar to Sphagnum are :—

1. Absence of **rhizoids** in the adult gametophore.

2. Origin of branches in **tufts** from the axil of every fourth leaf.

3. Absence of a **midrib** in the leaves.

4. **Unique structure** of the stem and the leaves. The cortex of the old stems is **spongy** or **porous** in nature. It consists of **hyaline cells** with large, oval pores and sometimes with spiral thickenings also. The leaf consists of a single layer of two kinds of cells : the large dead, **hyaline cells** with pores and the narrow, elongated green **assimilatory cells**.

5. Peculiar physiology of water absorption, retention and conduction.

6. Presence of some organic substance of a colloidal nature in the cell walls. It absorbs the base and releases the acid. For this reason the water in which *Sphagnum* grows is highly acidic.

REVISION QUESTIONS

1. List the salient features met with in the life cycle of *Sphagnum*.
2. Give reasons to explain the following :
   (*i*) Dried and dead remains of *Sphagnum* plant serve as an excellent absorbent.
   (*ii*) Sex organs are produced in abundance in *Sphagnum* but sporophytes are only rarely found.
3. Write a short note on the economic and ecological importance of *Sphagnum*.
4. Give an illustrated account of the life history of *Sphagnum*.
5. Discuss the affinities of *Sphagnum*.
6. Describe the structure and the development of the sex organs of *Sphagnum*.
7. Describe the external and internal morphology of the sporophyte of *Sphagnum*. Of what advantage is the seta to the Moss sporophyte? How does *Sphagnum* compensate for its absence ?

CHAPTER XII

BRYIDAE – FUNARIALES : FUNARIA

General Characteristics. The sub-class Bryidae include a great majority of the common mosses called the **true** or the **higher mosses**. They number about 14,000 species allotted to nearly 650 genera. The Bryidae are characterized by :—

1. Leaf one to several cells in thickness and often with a distinct **midrib**.

2. Early growth of the embryo by means of a two-sided **apical cell** situated both at the anterior and the posterior ends.

3. Archesporium differentiated from the **outer layer** of the **endothecium**.

4. **Archesporium** not arching over the columella.

5. Presence of a large **intercellular space** around the spore sac traversed by **trabaculae**.

6. Absence of a **pseudopodium**.

7. Presence of a well-developed **seta** which serves to elevate the capsule far above the surrounding leaves of the gametophore.

8. Columella extending right up to the lid and is surrounded by the spore sac.

9. Presence of **peristome** teeth around the mouth of the spore cavity.

10. Dehiscence of the capsule by the separation of a lid.

11. Calyptra well developed.

12. Greater elaboration and complexity in the structure of the **capsule**.

13. Filamentous **protonema**.

Classification. The sub-class Bryidae includes about 80 families. There is some difference of opinion when it comes to grouping families into orders. The majority of the bryologists at present follow Fleischer with slight modifications. He divides the sub-class into 15 orders as follows :—

Fissidentales	with one family.
Dicranales	with seven families.
Pottiales	with three families
Grimmiales	with one family

Funariales	with six familes
Schistostegales	with one family
Tetraphidales	with one family
Eubryales	with sixteen families
Isobryales	with twenty three families.
Hookeriales	with six families
Hypnobryales	with twelve families
Buxbaumiales	with two families
Diphysciales	with one family
Polytrichales	with one family
Dawsoniales	with one family

Of this long list the two important ones are the Funariales and the Polytrichales. The former includes 6 families and the latter only one. In this text has been considered the order Funariales.

FUNARIALES

The members included in this order are small, annual or biennial land mosses. They are characterised by the following features :—

(*i*) The leaves are sessile usually ovate in form with a drawn out broad base and generally arranged in a terminal rosette.

(*ii*) The broad capsule has a lid without a long beak.

(*iii*) The peristome teeth are arranged in two rows, the teeth of the inner ring are usually opposite the outer peristome.

The order comprises about 356 species grouped under 26 genera. They are allotted to 6 families which are the Gigaspermaceae, Funariaceae, Disceliaceae, Oedipodiaceae and Splachnaceae. Of these Funariaceae is widely known.

The members of the family **Funariaceae** grow in large dense patches. The other characteristic features of the family are :—

1. Leaves prominent, usually wide and one cell in thickness except the midrib.

2. Calyptra with a long, slender beak.

3. The pyriform capsule usually nodding at maturity, immersed or borne on a long, twisted seta.

The family comprises about 200 species. They are placed under nine genera. The best known and widely distributed genus of the family is *Funaria*. It is represented by more than half the number of species included in the family. Here we shall consider the life cycle of *Funaria*.

Systematic Position :

Bryophyta
  Bryopsida or Musci
    Bryidae
      Funariales
        Funariaceae
          Funaria (Schreb.)

Habit and habitat. *Funaria* is a common moss which grows in dense patches of bright, green colour. It usually grows in moist shady situations such as damp soil, shady banks, sometimes on the trunks of trees and on the walls. *Funaria* includes more than 117 species. Of these 15 species have been reported from India. *F. hygrometrica* is the most widely distributed species. It is said to prefer soils where there has been a fire.

GAMETOPHYTE

The gametophyte phase consists of two stages (Fig. 12·1). These are, (*i*) the **juvenile stage** represented by the **protonema** and (*ii*)

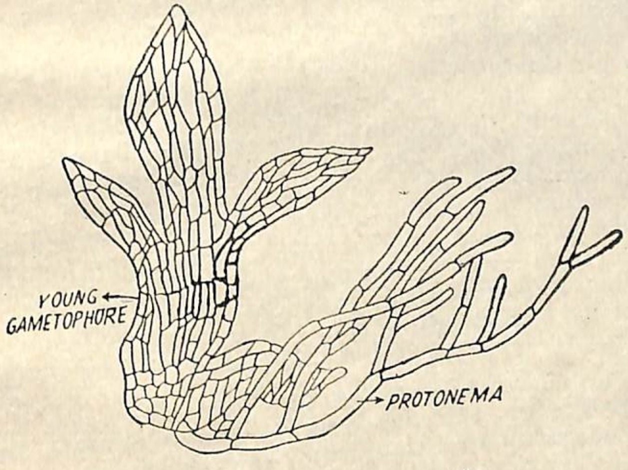


Fig. 12·1. Funaria hygrometrica.
Protonema bearing the young leafy gametophore.

the **leafy stage** represented by the adult leafy gametophore (Fig. 12·5A).

(*i*) *Juvenile stage* (Fig 12·22 C). It arises directly from the spore. When fully grown it consists of a slender, green, branching system of filaments called the **protonema**. The filamentous protonema branches freely. It forms a green, felt-like coating on the damp soil resembling algal growth. Many of the branches grow over the moist soil. They are green (chloronemal branches). The cells comprising them contain numerous, discoid chloroplasts and are separated by transverse cross walls. The other branches penetrate the soil. They are colourless or brown. The cells of these rhizoidal branches lack chloroplasts. They have oblique septa between them. The protonema stage in *Funaria* is only vegetative and transitory.

(*ii*) *Leafy stage.* It is the adult gametophore. It starts as a lateral bud on the protonema (Fig. 12·22 C). The bud develops into an erect, leafy shoot called the **gametophore**. The latter bears numerous rhizoids at its base which anchor it to the substratum. The protonema soon disappears. The leafy gametophore remains behind as the sole, independent and the most conspicuous representative of the gametophyte stage. It is also called the **moss plant**. It bears the sex organs.

Adult Gametophore.

(*a*) *External Features.* The mature *Funaria* plant (Fig. 12·5 A) has a slender, upright, central axis. It is about 13 mm. or a little more in height. It bears flat, green, lateral expansions inserted spirally. For convenience we call the central axis as **stem** and the green expansions as **leaves**. We cannot consider them as such for taxonomic purposes. Koch (1956) would call stems as **cauloids** and leaves **phylloids**. Besides these two principal organs of the moss gametophore, the third is the **rhizoid system**. It consists of numerous attaching filaments, the **rhizoids** which arise from the basal, naked, brown part of the stem. The rhizoids penetrate the substratum to a depth, at least, equal to the height of the leafy stem if not more. They are multicellular and branched. The septa between the cells are oblique and occur at long intervals. According to Goebel (1905) the oblique septa are an adaptation to promote rapid conduction. When young the rhizoids are colourless. The mature ones are coloured brown or dark brown.

The rhizoid system is analogous to the root system but more so to the root hairs. Like the latter the finer or ultimate branches of the rhizoid system are slender and colourless and have delicate cell walls. They are mainly absorptive in function like the root hairs. The older ones function in anchorage and conduction.

Because of their apparent **leaves, stem** and root-like **rhizoids** the *Mosses* might be mistaken for any small flowering plant. These structures, however, are neither homologous nor structurally similar to the roots, stems and leaves of the flowering plants. No doubt they perform the same functions. Such organs are called **analogous**. The Moss rhizoids, stem and leaves belong to the gametophyte stage. Their cells have nuclei with a **haploid** number of chromosomes. True roots, leaves and stems, as those of angiosperms, are sporophytic structures. The cells constituting them have $2n$ (**diploid**) number of chromosomes. These sporophytic organs are more complex. They show greater differentiation of tissues as compared with those of the *Mosses*. They have a well-defined and well-developed *epidermis* with stomata and guard cells (in the leaves and stems) and the vascular system. All these structures are absent in the stems and leaves of *Mosses*.

The so-called stem in *Funaria* is sparingly branched. The lateral branches arise from below the leaves. They are never axillary. The leaves are more crowded and large towards the apex. The spiral phyllotaxy is 3/8. The leaves are sessile and oblong-ovate in form with an entire margin and pointed apex. Each leaf has a distinct midrib and is inserted on the stem by a drawn out, fairly broad base.

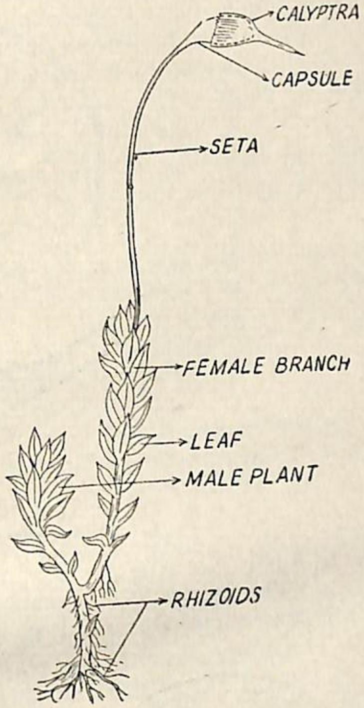


Fig. 12·2. Funaria hygrometrica. A leafy gametophyte bearing a nearly mature sporogonium at the apex of the female branch.

(*b*) Anatomy

(*i*) *Stem* (Fig. 12·3 A). A cross-section of the stem reveals a simple internal structure. There is no marked specialisation of cells. The cells are arranged in three distinct zones (Fig. 12·3 A); (*i*) the **central cylinder** or **strand**, (*ii*) the **cortex**, and (*iii*) the **epidermis**.

The **central cylinder** forms the core of the stem. It consists of vertically elongated, thin-walled, narrow, compactly arranged cells without protoplasm. It provides a certain amount of mechanical support. In addition it may function in the upward movement of water and solutes. Some botanists consider the central cylinder to be a vascular system of a primitive type. It has, however, no vascular structures like the vessels or tracheids characteristic of the true stems.

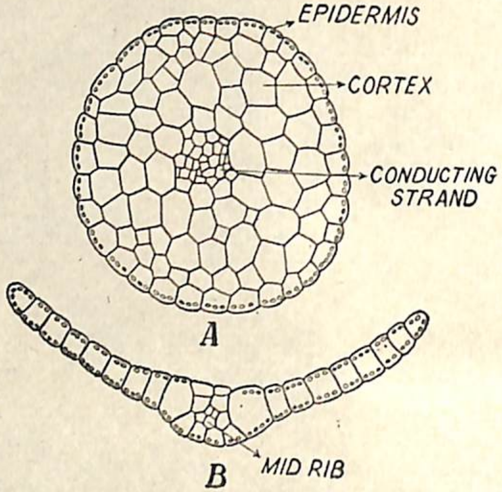


Fig. 12·3 (A—B). Funaria hygrometrica.
A. Transverse section of the stem.
B. Vertical cross-section of leaf.

The **cortex** is of a relatively greater thickness. It surrounds the central cylinder and is composed of undifferentiated, large, thin-walled, parenchymatous cells (Fig. 12·3 A). In young stems the cortical cells contain chloroplasts. The mature portion of the stem has the cortex usually differentiated into an outer, **thick-walled**, brown cortex and an inner, **thin-walled** cortex (Fig. 12·4). The latter lies next to the central cylinder.

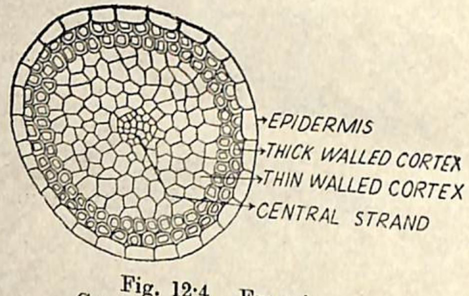


Fig. 12·4. Funaria.
Cross-section of stem through the older region.

The epidermis usually consists of a single surface layer of cells external to the cortex. The cells are small and contain chloroplasts in the younger portions of the stem. In the mature portions of the stem the epidermal cells become thick-walled and lack chloroplasts. The stomata characteristic of the true stems are absent.

(*ii*) *Leaf* (Fig. 12·3 B). Excepting the midrib the leaf consists of a single layer of undifferentiated parenchymatous cells. They are large and rectangular or hexagonal rectangular in surface view. The leaf cells are rich in chloroplasts which are comparatively

large and prominent. The marginal cells are specialized. They are narrow and thick-walled in contrast to the rest and afford strength to the frail moss leaves. The midrib is several cells thick. It has an upper and lower epidermis. Below the upper epidermis is a small group of thin-walled, large cells followed by a group of small, thick-walled cells with a narrow lumen. The structures characteristic of the leaves of the vascular plants such as the tracheids, the sieve tubes or the fibro vascular bundle are absent. There is no trace of the mesophyll tissue or the stomata.

True root in the *Mosses* is lacking. The rhizoids may perform some of the functions of roots such as anchorage and absorption of water and solutes from the soil.

Apical Growth. The stem grows by means of a single **apical cell**. It is located at the stem tip. The apical cell is pyramidal in shape. It cuts off segments parallel to its three sides. Each segment divides into an inner and outer part. The inner part divides to give rise to the major part of the stem. The outer part forms the leaves, buds and the outer part of the stem.

The growth of the leaf is carried on by means of a three sided apical cell. The rhizoids grow in length by means of an apical cell at the free end of each filament.

REPRODUCTION

Funaria reproduces by two methods which are **vegetative** and **sexual**. The production of meiospores is considered a stage in sexual reproduction by many botanists. The so-called leafy moss plant (**gametophore**) is concerned with vegetative reproduction and produces the sex organs. Production of meiospores is the function of a non-sexual individual which is the **sporogonium**.

1. Vegetative Reproduction

The gametophyte stage of *Funaria* is frequently propagated vegetatively by the following methods :—

(*i*) *Multiplication of the protonemal stage*. The primary protonema breaks into short fragments of living, green cells by the death of cells at intervals. Each detached fragment grows into a new protonema which bears a fresh crop of leafy gametophores.

(*ii*) *Secondary Protonema*. Filamentous protonema may also be formed from any cell of a detached injured portion of the stem, leaf and rhizoid when surrounded by moist air. It is known as the **secondary protonema**. From it arise the leafy gametophores as lateral buds in the same way as from the primary protonema.

(*iii*) *Bulbils*. These are small **resting buds** developed on the rhizoids or protonema. With the onset of conditions suitable for growth the bulbil produces a protonema which bears a crop of moss gametophores as lateral buds. According to the latest terminology the perennating structures produced on the rhizoids are called the **tubers**.

(*iv*) *Apospory*. Green protonemal filaments may arise from the unspecialised cells of the various parts of the sporogonium. These protonemal filaments bear lateral buds each of which develops into a leafy gametophore. The production of leafy gametophytes directly from the vegetative cells of the sporogonium without the intervention of spores is called **apospory**. The aposporously produced gametophores are normal in appearance. Genetically they are diploid.

2. Sexual Reproduction

Distribution of Sex Organs. Sexual reproduction takes place, as in the other bryophytes, by the formation of **antheridia** and **archegonia**. They are borne on the leafy gametophore and are never sunken. On the other hand they project freely from the surface of the plant. The sex organs are developed in **terminal clusters**. The formation of sex organs thus limits the growth of the vegetative axis.

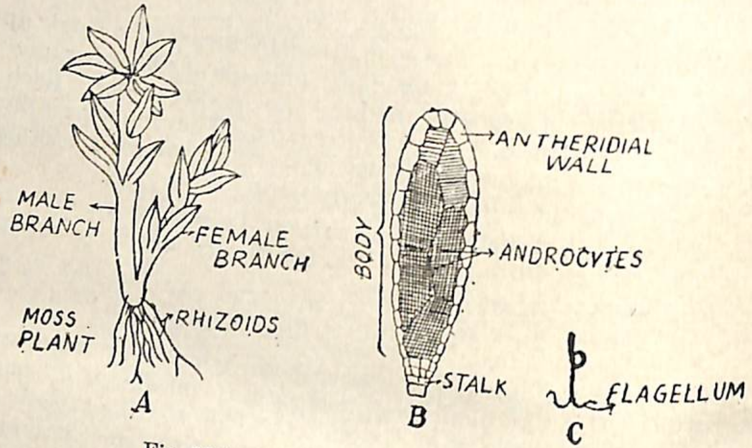


Fig. 12·5 (A—C). Funaria hygrometrica.
A. Gametophyte plant (Monoecious and autoicous).
B. Antheridium in section.
C. Sperm.

Apparently *Funaria* looks **dioecious**. In reality it is **monoecious** (Fig. 12·5 A). The antheridia are formed at the summit of a relatively small, main leafy shoot. Funaria is **protandrous**. The male shoot develops first. It is in fact the parent plant. The female branch arises later as a lateral outgrowth from the base of the parent male shoot. When the two kinds of sex organs are borne in separate clusters on two distinct branches of the same plant the arrangement is said to be **autoicous** and species **monoecious**.

Antheridia.

(*i*) *Position and Structure*. The antheridia are closely packed at the slightly flattened tip of the male shoot to form the male receptacle. To the naked eye the antheridial cluster appears as a tiny

orange spot (Fig. 12·6). The leaves surrounding the antheridial cluster are comparatively small. The small perigonial leaves are closely set and spread out in the form of a rosette to give protection to the sex organs. The central part of the rosette is of reddish colour. The antheridial cluster with the surrounding leaves is called the **perigonium**. The orange coloured mature antheridia and the rosette-like arrangement of the perigonial leaves make the male shoot conspicuous and easily recognisable. Antheridia at various stages of development occur in a single male receptacle which is thus capable of releasing sperms in succession over a long period extending over several weeks.

Associated with the antheridia in the cluster are numerous, green, sterile, hair-like filaments. They are multicellular and upright with large capitate heads and are called the **paraphyses** (Fig. 12·6 and 12·7 J). Each paraphysis is usually 4 to 5 or 6 cells in height. It consists of a single row of cells. The top cell is large and nearly sub-spherical in outline. The cells below it are elongated and narrow. All the cells are rich in chloroplasts. The top cells of the paraphysis meet over the antheridia. Thus the paraphysis afford protection and help to a limited extent in photosynthesis. Lorch (1931) suggested that they help to conserve moisture around the antheridia either by holding or secreting water. The water is held between them by capillarity. The other suggestion is that the paraphyses secrete mucilage which protects the young antheridia from undue water loss and also assists in the efficient discharge of sperms by building up pressure.

The mature **antheridium** (Fig. 12·5 B) of *Funaria hygrometrica* may be 0·25 mm in length. It has an elongate, club-shaped, orange coloured body seated on a short, multicellular stalk. The body has a jacket layer of polyhedral, flattened cells. The cells of the single layered wall contain chloroplasts when the antheridium is young. As it ripens the chloroplasts change into orange-coloured chromoplasts. Within the antheridial wall is a dense mass of small cells. They are known as the **androcytes**. Each androcyte produces a single biflagellate **sperm**. At maturity the free distal end of the antheridium is differentiated into a **cap-like** structure. It is the **operculum**. It consists of one or two cells and is formed from the apical cell of the young antheridium. The cells of the operculum are comparatively large in size. They have thicker walls and colourless contents.

