

REBOULIA HEMISPHERICA (L.) Raddi – Purple fringed liverwort

Rank	Scientific Name and Common Name
Kingdom	Plantae – Plants
Division	Hepaticophyta – Liverworts
Subdivision	Hepaticae
Class	Hepaticopsida
Subclass	Marchantiae
Order	Marchantiales
Family	Aytoniaceae
Genus	<i>Reboulia</i> Raddi, nom. cons.
Species	<i>Reboulia hemisphaerica</i> (L.) Raddi



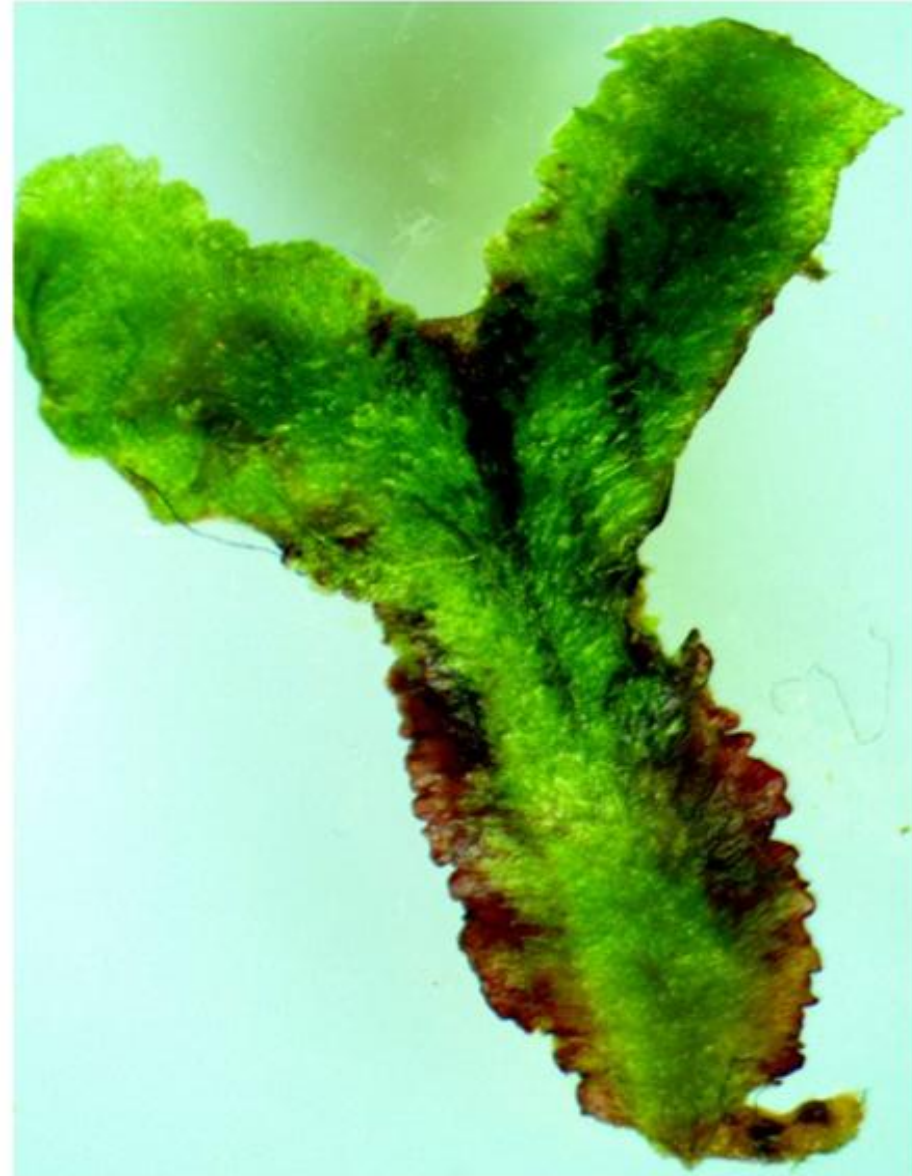
Figure 23.3 *Reboulia hemisphaerica* between brick pavers.

Distribution

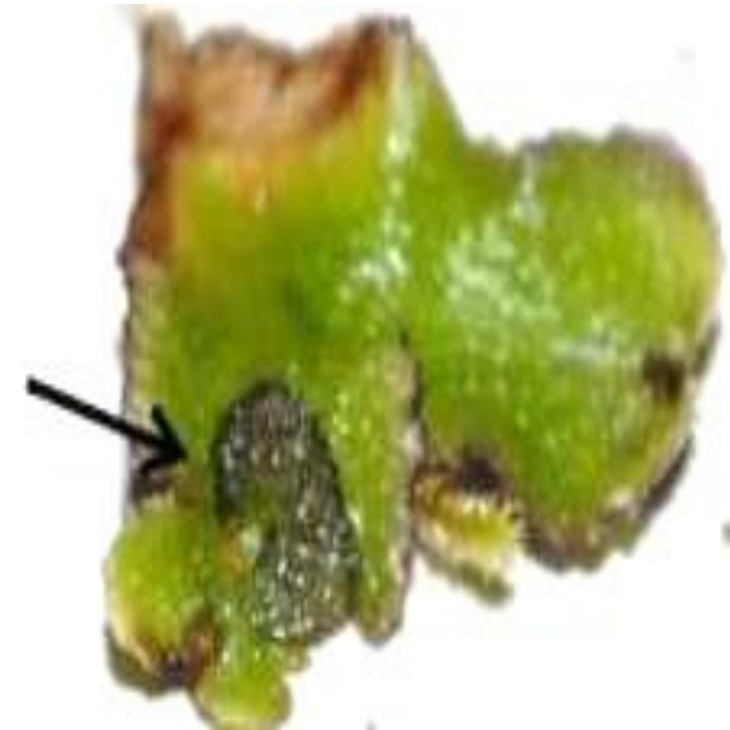
Description

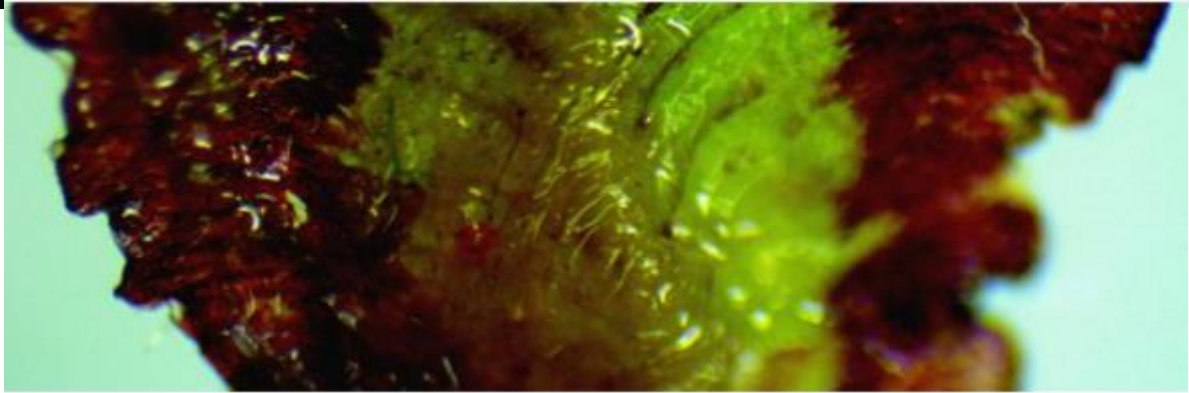
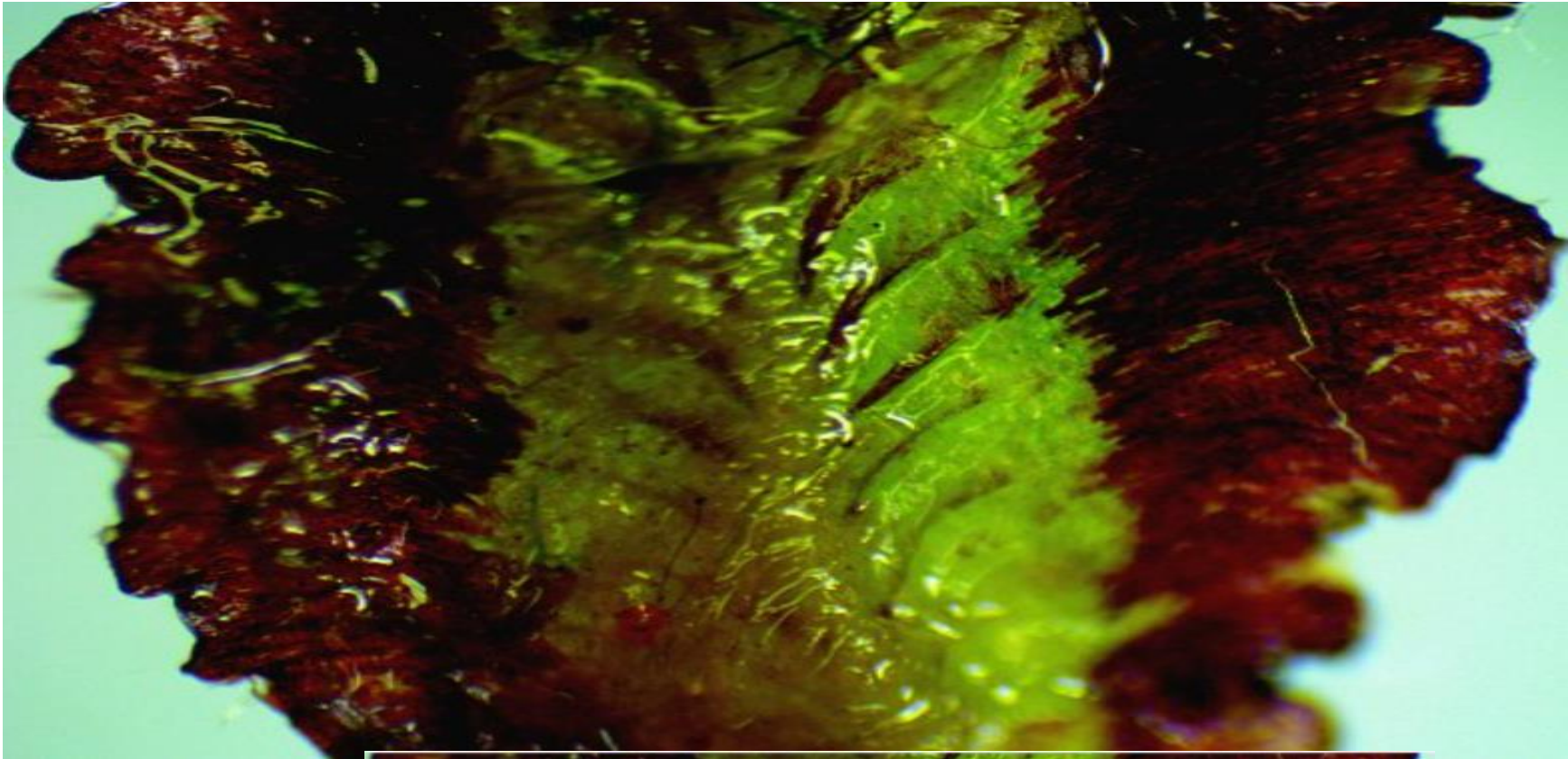
South India (Tamil Nadu: Nilgiri hills, Madras, Palni hills, Tirunelvely hills), Central India (Mt. Abu), North-east India (Mussoorie, Simla, Kulu, Kashmir, Darjeeling, Pachmahri, Khasi hills), China, Japan, Korea, Nepal, Afganistan, Pakistan, Java, Bonin, New Zealand, Australia, North & South America, Tahiti, Europe and Africa.

