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The Peristome Teeth of Selected Genera of Acrocarpous Musci of East Central Illinois

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INTRODUCTION

For well over a century bryologists have looked at, described, and attempted to classify the mosses using a variety of different morphological structures. One of the most variable and challenging taxonomically is a structure located around the mouth of the capsule called the peristome. The purpose of this study is to describe and illustrate the morphology of the peristomes of selected acrocarpous mosses.

The definition of an acrocarpous moss is any moss that bears sporophytes terminally on the gametophyte. In this group are found members of the Nematodontae and the Arthrodontae, with the latter being further divided into the Haplolepideae and the Diplolepideae. These divisions and sub-divisions show natural phylogenetic relationships, but the group Acrocarpi is an artificial one used for convenience by many bryologists.

Also included in this paper is a review of earlier literature and a discussion of the detailed development of the sporophyte, along with the development and morphology of the peristome using specific genera and species. It is hoped that this study will be of use to future students of bryology.

METHODS AND MATERIALS

The specimens studied were collected from Coles and Clark Counties in Illinois with the single exception of Rhabdoweisia, which was collected in Southern Indiana and included because of its uniqueness. Taxonomic keys used for determination of species were by Grout (1903, 1929-1940), Conard (1956), and Welch (1957).

Only fully mature capsules were chosen for use in this study. The capsules were allowed to soak in water for a period of about 15-30 minutes. After soaking the top one third of the capsule was cut off free hand using a single edge razor. A dissecting pick was used to remove most of the spores from this upper part. This ring of tissue was then cut longitudinally into two or three sections. The water was then removed and Hoyer's mounting medium added to the slide. The sections were arranged so that at least one dorsal view and one ventral view was obtained. A coverslip was applied and ringed with ordinary fingernail polish.

To make the illustrations a camera lucida was mounted on a monocular microscope. All measurements were taken with the aid of a calibrated ocular micrometer. At least three measurements were taken of both length and width of each species. These measurements represent the maximum sizes encountered in these specimens.

REVIEW OF LITERATURE

Johann Hedwig in 1801 was the first to use the peristome as a taxonomic structure for the bryophytes and his classical study remains the starting point for nomenclature of true mosses. However, the research done by Philibert (1884-1902), Fleischer (1900-1922), Goebel (1887, 1906, 1930), and others revealed that the peristome was of fundamental phylogenetic importance. Dixon (1932) stated "There are main types of peristomes that are of great phylogenetic importance, i.e., the Nematodontae and the Arthrodontae, the latter being divided into the Haplolepideae and Diplolepideae. No part of our classification based on gametophyte characters must cut across these broad lines."

Through the years the classification of the Musci has varied because of differing views on the origin of the sporophyte. One group of researchers, Bower (1908, 1935), Campbell (1918), and Cavers (1911), held the view that the simple sporophytes of Riccia are the most primitive and that the more advanced mosses developed through progressive sterilization of potentially sporogenous tissue. Church (1919), Goebel (1930), and Evans (1939), on the other hand, felt that Riccia is not a primitive type but is a reduced type evolved as a result of retrogressive evolution. Both groups have put forth good arguments to support their views and both should be kept in mind when looking at a classification system.

An early work which dealt with the peristome, its composition, its unity of plan, and its variation was done by Lantzius-Beninga (1847).

He was the first to observe that the peristome consists either of whole dead cells or only thickened portions of cell walls. He also called attention to the regularity of cell division giving rise to the teeth in multiples of four. Since the work of Lantzius-Beninga, investigations of the peristome have been focused on: (1) comparative morphology using mature peristomes; (2) its embryonal development; (3) its function and behavior; and (4) its minute structure and composition.

Although Sullivant (1864) was concerned primarily with the morphology of gametophytic structures of mosses, he also included drawings of the peristomes of many mosses. He did, however, have a tendency to draw the teeth too perfectly and left out some of the imperfections that are characteristic of certain species. Since his early work there have been other drawings included in studies but because of reduction and reproduction many do not have the clarity of the originals.

With the advent of the scanning electron microscope there has been a renewed interest in the comparative morphology of mature peristomes. Robinson (1971) used the scanning scope to compare several different peristomes and included two that are in the present study; Aulocomnium heterostichum and Dicranum scoparium. Vitt and Hamilton (1974) also included scanning electron pictures of the peristomes of the Encalyptaceae but were concerned primarily with spore morphology. Both studies agree with earlier literature and give a good three dimensional look at some peristomes.