(*ii*) *Dehiscence* (Fig. 12·6). The antheridia dehisce only in the presence of water. It is provided by rain or dew. On the access of water the walls of the opercular cell or cells become mucilaginous. They absorb water and swell. The pressure within the opercular cell eventually becomes sufficient to rupture, at first, its inner and latter the outer wall or break its connection with the adjacent cells. This distal rupture forms an open pore to the exterior. The pore, of course, is a small or narrow one. Through this pore oozes a slow stream of a viscous fluid containing the sperms still enclosed within their vesicles. The escape of the vesicles containing sperms is facilitated by the contraction of the distended antheridial wall and

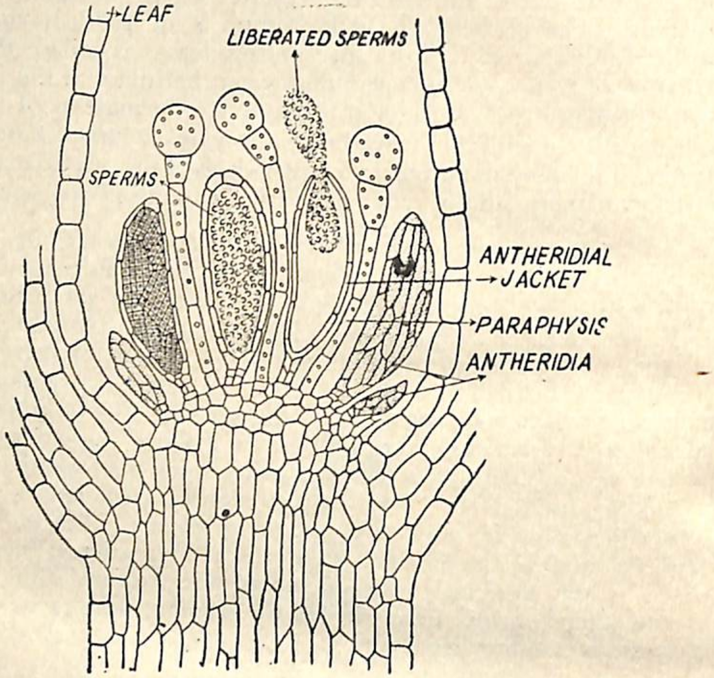


Fig. 12·6. Funaria hygrometrica
Longitudinal section through the tip of the male shoot.

the resultant hydrostatic pressure of the swollen contents within the antheridium. Soon after emergence, the extruded mass of vesicles floats to the surface of water surrounding the antheridial cluster. There the vesicles separate from each other and spread out in the form of a delicate, thin film. With the dissolution of vesicles the biflagellate sperms are set free (Fig. 12·7 I). They swim about actively in water that caused the rupture of the antheridium. The liberated **sperm** is an elongated, spirally coiled, biflagellate structure. The empty antheridia wither and die.

(*iii*) *Development* (Fig. 12·7). The antheridia develop from the superficial embryonic cells including even the apical cell at the expanded tip of the male shoot. Each antheridium originates from a single such cell. It is called the **antheridium initial** (Fig. 12·7 A). The antheridium initial grows into a **papillate** outgrowth. The latter projects above its neighbours. The papillate initial divides by a transverse wall into two cells (Fig. 12·7 B). Of these the inner or basal cell forms the embedded portion of the antheridial stalk. The outer or distal cell forms the entire antheridium.

In the outer cell there follows transverse segmentation. This results in a row of 2 or 3 cells (Fig. 12·7 C). The terminal cell of

the row henceforth functions as an **apical cell** with two cutting faces (Fig. 12·7 D). It cuts off segments alternately right and left by

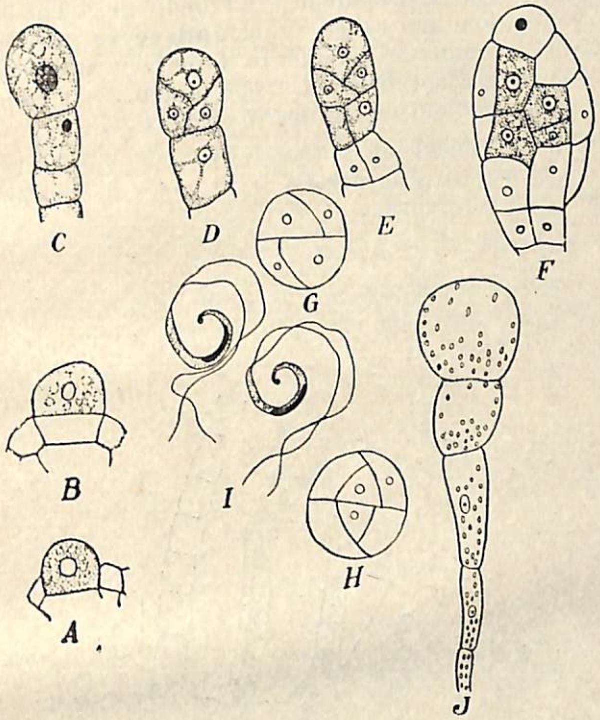


Fig. 12·7 (A—J). Funaria hygrometrica.
A—F. Stages in the development of the antheridium (median longitudinal sections).
G—H. Transverse sections.
I. Two sperms.
J. Paraphysis.

successive walls parallel to its cutting faces (Fig. 12·7 E). In this way 5-7 or even more segments are cut off. They are regularly arranged in two rows (Fig. 12·7 F). One of these segments which is 3 or 4 cells away from the apical cell divides by a periclinal wall (Fig. 12·7 G). Thereafter the segments above it (towards the apex) begin to divide in the same way. All these segments have denser contents than the remaining cells. The latter form the exposed portion of the stalk of the antheridium. The periclinal division in each segment with denser contents is in a diagonal vertical plane (Fig. 12·7G). The division is thus asymmetrical. The smaller daughter cell functions as the first **jacket initial**. The larger sister cell undergoes another similar division. It separates a **second jacket** initial on the outer side and a **primary androgonial cell** on the inner side (Fig. 12·7H). All the jacket initials divide only by anticlinal divisions to form a single layered wall of the antheridium. The apical cell forms the operculum or cap region of the antheridial wall. The antheridial wall encloses the primary androgonial cells. The latter divide and redivide. The cells of the last cell generation are called the **androcyte mother cells.** Each androcyte mother cell divides to form two **androcytes**. The division, however, is not diagonal. The protoplast of each androcyte gives rise to a single biflagellate sperm (Fig. 12·7 I).

The development of antheridia in the cluster is not simultaneous. Consequently antheridia at all stages of development may be found in the same cluster.

Archegonia.

(*i*) *Position and Structure* (Fig. 12·8). The archegonial branch springs from the base of the male shoot. The leaves surrounding the archegonial cluster (perichaetial leaves) overlap and close over at the top to protect the archegonia. Intermingled with archegonia in the cluster are the paraphyses.

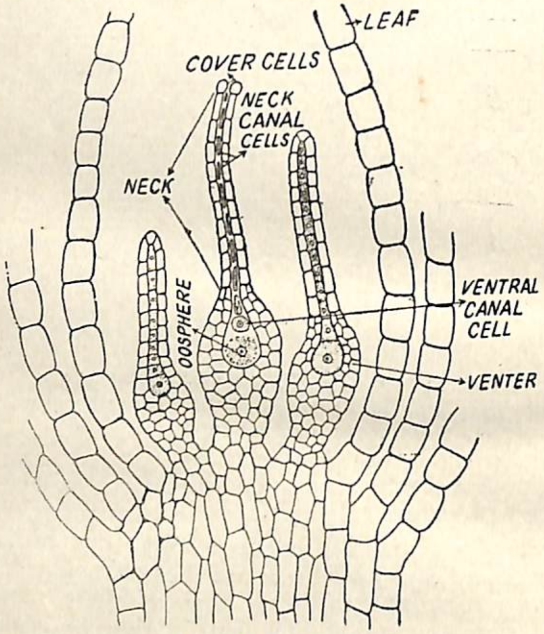


Fig. 12·8. Funaria.
Longitudinal section through the tip of the female branch.

The archegonia are typically flask-shaped (Fig. 12·8), each consisting of the two usual parts, the **venter** and the **neck**. It is borne on a distinct, multicellular stalk which is long and massive. The venter has a venter wall (jacket layer) of sterile cells two cell layers thick. In the hollow of the archegonial venter (**venter cavity**) is housed the **egg** and a **ventral canal cell** above. The long, tubular slightly twisted neck consists of six rows of neck cells which enclose an axial row of ten or more intensely protoplasmic **neck canal cells**. The archegonium is thus similar in structure to that of the liverworts differing only in the following respects :

(*i*) A long, massive, well developed stalk.

(*ii*) Somewhat enlarged venter with a two cell layers thick venter wall.

(*iii*) A long, twisted neck with a larger number of neck canal cells.

(*ii*) *Development* (Fig. 12·9). The archegonia arise from the embryonic cells at the tip of the archegonial branch including even the apical cell itself. Each archegonium develops from a single such cell. It is called the **archegonium initial** (Fig. 12·9 A). According to Campbell the archegonium initial in *Funaria* divides by a transverse wall. It separates a basal from a terminal cell (Fig. 12·9 B). The former divides and redivides to form the stalk of the archegonium. The terminal cell functions as the **archegonium mother cell**. It divides by three oblique walls to produce three **peripheral cells** surrounding a central **axial cell** (Fig. 12·9 C).

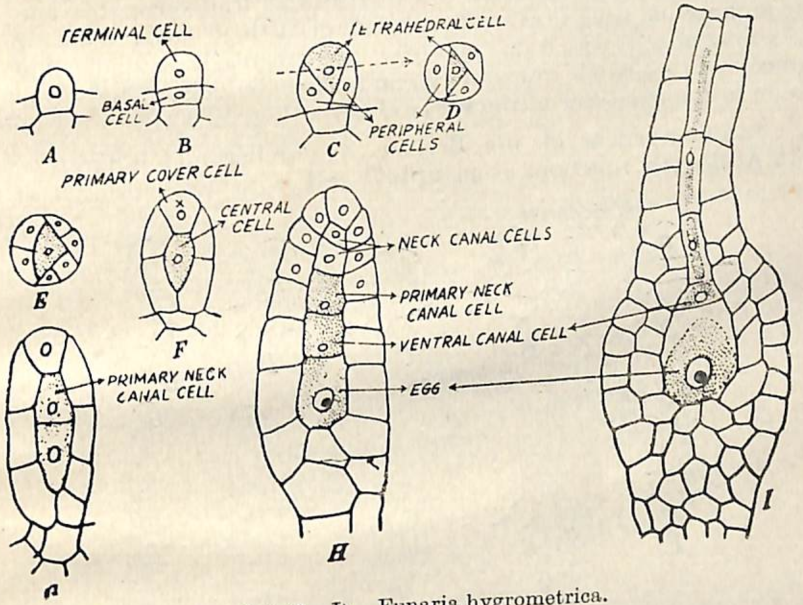


Fig. 12·9 (A—I). Funaria hygrometrica.
Development of Archegonium.

A—C, F and G. Early stages in longitudinal sections.
D and E. Transverse sections of the same.
H and I. Later stages in the development. (Diagrammatic).
(F, G and I after Campbell).

The latter is tetrahedral in form and is pointed below. The three peripheral cells undergo segmentation to form the single layered jacket or wall in the venter portion of the archegonium (Fig 12·9 F). During further growth it is doubled. The axial cell divides transversely to separate an inner cell from an outer cell (Fig. 12·9 F). The former functions as the **central cell** and divides to give rise to the **primary neck canal cell**, the **ventral canal cell**, and the **egg** (Fig. 12·9 G and H). The outer cell which corresponds to the **primary cover cell** of the liverworts behaves in a different way (Fig 12·9 F). It functions as an **apical cell** with four cutting faces, three lateral and one basal (Fig. 12·9 H). The apical cell thus cuts off four rows of segments. Three of these are lateral and one basal. The three lateral rows of segments function as **neck cells.** Each of these divides by a vertical wall to form six rows. The number of cells in each row increases by transverse cleavage. The archegonial neck thus finally consists of a single layer made up of six rows of cells which at maturity are irregularly twisted. The segments of the basal row undergo no further division. They contribute to the axial row of **neck canal cells** (Fig. 12·9 H).

In other genera of the Bryidae the archegonial initial (Fig. 12·10 A) directly functions as an **apical cell** with two cutting faces

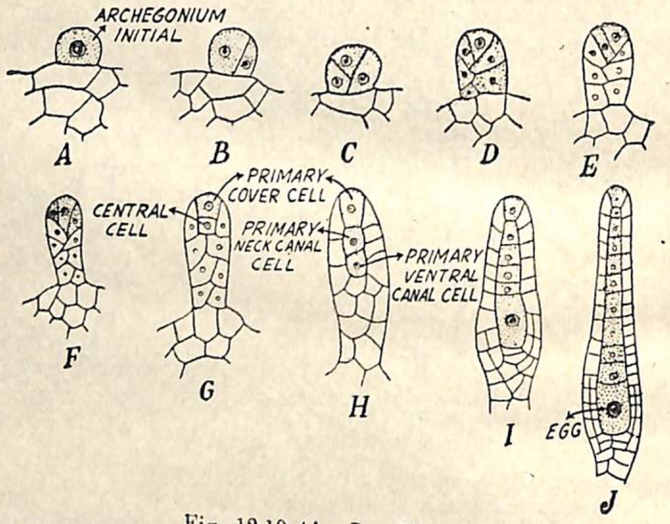


Fig. 12·10 (A—J). Moss.
Stages in the development of archegonium (median longitudinal sections).

(Fig. 12·10 B and C). It cuts off two rows of 4 to 8 segments by alternate cleavages (Fig. 12·10 D—F). These segments get bisected and in the course of time form the columnar stalk of the archegonium. Distally the apical cell is still there and active. However, it changes abruptly in nature. It assumes a tetrahedral form with a truncated base. It has three cutting faces. It cuts off three segments by walls parallel to each of its three lateral faces. Each of

these lateral segments divides by a vertical wall to form six **jacket** **initials**. The jacket initials surround the apical cell (Fig. 12·10 F). The latter henceforth functions as the **primary axial cell**. From the six jacket initials is formed the major part of the wall of the archegonium. It is doubled in the region of the venter.

With the differentiation of jacket initials the primary axial cell undergoes a transverse cleavage (Fig. 12·10 G). It separates the lower **central cell** from the upper **primary cover cell**. The central cell divides transversely to produce an upper **primary** **neck canal cell** and a lower **primary ventral cell** (Fig. 12·10 H). The latter eventually gives rise to the **ventral canal cell** and the **egg**. The primary neck canal cell by transverse segmentation forms an axial row of **neck canal cells** which occupy the median and the lower portion of the neck. The upper portion of the neck and the neck canal cells which fill it are formed from the derivatives of the primary cover cell which functions as an **apical cell** for some time. The segments cut off parallel to its three lateral faces form the upper part of the wall of the neck. The canal cells in this region are formed from the segments cut off from the truncated base of the apical cell.

Fertilisation (Fig. 12·11). Fertilisation can take place only when the archegonial and the antheridial clusters contain water provided by the rain or dew. On the access of water the antheridium ruptures at its distal end. The spirally coiled biflagellate sperms escape freely into the water surrounding the antheridial cluster. In the archegonial cluster the ripe archegonia have their neck canal and ventral canal cells break down to form a slimy mass. The latter swells. As a result the lid or cover cells are forced apart. The archegonial necks open at their tips (Fig. 12·11).

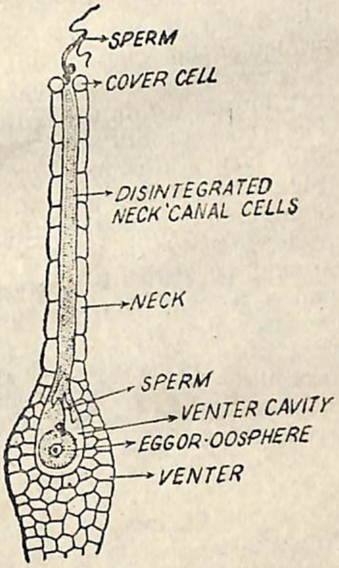


Fig. 12·11. Funaria sp.
Mature archegonium showing fertilisation (Diagrammatic).

The actual transfer of sperms to the archegonia in the autoicous Mosses, in which the two kinds of sex organs are borne on different branches, needs the help of some external agency. They may be transported in either of the following ways :—

1. The archegonial cluster on the female branch is situated at a lower level than the antheridial cluster on the main shoot. The water containing sperms may thus trickle down from the antheridial cluster at a higher level to the archegonial cluster at a lower level.

2. The rain drops falling on the antheridial cluster may splash the sperms on to the archegonial cluster situated at a lower level.

3. The sperms may be transported by the water currents to the neighbourhood of archegonia when the moss plants are submerged at the time of heavy rains.

4. There is a suggestion that the small, microscopic insects like mites, which visit the antheridial and the archegonial clusters for mucilage secreted by the paraphyses, serve as agents for carrying the sperms from the antheridial cluster to the water in the archegonial cluster.

Reaching the archegonial cluster the sperms swim to the archegonia. The source of attraction is the cane sugar present in the slimy mass given out from the open archegonial necks. Thus guided the sperms reach the archegonia. Eventually they enter the open necks and swim down their neck canals to reach the egg in the venter (Fig. 12·11). Only one sperm unites with the egg to accomplish fertilization. More than one archegonia may be fertilised. Normally only one zygote develops into a sporophyte.

Post-fertilisation Changes (Fig. 12·17 A—G).

The fertilised egg secretes a wall around it and is called the **zygote**. It increases in size and enters upon active segmentation. The segments are cut off alternately by two growing points, each located at the opposite end. The early development of the embryo in *Funaria* is thus **apical** (Fig. 12·17 E and F). A mass of cells is soon formed within the venter (Fig. 12·17 G). It is the **embryo**. The cells constituting the embryo divide, redivide and grow with little tissue differentiation. It becomes a long, slender structure (Fig. 12·17). The growth of the embryo is accompanied by the resumption of growth by the venter. The latter for a time keeps pace with the developing embryo and forms a protective covering around it. It is the **calyptra**. The lower end of the embryo makes its way through the stalk of the archegonium into the top of the female branch. The young sporophyte is thus surrounded by the tissues of the parent gametophyte. It take its nourishment from these tissues. The upper part of the embryo undergoes a high degree of differentiation and specialization to grow into a full-fledged **sporophyte**.

SPOROPHYTE

Production of Meiospores. The sporophyte originates from the zygote. It is the diploid, asexual individual usually called the **sporogonium**. The production of spores and their efficient disperal are its sole functions.

(*a*) **External Morphology of Sporogonium**. Funaria is an **acrocarpous** moss which means that the fruit or sporogonium is located at the distal end of the female branch (Fig. 12·2). The latter has by now outgrown and replaced the main shoot. The sporogonium is a complex and highly elaborate structure. It is differentiated into the **foot**, the **seta** and the **capsule**.

Foot. The foot forms the basal portion of the sporogonium. It is a small, dagger-like, conical object. In *Funaria it* is poorly developed. It is embedded in the tissues of the tip of the leafy female branch and functions both as an **anchorage** and an **absorbing** organ. It absorbs water and nutrient salts from the parent plant for the sporophyte. It is similar in function to the root of the fern plant. Both the organs are sporophytic structures. However, they are not homologous to each other. The two are quite different in their origin, in structure and to some extent in their nature of absorption.

Seta. The seta is a long, slender but tough, redish brown, stalk-like structure. It carries the capsule at its top and raises it more than an inch above the apex of the leafy gametophore. The seta is homologous to the stem of the Pteridophytes. The two are quite similar in origin and function. They differ only in the complexity of structure. The seta has a simple structure but shows more tissue differentiation than in the liverworts. It is differentiated into a central strand of small, thin-walled cells surrounded by a region of thick-walled cortex and epidermis. The central strand functions as a primitive type of vascular system. The thick-walled cortex gives strength to the slender seta. It enables the seta to bear the weight of the capsule. Conduction and support thus are the two functions of seta. The dry seta in the mature sporogonium is wavy and twisted. It is hygroscopic. In the humid atmosphere it becomes untwisted. As it does so the capsule at its summit swings round and round. When the air dries up its movements are reversed. The capsule now swings in the opposite direction.