- The gametophyte plant body of *Reboulia hemisphaerica* is a pale green, dichotomously branched thallus with slightly undulate margins and a distinct midrib.
- Rhizoids and scales arise from the ventral surface. Both smooth and pegged rhizoids occur, their ends often being highly contorted when in contact with soil particles.
- The dark red ventral scales are 2-ranked and point diagonally forward and outward. They do not arise from the splitting of a single scale as in most species of *Riccia*, but are separate from the beginning.
- The scales are 1 cell thick except near their place of attachment to the thallus where they are often 2 cells thick. They are un-appendaged.
- Fresh specimens of *Reboulia* have a distinct aroma and a sweet taste when crushed.
- The generic name is dedicated by the author to Eugen de Reboul (1781-1851), an Italian botanist from Florence



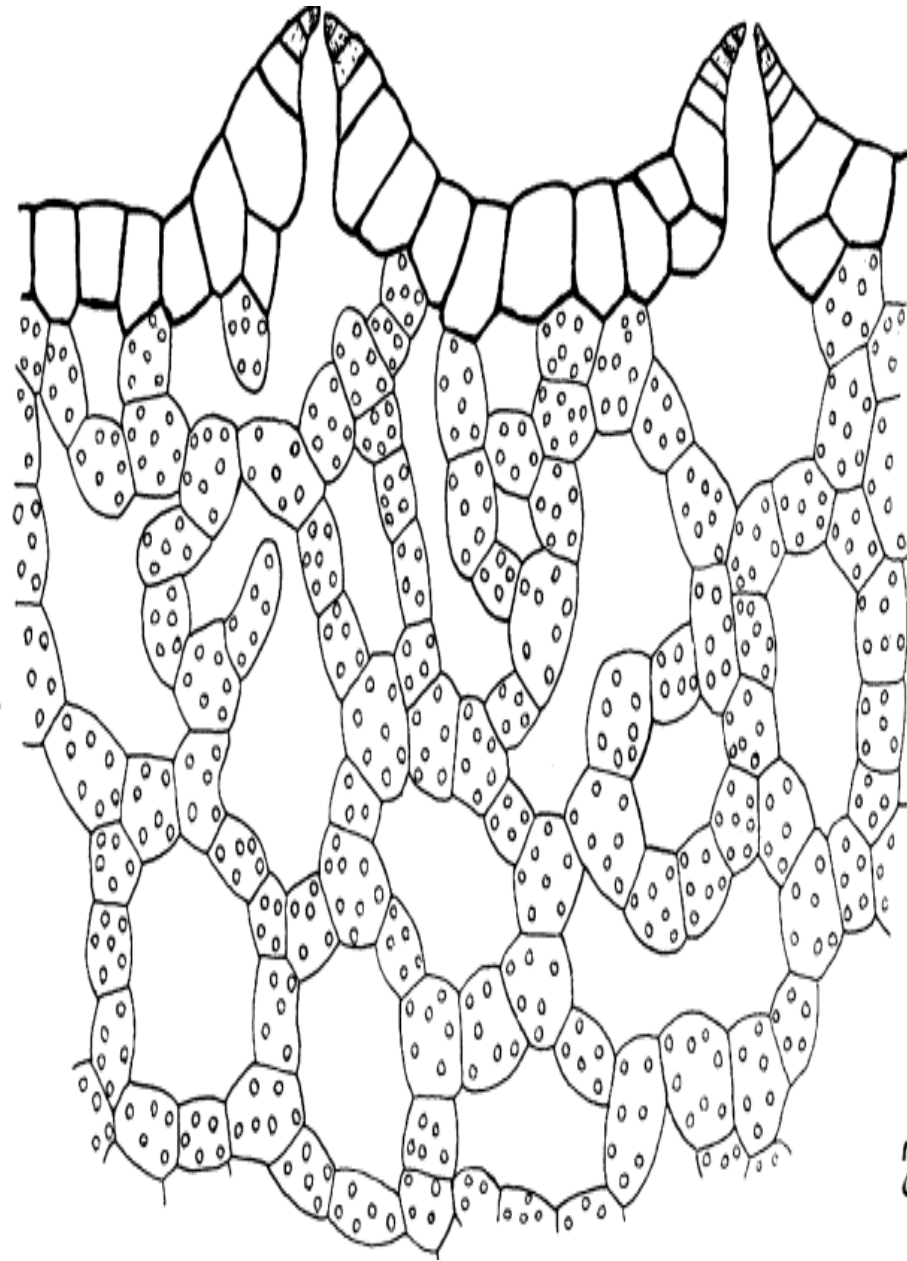
Comments: This is a moderate-sized thalloid liverwort. It is similar in appearance to several other thalloid liverworts, but it can be distinguished from these species by considering the following features: 1) its thalli are typically 6-8 mm. across, 2) the margins of its thalli are often purplish, 3) its mature thalli have purple undersides with 2 rows of purplish scales, 4) whitish air pores are barely visible with the naked eye on the upper surface of its thalli, 5) indentations separating the cells of air pores are not visible to the naked eye on the upper surface of its thalli, and 6) the margins of its thalli curl upward when they dry out, rather than remaining flat. If the male and female receptacles are present, they are also useful in identification: 1) the small male receptacles are kidney-shaped or crescent-shaped, purplish, and sessile, 2) the males receptacles are usually located only 1-10 mm. behind each female receptacle on a thallus, 3) there are white filaments at the apex and base of the stalk of the elevated female receptacle, and 4) the female receptacle has 4-7 rounded lobes at maturity. The most similar liverwort species



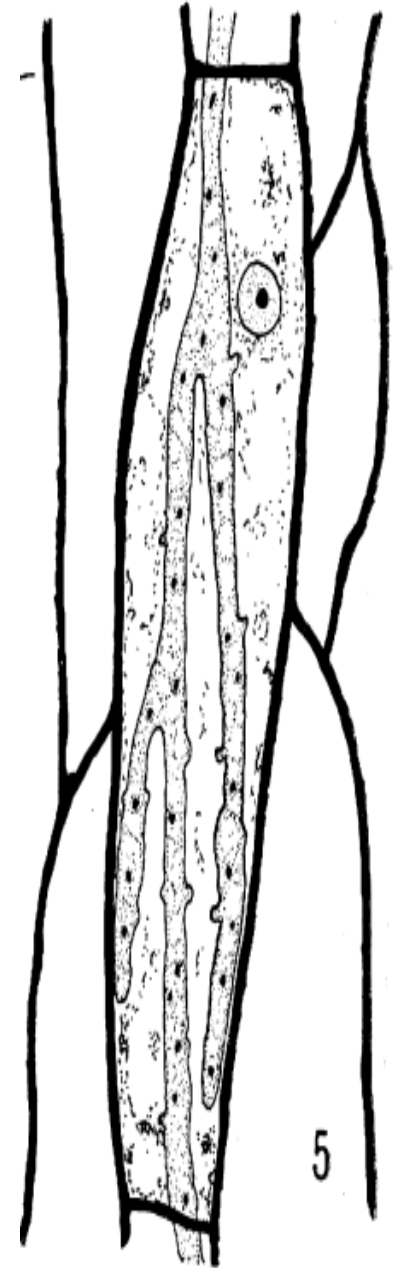


Internal Structure of Thallus

The body of the thallus is differentiated into a lower colorless region of compact elongated cells with rather thick walls, and an upper region of loose chlorophyllose tissue containing large air chambers. Intracellular fungi live in the lower region (5). The walls of the epidermal cells are slightly thickened and are devoid- of chloroplasts except near the growing point of the thallus (Fig. 2). The plastids in the air chamber region are rather large and contain several starch grains with distinct hila. Plastids in the cells in the growing region are small and contain no starch. Small oil globules are very abundant in the apical cell region and occur less abundantly in the cells of the older parts of the thallus. The formation of a definite oil cell from an ordinary vegetative cell is a common feature of the genus. No gemmae are produced.