Important investigations concerning the development of the sporophyte were conducted by Hofmeister (1851), who observed that development is from a two sided apical cell, by Kuhn (1870) who named the Grundquadrat, and by Kienitz-Gerloff (1878) who named the endothecium and amphithecium.

Kienitz-Gerloff further showed that the peristome develops from the amphithecium. Philibert (1884-1902) contributed much to the knowledge of both embryonal development and comparative morphology of the mature peristomes. Much of his work, however, was largely ignored until more recent times when Taylor (1962) translated and abridged it.

More specialized contributions to the development of the peristome were made by Goebel (1887) on Funaria and Polytrichum, by Strasburger (1902) on Mnium, by Campbell (1905) on Funaria, and by Kuntzen (1913) on Ceratodon purpureus. All these studies were incomplete, however. The first complete developmental study was done by Evans and Hooker (1913) on Ceratodon and they included a very good account of the deposition of thickenings on the peristomial layers. Working simultaneously but independently van der Wijk (1929), Lorch (1931), and Wenderoth (1931) made intensive investigations on the development of the peristome of Polytrichum.

The most recent study on development of the peristome is that of Proskauer (1958) on Funaria hygrometrica. This study brought together all the earlier literature and discussed the deposition of material on the cell walls.

Some of the early studies mentioned the possible function of the peristome as either to protect the spores from moisture or for spore dispersal. Patterson (1953) pointed out some aberrant peristome behavior that tended to show a more passive role in spore dispersal than earlier workers suggested. Lazarenko (1957) stated that the peristome is not for the protection of spores from moisture. He pointed to the fact that most sporophytes that are without peristomes are erect and that many pendant ones have a well developed double peristome. He also used

examples to show that the peristome sometimes has an active role in spore dispersal. Ingold (1959) agreed with Lazarenko and felt that the function of the peristome was to effect a gradual discharge of spores.

The first study of the minute structure and chemical composition was made by Derschau (1900). He concluded that cytoplasmic activity governs the first deposits of primarily cellulose and pectin and that later deposition is controlled by the nucleus and is related to the hygroscopic activity of the teeth. In the work on the peristome of Mnium cuspidatum Lorch (1931) gave considerable attention to the minute structure. A more recent study was conducted by Taylor (1959) who used polarized light to look at the cellulose chains, their direction, and how this affected the appearance of a tooth.

DEVELOPMENT AND MORPHOLOGY OF TWO TYPICAL ACROCARPOUS
SPOROPHYTES (USING FUNARIA AND POLYTRICHUM)

Development of Funaria Sporophyte

For a complete understanding of the development and function of the peristome, the development of the sporophyte needs to be discussed in detail. Studies using Funaria hygrometrica found that after fertilization the zygote undergoes a series of specific divisions and elongates rapidly through the activity of an apical cell. Normally a second apical cell develops at the base of the sporophyte and produces an acuminate foot. The alternating segments cut off by the upper pyramidal apical cell gives rise to the tissue of the capsule in the upper region of the embryo. The two alternating segments are divided in such a fashion to produce a central square of four cells surrounded by a layer of eight cells. The central group of cells is called the endothecium and the outer layer is the amphithecium (first named by Kienitz-Gerloff, 1878). These are the fundamental embryonic layers. For ease of study the capsule is divided into three regions: a) the upper region consisting of the operculum and peristome; b) the central region or the theca proper; and c) the lower region, the apophysis.

In the central region the four endothelial cells undergo divisions like the ones that formed the amphithecium and endothecium to produce a central group of four to eight peripheral cells. The four central cells divide twice again to form a group of sixteen cells which develop

into the columella" (Kienitz-Gerloff, 1878). According to Campbell (1895) the number of cells contributing to the columella is somewhat more variable than the stated sixteen of Kienitz-Gerloff (1878). The eight peripheral cells divide to form an inner and outer layer of cells. The outer layer divides again to form the archesporium. The inner layer next to the columella matures into the inner spore sac. The archesporium forms a single layer and occupies a small part of the capsule. This later becomes two-layered and every cell of the archesporium is a functional spore mother cell.