Capsule. (Fig. 12·12 A). The capsule is a highly organized

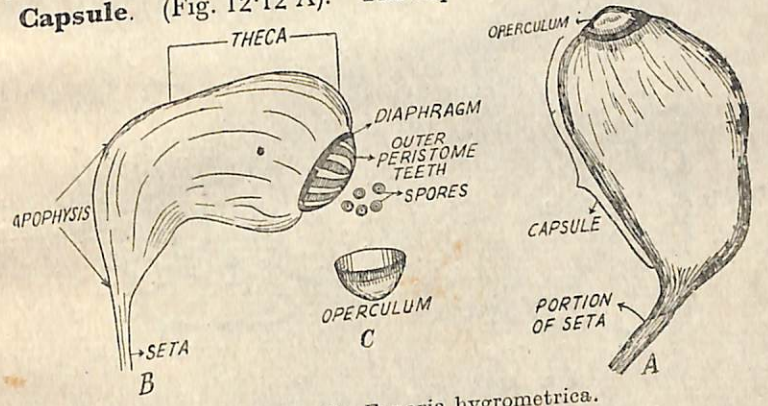


Fig. 12·12 (A–C). Funaria hygrometrica.

A. Mature capsule.
B. The same with the lid or operculum removed and outer peristome teeth exposed.
C. Detached operculum.

structure. It is pear-shaped and green at first but later turns yellow and then orange. Its upper portion is covered by a conical hood or a cap, the **calyptra** (Fig. 12·2). At first the capsule is upright on the seta. As it advances towards maturity it becomes pendent (nodding). Eventually it turns dark brown. The calyptra falls off laying bare its apex. The capsule is concerned with the production and dispersal of spores. Externally it shows three well marked regions, each specialized to perform a definite function. These regions are the (*i*) **apophysis**, (*ii*) **operculum** and (*iii*) **theca**.

The apophysis (Fig. 12·12 B) is the solid, somewhat swollen, basal, green portion of the capsule. It is the **photosynthetic region** of the capsule. It also helps in the conduction of water and food materials.

The apophysis is continuous above with a more swollen, urn-shaped, fertile region of the capsule called the **theca**. The theca forms the major and middle part of the body of the capsule. It is primarily a **spore producing region** of the capsule.

Above the theca, forming the apical portion of the capsule, is an obliquely placed cap-like structure. It is the **lid** or the **operculum** (Fig. 12·2). The latter functions in the **dehiscence** and the **dispersal** of spores. There is a well marked line of junction that delimits the operculum from the rest of the capsule. It is the **annulus**.

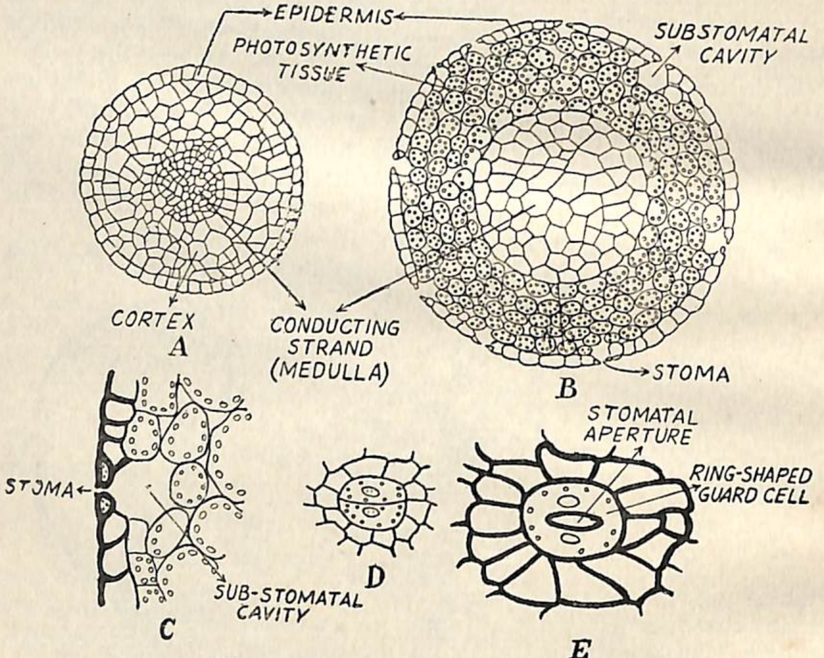


Fig. 12·13 (A—E). Funaria hygrometrica.
A. Transverse section seta.
B. Transverse section through apophysis.
C. A portion of B magnified to show stoma, substomatal cavity and photosynthetic tissue.
D. Young stoma in surface view.
E. Mature stoma in surface view.

(*b*) **Internal Structure of Capsule** (Fig. 12·15)

(*i*) *Apophysis*. On the outside the apophysis is covered by an **epidermal layer** (Fig. 12·15 B). Stomata occur in the epidermis. In structure the stomata are similar to those of the higher plants. Each stoma has a stomatal aperture guarded by two guard cells. Later the septa between the guard cells break down. In a mature stoma the aperture is thus surrounded by a ring-shaped guard cell (Fig. 12·13 E). Each stoma leads into an air space below called the **substomatal cavity**. Within the epidermis is a broad **spongy zone** of sterile cells rich in chloroplasts. There are distinct intercellular spaces between these cells. The spongy zone surrounds the central conducting strand composed of thin-walled, narrow, vertically elongated cells devoid of chloroplasts. The central strand is continuous below with the central strand of the seta. Above it is linked with the columella by means of a bundle of filaments (Fig. 12·15). Each filament consists of a few thin-walled, vertically elongated cells.

(*ii*) *Theca*. The capsule wall in this region is highly differentiated and several cells in thickness. The outermost layer is the **epidermis** (Fig. 12·15). It is continuous with the epidermis of the apophysis but contains fewer stomata. The cells within

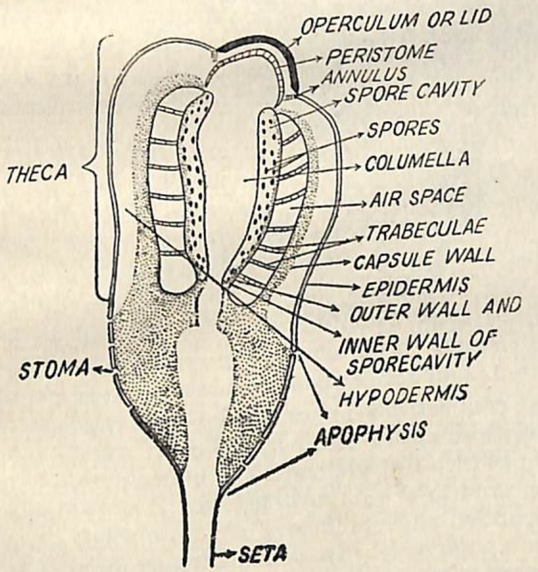


Fig. 12·14. Funaria hygrometrica.
Outline sketch of a median longitudinal section of capsule.

the epidermis are colourless. These colourless parenchymatous cells are compactly arranged in two hypodermal layers and constitute the **hypodermis**. Within the hypodermis is the **spongy layer**. It is one or, at the most, two cells in thickness. The cells constituting the spongy layer contain chloroplasts and are loosely arranged. The spongy layer is continuous with that of the apophysis where it becomes broader.

Within the capsule wall is a wide, cylindrical **air space** (Figs. 12·14 and 12·15). It is traversed by strands of narrow, elongated, green cells. These strands of green cells are called the **trabeculae**.

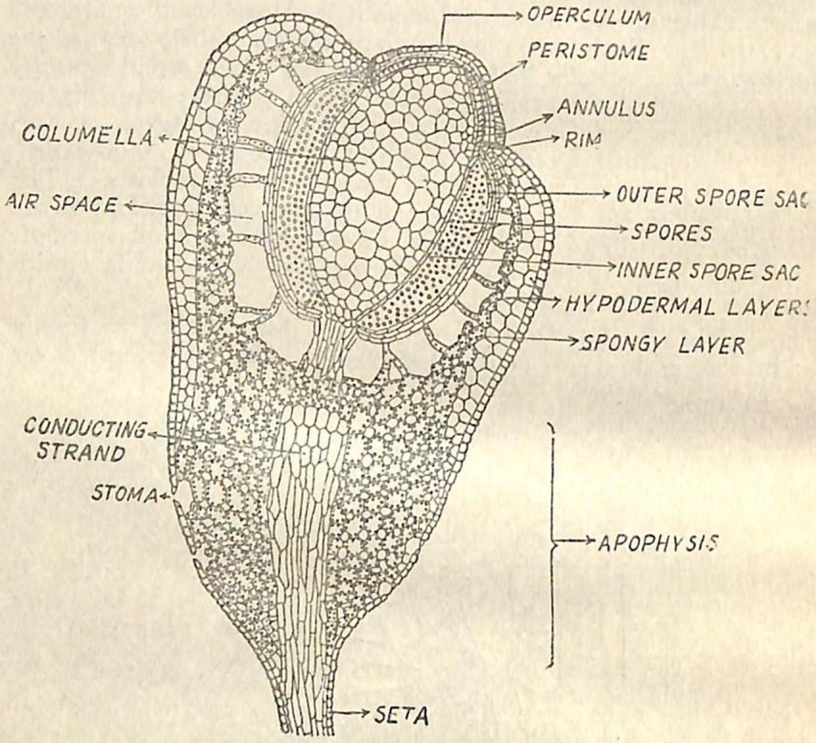


Fig. 12·15. Funaria hygrometrica. Longitudinal section of a mature capsule.

The trabeculae connect the innermost layer of the capsule wall with the outer wall of the **spore sac**. In the centre of the theca region is a solid cylinder of pith-like (delicate, colourless, compact parenchyma) cells. It is referred to as the **columella**. The columella is narrow below and expanded above. Below it is connected with the central strand of the apophysis. Just outside or surrounding the columella is the **spore sac**. It is a barrel-shaped structure open above and below. It surrounds the columella. The inner wall of the spore sac, often referred to as **inner spore sac**, is one cell in thickness. The outer wall or **outer spore sac** is three or four cells in thickness. These cells are colourless. Between the inner and the outer walls

is the cavity of the spore sac. It contains numerous **spores** at maturity but no **elaters**. The spores are formed from the spore mother cells in tetrads. In their formation the diploid nucleus of the spore mother cell undergoes the usual meiotic division. The spores are thus **haploid**. They are the first cells of the gametophyte generation.

(*iii*) *Operculum or Lid* (Fig. 12·15). The terminal, obliquely placed, conical, cap-like portion of the capsule is the **operculum**. It consists of 4 or 5 layers of cells. The inner 3-4 layers of cells are composed of small, thin-walled parenchyma cells. This thin-walled tissue forms the major portion of the operculum. It is bounded by a surface layer which consists of cells with greatly thickened walls. It is the **epidermis**. The operculum. at first, is continuous with the theca region. Eventually it becomes delimited by the appearance of a narrow, circular constriction. Below the constriction are 2-3 layers of special, radially elongated, thick-walled cells. These form a circular **rim** or **diaphragm**. The latter constitutes the upper end of the open theca. It joins the epidermis to the peristome within and is perforated in the centre by the thin-walled tissue in continuation with the columella.

Immediately underneath the operculum lies the **peristome** (Fig. 12·12 B). It consists of two sets of long, conical teeth, one within the other. There are sixteen teeth in each set. The teeth of both the sets are on the same radii and thus opposite to each other. The tapering distal ends of the teeth of the outer set converge towards each other and are united terminally in a small central disc of tissue. The peristome teeth close the opening of the spore sac. They are attached at the base to the rim or the diaphragm. The peristome teeth are elaborately sculptured. They are highly hygroscopic (Fig. 12·16) and thus play an important role in the dispersal of spores.

Fig. 12·16. Funaria hygrometrica. Peristome teeth (outer and inner).

Above the rim of the theca forming the broadest lower part of the operculum is the **annulus** (Fig. 12·15). It consists of 4 or 5 layers of cells (Fig. 12·21 C). The upper two or three layers form a special ring of modified cells constituting the edge of the detached operculum. The lower two layers constitute the annulus proper. It consists of thin-walled cells with distended form. By the destruction of these thin-walled annulus cells the operculum is, at first, loosened and later dropped of.

The remarkable feature of the moss capsule is its extremely reduced archesporium or fertile tissue as compared with its sterile tissue. The **sterile tissue** composing the capsule can be divided into the following four regions :—

(*i*) The sterile cells constituting the apophysis.

(*ii*) The sterile cells forming the several layers thick capsule wall.

(*iii*) The sterile cells forming the columella.

(*iv*) The sterile cells constituting the operculum and the peristome.

There is a suggestion that the **capsule** bears a rough resemblance to a **true leaf** of the pteridophytes. It is eminently fitted to carry on photosynthesis. In case we take the homology to be correct the **spore sac** will then correspond to the **sporangium**.

(*c*) Dehiscence of Capsule.

The mature capsule begins to dry up. Consequently the thin-walled cells of the operculum within the epidermis and the thin-walled cells of the annulus proper which hold the operculum in place, shrink and shrivel. This causes strain and eventual breakdown of the thin-walled cells. As a result the operculum is loosened from the underlying tissue. Soon it drops off exposing the peristome which form a fringe around the mouth of the opened capsule (Fig. 12·12 B). Dropping off of the operculum is said to be assisted by the upward hygroscopic movement of the underlying peristome teeth. By this time the columella and the adjoining thin-walled tissues have shrivelled leaving a central cavity. It is filled with spores,

In wet weather the exposed, rough, hygroscopic peristome teeth bend inward. They close together covering the mouth of the cavity containing the spores. This prevents the escape of spores in wet weather. In dry weather the teeth bend outward. As they do so they separate from each other. Consequently the slits between them open. At this time assisted by the swinging round of the open capsule on the twisting hygroscopic seta the spores sift out gradually through these slits, a few at a time. The spores are thus liberated in the dry weather when they are most likely to be carried by the air currents. The spores also escape through the open mouth when the wind shakes the capsule.

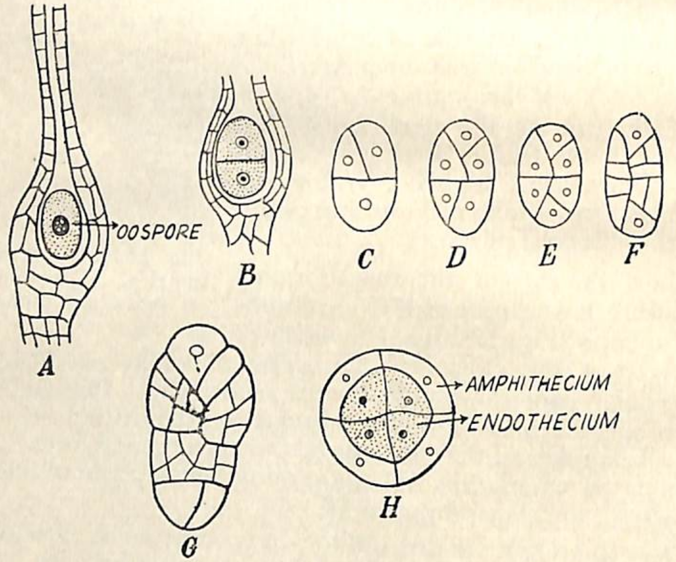


Fig. 12·17 (A—G). Funaria hygrometrica. Stages in the development of the embryo.
(Explanation in the text).

Development of Sporophyte (Fig. 12·17)

The sporophyte (sporogonium) originates from the diploid zygote. Its early development consists in the segmentation of the zygote. The details of segmentation of the zygote have been studied by many observers. They are as follows :—

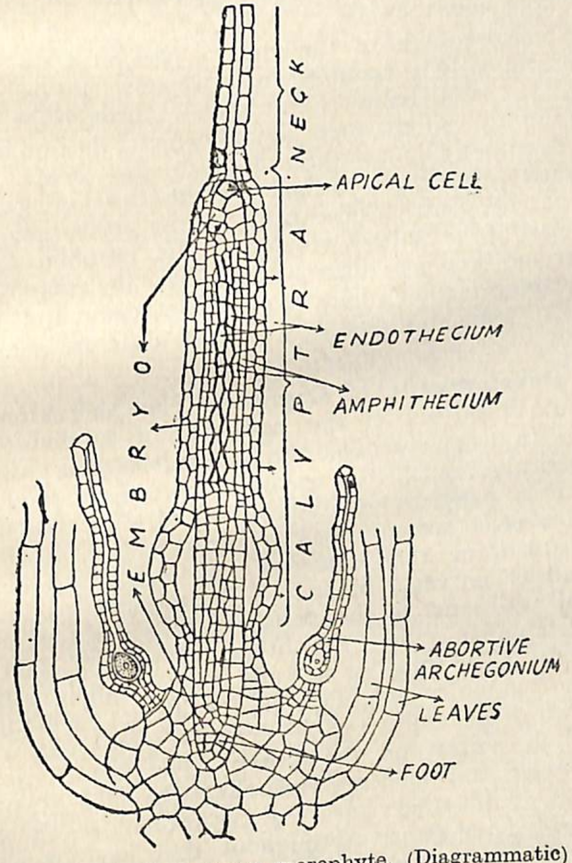


Fig. 12·18. Moss, young sporophyte. (Diagrammatic)

(1) **Segmentation of the Zygote**. The first division in the zygote is transverse (Fig. 12·17 B). It separates the upper **epibasal** half from the lower **hypobasal** half. Each of these regions undergoes two successive diagonal divisions. As a result an **apical cell** with two cutting faces is differentiated at each end (Fig. 12·17 C—E). The embryo thus grows from two growing points—a feature in sharp contrast to the other bryophytes. The two apical cells cut off segments right and left. These alternate cleavages from the two apical cells produce a spindle-shaped **embryo** (Fig. 12·17 G). The latter grows rapidly at the upper end. Here the segments are cut off in quick succession alternately right and left. The segments divide and re-divide to produce the capsule and the upper portion of the seta. The apical cell at the lower end of the embryo is not so active. The divisions at this end are less regular. The derivatives of the apical cell at this end differentiate into the foot and the lower portion of the seta.

The apical growth of the embryo goes on for a considerable time. Consequently it assumes an extremely elongated, cylindrical form (Fig. 12·18). Its lower end burrows through the archegonial stalk into the tip of the stem upon which the archegonium is seated. Eventually it enlarges to form the **foot**. The latter obtains water, nutrients and food for the developing sporophyte from the parent plant. Subsequent to the formation of the foot the upper part of the embryo elongates. Its terminal end enlarges in diameter and becomes differentiated into the **capsule region**. The narrow portion which joins the capsule region and the foot is the **seta**. It elongates gradually and is differentiated from the capsule late.

(2) **Development of Capsule**. The alternating segments cut off by the apical cell of the epibasal half subdivide with great regularity. In a cross-section the two alternating segments are nearly spherical (Fig 12·19 A) each being semi-circular in outline. Each of these segments divides by a radial vertical wall. The resultant four cells are arranged quadrately (Fig. 12·19 B). Each cell of the quadrant then undergoes an anticlinal division. The division wall is curved. Since it is in a plane perpendicular to an internal wall one of the daughter cells in a cross-section is nearly rectangular and the other more or less triangular (Fig. 12·19 C). The third set of walls are periclinal. They appear only in the rectangular daughter cells. With the formation of the periclinal walls the embryo in the capsule portion is divided into two regions, the **outer** and the **inner**. The former is called the **amphithecium** and the latter **endothecium** (Fig. 12·19 D). The endothecium, at this stage, forms a central column of four clearly defined rows. They extend throughout that part of the embryo which is destined to form the capsule. In a cross section the endothecium forms a central rectangular tract of four quadrately arranged cells (Fig. 12·19 D). It is surrounded by a single layered, eight celled amphithecium.