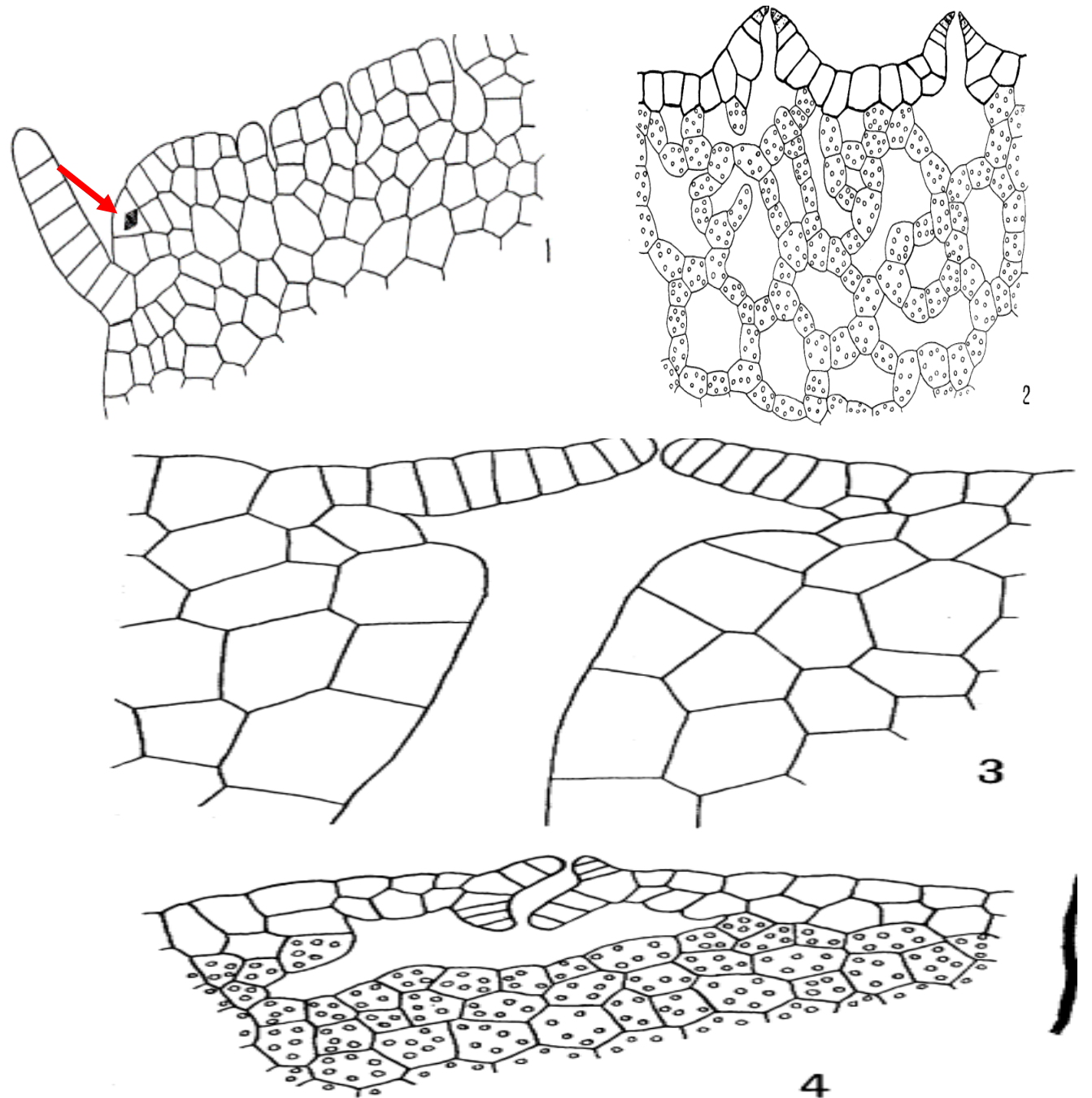
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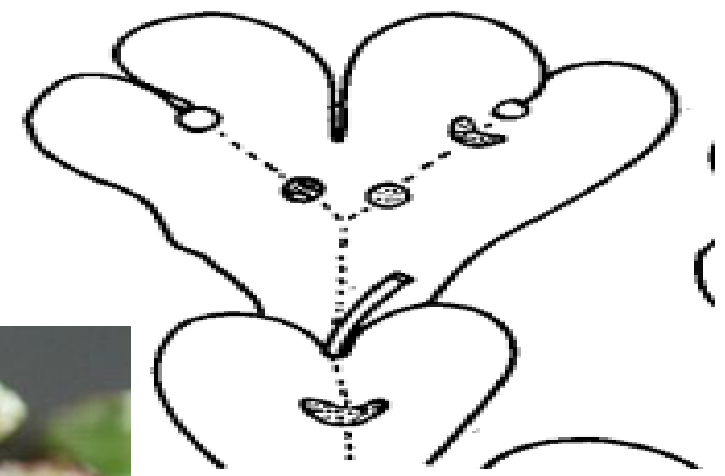
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The thallus grows by means of a single cuneate apical cell which cuts off segments from its four sides

(fig. 1). The air chambers form a very extensive system of irregular air passages separated by thin partitions, but more or less connected (fig. 2). No chlorophyllose filaments are formed. the secondary partitions arise from all sides of the primary air chambers and grow toward the center, and that the boundaries of the primary chambers are soon lost, resulting in the entire air chamber region becoming broken up into a uniform spongy tissue. The air chambers of *Reboulia* arise immediately behind the apical cell of the thallus by intercellular splittings which start at the surface of the thallus and progress inward (fig. 1), reaching the line of differentiation between the dorsal and ventral regions. The cells forming the air pore margins are attenuate, and are developed by segmentation from the adjacent epidermal cells (fig. 2). This type of air pore also occurs on the male receptacle (3), but those on the female receptacle are barrel-shaped (fig. 4). The air chambers in the female receptacle develop like those of the main body of the thallus