The amphithecium in the central region divides in a very regular fashion with the result being that any layer of cells has twice as many cells as the next inner layer. This regular division was named the Grundquadrat or 'fundamental square method' by Kuhn (1870), the end result being five rings of cells. The cells of the first ring divide radially to form a layer of 32 cells, which again divides to form a three-layered achlorophyllose spore sac. The cells of the second ring elongate, develop chloroplasts, and divide in such a manner as to produce a filament of three or four cells, which connect the outer spore sac to the outer layers of the capsule. The third ring usually remains one cell thick and its cells develop chloroplasts. The fourth ring divides to form two or three concentric rings of cells, which are larger and lack chloroplasts. The cells of the fifth ring divide and form a well-defined epidermis with greatly thickened outer walls.

The apical portion of the young capsule undergoes divisions so that the four central cells form a central thin-walled parenchymatous tissue, which is continuous with the columella. The amphithecial cells divide to form six concentric rings. "The peristome develops from the three

inner layers" (Proskaurer, 1958). Outside the peristome, the fourth, fifth, and sixth rings of cells contribute to the operculum. The fourth and fifth form the three layers of the operculum and the sixth ring forms the epidermis. The operculum is demarcated from the rest of the capsule by a shallow depression. This is the line of separation, above it is the annulus and below it is the rim. The cells of the annulus are distinguished from the epidermal cells because of their greater radial depth.

Between the seta and capsule is an enlargement of a zone which finally forms the apophysis. The general order of formation of tissues is the same as the central region except the archesporium and spore sac are not formed. The endothecium here becomes a central conducting strand which is continuous with the seta. The amphithecium gives rise to the spongy chlorophyllose tissue and the epidermis, which is interrupted by stomata.

During early development the body of the surrounding archegonium undergoes development to form the protective covering known as the calyptra, which keeps pace with the developing sporophyte so as to continuously enclose it. Later the calyptra ceases to keep pace and is finally ruptured, the upper part being carried to the top and the lower part forming a sheath around the foot. The calyptra covers the apical portion of the sporophyte and may remain until full maturity is attained.

Structure of Mature Sporophyte of Funaria

The mature sporophyte is composed of a foot, a seta, and a capsule. "The foot is a poorly developed, small, dagger-like, conical structure

imbedded in the apex of the archegonial branch, from which it absorbs water and mineral nutrients for the developing sporophyte" (Parihar, 1965). The seta is long, slender, twisted and bears the capsule at its upper end. The axial tissue forms a strand of elongated cells that continue up into the capsule. This strand, surrounded by a thick-walled cortex and epidermis, apparently has the function of conduction of some water but mainly is for support. The mature capsule is very complex in structure and will be discussed again by dividing it into three regions: the apophysis, the theca, and the upper region.

The seta expands above to form a swollen area in the basal region of the capsule and is called the apophysis. In the center of the apophysis is a conducting strand that is continuous with the central strand of the seta. "Surrounding the strand is a broad zone of spongy green tissue with conspicuous air spaces that resembles closely the leaf tissue of higher plants in their form, arrangement, and presence of abundant chloroplasts" (Parihar, 1965). The stomata are arranged more or less parallel with the long axis of the sporophyte. This region enables the sporophyte in part, if not altogether, to effect its own nutrition.

In the center of the theca proper (fertile region) is a sterile column of thin-walled parenchymatous tissue, the columella. It extends up to the operculum and is connected to the center of the apophysis by filaments of cells. The columella is surrounded by the spore sac, which is one-layered on the inside and three or four-layered on its outside wall. Between these walls are the spore mother cells, which give rise to spores by meiosis. Outside the spore sac there is a wide air space traversed by filaments of two to four cells, joined externally

to the inner surface of the capsule wall. The capsule wall in this area consists of two to three layers of cells bounded by a well-defined epidermis. The two outer layers consist of compact, colorless, parenchyma which forms the hypodermis. The innermost layer is composed of loosely arranged cells containing chloroplasts. The colorless hypodermal tissue of the capsule walls thins out below the fertile region, whereas the green inner tissue increases and is continuous with the green tissue of the apophysis.