These two regions (the amphithecium and the endothecium) are the **primary** or the **fundamental embryonic** layers of the

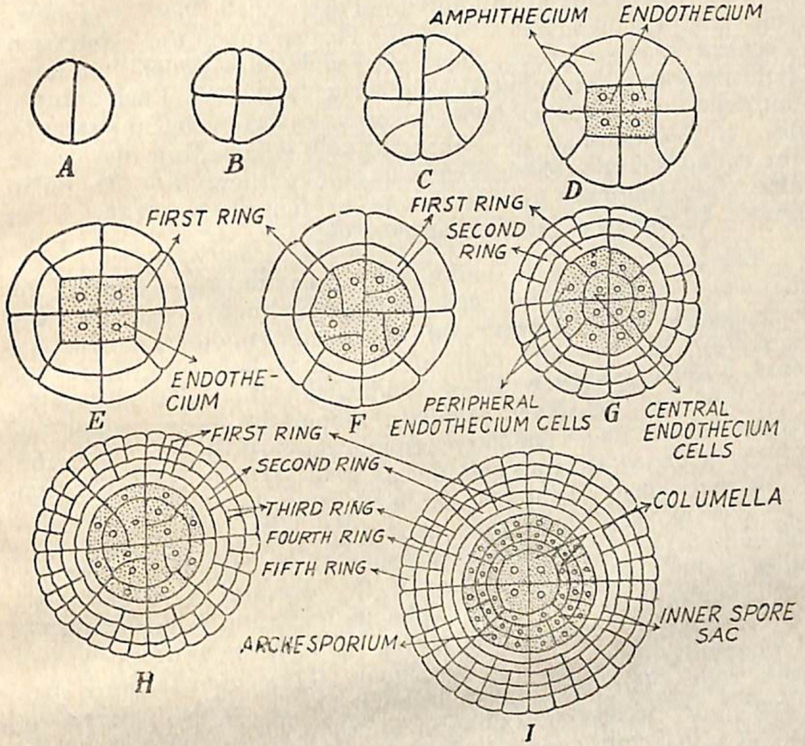


Fig. 12·19 (A—I). Funaria hygrometrica.
Diagrams of transverse sections of young capsule showing stages of development at successive levels below its apex.
A—D. Differentiation of amphithecium and endothecium.
E—I. Differentiation of five rings of cells from the amphithecium.
(Diagrammatic)

sporogonium. They are recognisable though to a lesser extent in the epibasal segments of the seta region as well. The inner region corresponding to the endothecium forms the central strand in the region of seta. The outer corresponding to the amphithecium forms the cortex. For the sake of convenience and clarity we consider the differentiation of tissues in the three well defined regions of the capsule separately as follows :

(*a*) **Differentiation of Tissues in the Middle or the Theca Region :**

(*i*). **Fate of the Primary Endothecium**. The next divisions appear in the amphithecium but we first trace the destiny of the endothecium. The four central quadrately arranged cells of the endothecium undergo cleavage in the same way as the four cells of the quadrants at the apex of the embryo (Fig. 12·19 C and D). The first walls are curved and anticlinal (Fig. 12·19 F). The following ones are periclinal (Fig. 12·19 G). This results in the separation of a central group of four endothecial cells surrounded by a layer of eight peripheral endothecial cells (Fig. 12·19 G). Each central endothecial cell undergoes two successive divisions by intersecting walls. In this way a group of about 16 cells is formed in the centre of the endothecium. These eventually differentiate into the **columella**. The columella forms the core of the theca region of the capsule. It consists of large colourless cells.

The eight peripheral endothecial cells undergo cleavage by radial walls. The daughter cells divide periclinally. In this way two concentric layers, **outer** and **inner**, of endothecial cells are formed (Fig. 134 I). The cells of the outer layer constitute the **primary archesporium**. They divide at first by radial walls only. The cells of the inner layer remain small and are transformed into the **inner spore sac**. The latter remains one cell thick. The archesporium in *Funaria* is thus endothecial in origin. It is formed from the outermost layer of the endothecium. Originally it consists of a single layer of cells. It is thus extremely reduced forming but a small and narrow part of the theca region of the capsule. It extends neither to the base nor to the apex of the capsule. It is a barrel-shaped tract open at both ends. The archesporium cells may undergo sub-division to form two cell layers thick **sporogenous tissue**. All the sporogenous cells are functional. They mature into spore mother cells. The elaters are lacking. Each spore mother cell undergoes the usual tetrad division to produce four haploid spores. The four celled embryonic or primary endothecium in the theca region thus gives rise to :

(*i*) The columella.

(*ii*) The single-layered inner spore sac.

(*iii*) The sporogenous tissue with all the cells are fertile and functional. No elaters are formed.

(*ii*) **Fate of the primary Amphithecium.** Meanwhile the eight cells of the primary amphithecium have undergone rapid segmentation. They divide both periclinally and anticlinally in a definite pattern and regular sequence to produce five concentric layers or rings of cells. The first division in the 8 primary amphithecium cells is periclinal. Two concentric layers of 8 cells each are formed (Fig. 12 19 E). The 8 cells of the *inner layer* constitute the **first ring**. The latter is in contact with the archesporium. It consists of cells smaller in size. The cells of the first ring divide by radial walls to increase in number. The derivatives undergo periclinal divisions to form three to four layers of cells. These mature into the **outer spore sac**. The cells of the outer spore sac lack chloroplasts.

The *outer layer* external to the first ring consists of 8 larger cells. These undergo two successive divisions. The first is anticlinal and next periclinal. Two concentric layers of 16 cells each is the result (Fig. 12·19 G). The inner of these two layers is known as the **second ring**. The outer layer of 16 cells again undergoes segmentation. The 16 cells of the second ring undergo a radical change. They develop chloroplasts and elongate radially. Owing to the increase in diameter of the theca region intercellular spaces appear between the radially stretched cells of the second ring. They thus become separated from each other laterally by these intercellular spaces (Fig. 12·20). The air spaces become wider and extend from the base towards the top of the theca region. Finally these radially elongated cells divide by transverse walls to become short filaments of three or four chlorophyll containing cells. These are called the **trabeculae**. The latter extend across the air space and link the outer spore sac with the several layers thick capsule wall.

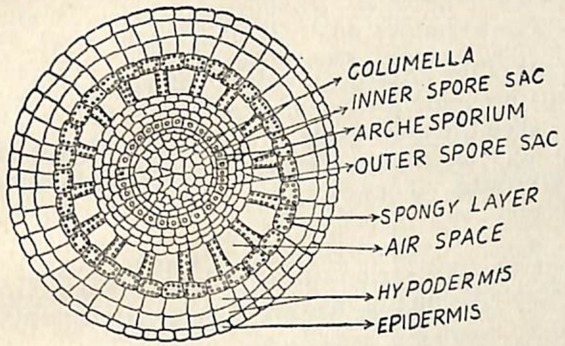


Fig. 12·20. Funaria hygrometrica.
Transverse section through the fertile portion of a young capsule. (Digrammatic).

The 16 cells of the layer external to the second ring undergo the anticlinal division followed by the periclinal one (Fig. 12·19 H). Two concentric layers of 32 cells each are produced. Of these the inner layer of 32 cells constitutes the **third ring**. The cells of the third ring develop chloroplasts. They mature into the inner layer of the capsule wall. It is called the **spongy layer**. It usually remains one or at the most becomes two cells thick in the theca region of the capsule.

The 32 cells of the layer external to the third ring divide only by periclinal walls. They do not undergo the anticlinal division. Two concentric layers of 32 cells each are formed (Fig. 12·19 I). The inner layer of 32 cells is known as the **fourth ring** and the outer **fifth ring**. The cells of the fourth ring later undergo periclinal divisions producing 2 to 3 layers of cells.

These mature into the **hypodermis** region of the capsule wall. The cells of the hypodermis are colourless as they lack chloroplasts. They are, however, larger in size and are thin-walled and parenchymatous.

The cells of the fifth ring divide by anticlinal walls only. They eventually mature into the single layered surface layer of the capsule wall. It is called the **epidermis**. The epidermal cells have greatly thickened walls. Here and there the epidermis is punctured with functional **stomata**. They are, however, more numerous in the apophysis region.

To sum up the various tissues derived from the primary or embryonic amphithecium in the theca region from without inwards are :—

(*i*) Single layered **epidermis**.

(*ii*) Two or three layers thick **hypodermis**.

(*iii*) One cell or at the most two cells thick **spongy layer**.

(*iv*) Short filaments of green cells or the **trabeculae** extending across the air space.

(*v*) Three or four cell layers thick **outer spore sac**.

(*b*) **Differentiation of Tissues in the Apical** *or* **Operculum Region** (Fig. 12·21, A—C). With the development of the theca region the apical portion of the capsule differentiates into a cone of tissues. It constitutes the **operculum** region. In this tissue originates the **peristome**. The surface layers of the operculum region cover the peristome.

(*i*) **Fate of Endothecium**. The operculum region originally consists of the same two embryonic layers. There is the central tract of four **primary endothecium cells** surrounded by a peripheral layer of 8 **primary amphithecium cells**. The former undergo repeated cleavage. A central mass of thin-walled parenchymatous cells in continuation with the columella is produced. The endothecium thus differentiates into that portion of the columella which lies in this region of the capsule.

(*ii*) **Fate of Amphithecium**. The eight primary amphithecium cells undergo the usual anticlinal and periclinal divisions (as in the theca region) to produce six concentric rings of amphithecium cells. It is from these rings that the **operculum** and the **peristome** tissues are differentiated as follows :—

Formation of Peristome. The account of the development of the peristome is mainly based on Proskauer's investigations (1958). The peristome in *Funaria* is developed from the **three**

inner rings of the amphithecium in the opercular region. The eight cells of the **first ring** undergo anticlinal divisions till this ring becomes 32 cells in perimeter. It is now called the **inner peristomial layer** (Fig. 12·21 A). The second ring which consists of 16 cells forms the **middle peristomial layer**. The cells in this layer undergo no division and thus determine the number of peristome teeth in each ring of the peristome of the mature capsule. The third ring which consists of 32 cells functions as the **outer peristomial layer**. The cells of the three peristomial layers are so disposed of with respect to one another that one cell of the middle layer is opposite two cells of outer and inner peristomial layers. These peristomial layers form a dome-shaped structure external to the columella in this region. From it are differentiated the **outer peristome** (**exostome**) and the **inner peristome** (**endostome**). The former originates at the juncture of the outer and middle peristomial layers. The **inner peristome** is formed at the juncture of the middle and inner peristomial layers. The next step is the deposition of additional wall material (cutin). It is laid on the tangial walls contiguous to the outer and middle peristomial layers in the case of outer peristome. In the case of the inner peristome the thickening wall material is

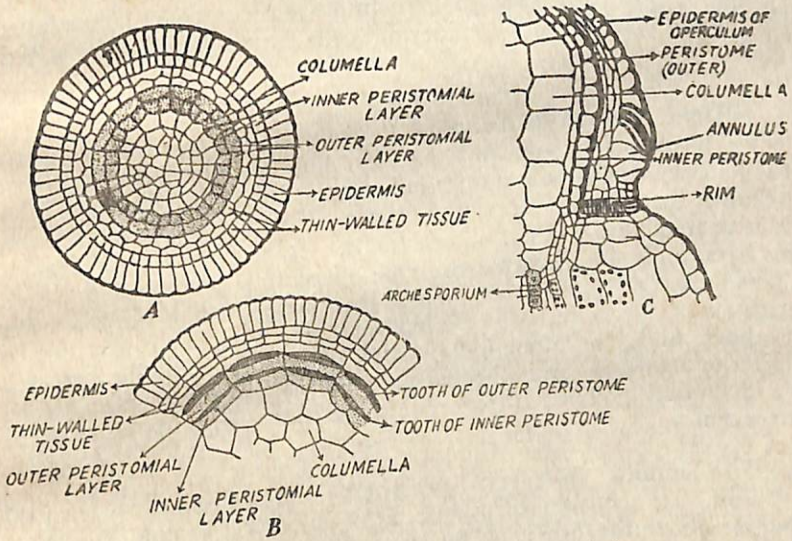


Fig. 12·21 (A—C). Funaria hygrometrica.

A. Transverse section through the operculum at a lower level.

B. A portion of the same from a still older capsule showing development of peristome teeth from the opposite walls of peristome cells.

C. A portion of a longitudinal section through the operculum and upper part of theca showing the relationship of peristome and rim.

deposited only on the outer wall of the inner peristomial layer (Fig. 12·21 B). The vertical anticlinal (radial) walls of the peristomial cells of the three layers undergo no noticeable thickening. It is along these unthickened anticlinal walls of the peristomial cells that splitting takes place. The unthickened radial cellulose walls and the contents of these cells disappear. Only the two thickened cutinized walls are left behind. These split longitudinally into two (outer and inner) rings of peristomial teeth with 16 teeth in each ring. These peristome teeth are built up of strips of specially thickened and cutinized cell walls. They are curved, narrow, triangular plates with thick, transverse bars on the brownish red, conical teeth of the outer series. The teeth of the inner series or endostome are comparatively smaller, more delicate and colourless. The outer peristome teeth converge towards their tapering distal ends to meet a small central disc.

Formation of Operculum. The three rings (4th to 6th) of the amphithecium which are on the outer side of the peristome form the **lid** or **operculam** (Fig. 12·21 A). The cells of the fourth and fifth rings jointly produce a tissue. It consists of thin-walled parenchymatous cells and is arranged in three layers. This thin-walled tissue forms the inner and major portion of the operculum. The cells of the 6th ring mature into the protective surface layer called the **epidermis**. The epidermal cells have greatly thickened outer walls.

Differentiation of Annulus. Very early in the development of the capsule there appears a narrow, shallow, circular depression at the junction of the operculum and the theca regions (Fig. 12·21 C). It delimits the former from the latter. In this depression lies a narrow zone of thin-walled, narrow cells. It serves as an **abscission layer**. It is here that the ripe operculum becomes detached. The epidermal cells above and below this narrow zone show active growth and elongate radially. Two distinct rings of cells are formed one above and the other below the narrow zone. The former is called the **annulus** and the latter **rim** or **diaphragm** of theca. The epidermal cells of these regions project beyond those of the narrow zone.

The annulus forms the periphery of the broadest part of the operculum. It consists of about 5 or 6 layers of epidermal cells lying one above the other. The cells of the upper three or four layers become specially modified. They are narrow and radially elongated. They have thicker walls and form the rim of the mature detached operculum. The cells of the two lower layers of the annulus, which constitute the **annulus proper**, remain thin-walled. They are reported to be filled with mucilage. The mucilaginous contents of these cells absorb water and swell as the capsule matures. Subsequently they are destroyed and the operculum is detached. To sum up the **amphithecium** in the region of the operculum gives rise to :—

(*i*) Surface layers of the operculum consisting of the epidermis and the three layers of thin-walled, parenchymatous cells internal to it. They cover the peristome.

(*ii*) The two rings of peristome teeth.

(*iii*) The annulus.

(*c*) **Differentiation of Tissues in the Basel or Apophysis Region** : A broad zone of cells between the theca and seta regions in the young capsule enlarges considerably. It forms the basal, swollen, sterile region of the capsule and is called the **apophysis** (Fig. 12·13 B). The four primary endothecium cells in this region divide and re-divide to form the **conducting strand**. It is continuous with the conducting strand of the seta. The archesporium and the inner spore sac characteristic of the theca region are not differentiated. The eight primary amphithecium cells divide and re-divide in the usual manner to form five concentric rings of cells. The latter get differentiated into the various tissues external to the conducting strand. The order of cell succession and differentiation is practically the same as in the theca region. The cells of the first, second, third and fourth rings form the broad **spongy zone** with cells rich in chloroplasts and intercellular spaces between them. The cells of the fifth ring mature into the single layered **epidermis** punctured here and there with stomata. There is neither any hypodermis nor any air space traversed by trabeculae. Apophysis is, therefore, the solid photosynthetic region of the capsule.

As these developmental changes have taken place the young sporogonium grows faster than the surrounding calyptra. The neck of the archegonium has by now dried up. It is, however, persistent. The seta elongates rapidly. Consequently the calyptra is ruptured around its base. The ruptured portion of the calyptra tipped by the persistent, dark brown, archegonial neck is carried up as a **conical hood** at the top of the elongating sporogonium. It surrounds and protects the developing theca. For a while the capsule is upright on the seta. Later it becomes pendent or nodding. Eventually the calyptra is stripped off and lost.

Comparison between the sporophytes of Sphagnum and Funaria. Having discussed the structure and the development of the sporogonium of *Funaria*, we are in a position to compare it with the sporophyte of *Sphagnum*. The two may be contrasted as follows :—

Sphagnum	Funaria
(a) Development :	
1. The early growth of the embryo is by transverse cleavage followed by **intercalary** enlargement of the segments. There is no apical growth.	1. The early growth of the embryo is **apical**. The segments are cut off alternately from the two apical cells each located at the opposite end. The apical growth later gives place to intercalary activity.
2. The entire endothecium gives rise to the **columella** which is a bulky mass of parenchyma cells. It has a rounded apex.	2. Only the inner part of the endothecium forms the **columella.**
3. The **archesporium** is derived from the inner layer of the **amphithecium.**	3. The **archesporium** arises from the outermost layer of the **endothecium.**
4. The archesporium forms a **dome** arching over the columella.	4. The archesporium is a **barrel-shaped** structure open both at the top and the base. It does not arch over the columella but surrounds it instead.
(b) Structure :	
5. The mature sporophyte consists of a **foot** and a spherical **capsule.** There is no seta. Its place is taken up by a **constriction.** The function of the seta is taken up by the **pseudopodium.** The foot is massive and functions as an **haustorium.**	5. It consists of a **foot**, a long, slender **seta** and a pear-shaped **capsule.** The **pseudopodium** is absent. The foot is poorly developed.
6. The capsule of *Sphagnum* is comparatively a simpler structure representing only the **theca** portion concerned with spore production and the **opercular** portion concerned with dehiscence. The **apophysis** is absent. So is the **peristome** from the opercular region. The theca region is also comparatively simple in structure.	6. The capsule shows complex structure with considerable differentiation of tissues. It shows three well marked regions :— (*a*) **Apophysis**—a solid, somewhat swollen, sterile, basal portion mainly concerned with photosynthesis and conduction. (*b*) **Theca**—a middle urn-shaped portion concerned with spore production. (*c*) **Operculum**—apical region closely related to dehiscence. Beneath the operculum is an elaborate mechanism for dispersal of spores in the form of **peristome** teeth.
7. The capsule is bounded by **epidermis** bearing functionless **stomata.** They have no **pores.** There are no substomatal air spaces. Thus the many layered capsule wall lacks ventilated photosynthetic tissue.	7. The capsule has a well developed **epidermis** punctured with functional **stomata,** particularly numerous, in the apophysis region. They open into sub-stomatal **air spaces** which communicate with a system of intercellular spaces aerating the green, photosynthetic **spongy tissue** in the capsule wall. The capsule wall in *Funaria* has thus a well ventilated, photosynthetic system. In the theca region there is the two cell layers thick hypodermis, in addition, beneath the epidermis.
8. Within the several layers thick capsule wall there is no intercellular space so that the capsule is a compact solid structure.	8. Within the several layers thick capsule wall is the wide air space. It is, in fact, a highly distended cavity in the spongy zone of the capsule wall. In the centre of this wide air space remains suspended by filaments of green cells (**trabeculae**) the **columella** surrounded by the **spore sac.**
9. The **spore sac** is a wide, dome-shaped structure over-arching the rounded tip of the massive central columella.	9. The **spore sac** is narrow and barrel-shaped. It is open at the top and the base. It does not over-arch but surrounds the columella which forms the central core of the capsule in the theca region.

(*Contd.*)

The points of resemblance between the two are :—

1. Absence of **elaters** in both.
2. Dehiscence of the capsule by the separation of a **lid** in both.
3. Rupturing of the **calyptra.**
4. Presence of a well defined columella in both.

Nutrition of Sporophyte. The sporophyte of *Funaria* has a well ventilated photosynthetic tissue in the apophysis and the theca regions of the capsule. It is thus able to synthesize a considerable portion (if not whole) of its own carbohydrate food from the time its photosynthetic tissue is developed. Its photosynthetic capacity has been estimated by certain bryologists and is considered equivalent to that of the fourteen leaves of the leafy gametophore. For water and mineral substances, which must come from the soil, it depends upon the parent plant. The sporophyte of *Funaria* thus is a **semi** or **partial parasite**.

Germination of spores. The spore (Fig. 12·22 A), on falling on a moist soil, immediately germinates. It, at first, absorbs water and swells. Consequently the exospore ruptures. The endospore protrudes out in the form of one or two tubular outgrowths called the **germ tubes** (Fig. 12·22 B). When the two germ tubes come out from the opposite sides of the germinating spore, a cross wall soon appears at the point of emergence of the germ tube. The cell thus separated turns green. It grows in length and divides by septa to form a filament of green cells (Fig. 12·22 C). The filament grows on the soil and branches freely. The growth is apical. The branched, green, alga-like filament is the **primary protonema** (Fig. 12·22 C). Most of the branches of the protonema grow on the moist soil surface. They are green and thus known as the **chloronemal branches**. Some, however, penetrate the soil and function as absorbing and anchoring organs. These **rhizoidal branches** are non green, thin and possess oblique septa between the cells. The moss protonema with its chloronemal and rhizoidal branches very much resembles the heterotrichous thallus of a green alga. It can, however, be distinguished from the latter by the presence of oblique septa in the prostrate rhizoidal branches. Soon buds arise on the chloronemal branches. They are formed when the protonema has reached a certain stage of development. The formation of buds is said to be induced by the presence of a naturally occurring growth factor known as **bryokinin**. Each bud by the activity of its apical cell grows into a leafy *Funaria* plant of the usual form.