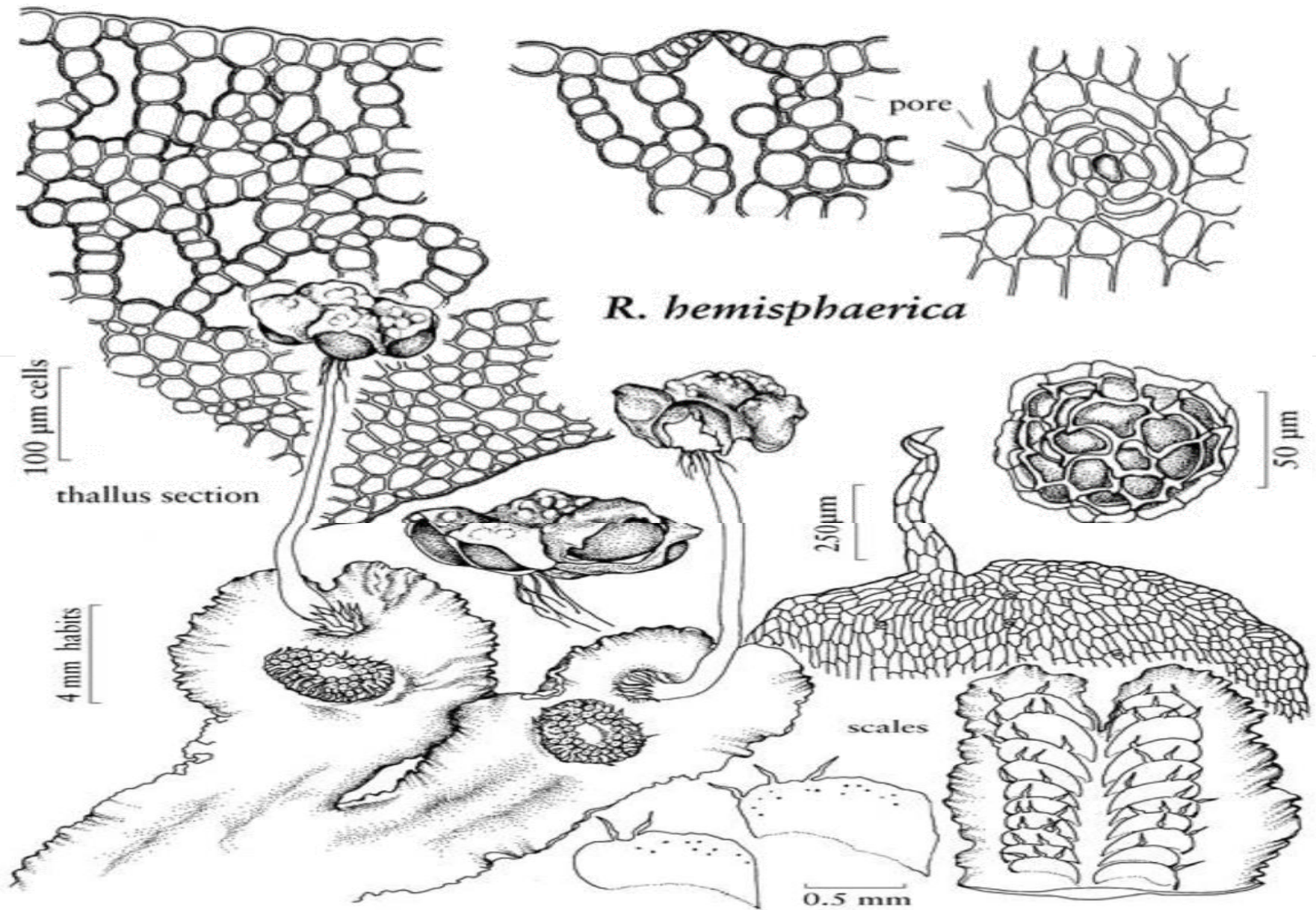
This liverwort is monoecious (at least in North America), as both male and female reproductive organs are present on the same plant (thallus). The female reproductive organs (archegonia) are contained in a shallow dome-shaped receptacle that develops within the notches of the growing tips on the upper surface of a thallus. When this happens, a thallus will stop growing, although it may form 2 branches. The female receptacle is green and speckled with white from an abundance of air pores along its upper surface. The male reproductive organs (antheridia) are located within one or more reniform (kidney-shaped) or lunate (crescent moon-shaped) receptacles that are usually purplish and shallowly elevated on the upper surface of a thallus. The male receptacles are usually located only 1-10 mm. behind the female receptacle on the same thallus body or branch. After fertilization occurs, the male receptacles become somewhat shriveled, while the female receptacle becomes elevated on a stalk (seta) about 1-3 cm. high. Depending on the local ecotype, environmental conditions, and its maturity, this stalk can be white, light green, yellow, light purple, or dark purple; it is mostly terete, except for a narrow slit along one side. The dome-shaped head of the female receptacle (carpocephalum) becomes more lobed as it matures; there are typically 4-7 rounded lobes that become partially separated from each other by downward-sloping indentations. Along the underside of the elevated female receptacle, there is a ring of 4-7 ovoid spore cases. A white-membranous covering of the spore cases splits apart as they develop; immature spore cases are light green or yellowish green, while mature spore cases become dark purple or black. At the base of the stalk (seta) of the female receptacle, there is a tuft of membranous-white filaments, while another tuft of membranous-white filaments occur at the apex of the stalk where the female receptacle is located. The spore cases split open to release their spores to the wind; because they are rather large in size for spores, they may not travel far. Individual spores are 65-80 micrometers across, globoid in shape, yellow to brown, and winged.











R. hemisphaerica

100 µm cells

thallus section

4 mm habits

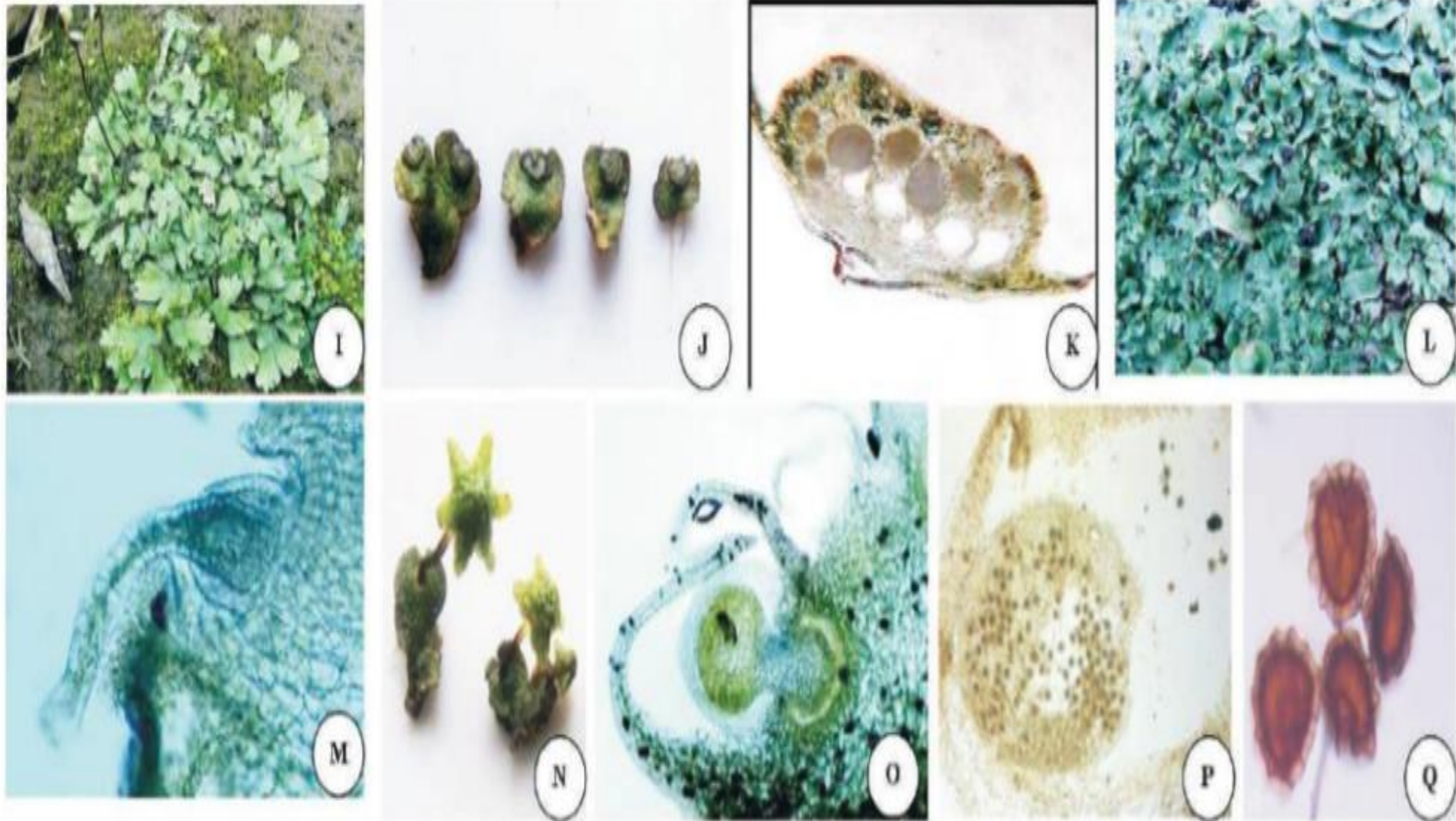
250µm

50 µm

scales

0.5 mm

REBOULIA



male receptacles (G); Sporophyte with spores and elaters (H); A patch of *Roboulia hemispherica* (I); Few male thalli (J) VS passing through male receptacles showing antheridia (K); A patch with female receptacles (L); VS passing through young female receptacle (M); Few thalli with mature female receptacles (N); VS passing through mature female receptacle (O); Spore mother cells in a capsule (P); Magnified view of spores (Q).



Figure 23.4 Hemispherical structures that presumably inspired the name *hemisphaerica*. Each is a female reproductive organ (archegonium). The dark structure above each hemisphere is the male reproductive organ (antheridium). To fertilize eggs, sperm must swim from male to female organs in rainwater, dew, or meltwater. Photographed January 12, 2008.