The upper region of the capsule is highly modified in relation to dispersal of spores. This region consists of the operculum and the peristome, and is marked off from the theca proper by a constriction. Below this constriction is the rim, which is shaped like a circular ledge. The rim stretches inward from the epidermis of the capsule wall and joins the peristome to the epidermis. When the operculum separates from the capsule, these layers form the thickened rim of the open capsule. Immediately above the rim is the annulus, which is composed of layers of superimposed epidermal cells. The two lower layers (the annulus proper) have thinner walls and are distended. Dehiscence of the operculum eventually takes place by the destruction of these swollen cells. Attached below to the edge of the diaphragm is the peristome, which in Funaria consists of two rows of curved, narrow, triangular, plate-like teeth, sixteen in each row. "These teeth are twisted and converge together to a small central persistent disc" (Proskauer, 1958). The inner teeth are shorter and more delicate. At their bases they are directly covered by the outer teeth, but towards the center they curve so that they narrow the openings between the teeth of the outer peristome.

At maturity the capsule begins to dry up and the columella, along with other thin-walled tissues, loses water and shrivels up, leaving open the space in which the spores lie. The annulus proper, which consists of elastic and hygroscopic cells, aids in the removal of the operculum. These cells are very responsive to changes in the relative humidity. "When moisture is available the cells of the annulus proper swell rapidly with the result that the annulus breaks free from the rim of the capsule and suddenly rolls back throwing off the operculum" (Parihar, 1965). After the operculum is thrown off, the peristome teeth seem to aid in the dispersal of spores.

Structure of Mature Sporophyte of Polytrichum

The mature sporophyte of Polytrichum consists of a foot, a long seta, and a capsule. The foot is imbedded in the tissue of the apex of the gametophyte and consists of thin-walled parenchymatous cells. Just above the foot is the long slender seta, which supports the capsule. On the outside of the seta is a superficial layer of cells with thick walls. Inside the superficial layer is a band of brown sclerenchymatous tissue with intercellular spaces. The axial tissue forms a central strand of thick-walled cells. At the base of the capsule the seta enlarges to form the apophysis, which is separated from the sporogenous portion by a groove. The apophysis has a distinct epidermis with stomata, inside of which is a mass of chlorophyllose tissue. The stomata are usually restricted to the groove and are large and raised above the level of the epidermis. "The number of guard cells are usually two, but occasionally single annular guard cells are seen" (Paton, 1957).

The capsule is usually angular and shows a polygonal outline in cross-section. The wall of the capsule is composed of several layers

of chlorophyllose cells, the outermost layer of which is differentiated into an epidermis with thick outer walls. Inside the wall there is an outer lacuna (air space) traversed by filaments of chlorophyll containing cells, which are connected to the outer wall of the spore sac. The spore sac is limited internally by an inner lacuna, which is again bridged by filaments of cells connecting the spore sac with the columella. The spore sac is bounded on the inside and outside by layers of thin-walled cells, the number of which depends on the age, up to four or six layers in the adult. All cells of the sporogenous tissue gives rise to spores.

At the top of the capsule there is an operculum which appears as a conical lid with a beak or rostrum. A distinct annulus is not present but a thickened diaphragm (rim) is present. At the base of the operculum is a transverse band of thin membranous tissue. This tissue stretches over the opening of the capsule and is called the epiphragm. At maturity the peristome is composed of 32 or 64 short, pyramidal teeth, connected below to the mouth of the capsule and united above with the margin of the epiphragm. As in Funaria, the calyptra is carried upward on the top of the capsule forming a dry fibrous hood over the apex of the capsule. The calyptra consists externally of dry, branched, hypha-like filaments loosely matted together.

General Sporophyte Morphology

"The sporophytes of most bryophytes remain relatively small due to several factors: a) to a certain extent the physiological dependence on the gametophyte, b) the localized apical growth is either absent or arrested early in development, c) spores are formed and mature simultaneously in most bryophytes, and d) branching and lateral

appendages are lacking" (Parihar, 1965). The mature sporophyte consists of the foot, seta, and capsule with variations of this basic pattern.

The foot is the basal portion of the sporophyte and is usually wider than the seta. It is generally believed to be the connection with the gametophyte through which water and nutrients move, but as Watson (1964) points out there is very little experimental work to prove this idea. In most mosses the foot is acuminate. "In several species of musci the foot shows tissue differentiation, the outer portion is composed of highly protoplasmic haustorial cells, the intermediate zone is made up of parenchyma, and the central region has narrow elongate cells" (Watson, 1964).