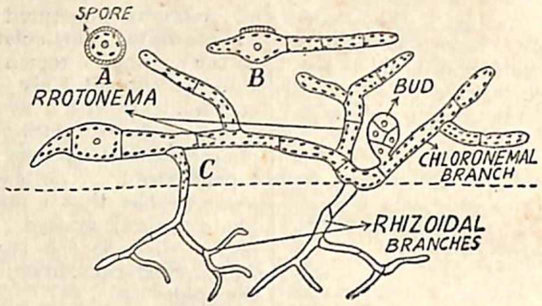


Fig. 12·22 (A–C). Funaria.
A. Mature spore.
B. Germinating spore.
C. Protonema.

Alternation of Generations (Fig. 12·23). In the life cycle of *Funaria* there occur two distinct individuals. They are unlike each other. One of these is **haploid**. It is the independent **leafy, moss plant**. The other is **diploid**. The diploid individual is the **sporogonium**. It is partially dependent on the gametophyte for its nutrition. The nuclei in the cells of the leafy plant contain n chromosomes and in the sporogonium $2n$ chromosomes. The haploid leafy plant reproduces by **gametes**. The diploid plant reproduces by **spores**. Because of its characteristic method of reproduction by gametes, the haploid leafy plant is often called the **gametophyte**. The diploid plant because of its reproduction by spores is known as the **sporophyte**. The leafy gametophyte represents the **sexual generation** and the sporophyte or sporogonium **asexual generation**. The gametophyte is developed from the spore. The sporophyte is formed from the zygote. The latter is the result of the union of two gametes (male and female). The two kinds of individual (sporophyte and gametophyte) alternate with each other in the life cycle. In fact one of them is the parent of the other. This phenomenon is expressed by the phrase **Alternation of Generations**. It means the alternation in a single life cycle of two vegetative individuals with different functions and different genetic constitution. The structures developed during the gametophyte phase are the *spores*, the *protonema*, the *leafy gametophore*, the *sex organs* (antheridia and archegonia) and the *gametes* (sperms and the eggs). The structures developed during the sporophyte stage in order of their appearance are the *zygote*, the *embryo*, the mature *sporogonium* consisting of a *foot*, a *seta* and a *capsule*, and the *spore mother cells*. The spore mother cells are the last structures of the sporophyte gerneration. They differentiate by meiosis into spores which are haploid. The meiospores are therefore the first structures of the next gametophyte generation.

SUMMARY OF THE LIFE HISTORY OF FUNARIA (Fig. 12·23)

1. **Gametophyte.** There occur two distinct individuals in the life cycle of *Funaria*. They are the leafy **gametophore** (Fig 12·23, 1), and the **sporophyte** (Fig. 12·23, 7). Leafy gametophyte is far more conspicuous of the two. It is developed from a germinating spore (Fig. 12·23, 10). The spore germinates as it falls on the moist soil and produces a freely branched, green filament of cells called the **protonema** (Fig. 12·23, 11). The protonema is the juvenile stage in the life cycle. It is purely vegetative. It has two kinds of branches, the **chloronemal** and the **rhizoidal** branches. The former grow horizontally on the moist soil and the latter penetrate the substratum. The chloronemal branches manufacture food and the rhizoidal function as anchoring and absorbing organs. Sooner or later certain of the older cells of the chloronemal branches grow into buds. Each bud has an apical cell with three cutting faces. With the activity of its apical cell each bud finally grows into a leafy shoot anchored to the substratum by the rhizoids. With the development of leafy shoots the protonema dies leaving each leafy axis as the sole, independent representative of the gametophyte phase. It is the so-called **moss plant**. The

protonema and the leafy shoot are the two stages of the gametophyte generation. The former is purely vegetative in function. The leafy gametophore is reproductive It bears the sex organs.

The adult *Funaria plant* (Fig. 12·23, 1) is an upright, leafy axis about 12–20 mm. in height. It has a slender, central axis, the so-called **stem**. The latter bears multicellular, branched **rhizoids** at its base and leaf-like expansions throughout its length. The leaves are arranged spirally and are more crowded towards the apex. They are sessile and ablong-ovate with entire margin and pointed apex. Each leaf is traversed by a distinct midrib.

Internally the stem is differentiated into an **epidermis**, a **cortex** and a **central strand**. Excepting the midrib the leaf is composed of a single layer of parenchymatous, rectangular cells rich in chloroplasts. The few layers thick midrib has a small conducting strand.

Sex Organs. The leafy gametophore is concerned with sexual reproduction by the formation of antheridia and archegonia. They are borne in separate terminal clusters on distinct branches of the same plant. The antheridia are borne at the tip of the main shoot and the archegonia on a lateral branch, that arises from the base of the male shoot.

The perigonial leaves surrounding the antheridial cluster are crowded together and spread out to form a rosette-like structure. The leaves on the inner side of the rosette are reddish in colour. Intermingled with the antheridia are the **paraphyses**. Each mature **antheridium** (Fig. 12·23, 2) is more or less a club-shaped, orange coloured structure. It consists of a short, multicellular **stalk** and a **body**. The body of the antheridium has a jacket or wall one cell in thickness. At the free, distal end of the antheridium the antheridial wall is differentiated into a lid-like structure. It is the **operculum**. It consists of one or two large cells derived from the apical cell by the activity of which the antheridium grows in its early stages of development. Within the wall is a dense mass of small, closely packed cells, the **androcytes**. Each of the latter gives rise to a biflagellate, spirally coiled **sperm** (Fig. 12·23, 3). On the access of water the opercular cells at the apex of the mature antheridium disintegrate or separate by hydrolysis. A viscous fluid containing the androcytes oozes out. With the dissolution of the walls of the androcytes the sperms escape and swim about in the water surrounding the antheridial cluster.

The archegonia (Fig. 12·23, 2′) are typically flask-shaped structures each borne on a short, multicellular stalk. The long, slightly twisted neck has one cell thick jacket layer of cells enclosing the neck canal cells. The jacket is doubled in the enlarged basal portion or the venter of the archegonium. The venter cavity contains an ovum with a ventral canal cell above it. On the access of water the axial row of cells in the archegonium, excepting the ovum, gets disintegrated to form a mass of mucilage. The mucilage in the canal absorbs water and swells. Consequently the end cells of the archegonial neck are forced apart.

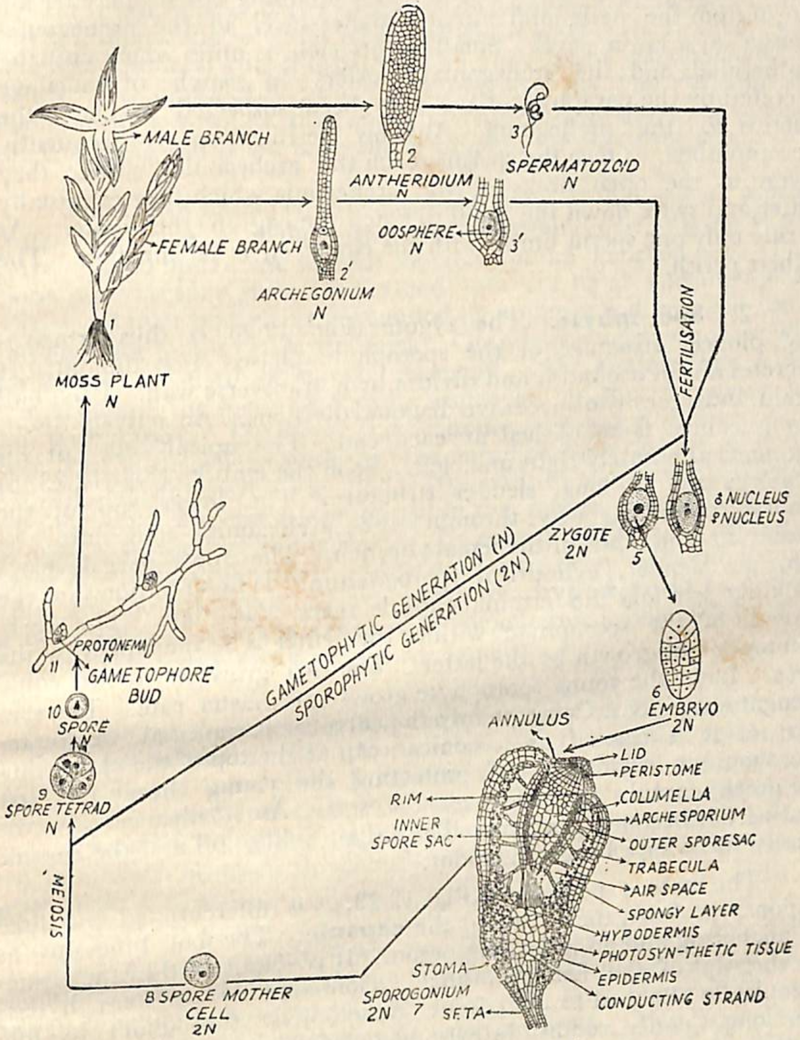


Fig. 12·23. Funaria hygrometrica.
Diagrammatic representation of the life cycle.

Fertilisation. The antheridia and the archegonia are borne in separate clusters of different branches. Naturally they are always some distance apart. The sperms from the perigonial rosette must be transported by some external agency to the archegonia. How it takes place is all a guess ? There is a suggestion that the sperms may be splashed out of the perigonial rosette by rain drops on to the archegonial cluster situated at a lower level. The other possibility is that water containing sperms may trickle down from the perigonial cup at a higher level to the archegonial cluster at a lower level. Small insects such as mites which visit the antheridial and the archegonial clusters in search of mucilage secreted by the paraphysis, have also been suspected to carry the sperms to the archegonia. Anyhow fertilization is frequently accomplished. Once the sperms reach the archegonial cluster they swim to the open necks of the archegonia which they eventually enter and swim down the canal to reach the egg in the venter. As a rule only one sperm unites with the egg to effect fertilization. The others perish.

2. **Sporophyte**. The zygote (Fig. 12·23, 5) thus formed is the pioneer structure of the sporophyte phase. It is diploid. It secretes a wall around it and divides by a transverse wall. Each half again undergoes two successive diagonal divisions. An actively dividing apical cell is established at each end. The apical cells cut off segments alternately right and left. Soon the embryo (Fig. 12·23, 6) develops into a long, slender structure. The lower end of the embryo makes its way through the archegonial stalk into the tissues at the apex of the female branch. The upper part develops into the slender, cylindrical sporogonium. Differentiation into the stalk-like seta and the terminal capsule takes place late. The early growth of the sporophyte within the venter is accompanied by the resumption of growth by the latter. The two grow at about equal pace. Later the young sporophyte grows at a faster rate. The seta elongates rapidly. Consequently the calyptra is ruptured. A greater part of it is carried as a conical cap at the top of the elongating sporogonium enclosing and protecting the young theca. At first the green capsule is upright on the seta. As it advances towards maturity it becomes pendent. The calyptra falls off and the capsule finally turns dark brown in colour.

The mature sporophyte (Fig. 12·23, 7) is differentiated into three regions, the **foot**, the **seta** and the **capsule**. The foot functions as an anchoring and an absorbing organ. It is embedded in the tissues at the tip of the female branch. Consequently the sporophyte is organically attached to the parent gametophyte throughout its life. The long, slender, reddish brown seta elevates the capsule more than 25 mm. above the surrounding leaves of the gametophyte. It consists of a central strand of thin-walled, elongated cells surrounded by the thick walled cortex. The pear-shaped capsule is a highly organised and elaborate structure. The elaboration is more internal than external. Externally the capsule is well marked into three regions : the **apophysis**, the **theca** and the **operculum**.

The **apophysis** is bounded by a well defined, protective surface layer, the **epidermis**. It bears numerous functional **stomata** each leading into a sub-stomatal air space. Within the epidermis is

the nutritive tissue or the **spongy parenchyma**. The sub-stomatal air spaces communicate with a system of intercellular spaces ventilating the green, spongy parenchyma. The capsule of *Funaria* is therefore self-supporting so far as its carbohydrate food is concerned. For water and mineral salts it is parasitic on the parent gametophyte to which it is organically attached throughout its life. Within the photosynthetic tissue is the conducting strand continuous above with the columella and below with the conducting strand of the seta.

The **theca** has a centrally located column of thin-walled, sterile, parenchyma cells. It is the **columella**. Surrounding the latter is the barrel-shaped **spore sac** with its top and bottom knocked out. The spore sac therefore does not extend into the basal and the apical portions of the capsule. It is bounded by an inner wall one cell thick and an outer 3 or 4 cell layers thick. Outside the spore sac is a wide **air-space** traversed by green filaments, the **trabeculae**. The columella and the spore sac thus lie suspended in the air space by the **trabeculae**. The spore sac contains the spore mother cells (Fig. 12·23, 8) which undergo the tetrad division (Fig. 12·23, 9) to form the haploid spores (Fig. 12·23, 10) All the spore mother cells are functional. No elaters are formed in the mosses. External to the air space is the wall of the theca. It consists of the inner **spongy layer** one or two cells thick. It is continuous below with the spongy tissue of the apophysis. Then comes the **hypodermis** consisting of two layers of colourless cells. The hypodermis is bounded by the single layered **epidermis** with fewer stomata.

Above the theca constituting the apical portion of the capsule is the **operculum** or **lid**. A transverse ring of modified epidermal cells delimits the operculum from the theca. It is the **annulus**. Beneath the operculum are two rings of conical teeth constituting the **peristome**. Together the peristome teeth form a cone-like structure which obstructs the mouth of the spore sac. The teeth are hygroscopic.

The mature capsule dries up. The thin-walled cells of the annulus proper, which hold the operculum in place, shrink and shrivel. Finally they rupture. The lid or the operculum drops off exposing the dome-like hygroscopic peristome teeth. The latter close over the central cavity formed by the drying up and shrivelling of the columella and the adjoining tissues. This cavity is now filled with spores. The escape of these spores is prevented in the wet weather as the peristome teeth close together. In dry weather the teeth bend outward. In doing so they separate from each other. The slits between them open. Through these slits the spores escape a few at a time when they are likely to be carried and thus dispersed by air currents. Falling on a suitable substratum and under favourable conditions the spores germinate, each producing a protonema, the juvenile stage of *Funaria*.

Significant steps in the life history of Funaria

A. **Gametophyte**

1. It consists of (*a*) a branched, green, alga-like filament, the **protonema** and (*b*) a leafy gametophore the so called **moss plant**. The protonema is short-lived.

2. The leafy gametophore consists of a slender, stem-like central axis bearing rhizoids at its base and leaf-like expansions throughout its length. It is independent.

3. The so-called **leaf** is traversed by a definite midrib more than one cell in the thickness.

4. The **rhizoids** are branched and multicellular. The septa between the cells are oblique.

5. The **sex organs** (antheridia and archegonia) are borne in terminal clusters, at the tips of separate branches of the leafy gametophyte.

6. Early development of the sex organs is by means of the activity of an **apical cell**.

B. **Sporophyte.**

7. The embryo sporophyte grows from two growing points, each located at the opposite end. The growth of the embryo is thus **apical**.

8. The mature sporogonium is differentiated into the **foot**, the **seta** and the pear-shaped **capsule** of great complexity. The seta is long and carries the capsule far above the leafy gametophore.

9. The mature capsule is differentiated externally into **apophysis**, **theca** and **operculum** regions. Internally it consists of several tissues. There is a well developed **ventilated photosynthetic tissue** and a large **air space** in which lies suspended the **spore sac** and the **columella** by filaments of green cells. The capsule has a complex organisation in the form of an **operculum** and **peristome** for the dehiscence and dispersal of spores at its apical portion.

10. The archesporium does not arch over the columella, and is derived from the exterior portion of the **endothecium**. It is reduced to a single layer. The progressive sterilisation of the potentially fertile tissue has thus reached its extreme in *Funaria*.

The chief differences between Funaria and the Liverworts

A. **Gametophyte.**

1. Presence of protonema in the mosses and its usual absence in the liverworts.

2. Radial symmetry of the upright moss plant as compared with the dorsiventral symmetry of the liverworts.

3. More elaborate external appearance and greater differentiation of tissues of moss gametophyte as compared with the liverworts.

4. The branched and multicellular rhizoids as compared with the unbranched, unicellular rhizoids of liverworts.

5. Early apical growth of the sex organs.

B. **Sporophyte**

6. Development of the embryo sporophyte is **bi-apical**. It takes place by two growing points as against by successive transverse cleavage in the liverworts.

7. The foot is usually dagger-shaped and the seta longer, stronger, hygroscopic and much longer-lived than in the liverworts.

8. The seta lengthens earlier than that of the liverworts and shows greater tissue differentiation.

9. Highly organised mature capsule externally differentiated into the basal, photosynthetic **apophysis region**, middle fertile **theca region** and the terminal **lid** or **operculum region** as compared with the simple capsule of liverworts represented by the theca region only.

10. Presence of a well developed, **ventilated photosynthetic system** in the several cell layers thick capsule wall of *Funaria* and its absence in the liverworts.

11. The characteristic wide **air space** in which lies suspended the spore sac and the columella by green filaments in the capsule of *Funaria*, is absent in the liverworts.

12. Single layered **archesporium** derived from the external layer of the endothecium in *Funaria* as against the massive archesporium derived from the entire endothecium in the *liverworts*.

13. Presence in *Funaria* of a central column of sterile tissue, the **columella** which is absent in the liverworts.

14. The mechanism of dehiscence and dispersal of spores in the form of **operculum** and **peristome** is much more elaborate and efficient in *Funaria* than in the liverworts in which capsule usually dehisces by valves or by the separation of a lid only. The peristome is absent in the liverworts and the lid when present is very simple in structure.

REVISION QUESTIONS

1. List the chief characteristics of the sub-class Bryidae and the family Funariaceae.
2. Enumerate significant steps in the life cycle of *Funaria*.
3. In what respects does *Funaria* differ from the Liverworts ?
4. Give an illustrated account of the phenomenon of alternation of generations in *Funaria*.
5. Compare the sporophytes of *Sphagnum* and *Funaria*.
6. With the help of labelled sketches only trace the life history of *Funaria*. (*A.U. 1959*)

7. Describe the external and internal structure of the capsule of *Funaria*.

8. Give an account of the fate of the amphithecium and endothecium in the three regions of the capsule (apophysis, theca and opercular regions) of *Funaria*.

9. Describe the structure and development of sex organs in *Funaria*. How does fertilisation take place in this plant ?

10. Describe the external features and internal structure of the vegetative organs of the gametophytic phase of any moss you have studied.

11. Draw a neat, fully labelled sketch of a median longitudinal section of the capsule of any moss you have studied.

CHAPTER XIII

GENERAL CONCLUSIONS

Origin of Bryophyta. Nothing definite is known about this subject. The little geologic record that we have is of little help. In fact no fossil forms more primitive than the present day bryophytes have been found. All the views about their origin must therefore be based on the evidence under the following three heads :—

(I) Evidence from comparative morphology of the living plants.

(II) Evidence from ontogony of the living plants.

(III) Evidence based on analogies with the living plants of other groups.

Bryologists are divided into two camps on the origin of bryophytes. The followers of one camp hold that the bryophytes have descended from the Pteridophytes. This is called the **Pteridophytean hypothesis** of the origin of bryophytes. The ardent supporters of this view are Scott, Lang and Kidston, Haskall, Kashyap and others.

The adherents of the second school believe in the aquatic ancestry of the bryophytes. They hold that the bryophytes have evolved from the Algae. This viewpoint has come to be known as the **Algal hypothesis** of the origin of bryophytes. Bower, Cavers, Smith, Campbell and Fritsch are the eminent supporters of this hypothesis. These two hypotheses which attempt to explain the origin of the bryophytes are thus diametrically opposed to each other.

(*a*) **Pteridophytean Hypothesis**. The supporters of this view formulated their argument on the basis of the following two features :—

(*i*) Close similarity between the sex organs of the two groups.

(*ii*) Resemblance between the sporogonium of *Anthoceros* and the terminal sporangium of the fossil pteridophytes such as *Sporogonites* and *Horneophyton*.

The kinship between the two groups is further strengthened by the similarity in their pigments, structure of cell walls, food reserve, reproductive methods and life cycle. These similarities between the bryophytes and the pteridophytes encouraged the followers of this school of thought to presume that the former have evolved from the latter by **progressive simplification** or **reduction**.

Scott (1911) was the first to moot this idea on the basis of the presence of chlorophyll and plastids in the sporogonium of mosses, liverworts and *Anthoceros* and also the presence of stomata of the type met with in the primitive vascular plants on the sporogonium of *Anthoceros* and the apophysis region of the capsule of mosses. He interpreted these features as ancestral characters retained from the time when the sporophyte was an independent plant (as in the pteridophytes). The sporogonium of *Anthoceros* which is to a great extent independent of the parent thallus plant (gametophyte) was believed to be the immediate descendant in all the bryophytes.