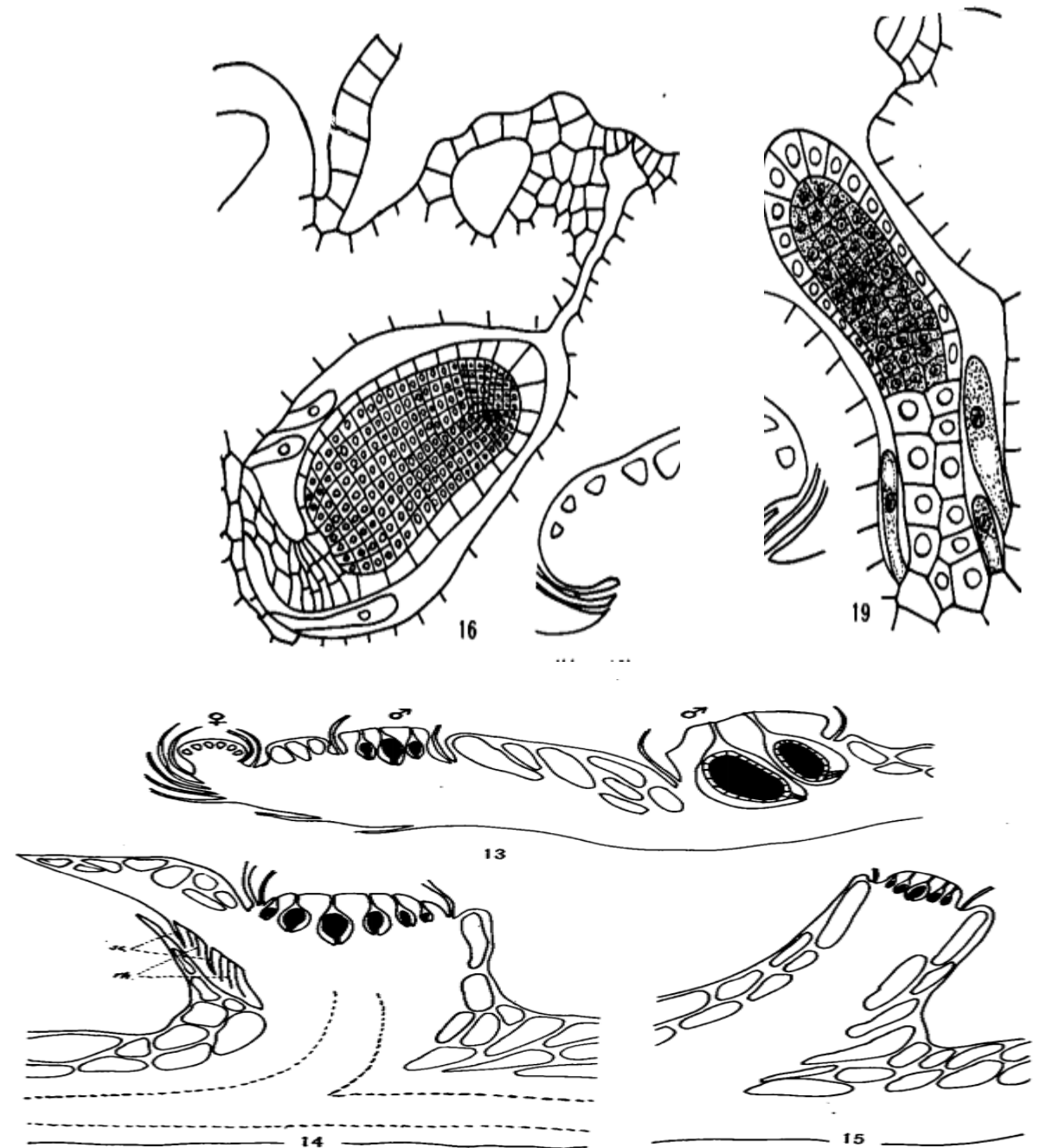
SEX ORGANS OF REBOULIA

The plants of *Reboulia* are monoecious, and the antheridia and archegonia are borne in separate median groups on the dorsal surface of the thallus. The antheridial group is only slightly raised above the general surface of the thallus, and the archegonial receptacle becomes lifted up on a stalk only after the sporophytes are approaching maturity. The archegonia appear in the autumn, fertilization occurs, and the embryo develops immediately. The sporophyte, however, does not mature until the following spring.

Structure of male receptacle.

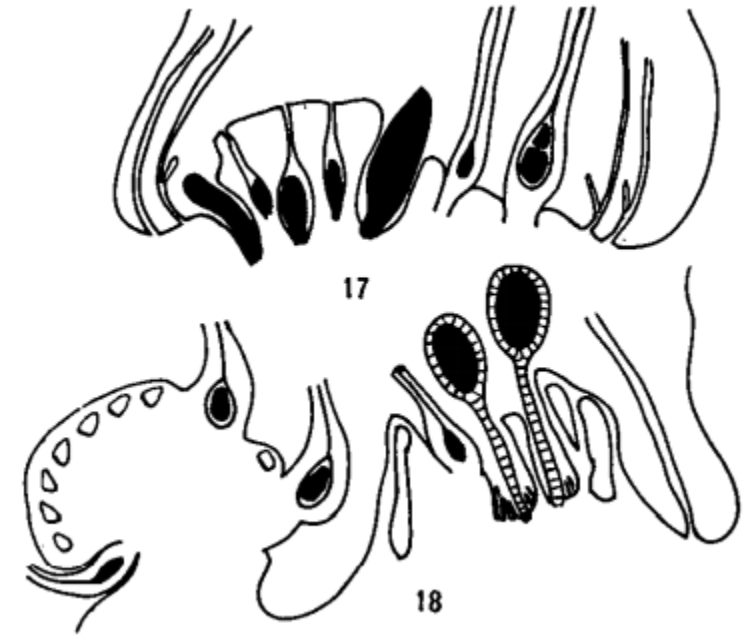
The tissue of the young male disc is rather compact, but with the development of the antheridia the growth of the disc tissue exceeds that of the sex organs which thus become deeply imbedded in deep chambers opening to the exterior by narrow canals and simple air pores (fig. 16). Small air chambers develop between the canals. These chambers have simple pores. Small barrel-type openings to occur occasionally. The disc is usually surrounded by a groove within which small narrow scales develop, similar to those around the female receptacle. Mucilage cells arise from the base of the antheridial chamber (figs. 16, 19)

Usually the receptacle is raised only a slight distance above the general surface of the thallus (fig. 13), but it may, in some cases, be elevated on a short stalk (figs. 14, 15), the stalk being formed by intercalary growth of the ventral tissue forming a central core surrounded by air chamber tissue like that of the thallus itself. The fungal hyphae of the compact tissue may penetrate the stalk, and in one case the raised portion bore a few ventral scales and a few pegged rhizoids on the posterior margin (fig. 14)



1. The male receptacle of *Reboulia hemisphaerica* occupies a dorsal position, as a rule, posterior to the female receptacle which terminates the branch.
2. The receptacle is usually more or less lunate in outline, although it may be circular, or more or less irregular. It is sessile, as a rule, although in rare cases it may be elevated on a very short stalk.
3. *R. hemisphaerica* is monoecious, with the sex organs in distinct groups, although bisexual receptacles may occur.
4. The antheridia show a tendency toward centrifugal development. Variations from the usual marchantiaceous type of development occur, such as the occasional appearance of an apical cell with two cutting faces and the occasional formation of only two primary spermatogenous cells in a segment.
5. The male receptacle is a plastic structure, probably representing an elementary stage of a branch system and showing transitions from the "dorsal outgrowth" type to the "composite branch-system" type.

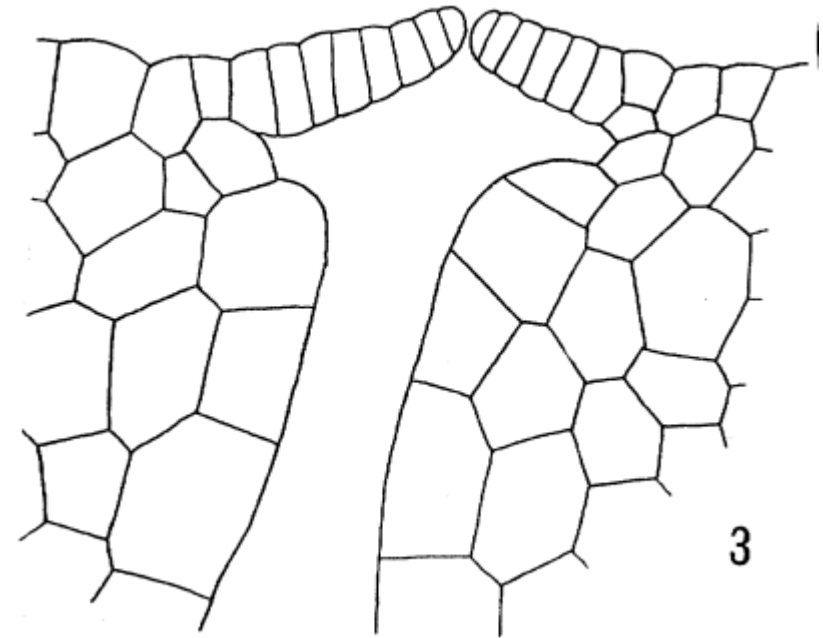
In a few such cases in *Reboulia*, where archegonia may occur on the male receptacle (figs. 17, 18) or antheridia on a female receptacle. The young antheridia found on the female receptacle were deeply imbedded within the tissue.