In most mosses, the seta lengthens gradually, becoming at maturity a slender but comparatively tough and fairly long-lived structure. This elongated organ is specialized for support and conduction and has a well-marked central strand surrounded by cortex and epidermis. In some mosses such as Ephemerum and Phascum the seta is very small and in some, Sphagnum and Andrea, the function of the seta is taken up by a gametophytic structure, the pseudopodium.

The simplest capsule construction is found in those genera which produce few and relatively large spores. "In one genus, Ephemerum, the cells of the columella are resorbed before the division of the spore mother cells and serve to nourish the large spores which fill the cavity of the ovoid capsule" (Parihar, 1965). The seta is short and special structures for spore dispersal are not present, the capsule lacks the operculum, peristome, and annulus. This type of moss which lacks a definite operculum or any regular method of dehiscence is known as a cleistocarpous moss.

In other mosses, known as stegocarpous mosses, the upper region of the capsule is specialized for spore dispersal into an operculum and peristome. The simplest example of a stegocarpous moss is Tetraphis. The capsule of Tetraphis is an upright cylindrical body with a conical operculum and is borne on a short seta. The operculum is a single layer of indurated cells. The peristome consists of four massive pointed teeth composed of solid cellular tissue and arranged in single series.

The length of development of the sporophytes of different mosses varies greatly as might be expected. Watson (1964) stated that the length from fertilization to maturity varied from a few weeks in early winter ephemerals to a full thirteen months in Polytrichum. Garner and Paolillo (1973) studied Funaria hygrometrica under greenhouse conditions and found that from the time of first appearance of the young sporophyte to full maturity took approximately 65 to 70 days.

DEVELOPMENT AND MORPHOLOGY OF SELECTED
ACROCARPOUS PERISTOMES

On the basis of origin and fundamental structure peristomes are divided into main divisions (clans), the Nematodontae and the Arthrodontae. The nematodontous peristome-forming zone consists of several concentric layers of the amphithecium. The peristome teeth are solid, consisting of several bundles of whole dead cells without articulations or markings other than cell outlines. In contrast, the arthrodontous peristome is formed from two or three concentric cell layers. The teeth are thin, membranous, transversely barred and articulated, not made up of cells but consist solely of plates representing the thickened portions of the walls of the cell layers.

The nematodontous peristome shows variations in different orders. The simplest type is in the order Tetraphidales, in which the entire tissue within the single layered operculum splits into four conical teeth. In the order Polytrichales the peristome consists of 32 or 64 short, pyramidal, solid teeth. Each tooth has a central pillar of fiber-like cells. In the Dawsoniales the peristome-forming region is broad and is made up of several concentric layers. The peristome consists of numerous, much elongated filaments. The long filamentous cells are simple and continuous throughout with no trace of crosswalls. In the order Buxbaumiales the peristome is intermediate between the nematodontous and arthrodontous types. The peristome consists of one or two layers of teeth, which are composed of cell wall materials, but

not entire cells. Because there are several concentric layers of the amphithecium involved, it is said to be nematodontous. Therefore, the origin is nematodontous but the structure is arthrodontous.

The Arthrodontae are often divided into two sub-clans, the Haplolepidae and the Diplolepidae. The haplolepidous peristome consists of a single series of teeth formed from two concentric layers of cells. Sometimes it consists of a thin membrane rising over the mouth of the capsule, leaving only a small aperture at the top. Commonly this membrane is split into a number of filaments called teeth that are in multiples of four. The teeth are usually delicate in texture and composed of two layers of thin plates, divided transversely into segments with more or less distinct lines at the point of division. The teeth may be entire or often forked above, but usually undivided at the base. The dorsal layer of a tooth is formed of a single row of thin plates in the form of a rectangle with the long side running the width of the tooth. The ventral layer is formed of trapezoid sections, higher but narrower than the outer plates. There are usually two or three rows in the width of the outer plates causing, when viewed from the inside, a fine vertical line down the center of the tooth. Philibert (1884) was the first to name this type of tooth haplolepidous, because of the single row of dorsal plates.