Kashyap (1919) another ardent supporter of this hypothesis considered the liverworts to have evolved from the Equisetales along three independent lines namely the Marchantiales, Jungermanniales and Anthocerotales. It may be worthwhile to note that uptill then the Psilophytales had not yet been known.

Haskell (1949) advocated the origin of the bryophytes from the algae through the Psilophytales by simplification. The resemblance between the *Anthoceros* sporogonium and terminal sporogonium of *Horneophyton* and the presence of stomata typical of the vascular plants on the *Anthoceros* sporogonium and apophysis region of the capsule of mosses were the two chief features on which he based his view point. The subsequent disappearance of stomata in other members of the Anthocerotales was linked with the parasitic habit of their sporogonia.

To sum up the supporters of Pteridophytean hypothesis believe that the bryophytes represent a degenerate evolutionary line of the pteridophytes. In their view it is difficult to explain these similarities between the two groups otherwise. However this hypothesis now stands discarded. The opponents of this hypothesis point out to complete absence of any relic of the lost vascular system in the sporophyte of all the bryophytes including the sturdy mosses. Mehra (1967) writes, "We know of many vascular plants including the water ferns that have taken to aquatic modes of life since the ages or have assumed parasitic mode of life but even then retain the vascular system."

(*b*) **Algal Hypothesis**. The occurrence of flagellated sperms (in the bryophytes) which necessitates the presence of free water, at least, at the time of fertilisation is a clear sign of their aquatic ancestry. The development of a green, filamentous, alga-like protonema as a **juvenile stage** in the life cycle of some of the bryophytes shows beyond doubt that the bryophytes had their origin in some algal form. It is a biological principle that the juvenile stage of an organism resembles its ancestral form.

The consenses of opinion, at present, favours the view that the bryophytes have evolved from the green algae rather than the brown. This view is supported by the several similarities that exist between the two. These are identical photosynthetic pigment (chlorophyll and xanthophyll), essentially thallus-like plant body lacking vascular tissues, starch as a food reserve, cellulose as the main component of cell wall and the type (whiplash) and number of flagella.

The above mentioned similarities between the green algae and the bryophytes serve to denote that the latter have arisen from the former. This is the *Chlorophycean Hypothesis* of the origin of the bryophytes.

The bryophytes, on the other hand, are more advanced and highly organized than the green algae in their land habit, more complex and elaborate thallus, multicellular and protected sex organs, retention of the zygote within the venter and its germination in situ, production of wind disseminated spores and heteromorphic type of alternation of generations. How these changes actually occurred during the evolution of bryophytes from the green algae still remains an unsolved problem. The species which constituted the links between the two have long since disappeared. These transitional species must have been small, delicate, thallose organisms. They could not be handed down to us in fossil form. We are therefore left no alternative but to speculate what these bridging species might have looked like. It is suggested that the transitional species probably were heterotrichous in habit. The presence of a small, flat, plate-like protonema in *Sphagnum* suggests the possibility of a green alga with a small, simple Sphaerocarpus-like thallus having become adapted to a life on land.

Smith, an ardent supporter of this hypothesis, has suggested *Fritschiella* as the probable nearer approach to the primitive ancestral form from which evolved the bryophytes. It is an amphibious green alga of the family Chaetophoraceae. It appears on the moist silt of the drying pools. Bower writes, "this amphibial plant possesses the essentials of a three dimensional, photosynthetic, sub-aerial thallus originating from a simple filament."

The occurrence in the bryophytes of multicellular sex organs with their sterile jackets is, however, difficult to explain. There are no known parallels among the living or fossil Chlorophyceae. The presence of a protective sterile jacket around the sex organs, it seems, is an adaptation to a land habit. The jacketed sex organs have a better chance of survival when exposed to the drying effects of the air. Bower writes, "in the amphibial green algae this is distantly adumberated by the nucule of the *Characeae* or still less prefectly by the protective filaments surrounding the zygote of *Coleochaete*."

The algal ancestry of the bryophytes is now acknowledged by all the botanists. The older view advocated by Smith (1955) that the bryophytes arose from the algae and then gave rise to the simple pteridophytes (primitive vascular plants) is no longer considered tenable. On the contrary the modern bryologists hold that the bryophytes represent a blind alley in evolution. Their viewpoint is that to avoid increased competition in water a group of remote ancestors of the green algae migrated to a subaerial habitat. These primitive amphibious plants developed multicellular sex organs as an adaptation to a life on land. From this hypothetical group arose both the bryophytes and the primitive vascular plants (pteridophytes) along two parallel lines.

The supporters of the algal origin differ among themselves as regards the origin of the two main groups of bryophytes. According to one school which support the polyphylletic origin the three groups of the bryophytes namely liverworts, hornworts (*Anthoceros*) and mosses represent three independent evolutionary lines, each having an independent origin from the transitional archegoniale forms which evolved from still earlier, different, hypothetical green algal stocks that migrated to the land. The supporters of the monophylletic origin advocate that the mosses are more primitive than the other bryophytes. The latter have evolved from the moss-like ancestors by simplification or reduction. According to this view the mosses are nearer to the supposed algal ancestors than the other bryophytes.

Systematic Position. The bryophytes are a group of interesting plants. They resemble the green algae in certain respects and differ from them in others. The features in which they agree with the green algae are :

(*i*) The simple, green, thalloid plant body.

(*ii*) Lack of vascular tissue and absence of roots.

(*iii*) Predominant plant in the life cycle being the gametophyte.

(*iv*) Autotrophic mode of nutrition.

(*v*) The retention of motility by the male gametes.

They differ from the green algae in the following respects :

(*i*) Terrestrial habit.

(*ii*) Multicellular sex organs each with a jacket layer of sterile cells.

(*iii*) Embryo formation.

(*iv*) Constant occurrence in the life cycle of a heterologous type of alternation of generations.

(*v*) Development of a remarkable female sex organ, the **archegonium**. It corresponds no doubt to the oogonium of the green algae but has no exact counterpart among them.

(*vi*) Origin and early development of the future sporophyte within the archegonium.

(*vii*) Sporophyte attached throughout life to and dependent for nutrition upon the parent gametophyte.

Because of the above-mentioned differences these thallus-bearing plants (bryophytes) are not included among the other thallus bearing plants such as the green algae to which they resemble in certain other respects. They are thus separated from the division *Thallophyta*.

The features in which the bryophytes differ from the green algae they share with the primitive vascular plants pteridophytes except point (*vii*). But they cannot be included among the pteridophytes as they are very unlike them in the following important respects besides others :

(*i*) Absence of vascular tissue.

(*ii*) The dominant phase in the life cycle being the gametophyte and not the sporophyte.

It is for this reason that the bryophytes are placed in a separate division Bryophyta occupying a position intermediate between the Thallophyta and the Pteridophyta.

Biological Importance. This group of lowly organisms illustrates that plants may be successful (widespread and numerous) despite their small size.

(*a*) *Origin of Land Habit among Plants*. To the botanist the group is of a singular interest. It throws light on the origin of land habit among plants. This event of change in habit from a life in water to a life on land must have been a red letter day in the history of plant life. It is so because it made possible all subsequent progress in the plant world. The group bryophyta includes the most primitive land plants which illustrate some of the steps this change in habit from water to land involved. Their structure, physiology and reproductive habits provide a striking evidence of their having evolved from the aquatic ancestors such as the Algae. The retention of swimming habit by the male gametes of the group is a clear sign of their aquatic ancestry. The important structural adaptations to a terrestrial existence shown by the bryophytes are :—

(*i*) Their compact plant bodies usually protected by epidermis containing air pores.

(*ii*) Primitive type of conducting strand.

(*iii*) To facilitate absorption of water and salts from the soil the plant body is provided with rhizoids. The latter in addition function as organs of attachment.

(*iv*) Jacketed, multicellular sex organs.

(*v*) Retention of the zygote within the archegonium. It serves a double purpose namely ensures food and water from the parent plant as it develops into a multicellular embryo and affords protection from drying.

(*vi*) Thick-walled, wind disseminated spores.

It seems the nature in its quest for a suitable plant body for a life on land tried two schemes. One of these is the upright leafy body habit of the Mosses. It favours photosynthesis as it presents greater photosynthetic surface to light. It, however, presents difficulties in the way of fertilisation as the sex organs are elevated. The elevated position of the moss sporophyte is, no doubt, ideal for spore dispersal but how can there be a sporophyte without fertilisation. The two physiological processes fertilisation and photosynthesis have opposite requirements. The former is facilitated by flat, thalloid body and the latter is favoured by a tall, upright body. Hence the scheme of combining photosynthesis with fertilisation as the functions of the gametophyte failed. It proved an unprogressive evolutionary trend. This is the main reason why the Mosses end blindly in the evolutionary line. They have given rise to no new plants. Nor have they progressed beyond this stage. The gametophyte plant in the mosses both morphologically and anatomically shows highest development of the vegetative body in the bryophytes. But there can be no progress beyond this stage The two main factors which check further growth are :—

(*i*) Absence of root and vascular tissue. The rhizoids as absorbing organs proved inefficient.

(*ii*) Dependence upon water for fertilisation. It also hinders further growth.

Hence the plan of combining photosynthesis with fertilisation as functions of the gametophyte failed. It permitted no further progress.

In the second scheme nature tried the combination of photosynthesis with spore dispersal as functions of the sporophyte. Both the processes have the same requirements. They are favoured by an upright, tall body. It thus proved an ideal combination as it permits further progress. On the other hand fertilisation is favoured by a flat, thalloid body. This combination we find in *Anthoceros*. It has a flat, thalloid gametophyte ideal for fertilisation. The gametophyte bears an erect, tall cylindrical sporophyte with a well ventilated green tissue in the capsule wall for photosynthesis. From such a sporophyte, some botanists believe, may have arisen the sporophyte of the simplest and the primitive vascular plants (pteridophytes).

(*b*) *Stabilisation of alternation of generations.* This important biological phenomenon is found in the life cycles of a few of the thallophytes but is far from being fixed. The two generations in their life cycles are either quite similar or somewhat different. In the bryophytes, however, this phenomenon is stabilised. It becomes a constant feature of their life cycles. Besides the vegetative individuals of the two generations differ markedly in their physiological and anatomical details.

Economic Importance. The bryophytes, in general, are of little **economic** importance. Some mosses provide food for herbivorous mammals, birds and other animals. On the whole none of them is directly important to man except a number of species of *Sphagnum*. They grow and multiply enormously in water thus filling the ponds and lakes with its growth. The barren sheet of water is converted into a solid land. The peat has long been used as fuel. Dried up specimens of *Sphagnum* are used as an absorbent in surgical dressings, as a packing material in upholstry and for transhipment of living plants, as a material to increase the water retaining property of certain poor types of soil, and as a means of retaining high soil acidity required by certain decorative and economically important plants (as a garden mulch). Flowers packed in moistened peat mosses keep fresh for a considerable period.

Oecologically the mosses are of considerable importance as soil formers in soil production and in soil conservation. They provide essential steps in the development of the soil. The mosses grow on barren soils. They along with the lichens grow even on dry rocks where growth of higher plants is impossible. In the course of time their bodies die and decay forming humus. The humus increases the fertility of the soil. Eventually humus containing soil becomes favourable for the growth of higher plants. Even forests grow on such soils.

The mosses usually form dense, extensive mats on the soil, which diminish the force of falling rain and thus prevent soil erosion. The rhizoids absorb large quantities of water and are so firmly intertwined around the soil particles that there can be little erosion even on a steep hill side.

Origin and Fate of the Archesporium. In the bryophytes archesporium originates as a continuous tract of primary cells. These divide and redivide to give rise to a mass of cells forming, at first, a solid tissue. The cells of the last cell generation of this solid tissue separate from each other. All or a part of them function as **spore mother cells** and give rise to spores. So this solid tissue derived from the archesporium comes to be called as the **sporogenous tissue**. On this basis archesporium is defined as the first generation of the sporogenous tissue. The origin and consequently the position of this tissue varies in different classes of the Bryophytes. The fate may vary in different genera of the same order :–

Classes and Orders	Origin	Position	Fate
1. Hepaticopsida			
(*a*) *Marchantiales* :			
Riccia	The entire endothecium becomes the archesporium, and forms the sporogenous tissue.	It is central in position and forms the bulk of the sporophyte except the single layered wall.	Practically all the sporogenous cells function as **spore mother cells** and form the spores. A few at the periphery degenerate to form a nutritive fluid. These are called the **nurse cells.**
Marchantia	The whole mass of endothecium forms the archesporium which divides and redivides to form the sporogenous tissue.	It fills the cavity of the capsule within the single layered capsule wall.	Half the sporogenous tissue yields the **spore mother cells** and the other half gives rise to the **elaters.** A few towards the top may remain sterile and form the **apical cap.**
(*b*) *Jungermanniales* :			
Pellia	The entire endothecium forms the archesporium. The archesporium gives rise to the sporogenous tissue.	It fills the entire cavity of the capsule within the two or more cell layers thick capsule wall.	A central mass of sporogenous cells forms the **basal elaterophore**. The rest form the **spore mother cells** and the **elaters.**
Porella	As in *Pellia.*	As in *Pellia.*	There is no elaterophore. The entire sporogenous tissue forms the **spore-mother cells** and the **elaters**
2. Anthocerotopsida			
(*a*) *Anthocerotales* :			
Anthoceros	Archesporium arises from the innermost layer of the amphithecium. It divides to form 2-4 layers thick sporogenous tissue.	It is more superficial in position than the Hepaticopsida. It overarches the tip of the columella and lies between the central columella and the several layers thick capsule wall	It differentiates into the **spore mother cells** and the **pseudo-elaters.**
3. Bryopsida (**Musci**)			
(*a*) *Sphagnidae*—			
Sphagnales : *Sphagnum*	Archesporium as in *Anthoceros* originates from the inner layer of the amphithecium. By division it forms 4 layers thick sporogenous tissue.	As in *Anthoceros* it is superficial in position. It is dome-shaped and lies in the upper part of a capsule overarching the top of the massive central columella within the capsule wall.	The entire sporogenous tissue is devoted to the formation of **spores.** The sporogenous tissue thus forms a coherent tract of fertile cells in the capsule.
(*b*) *Bryidae*—			
Funariales *Funaria*	The archesporium originates from the outermost layer of the endothecium. It gives rise to the sporogenous tissue, 2 cells in thickness.	It is superficial and surrounds the columella like a barrel.	All the sporogenous cells are fertile and form the **spores.** The sporogenous tissue thus forms a coherent tract of fertile cells as in *Sphagnum.*

EVOLUTION OF THE SPOROPHYTE

The sporophyte of the bryophytes, at first, is a solid object radial in construction. It lacks lateral appendages and is incapable of self-nutrition. It obtains its nutrition wholly or partially from the parent gametophyte to which it remains organically attached throughout its life. Its chief function is the production and dispersal of spores. In form it varies from only a spherical spore producing case as in *Riccia* to an elaborate object differentiated into foot and capsule (*Corsinia*) or more usually into the foot, seta and the capsule The foot functions as an anchoring and absorbing organ. The seta may either be small and constriction-like or a long, slender stalk. It helps in conduction and aids in spore dispersal. The capsule also varies in form. It may be spherical, oval, cylindrical or pear-shaped, etc. It varies in its elaboration. The elaboration, however, is internal rather than external.

According to the complexity of structure the sporophytes of bryophytes may be arranged in a series between the simplest and the most elaborate. The series starts with the simple sporophyte of *Riccia* runs through that of *Marchantia*, *Pellia*, *Anthoceros* and finally ends in the highly complex sporophyte of *Funaria*. So seriated the sporophytes of the bryophytes suggest a possible line of evolution.

(*a*) **Theory of Sterilisation**. Bower holds that the series runs in an upward direction. It illustrates a natural advance in the progressive elaboration and complexity of the sporophyte. The fundamental principle upon which he formulated his argument is the "*progressive sterilisation of the potentially fertile cells* (*sporogenous tissue*)." Instead of forming spores and serving a propagative function they remain sterile. These sterile cells are put to other uses such as nutrition, support, dehiscence, dispersal, etc. This hypothesis of Bower is called the **theory of sterilisation**. It attempts to explain the evolution of the sporophyte in the bryophytes on the basis of progressive elaboration. The ardent supporters of this theory are Cavers, Campbell and Smith. Let us apply Bower's theory of sterilisation to the individual sporophytes of this group and see if it stands the test.

1. **Riccia Sporophyte**. The zygote enters upon active segmentation to form a spherical mass of 23—30 undifferentiated cells (Fig. 4·12 A—E). Periclinal segmentation at this stage defines an inner mass of **endothecium** from an outer single layered **amphithecium** (Fig. 4·12 D and E). The amphithecium forms the single layered capsule wall. The endothecium which occupies the central position, as a rule, in whole becomes the archesporium. The latter divides and redivides to form the sporogenous tissue. Practically all the sporogenous cells are fertile. However a few at the periphery undergo degeneration to form a nutritive fluid (Fig. 4·13 D). These are the **nurse cells**. There is a large output of spores and no or very little sterilisation of the potentially fertile cells.

The sporophyte of *Riccia* is thus the simplest among the bryophytes and has the least amount of sterile tissue. The entire embryo forms the spore producing capsule. There is no foot and no seta (Fig. 4·15). It is simply a spore producing organ without any distributing function. It does not dehisce to allow the spores to escape.

2. **Marchantia Sporophyte** (Fig. 5·21). Half of the embryo derived from the **hypobasal region** remains sterile. It forms the **foot** and the **seta** (Fig. 5·19). It is only the upper **epibasal half** of the embryo which forms the spore producing capsule. The amphithecium forms the single layered capsule wall. Towards maturity ring-like thickenings appear on the walls of these cells. The entire mass of endothecium becomes the archesporium as in *Riccia*. The archesporium cells divide and re-divide to form the sporogenous tissue. Unlike *Riccia* only half of the sporogenous cells differentiate into spore mother cells. The other half remain sterile. These sterile cells elongate, develop spirally thickened bands on their walls and become the **elaters**. The elaters are hygroscopic. They help in the scattering of spores. A few of the sporogenous cells at the top may differentiate into the sterile, apical cap. The capsule of *Marchantia* has specialised both as a spore producing and spore distributing body. It illustrates a step further in the progressive sterilisation of the sporogenous tissue and consequent elaboration of its sporophyte.

3. **Pellia Sporophyte** (Fig. 7·8). **Hypobasal half** of the zygote takes no part in the development of the embryo sporophyte. The entire sporophyte including the **foot** and the **seta** is developed from the **epibasal half** (Fig. 7·9 F). Periclinal divisions in the embryonic capsule differentiate into an outer amphithecium surrounding the inner endothecium. The amphithecium forms the capsule wall 2 or more cell layers thick. The cells of the outer layer develop radial thickening bands and those of the inner layer develop semi-lunar thickening bands. The endothecium in whole becomes the archesporium as in *Riccia* and *Marchantia*. The archesporial cells divide and redivide to form the sporogenous tissue. Unlike *Riccia* and *Marchantia* a central mass of sporogenous cells, at the base of the capsule, remains sterile. These sterile cells elongate considerably and develop spiral thickenings on their walls to become elater-like. The central solid mass of elater-like cells attached at their lower ends to the cavity of the capsule is called the **basal elaterophore**. It is the result of progressive sterilisation of the potentially fertile cells of the sporogenous tissue. In addition some other widely diffused cells in the rest of the sporogenous tissue form **elaters** which remain unattached. The remaining sporogenous cells form the **spore mother cells**. The attached basal elaterophore is mechanically more effective in the dispersal of spores. The advancing sterilisation of the sporogenous tissue is thus associated with more efficient mechanism for spore dispersal. The other evolutionary trend has been the **decentralisation** of the remaining fertile tissue. This is achieved by sterilisation at the centre.

4. **Anthoceros Sporophyte** (Fig. 9·9 A). It illustrates a step further than *Pellia* in the progressive sterilisation of the potentially fertile tissue. There is complete sterilisation at the centre. The entire endothecium remains sterile. It forms a central column of sterile cells with a rounded apex. It is the **columella**. Consequently the office of spore formation is transferred to a more superficial tissue. The archesporium thus arises from the innermost layer of the amphithecium. It over-arches the free tip of the columella

and surrounds it. The sporogenous cells become differentiated into **spore mother cells** and **pseudoelaters**. The archesporium in *Anthoceros* is thus extremely reduced. It forms only a small narrow part of the capsule. The outer amphithecium gives rise to the several layers thick capsule wall. The capsule wall develops a well-ventilated photosynthetic tissue protected by the epidermis containing perfect stomata like those of the vascular plants.