ANTHERIDIUM AND ITS DEVELOPMENT

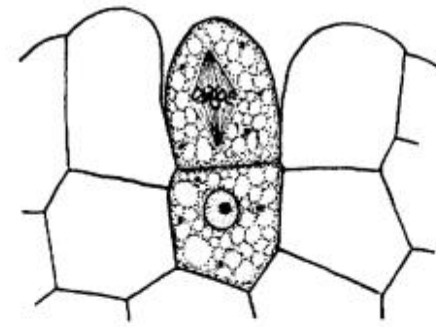
The antheridia occur in sessile lunate receptacles which are sometimes irregular in outline and broken up into several pieces. The receptacle is cushion-shaped and slightly raised above the general level of the thallus, but the antheridia themselves are rather deeply sunken in the main body of the thallus. Four, or occasionally 5, antheridia are usually seen in cross-section, and 4-6 in longitudinal section, but often more, and in rare cases as many as 24 were counted in longitudinal section. The number of antheridia in a receptacle, therefore, varies from about 16 to over 100. Usually 2 and rarely 3 groups of antheridia are produced successively on the thallus before the appearance of the archegonial receptacle. They are formed in rather close proximity (about 7-10 cells removed) to the apical cell, and each group becomes isolated by a rather wide area of sterile tissue of the thallus. In all cases the antheridia develop strictly in acropetal succession from segments of the apical cell. Air chambers are abundantly formed in the raised portion of the thallus which communicate with the surface by means of air pores similar to those which occur on the rest of the thallus. By growth of the epidermal cells around the pores which communicate with the antheridial cavities, a plate of cells is formed containing a small central perforation through which the sperms escape (fig. 3).

the explosive discharge of the sperms, as high as 5 cm.

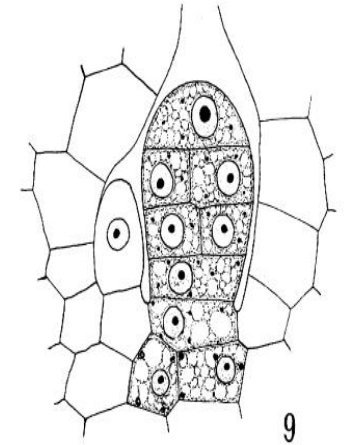


The development of the antheridia of *Reboulia* is similar to that of the other *Marchantiales* which have been investigated. The superficial papillate initial is soon overgrown by the adjacent cells of the thallus, so that the antheridium comes to lie in a pit, the development of the antheridial pit is therefore very different from that of the air chambers. The first division of the initial is transverse and separates the imbedded portion of the stalks from the rest of the antheridium (fig. 7). Additional transverse walls appear in the outer cell without a definite sequence, resulting in a filament of 4 cells (fig. 8). Vertical walls are then formed in two planes at right angles to each other, which usually are first developed in the basal tiers, or sometimes elsewhere (fig. 9). After the formation of the first vertical walls in the lower tiers, additional transverse divisions usually occur below, and as a consequence 5 or 6 tiers of cells are formed (Fig 10)

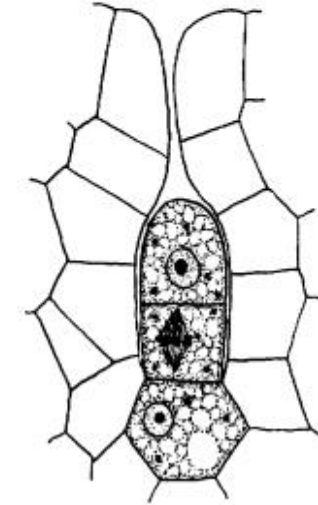
Periclinal divisions next occur invariably in the 3 uppermost tiers of cells (figs. 11 & 13), separating the inner spermatogenous cells from the outer sterile wall cells. The cells in which no periclinal appears form the stalk. The further development of the spermatogenous tissue is like that of the other *Marchantiales*. The sperms differ in no way from those of the other members of the group. "With the coming in of the first vertical walls in the young antheridium, several mucilage hairs arise from the cells which line the antheridial cavity. These arise near the base of the antheridial stalk as 1-celled, slightly elongated structures with a nucleus and a highly vacuolated cytoplasm (figs. 9-13). They elongate considerably and secrete abundant mucilage around the mature antheridia.



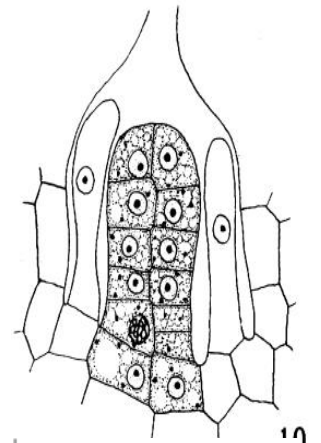
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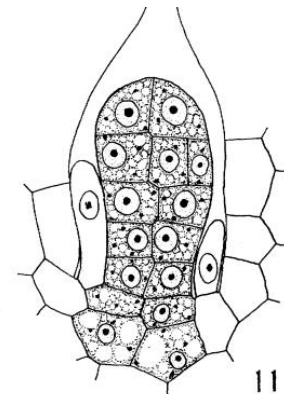
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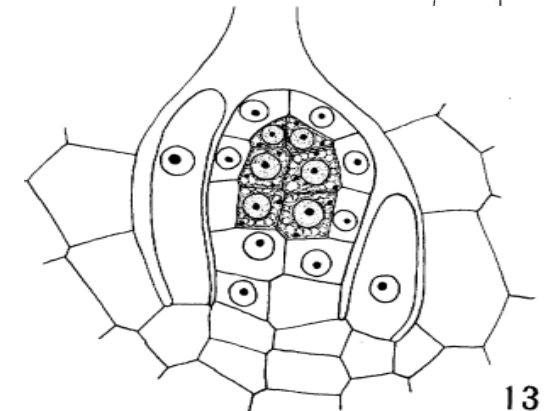
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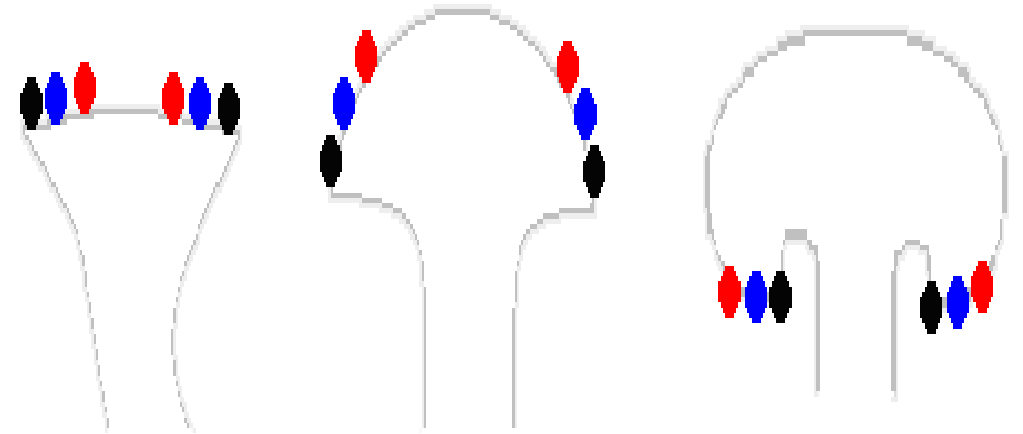
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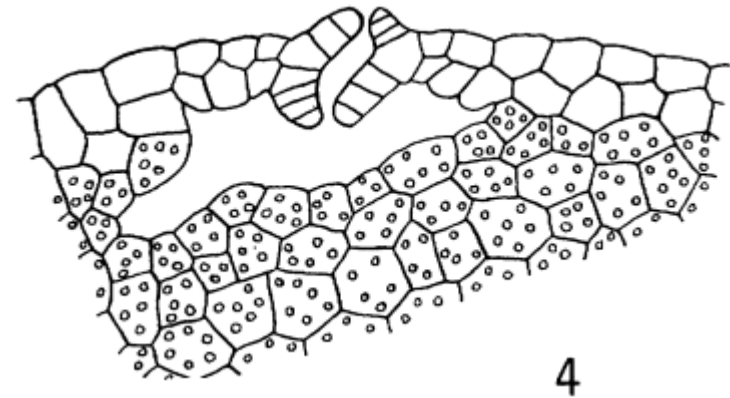
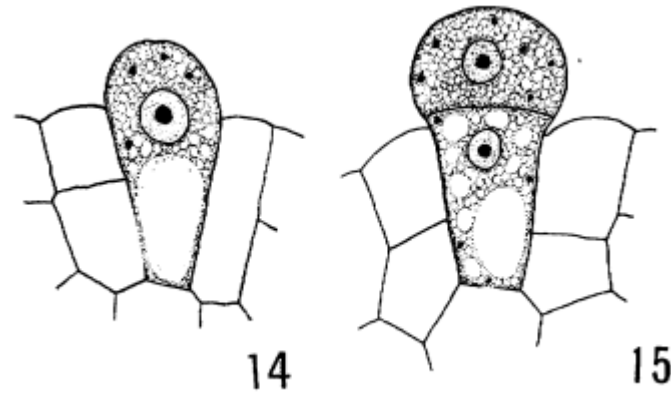
Female Receptacle

A number of thallose liverworts produce their sporophytes in umbrella-like structures. An example is the genus *Marchantia*. Here is a differently shaped "umbrella" top from a different species of *Marchantia*. Each such "umbrella", or **archegoniophore**, is not itself a sporophyte but is in fact gametophyte tissue. The part of the "umbrella" at the top of the stem is called the female **receptacle** or **carpocephalum**. The receptacle is initially on the thallus surface and the stalk grows to raise it. The archegonia are found on the female receptacle and initially they are in the upper surface and face upward. They are fertilized when the stem is still fairly short. The stem continues to grow and the receptacle continues to grow by centrally added tissue. This moves the fertilized archegonia outward and the receptacle eventually folds over to orient the developing sporophytes so that they face down. The following stylized diagram shows three stages in that process with the coloured dots indicating the positions of six archegonia. A number of sporophytes develop under each receptacle and each sporophyte has a short, robust seta. Each fluffy, yellow mass is a mix of spores and **ELATERS** that has been exposed upon the rupture of a spore capsule.