The best example of a haplolepidous peristome is found in the genus Dicranum and is commonly called the dicranoid type. The typical dicranoid type of peristome has sixteen teeth which are usually split above, sometimes to the base, with the two sections of the ventral layer being separated by the split. The typical form is broad at the base and the dorsal plates are thin with vertical striations, while

the inner plates are thicker and have projecting trabeculae at their articulations. This type of peristome is found in the order Dicranales, Fissidentales, and Grimmiales.

The diplolepidous peristome is usually double, but sometimes has the appearance of being single as in the Splachnaceae and sometimes in the Orthotrichaceae. The outer peristome is usually called the exostome and the inner peristome is called the endostome. Each tooth of the exostome is made of two layers of plates. The dorsal layer is formed of two rows of plates divided by a thin vertical line, thus the name diplolepidous. The ventral layer is formed of a single row of plates extending the width of the tooth. Each segment of the endostome is composed of two layers of plates. The dorsal layer is composed of only the primary cell wall while the ventral layer is composed of both primary and secondary walls. These layers are generally thin and hard to separate. The plates on the dorsal layer of the endostome correspond to the plates of the ventral layer of the exostome both in number and placement. The exostome superficially resembles a haplolepidous peristome with some differences in structure. The endostome presents a great variety of form. It sometimes consists of eight to sixteen delicate filaments that alternate with the outer teeth. In some groups these processes are wider, meeting at their bases. In its typical form these processes are united below to form a collar-like basal membrane surrounding the orifice and is usually sharply folded or keeled, while the upper portions remain free. The spaces left between the free upper portions are often occupied by slender projections off the basal membrane called cilia. Occasionally the basal membrane is continued to the apex, forming a dome-like structure with a small opening, or parts can be reabsorbed forming a lattice work of open meshes.

Development of Funaria Peristome

Much of the early study of the peristome was conducted using the diplolepidous Funaria hygrometrica, probably because of its cosmopolitan nature and its world wide distribution. One of the first papers dealing with the peristome of Funaria is in a series of articles written by Philibert (1884-1902). In his seventh article (1888) he describes the structure of the mature peristome of Funaria and it is in this paper he states that the inner peristome of diplolepidous mosses is homologous with the peristome of haplolepidous mosses. These studies were largely ignored by other early bryologists, possibly because as Taylor (1962) says, "Philibert had a tendency for wordiness and repetition," and this made it very difficult to understand the main points he was trying to convey. Today it is still one of the best studies on the peristomes of mosses and Taylor's abridged translation makes it more readable and accessible to modern bryologists.

Other early works on the development of the peristome of Funaria were done by Goebel (1887), Campbell (1905), and Smith (1955). Proskauer (1958) reviewed this early literature, did a detailed study on the development of the peristome, and corrected some earlier misinterpretations.

According to Proskauer (1958) the apical portion of the capsule has the usual differentiation into two fundamental embryonic layers, the endothecium and amphithecium. The four central cells of the endothecium divide and redivide to form a central thin-walled parenchymatous tissue which is continuous with the columella. The eight amphithecial cells by regular alternation of periclinal and anticlinal divisions form six concentric layers of cells each of which has twice as many cells as the next inner layer. The tissues of the operculum and peristome are formed from these six rings.

The double peristome is formed from the three innermost cell layers (first, second, and third, counted from the inside). The cells of the first layer divide by anticlinal walls to form the inner peristomial layer, 32 cells in perimeter. The second ring of cells becomes the middle (primary) peristomial layer. The cells of this layer divide no further and the number of cells of which it is composed (16 in this species) determines the number of peristome teeth in the mature capsule. The third ring of cells, which is 32 cells in perimeter, forms the outer peristomial layer.

Maturation of the peristome occurs with the deposition of additional cell wall material on the tangential walls of the peristomial layers. According to Proskaurer (1958), the outer peristome develops at the juncture of the outer and middle peristomial layers and is formed from the deposition of cell wall material on the outer tangential walls of the middle peristomial layer, contiguous to another deposit on the inner tangential walls of the outer peristomial layer. The thickening on the outer walls of the middle peristomial layer is more or less homogeneous. This thickening extends considerably on the horizontal radial walls, ultimately giving rise to the bars of the teeth.