5. **Funaria Sporophyte** (Fig. 12·15). Major portion of the embryo sporophyte remains sterile to form the **foot** and the **seta**. The embryonic capsule region becomes differentiated into an inner central column of endothecium surrounded by many layered amphithecium. The amphithecium becomes differentiated into the epidermis, the photosynthetic tissue of the capsule wall and the outer spore sac. Excepting the superficial layer there is complete sterilisation of the endothecium to form the central columella which is continuous right up to the top of the capsule. The archesporium arises from the outermost layer of the endothecium. It is thus extremely reduced and consists of a single layer of cells. Besides its fertility is limited above in the operculum region and below in the apophysis region. Consequently the archesporium becomes barrel-shaped. It is confined to the theca region only. The barrel is open at both the ends. The sterilisation of archesporium towards the base results in the increase in size of the photosynthetic tissue in the apophysis region. The arrest of fertility towards the top according to Bower may be correlated with the specialisation of this region for spore distribution. This view is supported by the presence of peristome, operculum and annulus in this region. In fact the archesporium stops short just at the base of the annulus and the peristome. The accessory dehiscing apparatus of the Moss capsule is mechanically more efficient in scattering the spores. Consequently the reduced archesporium with all its cells fertile and no elaters suffices for all the needs.

Bower's theory of sterilisation offers a plausible explanation of the evolution of the sporophyte in this group in the upward direction. It is appealing.

(*b*) **Reduction Theory**. There is, however, an opposite school of thought led by Kashyap, Church, Goebel and Evans. They hold that so seriated the evolution of the sporophyte has been in the downward direction. The series they believe furnishes an example of retrogressive evolution. There is ample evidence of reduction rather than progressive elaboration of the sporophytes of this group. The reduction is accompanied by simplification of the structure of the sporophyte in the series. On the basis of this view the simplest sporophyte of *Riccia* will be considered as highly evolved or advanced though reduced as a result of progressive simplification. The significant steps in the reduction series are :—

(*i*) Simplification of the dehiscence apparatus.

(*ii*) Reduction of the green photosynthetic tissue in the capsule wall.

(*iii*) Associated with the above is the disappearance of stomata and intercellular spaces.

(*iv*) Decrease in the thickness of the capsule wall along with the disappearance of thickening of all types of wall material from the walls of the cells.

(*v*) Side by side with the above changes is the gradual elimination of the seta and subsequently the disappearance of the foot.

(*vi*) All these changes are accompanied by the progressive increase in the fertility of the sporogenous cells. This change eliminates the presence of sterile cells and elaters in the capsule.

Evidence from comparative morphology and experimental genetics support the view that the simple sporophyte of *Riccia* is an advanced but a reduced structure.

COMPARISON BETWEEN THE GAMETOPHYTES OF

	Riccia	Marchantia	Pellia	Porella or Madotheca	Anthoceros	Funaria
Habitat	Most of the species are terrestrial. They grow on moist soil. A few are aquatic. The latter grow floating or submerged in the water of quiet ponds and lakes.	It is more terrestrial in habit than *Riccia*. It grows in moist situations such as damp earth, walls of wells, along streams and wet rocks. No aquatic species has so far been reported.	It occurs commonly on damp soil by the sides of streams, springs, wells, sometimes actually under water and rarely on moist rocks.	It grows in damp, shady places on logs, tree trunks, branches, wet rocks etc. It often occurs in large mats in the tropics.	It is terrestrial and grows on soil generally in very moist, shady places on the sides of slopes, ditches and in moist hollows among rocks. The plants grow in dense clusters.	It grows in dense patches in moist situations such as damp soil, on the walls, on moist rocks and on lands burnt by fire.
Thallus *i) External Features*	The plant body is a small, green thallus. It is dorsiventral and grows prostrate on the ground. It branches freely by dichotomy and frequently takes on a circular form. Each thallus lobe has a distinct **midrib**, a dorsal median **groove** or **furrow** and ends in a **terminal notch**. The areolae and the gemma cups are absent.	The plant body as in *Riccia*, is a green, prostrate, dichotomously branched thallus, fleshy in texture. Each thallus lobe has a distinct **midrib** but no dorsal furrow. It ends in a **terminal notch**. The thallus of *Marchantia* is, however, more terrestrial in habit. It has a definitely large size, broader and thicker lobes, more prominent, expanded midrib and upper surface marked by rhomboidal areas (**areolae**) each with a distinct central *pore*. Presence of **gemma cups** is another distinguishing feature.	The plant body as in *Riccia*, and *Marchantia* is a simple, dorsiventral thallus. It is thin, flat, green and lobed. The upper surface is smooth. The margin is sinuous and irregularly lobed. The lobes often overlap one another. The branching is dichotomous. Each lobe has a slightly thickened *midrib* and a *terminal notch*. The median dorsal groove characteristic of the thallus of *Riccia* and the rhomboidal areas (areolae) characteristic of the thallus of *Marchantia* are absent.	The plant body is generally epiphytic in habit. The thallus is prostrate and dorsiventral. In external appearance it is, however, more elaborate than *Riccia*, *Pellia* and *Marchantia* being **leafy**. It consists of a more or less branched central axis with leaves arranged in three rows. There are two rows of lateral and symmetric leaves on the upper surface of the axis. The third row of reduced leaves is on the lower side of the axis. The dorsal leaves are **bilobed** and **incubously** arranged. They are without a midrib. The branching of the axis is **monopodial**. Dichotomous. branching is absent.	The plant body is a simple, somewhat fleshy dorsiventral, green, non-leafy thallus as in *Riccia*, *Marchantia* and *Pellia*. The thalli are deeply lobed. The lobes overlap. Branching is dichotomous but due to unequal growth of the two parts of dichotomy the thallus usually becomes irregular in outline. The margin of the lobes is variable. It may be entire, toothed, folded or fringed. There is neither any **midrib** nor a dorsal **furrow**. The upper surface is smooth there being no rhomboidal areas characteristic of the thallus of *Marchantia*. The thallus is usually inhabited by *Nostoc* colonies seen as small, dark, blue green specks or spots in surface view.	The plant body is leafy, green **upright** and **ridial** in symmetry. It consists of an erect, sparingly branched central axis 12—20 mm. in height bearing green leaf-like expansions. The leaves are spirally arranged. They are sessile, oblong-ovate with a smooth margin, pointed apex and distinct midrib. The branching is **monopodial**. The branches are never axillary. They arise from below the leaves. In its external appearance the moss gametophyte is the most highly developed of all the bryophytes.
	From the ventral surface of the thallus arise the **scales** and the **rhizoids**. The scales arise along the margin and project beyond it. In some species they are absent and in still others rudimentary. The rhizoids are unicellular and unbranched. They anchor the thallus to the substratum and	From the ventral surface of the thallus arise both the **scales** and the **rhizoids.** The scales are arranged in two or three rows on either side of midrib. They are not marginal. The rhizoids as in *Riccia* serve to attach the thallus to the substratum and are of the two usual kinds **smooth-walled**	From the under surface of the thallus arise only the rhizoids The **scales** are absent in *Pellia*. The rhizoids are also of **smooth-walled** type. The tuberculate rhizoids are lacking. The unicellular, unbranched, smooth walled rhizoids secure the thallus to the substratum.	The **scales** are absent in *Porella*. The unicellular rhizoids are also of one kind only. They are **smooth-walled** and unbranched. They arise from the lower surface of the stem from the basal portions of the ventral leaves. They serve to attach the thallus to the substratum. The tuberculate	As in *Pellia* and *Porella* the scales and the tuberculate rhizoids are absent on the ventral surface of the thallus. It is fixed to the substratum by unbranched **smooth walled** rhizoids only.	The plant being upright there is no distinction into the upper and the lower surfaces. The rhizoids, which are the attaching organs, arise from the brown, naked, basal part of the stem. They are multicellular and branched. The septa between the cells are **oblique** and at

	Riccia	Marchantia	Pellia	Porella or Madotheca	Anthoceros	Funaria
	are usually of two types, **smooth-walled** and **tuberculate**.	and **tuberculate.** The ventral scales help to retain moisture below the thallus which can be absorbed by the rhizoids. This enables *Marchantia* to grow in drier habitats as compared with *Riccia*.		rhizoids are lacking.		long intervals. There are no scales. Nor is there any distinction into smooth-walled and tuberculate rhizoids.
(*b*) *Anatomy*	Internally the thallus is several cells thick. The cells are differentiated and arranged in two distinct regions, the upper, green **photosynthetic region** and the lower **storage region**.	As in *Riccia* internally the thallus is several cells thick. These cells are better differentiated and arranged in three distinct regions instead of two as in *Riccia*. These are :—	Internally the thallus is simple as compared to that of *Riccia* or *Marchantia*. It is several layers of cells thick in the median portion but there is no or little tissue differentiation. The cells are not arranged in any distinct regions such as the upper photosynthetic and the lower storage regions.	Internally the young central axis is very simple in structure. It is made up of perfectly uniform, green parenchyma cells. It shows no differentiation of tissues.	Internally the thallus is very simple in structure. It is several cells thick in the median portion. The cells, however, show no or little tissue differentiation. Nor are they arranged in photo synthetic and storage regions, All the cells are uniform, compactly arranged and parenchymatous except the surface layer.	Internally as well the so called moss stem shows certain amount of tissue differentiation. The cells are arranged in three distinct regions : **epidermis, cortex** and **central cylinder**.
	(*i*) There is no well-defined epidermal layer. It is represented by the terminal, colourless cells of the vertical rows of green cells. Together the hyaline cells of the neighbouring green filaments form an ill-defined, discontinuous **upper epidermis**, one cell in thickness.	(*i*) *Epidermal region*. It consists of a well-defined upper epidermis with true, barrel-shaped pores. The epidermal cells have slightly thickened walls. They are protective in function and tend to check evaporation from the underlying tissue over which the epidermis forms a single-layered roof.	(*i*) There is no well developed and well defined upper epidermis. Of course the surface layer is often referred to as epidermis but the epidermal cells are not in any way different from the other cells of the thallus.	(*i*) The epidermal layer is not well defined. Nor is there any trace of a central strand.	(*i*) The cells of the surface layer are smaller but not cuticularized or otherwise modified as epidermal cells. Hence there is no organised epidermis.	(*i*) *Epidermis*. It is the surface layer. In the mature portions of the stem the epidermal cells are thick-walled and lack chloroplasts. There are neither any air pores nor stomata.
	(*ii*) The photosynthetic region consists of a loose, green tissue. The green cells rich in chloroplasts are arranged in vertical rows usually with **narrow slits** between them. The empty air-chambers open to the exterior	(*ii*) *Photosynthetic Region*. It lies beneath the upper epidermis and consists of a chlorophyll bearing tissue with **air chambers**. The chambers are arranged in a single horizontal layer and are of fairly regular size. Each chamber	(*ii*) The air pores and air chambers characteristic of *Marchantia* are absent. The entire thallus consists of uniform tissue of chlorophyll bearing polyhedral, parenchyma cells arranged compactly. The cells of the upper	(*ii*) In older portions of the stem, however, there is differentiation into the outer **cortical** and inner **medullary** regions. The cortex consists of small cells with slightly thickened walls. The medulla is	(*ii*) There are no chambers, and air pores. In fact in its structure the *Anthoceros* thallus approaches that of *Pellia* as it does in the absence of scales and tuberculate rhizoids. There are, however, differences in detail.	(*ii*) *Cortex*. It is several cell layers thick and consists of large, thin-walled cells. They are compactly arranged and in young stems contain chloroplasts. The mature portions of the stem have the cortex differentiated into an outer **thick-**

	Riccia	Marchantia	Pellia	Porella or Madotheca	Anthoceros	Funaria
	through air-pores which are simply intercellular spaces bounded by 4—8 epidermal cells. The photosynthetic filaments and the true pores characteristic of *Marchantia* are absent in *Riccia*.	is separated from its neighbours by partitions of green cells 3 or 4 cells in height. It opens to the exterior through a centrally placed barrel-shaped, epidermal **air pore**. From the floor of each chamber arise short, simple, or branched filaments of cells rich in chloroplasts.	layers contain abundant chloroplasts. Starch grains occur in all the cells.	composed of comparatively larger cells with thinner walls.		**walled cortex** and an inner **thin-walled cortex.** There are no air spaces.
	(*iii*) The lower storage region is colourless and several layers thick. It consists of closely packed, undifferentiated, parenchymatous cells which may contain starch. A few cells contain oil. These cells thus serve for food and water storage. There are no mucilage cells.	(*iii*) *Storage Region.* It is the lowermost region of the thallus where food and water are stored. It is more extensive and many layers thick. It is compact and colourless. The cells of the upper layers of this region may contain few or no chloroplasts. It consists of relatively large, thin-walled, colourless, parenchyma cells. Most of them contain starch. Isolated cells in this region may contain a single oil body or be filled with mucilage. The former are called **oil cells** and the latter **mucilage cells**.	(*iii*) There is no distinct storage region.		(*iii*) All the cells have a single large chloroplast each with a pyrenoid in the centre—an unusual feature. Some cells contain mucilage. The distinction of the thallus into the ventral storage and the dorsal photosynthetic region as is characteristic of the Marchantiaceae is lacking. In some species of *Anthoceros* the superficial cells on the lower surface of the thallus separate from each other to form intercellular spaces which are filled with mucilage. These mucilage pits often deepen and broaden to form large, rounded cavities. They are filled with soft, mucilage and open on the ventral surface by stoma-like clefts. Very often *Nostoc* finds its way into these intercellular, spaces through the slit like or circular openings of the mucilage clefts. Once lodged within, the alga multiplies extensively in the	(*iii*) *Central Cylinder.* It occupies the core of the stem and consists of vertically elongated, thin-walled cells. They are narrow and compactly arranged. It provides mechanical support to a certain extent and functions in conduction.
				The leaf consists of a plate of cells one-cell layer thick. The cells are rich in chloroplasts and are polygonal in form. There is no midrib. The axis is cylindrical in outline.		The so-called leaf consists of a single layer of cells rich in chloroplasts. The midrib is several cells thick. It contains a narrow strand of thin-walled, elongated cells.

	Riccia	**Marchantia**	**Pellia**	**Porella or Madotheca**	**Anthorceros**	**Funaria**
					intercellular spaces. The latter by the disorganisation of the neighbouring cells broaden into conspicuous cavities inhabited by the alga.	
	(*iv*) The lowermost cells of this region are smaller in size and more regularly arranged to form the lower epidermis.	(*iv*) The lower epidermis is distinct and well developed. It is continuous.	(*iv*) A single layer of regularly arranged cells on the lower surface of the thallus is referred to as the lower epidermis.		(*iv*) There is no distinct lower epidermis.	
Apical growth	Growth in length of the thallus takes place by means of a group of apical initials constituting the growing point. It lies in the deeply emarginate apex of each lobe.	As in *Riccia* the growing point lies at the bottom of a terminal notch of each thallus lobe. It consists of a group of apical initials. By the activity of these the thallus grows in length.	Growth takes place by the activity of a single large **apical cell**. It lies in a notch at the forward end of each thallus lobe.	The thallus grows by means of a single pyramidal **apical cell** with three cutting faces. It lies at the tip of the main axis and each of the branches.	Campbell, Bower and others report the occurrence of a single four-sided pyramidal **apical cell** at the growing point which lies in a shallow depression at the anterior end of each thallus lobe. Leitgeb recognized several marginal cells of equal rank. Mehra and Handoo confirm Leitgeb's observation. They hold that in *A. erectus* and *A. himalayensis* there is a group of cells which initiate growth. They are protected by mucilage.	It takas place by means of a single pyramidal **apica cell** at stem tip. It has three cutting faces.
Juvenile Stage	There is no juvenile stage or protonema. The thalloid gametophyte is formed directly from the germinating spore.	The same as in *Riccia*.	The same as in *Riccia* and *Marchantia*.	The adult leafy thallus is preceded by a **juvenile stage** or **protonema** which is of a simple type. It is multicellular and develops one or more rhizoids prior to the differentiation of the apical cell of the leafy thallus (gametophyte).	There is no juvenile stage as in *Riccia*, *Marchantia* and *Pellia*.	The upright, leafy gametophyte is preceded by the **juvenile** or **protonema** stage which is a green branched system of filaments.

COMPARISON BETWEEN THE SEX ORGANS OF :

	Riccia	*Marchantia*	*Pellia*	*Porella*	*Anthoceros*	*Funaria*
Distribution of sez organs	(*i*) Many species are **monoecious** but a few are **dioecious.**	(*i*) Without exception all species of *Marchantia* are dioecious.	(*i*) Some species are **monoecious,** others **dioecious.** The monoecious species are distinctly **protandrous.**	(*i*) All species are reported to be dioecious.	(*i*) Some species are **monoecious** and others dioecious. The monocious species are reported to be **protandrous.**	(*i*) *Funaria hygrometrica* is **monoecious** and **autoicous.** Some mosses are **monoecious** and **pariocous** others **monoecious** and **synoicous, Dioecious** mosses are also common.
	(*ii*) In the dioecious species the two kinds of thalli are similar but in *R. himalayensis* the male plants are smaller than the females.	(*ii*) The male and the female thalli are similar.	(*ii*) The male and the female thalli in the dioecious species are similar.	(*ii*) The male and female plants are **dimorphic,** the former being decidedly smaller than the latter.	(*ii*) In the dioecious species the male and the female thalli are similar.	(*ii*) The male and the female branches do not exhibit dimorphism.
	(*iii*) The sex organs lie in the dorsal furrow on the upper surface of the thallus and not on any special sexual branches.	(*iii*) They are borne on special sexual upright branches of the thallus called the **gametophores,** which are terminal in position on the thallus lobes.	(*iii*) The sex organs are developed on the upper surface of the thallus and not on any special sexual branches.	(*iii*) The sex organs are borne on specialised sexual branches.	(*iii*) The sex organs are not borne on any specialised sexual branches.	(*iii*) The sex organs occur at the tips of branches which are not in any way specialised.
	(*iv*) The sex organs are developed in lines back from the apex, in acropetal order.	(*iv*) In contrast to the scattered arrangement in *Riccia*, the sex organs are developed in localized areas called the **receptacles** which are elevated, later on, on long stalks.	(*iv*) The antheridia occur irregularly scattered in two or more rows in the broad midrib region.	(*iv*) The antheridia occur singly in the axils of closely imbricated, light green bracts on the antheridial branches which stand at right angles to the main axis.	(*iv*) The antheridia occur scattered singly or in groups immersed beneath the upper surface of the thallus.	(*iv*) The antheridia occur in a cluster at the apex of the male branch which is the main shoot. Intermingled with the antheridia are found the paraphysis.
			(*v*) The archegonia occur in a cluster close to the growing apex on a ridge of tissue called the **receptacle.** The receptacle remains sessile.	(*v*) The archegonia occur in a terminal cluster on the female branches which are very short and bear 2 or 3 leaves only.	(*v*) The archegonia occur singly and not in clusters embedded in the upper surface of the thallus.	(*v*) The archegonia are borne in a cluster at the apex of the female branch which arises as a lateral outgrowth from the base of the male shoot. Intermingled with the archegonia are found the paraphyses.
Position and origin of sex organs	(*i*) Both (antheridia and archegonia) lie immersed, each in a separate cavity or chamber on the dorsal surface of the thallus.	(*i*) The antheridia lie embedded on the upper surface of the male receptacle, each in a pit which opens by a pore on the surface of the disc.	(*i*) The antheridia lie embedded on the upper surface of the thallus, each in its own pit which opens by a pore on the upper surface of the thallus	(*i*) The antheridia occur singly projecting in the axils of small bracts on the antheridial branches.	(*i*) The antheridia occur singly or in groups inside closed antheridial chambers on the upper surface of the thallus.	(*i*) The antheridia occur in a cluster projecting at the tip of the male shoot.
		(*ii*) The archegonia are pro-	(*ii*) The archegonia occur in a	(*ii*) The archegonia occur pro-	(*ii*) The archegonia occur	(*ii*) The archegonia occur pro-