The archegonia are borne on receptacles which arise as dome-like areas at the growing point of the thallus. The formation of the archegonial receptacle involves the apical cell of the thallus, so that growth for the season is checked. Several (up to 6) growing points are organized in the young receptacle from segments of the main apical cell of the thallus, and thereby a new apical cell is formed in each receptacle notch.

The archegonium initials arise from the third or fourth segment of each apical cell, and do not appear until the young receptacle is conspicuously dome-shaped. The initial arises as a superficial cell which becomes papillate, and the first transverse wall cuts off a basal cell from an outer cell (figs. 14, 15). Three vertical walls then appear in the outer cell, and the primary axial cell and primary wall cells are differentiated as in all of the Bryophytes (fig. 16). The basal cell usually divides by a transverse (figs. 16, 17) or vertical walls. Further development of the archegonium is typical (figs. 17-20). The cover cell divides by a vertical wall which accompanies the first division of the primary neck canal cell. No evidence was found to lead to the suspicion that earlier than this stage the cover cell contributes to the development of the neck cells. Numerous mitotic figures in the neck cells prove that they increase in number by intercalary divisions.



The ventral canal cell and egg are formed, from the primary ventral cell rather early (fig. 20), and the former is unusually small. As soon as the egg is formed, the venter of the archegonium develops 2 layers of cells, and this condition prevails until after fertilization. The archegonial stalk is short, and the neck invariably curves outward and upward (fig. 21) so as to facilitate the entrance of the sperms, as in other forms in which the archegonia are borne similarly. The mature archegonium contains 18-20 neck canal cells which break down soon after their formation. The neck in all cases shows 6 cells in cross-section.

In the great majority of cases only one archegonium is formed from a single segment of each apical cell, and usually the egg of each develops a sporophyte. Occasionally 2 archegonia may be produced in the same receptacle notch. The apical cells of the female receptacle are checked by the formation of the archegonia and soon become lost. The lobes which develop between the archegonia grow entirely by intercalary divisions. Slender filaments arise below each archegonium, and grow to a considerable length. The filaments become quite numerous in each receptacle notch, and persist until the spores are shed. They are probably protective in function. The mature egg is oval and contains many plastids and several large oil globules (fig. 21). These oil drops are much larger than those found in the cells of the thallus, and they persist in the early stages of the embryo. The mature egg does not develop a cellulose wall until after fertilization. The number of lobes developed by the mature female receptacle corresponds with the number of growing points organized in the young receptacle. The lobes are not conspicuous

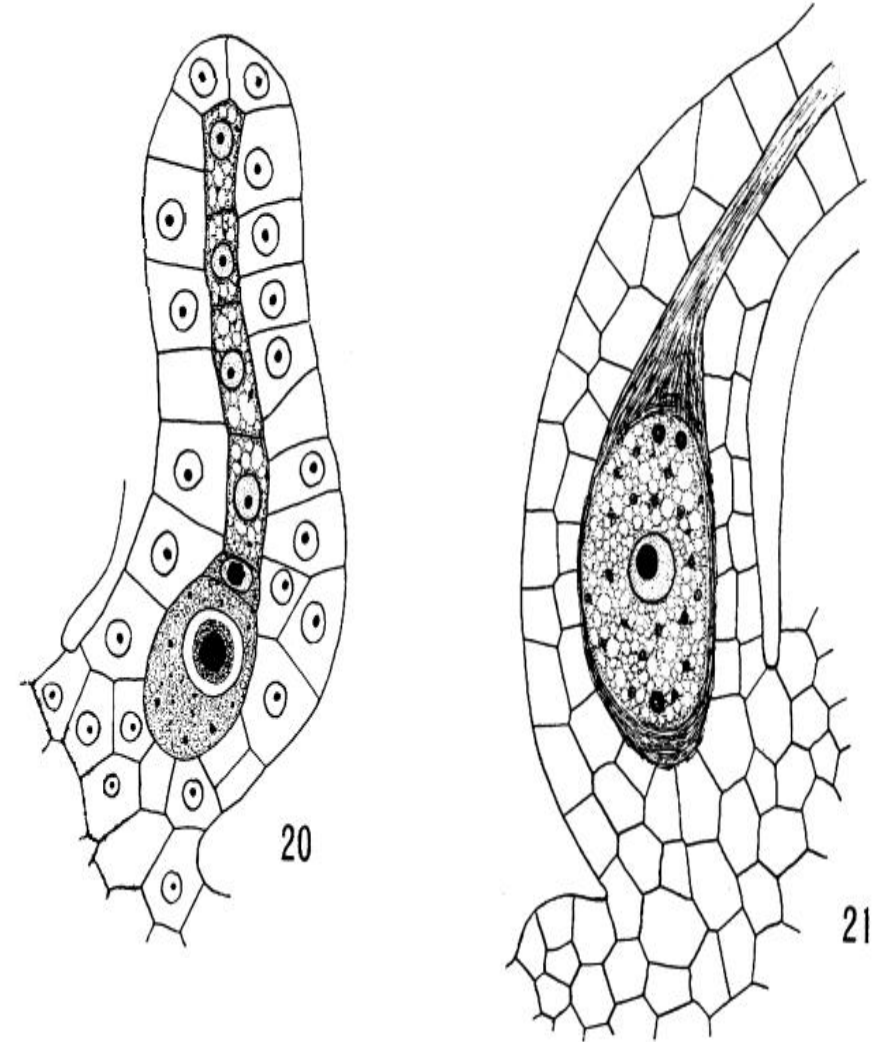


FIG. 21.—Venter of mature archegonium showing egg ready for fertilization, $\times 660$.

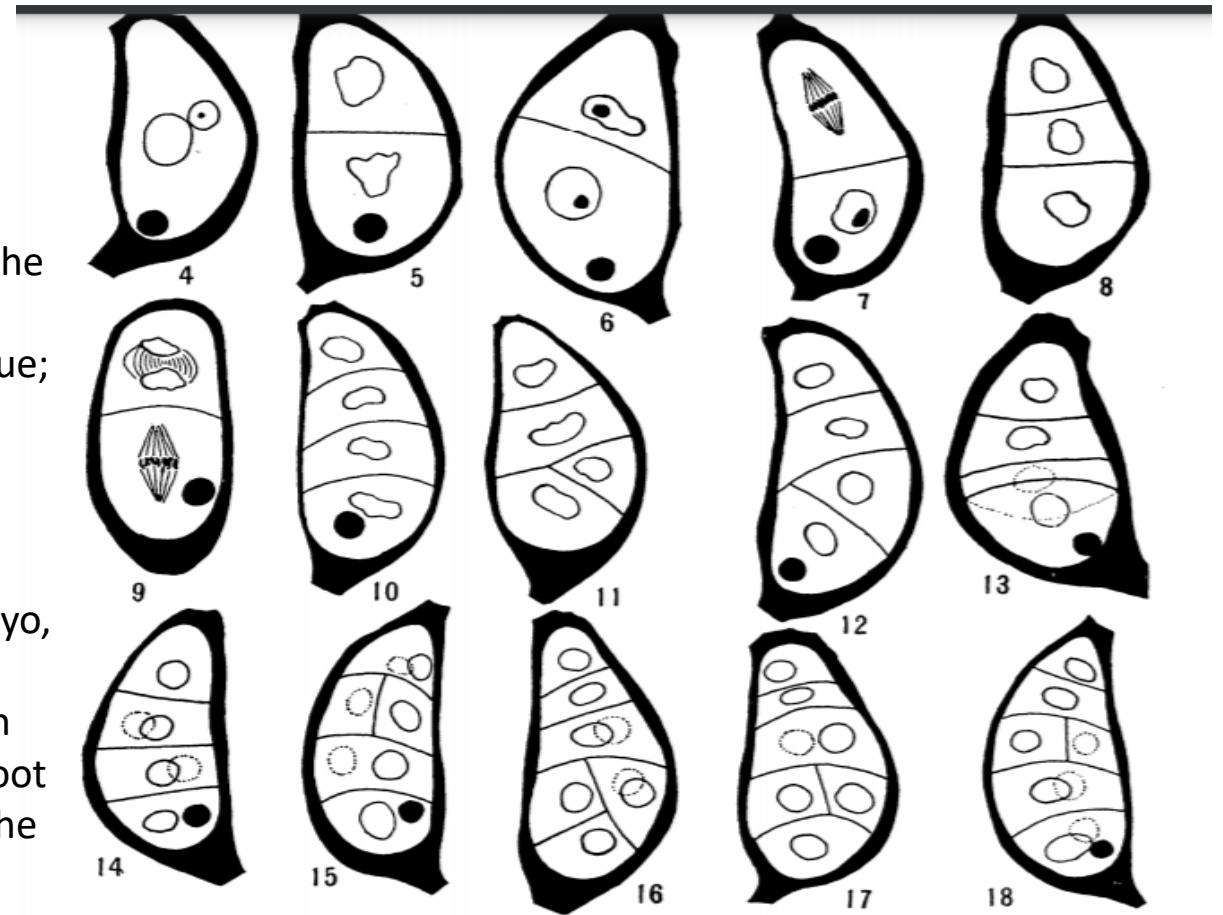
Fertilization

The close proximity of the male and female receptacles on the same branch of the thallus usually insures fertilization, although occasionally it fails to occur.