In the outer peristomial layer there are two smaller cells equaling the width of one cell of the middle peristomial layer. When thickening occurs there is a very small amount on the vertical radial walls of the outer peristomial layer. These are opposite the thickenings which occur on the outer tangential walls of the middle peristomial layer. This thickening gives rise to the median dorsal line of the diplolepidous mosses.

The inner peristome develops at the juncture of the middle and inner peristomial layers, but the additional cell wall material is laid down only on the outer tangential wall of the inner peristomial layer. None occurs on the inner tangential wall of the middle peristomial layer. In Funaria the number of cells in the inner layer is twice that of the middle layer, thus giving rise to the vertical ventral line on the inner peristome. The thickenings on the walls of the inner and outer peristomial layers are similar to each other but very different from the thickening on the middle peristomial layer. "Ultimately a papillate thickening is superimposed on all three thickenings. Usually there is no noticeable thickening of the vertical anticlinal walls of these cells. At maturity the thin vertical walls break up and disappear and the peristomial layers split along sixteen radial clefts from the apex to the edge of the capsule" (Proskauer, 1958). Thus two series of curved, narrow, triangular teeth are formed. Each set of teeth is attached to the edge of the diaphragm of the capsule.

Funaria is used as the example for diplolepidous mosses; however, it is different from many of the Diplolepidaceae in that the segments of the endostome are exactly opposite the outer teeth, instead of alternating as in a great number of genera. This occurs because of the difference in the thickening of the elements as the capsule matures. In many genera the thickening lies mainly on portions of the original membrane which alternate with the teeth. In Funaria the thickening lies solely on those parts of the membrane opposite each tooth.

Philibert (1888) used Funaria as the example to show that the inner peristome of a diplolepidous moss is homologous to the peristome of a haplolepidous moss. He pointed out, "the dorsal plates of Dicranum,

arranged in a single row, have the form of rectangles narrow vertically and wider transversely, separated by quite parallel horizontal lines, which is absolutely similar to the rectangles of the dorsal layer of the inner peristome of Funaria." He further went on to state, "in a young capsule of Dicranum, before thickening of the walls, there is a trapezoid mesh bounded by sinuous lines outlining a net altogether similar to that of the ventral layer of the inner membrane of the Diplolepidae. In most of the Dicranaceae there are but two rows of this mesh to each tooth, and the outer margins of each of these rows are generally resorbed with the vertical lines which separate the dorsal plates; this is just what occurs with the inner peristome of Funaria." This and other evidence that he uses explains why a moss with a single row of dorsal plates on the teeth never have an inner peristome; they have come from a diplolepidous ancestor which has lost its ability to produce an outer peristome.

A study on another diplolepidous member of the Arthrodonteae was done by Blomquist and Robertson (1941) on Aulocomnium heterostichum. They found the number of peristomial layers is the same as in Funaria, but in Aulocomnium a basal membrane and cilia are produced along the same plan as in many other genera of the Bryales. This study is the one that probably should be referred to when looking at a diplolepidous moss which produces an endostome with a basal membrane. They concluded that the keeled condition of the segments of the endostome was due to the convexity of the inner walls of the primary (middle) peristomial layer. They also noted a variation in the number of cells in the inner peristomial layer subtending one cell of the primary layer. This variation in number of cells causes a variation in the number of cilia produced when thickenings are laid down on the walls of the inner peristomial layer.

The Nematodontous Peristome

In a nematodontous moss, the structure of the peristome is completely different and is formed on an entirely different plan from that of an arthroodontous moss. The simplest nematodontous peristome occurs in Tetraphis pellucida. The entire tissue lying inside the single-layered operculum splits almost equally into four sectors along radial planes forming four conical teeth. On the dorsal side of these teeth are two or three cell layers of unequal cells having thickened and colored walls. The ventral surface consists of a layer of large, hexagonal, colorless cells. The number of longitudinal rows of cells is variable in the outer layer from twelve to fifteen at the base of each segment. "In transverse section these outer cells appear oval, of unequal size, alternating from one layer to another and forming together a rather irregular tissue and their walls are strongly thickened" (Taylor, 1962). In Tetraphis these fibers extend only part of the length of the tooth. Toward the apex of the tooth the cells average 10-15 times as long as wide, and they seem to often end in a pointed apex. Often though, there is a mixture of shorter and wider cells separated from each other by horizontal walls.