	Riccia	Marchantia	Pellia	Porella	Anthoceros	Funaria
		jecting. In the young receptacle they are borne on the upper surface with their necks directed upwards. They are not sunk in separate pits. In the mature receptacle they hang downwards from the undersurface of the disc with their necks directed downwards.	cluster projecting on the upper surface of the thallus.	jecting in a cluster at the apex of the female branch.	singly sunk deep in the fleshy thallus on its upper surface with the tip projecting out.	jecting in a cluster at the apex of the female branch.
	(*iii*) The sex organs are **exogenous** in origin.	(*iii*) The sex organs are **exogenous** in origin.	(*iii*) The sex organs are **exogenous** in origin.	(*iii*) The sex organs are **exogenous** in origin.	(*iii*) The antheridia are **endogenous** in origin whereas archegonia are **exogenous**.	(*iii*) Both the sex organs are **exogenous** in origin.
(*a*) **Antheridia**	(*i*) The mature antheridium consists of an ovoid or pear-shaped body attached at its broader end to the bottom of the antheridial chamber by a short, multicellular stalk.	(*i*) The mature antheridium is essentially similar to that of *Riccia*. It has an ovoid body supported on a short, multicellular stalk. The latter arises from the bottom of the antheridial chamber.	(*i*) The mature antheridium as in *Riccia* and *Marchantia* consists of a body and a stalk. The stalk is short but multicellular. It arises from the bottom of a round flask-shaped antheridial chamber.	(*i*) The mature antheridium of *Porella* has a globose or globular body elevated on a long slender stalk. The stalk consists of two rows of cells.	(*i*) The mature antheridium is orange coloured. The club-shaped or pouch-like body is raised on a long multicellular, four rowed stalk arising from the floor of a roofed over chamber.	(*i*) The mature antheridium is club-shaped and orange coloured. It is shortly stalked. The stalk is multicellular.
	(*ii*) The body of the antheridium is made up of a central mass of numerous small, internal cells protected and covered by a layer of larger, sterile cells forming the **jacket** or **antheridial wall**. The internal cells of the last cell generation produce the biflagellate **sperms**.	(*ii*) The body of the antheridium has a jacket layer one cell in thickness. It encloses a mass of **androcytes**. Each androcyte gives rise to a biflagellate sperm.	(*ii*) The globular or globose body of the antheridium has a jacket one cell-layer in thickness. The cells contain chloroplasts. The jacket layer encloses a mass of **androcytes**. Each androcyte metamorphosis into a biflagellate sperm.	(*ii*) The body has a jacket layer 2-3 cells thick towards the base. It encloses a mass of colourless internal cells which produce the sperms. The ripe antheridium is reported to be almost pure white. The antheridium thus differs from those of *Riccia*, *Marchantia* and *Pellia* in its large size, long stalk, jacket 2-3 cells thick at the base and no antheridial chamber.	(*ii*) The body of the antheridium has a single layered jacket forming the wall. The jacket cells in some species are rectangular and arranged in four tiers. The cells of the upper tier constitute the dehiscence cap. Within the wall is a mass of androcytes which produce the sperms. The roof of the antheridial chamber bursts open when the sperms are ripe.	(*ii*) The body of the antheridium consists of a jacket layer one cell in thickness. The cells contain chloroplasts. The jacket has a cap of one or two large cells at its distal end. Within the jacket is a mass of sperm producing cells.
	(*iii*) Each sperm is a minute, slender, curved structure furnished with a pair of flagella at its anterior end.	(*iii*) The sperm has a narrowly curved or rod-like body furnished with two apical flagella.	(*iii*) The sperm has a spirally coiled body with two flagella attached at its forward narrow end. The sperms of *Pellia* are	(*iii*) The sperm is a slender structure. It has a body consisting of about 2 complete coils. A small, vesicle is attached at its	(*iii*) The liberated sperm has a small, slender linear or slightly curved body furnished with two flagella at its forward end.	(*iii*) The liberated sperms are minute, biflagellate spirally coiled structures.

	Riccia	Marchantia	Pellia	Porella	Anthoceros	Funaria
			larger than those of *Riccia* and *Marchantia* and have more coils.	posterior end. The two flagella are somewhat longer than the body and are inserted at the pointed anterior end.	The flagella are almost equal in length.	
(*b*) **Archegonia**	The somewhat flask-shaped archegonium consists of an enlarged, basal **venter** and a long slender **neck**. The venter is usually directly attached to the thallus there being no visible stalk. The neck consists of a narrow, vertical neck canal filled by a row of **four** neck canal cells surrounded by a layer of neck cells arranged in six longitudinal rows. The tip of the neck is made up of four large **cap** or **lid cells**. The distal portion of the neck projects above the surface of the thallus into the dorsal furrow.	In form and structure the archegonia of *Marchantia* are similar to those of *Riccia*. The only differences are :— 1. Presence of a short but distinct stalk which attaches the venter to the receptacle. 2. Slightly longer neck. 3. Greater number of neck canal cells which varies from 4-6. 4. Hang downwards from the under surface of the receptacle.	The archegonium of *Pellia* is typically flask-shaped and essentially similar to that of *Riccia* and *Marchantia* except : 1. It is borne on a short but stout, massive stalk. 2. The neck consists of 5 longitudinal rows of neck cells instead of 6 characteristics of Marchantiales. 3. The number of neck canal cells varies from 6—8. 4. The neck is not sharply marked off from the venter.	The mature archegonium is more or less a cylindrical object. It is seated on a stalk. The neck consists of 5 vertical rows of cells as in *Pellia*. They enclose the neck canal. The neck canal is filled with usually 8 broad neck canal cells. The venter is but little enlarged. As in *Pellia* the ventral wall consists of 2-layers of cells.	In structure the archegonium of *Anthoceros* differs from that of the bryophytes and resembles that of certain Pteridophytes :— It has no stalk and is embedded in the tissue of the thallus. There is a central row of 4-5 neck canal cells but there is no jacket of sterile neck cells around it except the uppermost tier of neck cells which form the tip and project above the surface of the thallus.	The archegonium is typically flask-shaped. It is supported on a long, stoutly developed stalk which attaches it to the tip of the female branch. It projects above the adjacent vegetative tissue. The neck is long and twisted. There are numerous (8 to 10) neck canal cells.
	The venter consists of a layer of jacket cells enclosing the lower larger egg cell and an upper smaller ventral canal cell.	5. The same as in *Riccia*.	5. The venter wall consists of two layers of cells instead of one characteristic of *Riccia* and *Marchantia*. It encloses the egg and the ventral canal cells. Sometimes the lower portion of the neck also becomes two cell layers thick.		The venter contains the egg and the ventral canal cell but there is no venter wall of sterile cells around them.	The ventral wall is two cell layers thick. The venter cavity contains the egg and the ventral canal cell above it.
	Protected by the surrounding archegonial chamber. The protective sheaths like the perigonium and perichaetium are absent.	6. Presence of a collar-like structure at the base of the venter of each archegonium. It is the **perigynium**. Presence of a two lipped curtain-like **perichaetium** with fimbriated margins around each series of archegonia.	The perigynium is absent. The **involucre** which is homologous to the perichaetium of *Marchantia* surrounds and protects the archegonial cluster.	Protected by the surrounding perichaetial bracts, the upper ones forming the **perianth** and the lower ones constituting the **involucre**.	The protection to the axial row of cells is afforded by the adjacent thallus tissue. The protective investments such as the perigynium and the perichaetium are lacking.	The protective sheaths in the form of perigynium and perichaetium are absent.

COMPARISON BETWEEN THE SPOROPHYTES OF

Riccia	Marchantia	Pellia	Anthoceros	Sphagnum	Funaria
SPOROPHYTE					
(*i*) The sporophyte of *Riccia* is the simplest known among the bryophytes.	(*i*) It is larger than and more complex than that of *Riccia*.	(*i*) It is more elaborate than those of *Riccia*, and *Marchantia*.	(*i*) It is larger and more complex than those of *Riccia* *Marchantia* and *Pellia*. The elaboration is internal.	(*i*) It is much simpler than that of the other mosses. In certain features it resembles that of **Anthoceros** and in a few others that of *Funaria*.	(*i*) It is far more elaborate both externally as well as internally than that of any other bryophyte.
(*ii*) It consists of a **spore sac** or capsule only. There is no foot and no seta.	(*ii*) It is differentiated into **foot**, short **seta** and **capsule**.	(*ii*) It consists of a **foot**, a long **seta** and a **capsule**.	(*ii*) It is differentiated into a **foot**, a constriction-like **intermediate zone** and a **capsule**. There is no seta.	(*ii*) It consists of a **foot** and a **capsule**. Between the two is a constriction-like structure apparently resembling that of *Anthoceros*. The seta is absent.	(*ii*) The sporophyte consists of a **foot**, a long slender **seta** and a **capsule**.
(*iii*) It lies completely sunk in the tissue of the thallus and has no protective sheaths around it except the calyptra.	(*iii*) It hangs freely from the under surface of the female receptacle surrounded by the **perigynium** and the **perichaetium**.	(*iii*) It arises from the dorsal surface of the thallus surrounded by the **involucre** at the base. There is no **perigynium**.	(*iii*) Arise in clusters from the dorsal surface of the thallus each surrounded at the base by a tubular **involucre** only.	(*iii*) Arises from the apex of the female branch elevated by a leafless, stalk-like **pseudopodium**. The protective sheaths are absent.	(*iii*) It is situated at the distal end of the female branch. There is no pseudopodium. The protective sheaths are lacking.
(*iv*) The foot is lacking.	(*iv*) The foot is well developed and broad. It functions as an attaching and absorbing organ.	(*iv*) It is conical with its edges projecting upwards forming a collar-like structure at the base of the seta. Functions both in absorption and attachment.	(*iv*) It is a rounded, bulbous structure keeping the long capsule well-anchored upon and attached to the thallus, often develops rhizoid-like outgrowths increasing its absorptive surface.	(*iv*) The foot is well-developed and massive as in *Anthoceros* but develops no rhizoid-like outgrowths. Functions both in absorption and attachment.	(*iv*) It is a small, poorly developed dagger-like conical object which functions both as an attaching and absorbing organ.
(*v*) The seta is absent.	(*v*) The short seta elongates rapidly but slightly, simply, to push the mature capsule through and beyond the surrounding protective sheaths.	(*v*) The seta is long, of pure white colour, almost transparent. It elongates rapidly after the ripening of the spores to elevate the capsule far above the surrounding protective sheath and thus helps in the dispersal of spores.	(*v*) The seta is absent. Its place is taken up by the constriction-like intermediate zone which is meristematic. This intercalary meristem constantly adds new cells at the base of capsule which progressively become differentiated into the various tissues of the capsule.	(*v*) The seta is absent. The constriction-like intermediate zone which apparently resembles that of *Anthoceros* lacks the meristem. The absence of seta is compensated by the presence of **pseudopodium**. The latter helps in the dispersal of spores by elevating the capsule.	(*v*) The long, slender seta elevates the capsule far above the surrounding perichaetial leaves and helps in the dispersal of spores. It is hygroscopic.
(*vi*) The capsule is a spherical spore sac. Its chief function is the production of spores. It has no distributing function.	(*vi*) At maturity the capsule is an oval, yellow body concerned both in the production and distribution of spores.	(*vi*) The ripe, black capsule is spherical and specialised both as a spore producing and spore distributing organ.	(*vi*) It is a long, slender, cylindrical, upright object of fairly uniform thickness throughout its length. Its unusual length compensates for the absence of the seta. Functions both in the production and	(*vi*) The spherical capsule is externally more elaborate than that of the liverworts. It is differentiated into the theca portion concerned with spore production and lid-portion concerned with dehiscence.	(*vi*) The pear-shaped usually nodding capsule is far more elaborate both internally as well as externally than that of any other bryophyte. Externally it is differentiated into three regions, the basal **apophysis** for

Riccia	Marchantia	Pellia	Anthoceros	Sphagnum	Funaria
			dispersal of spores.		photosynthesis, middle **theca** for production of spores and the apical **opercular** or **lid portion** concerned with dehiscence.
Structurally the capsule of *Riccia* is the simplest among the bryophytes. The capsule wall consists of a single layer of cells.	It is slightly more elaborate in structure than that of *Riccia*. The capsule wall is single-layered in thickness. The wall cells towards maturity develop ring-like thickenings on their walls.	It is still more complex than that of *Riccia* and *Marchantia*. The capsule wall is 2 or more cell layers thick. The walls of these cells are strengthened by bands of thickening material. In addition the capsule wall at maturity has on its surface 4 vertical strips of thin-walled cells. These are the **lines of dehiscence.** They are absent in *Riccia* and *Marchantia*.	the capsule of *Anthoceros* displays striking complexity in its internal structure. The capsule wall is several layers of cells (4-6) in thickness. The outermost layer is called the **epidermis.** It is punctured here and there by the presence of true **stomata.** Within the epidermis is the typically ventilated **photosynthetic tissue** consisting of chlorenchymatous cells with intercellular spaces between them. It is absent in *Riccia, Marchantia* and *Pellia*. The capsule wall has on its surface generally two vertical **lines of dehiscence** on the opposite sides of the capsule each in a shallow depression.	The capsule wall as in *Anthoceros* is 4 to 6 layers in thickness. The outermost layer is the **epidermis.** It bears rudimentary stomata which lack the stomatal aperture. Within the epidermis is the non-ventilated photosynthetic tissue consisting of chlorenchymatous cells with no intercellular spaces between them.	The capsule wall is several layers thick and is highly differentiated. The outermost layer is the **epidermis.** It contains numerous stomata in the apophysis region, fewer in the theca region and none in the opercular region. The epidermal cells in the operculum have greatly thickened walls excepting the **annulus.** Within the epidermis and restricted to the theca region only are the colourless, compactly arranged two layers of cells constituting the **hypodermis.** Within the hypodermis in this region is the narrow **spongy layer** which is continuous below with that of the apophysis where it becomes broader. Inside the spongy layer in the theca region is the wide **air space** traversed by the trabeculae which connect the spongy layer with the outer 3 to 4 layer thick wall of the **spore sac.** The air space, the trabeculae and the outer spore sac are absent in the apophysis and operculum regions. Within the epidermis in the apophysis region is the broad spongy zone and in the operculum 3-4 layers of small parenchyma cells and then a double ring of peristome teeth.

Riccia	Marchantia	Pellia	Anthoceros	Sphagnum	Funaria
The capsule wall is formed from the entire amphithecium.	The capsule wall is formed from the entire amphithecium.	The capsule wall is formed from the entire amphithecium.	The capsule wall is differentiated from the outer layer of the amphithecium.	As in *Anthoceros* the capsule wall is formed from the outer layer of the amphithecium.	They are all derived from the **amphithecium.**
Prior to maturity the capsule wall disorganises and disappears.	The capsule wall is persistent.	The capsule wall is persistent.	The capsule wall is persistent.	The capsule wall is persistent.	The capsule wall is persistent.
The **archesporium** is formed from the entire **endothecium.**	The entire **endothecium** forms the **archesporium** as in *Riccia.*	The entire **endothecium** functions as the **archesporium** as in *Riccia* and *Marchantia.*	The **archesporium** is formed from the **inner layer** of the **amphithecium.**	The **archesporium** develops from the **inner layer** of the **amphithecium** as in *Anthoceros.*	The **archesporium** and inner spore sac orginate from the **outer layers** of the **endothecium.**
The columella is absent.	The **columella** is absent.	The **columella** is absent. Some scientists consider **elaterophore** as the **forerunner** of the columella.	The **columella** forms the central core of the capsule. It is formed from the entire endothecium which in *Riccia, Marchantia* and *Pellia* forms the archesporium.	As in *Anthoceros* the entire endothecium forms the **columella** which forms the central bulky mass of sterile tissue.	The major central portion of the endothecium forms the **columella** continuous below with the enducting strand of the apophysis.
The primary archesporium divides to form the **sporogenous tissue** which fills the entire space within the capsule wall.	The same as in *Riccia.*	The same as in *Riccia* and *Marchantia.*	The archesporium divides to form the **sporogenous tissue** one to 4 layers in thickness. It is narrow and overarches the rounded apex of the columella like a dome and surrounds it.	The archesporium divides to form the sporogenous tissue 2-4 layers in thickness. It overarches the rounded apex of the massive columella and forms a dome-shaped zone in the upper part of the capsule only.	The archesporium may undergo division to form two layers thick **sporogenous tissue.** It is thus extremely reduced forming but a small and narrow part of the theca region of the capsule. It neither extends to the base nor apex of the capsule. It simply surrounds the columella and does not overarch it.
Major portion of the sporogenous tissue is differentiated into the **apore mother cells.** Only a few peripheral cells remain abortive and function as **nurse cells.** By some scientists the nurse cells are considered as **forerunners** of the **elaters** of *Marchantia.*	Half of the sporogenous tissue differentiates into the **spore mother cells** and the rest into **elater mother cells.** The latter give rise to the sterile, hygroscopic **elaters** which help in scattering the spores differentiated from the spore mother cells.	A central mass of **sporogenous cells** at the base of the capsule becomes differentiated into the **elaterophore** whereas the remaining sporogenous cells surrounding the elaterophore form the **spore mother cells** and the **elaters.**	The sporogenous tissue differentiates into fertile **spore mother cells** and the sterile **pseudo-elater** mother cells. The former give rise to the spores and the latter to the **pseudoelaters.**	The entire sporogenous tissue gives rise to the **spore mother cells.** The **elaters** are absent.	The entire sporogenous tissue as in *Sphagnum* differentiates into the **spore mother cells.** The **elaters** are absent.
There is no regular method of dehiscence to allow the spores to escape. The surviving outer layer of the calyptra and the adjacent thallus	The capsule of *Merchantia* dehisces to allow the spores to escape. The capsule wall splits open into several usually 4-6 irregular teeth-	The capsule dehisces in a more regular manner as compared with *Marchantia.* It dehisces by crossed cleavages along the four lines of	Dehiscence is very regular. The mature capsule splits along 1-4 lines of dehiscence. The splits extend downwards separating into valves	Dehiscence is by the separation of a lid and is explosive. The spores are forcibly blown out.	The annulus cells perish and the operculum falls off exposing the peristome teeth. The latter by their peculiar disposition and hygro-

Riccia	Marchantia	Pellia	Anthoceros	Sphagnum	Funaria
tissue undergo decay. The spores are simply left behind in the soil to be dispersed by the wind.	like structures from the apex to about the middle of the capsule exposing the mass of spores and elaters.	dehiscence into four valves which get reflexed.	which remain united at the tip. Pseudoelaters help in spore dispersal.		scopic movement release a few spores at a time during dry weather.
The sporophyte is **totally parasitic** for its nutrition on the parent thallus (gametophyte).	As in *Riccia* the sporophyte is **totally parasitic** for its nutrition on the parent thallus (gametophyte).	As in *Riccia* and *Marchantia* the photosynthetic tissue is absent in the capsule wall. So the sporophyte is **parasitic** for its nutrition on the parent thallus (gametophyte).	Unlike *Riccia*, *Marchantia* and *Pellia* there is a well developed well ventilated photosynthetic tissue in the capsule wall. The sporophyte is thus able to prepare its carbohydrate food. For water and minerals in solution it still depends on the parent gametophyte. It is therefore a **semi-parasite.**	The photosynthetic tissue in the capsule wall is poorly developed and non-ventilated. It cannot fully meet the carbohydrate requirements of the sporophyte which is thus **mainly dependent** for its nutrition on the gametophyte.	There is a well developed and well ventilated photosynthetic tissue in the apophysis region. The sporophyte thus depends on the parent gametophore only for its supply of water and mineral salts. It is a **semi-parasite.**
The sporophyte is **a** short-lived structure. The whole sporophytic tissue perishes by the time the spores reach maturity.	The sporophyte is a short-lived structure. It dies as soon as the spores are shed.	The sporophyte dies as soon as the spores are shed.	The sporophyte is comparatively a long-lived structure. With the help of its intercalary meristem it continues to live and produce spores as long as the thallus lives.	The sporophyte perishes as soon as the spores are shed.	With the complete shedding of spores, which are released in successive showers and not all simultaneously, the sporophyte dies.

REVISION QUESTIONS

1. Describe the evolution of the sporophyte in the bryophytes studied by you. *(Agra Univ., 1962)*
2. Compare the sporophyte of *Marchantia* with any Moss studied by you. Give labelled sketches. *(Agra Univ., 1958)*
3. Compare the structure of the sporophyte of *Riccia* with that of *Anthoceros.* *(Agra Univ. 1959)*
4. Write a comparative account of (*a*) the structure of the thallus and (*b*) the organisation of the sporophyte in *Marchantia* and *Anthoceros.* *(Agra Univ., 1960)*
5. Compare the gametophyte of *Riccia* with that of *Marchantia.* *(Agra Univ., 1951, 57)*
6. Compare the sporophytes of *Riccia, Anthoceros* and *Funaria.* *(Agra Univ. 1956)*
7. Give a comparative account of the sex organs of *Riccia, Marchantia, Anthoceros* and *Funaria.*
8. Discuss the systematic position of division of Bryophyta.
9. Describe the various views on the origin of Bryophyta.
10. Discuss the biological and economic importance of Bryophyta.
11. What is archesporium ? Give an account of the origin and fate of this tissue in a tabular form in the bryophytes studied by you.

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