WOODBURN calls attention to the change which the motile sperm undergoes from the time it leaves the antheridium until its nucleus is ready to fuse with the egg nucleus. The writer found a number of cases in which the sperm nucleus had penetrated the egg cytoplasm and lay close to the egg nucleus . At this time the egg nucleus has about twice the diameter of the sperm nucleus, whose more compacted chromatin results in a denser staining body. No attempt was made to study the nuclear changes involved in fertilization. Apparently the fusion nucleus passes into the resting stage before division of the egg takes plac

1. The mature egg and early embryo are elongated, slightly curved, bilaterally symmetrical bodies.
2. Fertilization takes place in October, the development of the embryo beginning at once, the sporogenous tissue becoming differentiated by winter, the sporophyte maturing in May and June.
3. The early embryo shows considerable variation in its development, the chief features being:

- (1) the first division of the egg may be transverse or oblique;
- (2) transverse division of both hypobasal and epibasal cells results in a filamentous embryo of four cells;
- (3) vertical wall formation occurs in these four cells, with the exception, commonly, of the basal cell;
- (4) oblique walls may occur in any part of the embryo, and are not uncommonly to be found in the apical region where they may form a triangular apical cell, functional in the cutting off of a few segments;
- (5) the foot and stalk are probably derived from the hypobasal cell, the epibasal cell giving rise to the capsule, although it may conceivably make some contribution to the stalk as well;
- (6) the basal cell of the row of four varies in its contribution to the tissue of the foot, at times apparently remaining undivided, in which case the remainder of the foot and the stalk is derived from its sister cell.

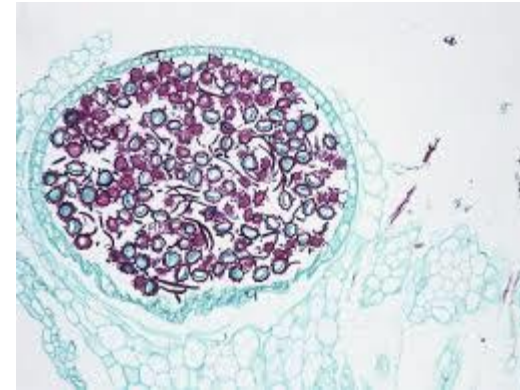


FIGS. 4-18.—Fig. 4, egg with male and female nuclei, black circle representing oil drop; fig. 5, first wall transverse; fig. 6, first wall oblique; fig. 7, mitosis in hypobasal cell; fig. 8, embryo of three cells; fig. 9, mitosis in both epibasal and hypobasal cells; fig. 10, typical filamentous embryo of four cells; figs. 11-13, epibasal cell divided by oblique wall; fig. 14, vertical division of two middle cells of row, basal and apical cells undivided as yet; fig. 15, apical cell not yet divided by vertical wall; fig. 16, epibasal cell divided by oblique wall, vertical division in middle of embryo, basal cell of row of four probably transversely divided; figs. 17, 18, two cells at base probably resulting from transverse division of basal cell; $\times 430$.

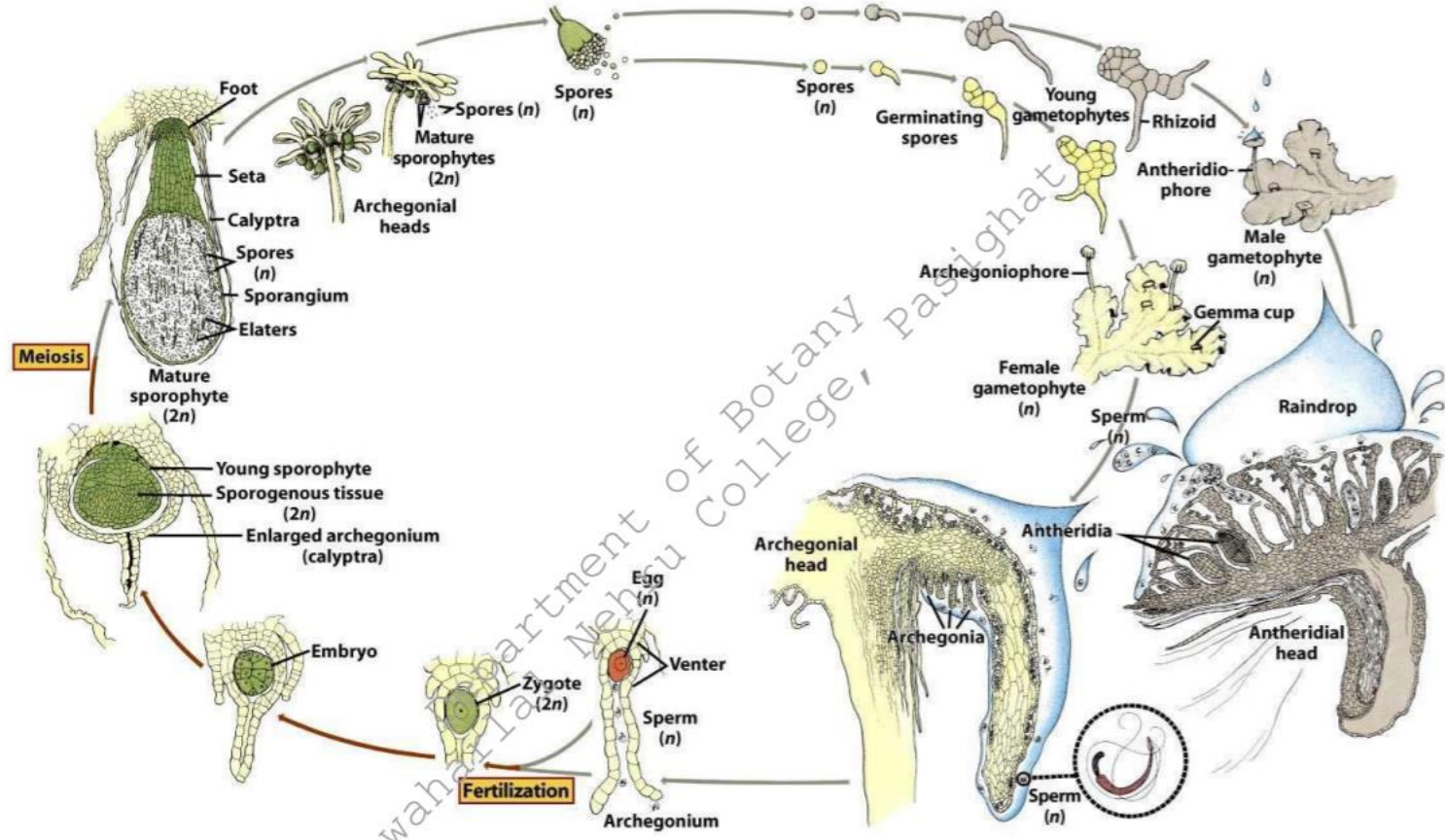
Sporogonium:

It possesses a spherical capsule, seta and foot. Capsule has a single-layered jacket, and dehisces irregularly at the apex. Spores are spherical, brown, reticulate – lamellate and about 65 – 75 μm in diameter. Elaters are with 2-3 spirals, coiled, 300 – 400 μm long

carpocephalum hemispheric, the proximal half lobed, each lobe with a 2-labiate slit, and containing one sporophyte; pseudoperianth absent. **Sporophyte** seta not elongating. **Capsule** spherical, irregularly circumscissile, the distal portion disintegrating; capsule wall without thickenings. **Spores** areolate, the areolae bordered by winglike ridges; elaters 2--4 spiral.



LIFE CYCLE



SUMMARY

1. *Reboulia* comprises a single polymorphic species, *R. hemisphaerica*, belonging to the Operculatae division of the subfamily Marchantioideae.
2. The thallus bears smooth and pegged rhizoids and 2-ranked ventral scales without appendages. The body is differentiated into a dorsal and ventral region, and grows by means of a single cuneate apical cell.
3. Air chambers are abundantly formed and develop by centripetal splittings. Secondary partitions separate the primary air chambers. No chlorophyllose filaments are formed.
4. Barrel-shaped air pores are developed on the female receptacle. Those of the thallus and male receptacle are made up of a single layer of concentric cells.
5. *Reboulia* is monoecious (autoicous). The antheridial receptacle is sessile, and several may be produced during the growing season, but the formation of the archegonial receptacle terminates apical growth of the thallus and represents a definite branch system, as among the higher members of the order.
6. The antheridia develop like those of the other Marchantiales.
7. In the development of the archegonium the 3 vertical walls follow the appearance of a transverse wall in the initial cell, and further development is typical. Eighteen to 20 neck canal cells are formed, but only 4 are present at the time of division of the ventral cell.
8. Several growing points are organized in the female receptacle from segments of the apical cell of the thallus, and each new apical cell comes to lie in a receptacle notch. Only 1 (rarely 2) archegonium is formed from the immediate segment of each apical cell