A more specialized and advanced type of nematodontous peristome occurs in the genus Polytrichum. Intensive developmental studies were conducted by van der Wijk (1929), Lorch (1931), and Wenderoth (1931) on this genus. In a transverse section of a tooth of Polytrichum there are about six or seven rows of cell cavities. "These cavities are oval in section towards the middle of the tooth, almost linear on the margins. In the direction of the length of the tooth these cell cavities correspond to elongate cells which continue without crosswalls in a curve from the

base to the apex of the tooth" (Taylor, 1962). Further up in the tooth as the tooth flattens out the cavities contract and almost disappear. "Below the teeth the peristome extends as a thicker undivided membrane formed of several concentric layers of cells; there the cellular cavities are more numerous, wider and less elongate; there are horizontal as well as vertical walls, forming as a whole a dense tissue" (Taylor, 1962).

Peristome Function

In many of the studies done on peristome morphology there are statements made about the possible function of the peristome in spore dispersal. Other researchers felt that the function of the peristome was to protect the spores from moisture.

Those researchers who felt the main function was spore dispersal found that the teeth are extremely sensitive to changes in humidity. It should be remembered each tooth of the outer peristome is essentially a two-ply structure. The dorsal layer of each tooth of the exostome lengthens when wet and shortens when dry, but the ventral layer is not affected by changes in moisture. When the exostome absorbs water the dorsal layer increases in length and the teeth curve together inward and reconstitute a dome, the results being that the opening left by the shedding of the operculum is almost completely closed and spores cannot escape. During dry weather when the exostome loses water the dorsal layer shortens more than the ventral layer and they bend outward with jerky movements as they separate from one another. The endostome does not seem to show a marked response to changes in humidity and as the slits between the outer teeth become wider the endostome acts as a sieve allowing only gradual discharge of spores. The spores are

released over a longer period and only when they are likely to be carried by the breeze to some distance from the parent plant.

Goebel (1905) used the criterion of how the peristome functioned in spore dispersal to classify peristomes into primitive, intermediate, and complex types. In his primitive grouping he placed genera like Barbula and Tortula, whose long spirally twisted peristomes show movement but play little or no part in spore dispersal. In his intermediate grouping he placed genera like Dicranella in which spores that accumulate under the mouth of the shrinking capsule are caught among slowly moving teeth and are shed. In his complex grouping he placed genera like Bryum and Mnium, whose peristomes are double and show active participation in spore dispersal.

Ingold (1939) noted that in some species the inner peristome stands up as a pale cone and the tips of the arched outer teeth become inserted between structures of the endostome. Occasionally the teeth are caught as they are reflexing and snap out suddenly, actively flipping spores outwardly. Ingold (1959) also noted that in the pendulous capsules the spores are not sticky and fall out slowly. Watson (1964) pointed out, however, that during dry conditions, "one has only to agitate the seta to induce the liberation of visible clouds of spores. With wind and animal movements in nature it makes one wonder if gradual discharge demonstrated in the lab occurs in the field." Patterson (1953) also noted that certain species show aberrant behavior. He notes, "in Forsstromia ohioensis the teeth move from horizontally reflexed when wet to inflexed along the inside wall when dry." He further suggested that "the spores may be washed by rain to the lower part of the same tree, and distributed by air currents to other trees when dry."

Lazarenko (1957) said that the peristome is not for protection against moisture, as some earlier workers had proposed, but for spore dispersal. He pointed out that many pendant species have double, well-developed peristomes while many erect ones have peristomes that are single, degenerate, or lacking. He also noted that the hygroscopic movement takes place most at the beginning and ending of a rain, so that spores are dispersed farther but are more likely to land when suitable moisture is present. More complete studies on spore discharge are needed to learn more of the real significance of the peristome.

MORPHOLOGICAL STUDIES ON THE PERISTOMES OF
ACROCARPOUS MOSSES

In the following section are descriptions of the gametophytes, sporophytes, and peristomes of selected acrocarpous mosses. Accompanying each description is an illustration. For the nematodontous and haplolepidous mosses there is a single plate per species. For the diplolepidous mosses there are two plates per species, one showing the exostome and one showing the endostome. Each peristome is illustrated using the dorsal view and has been enlarged 510 x its original size.

Tetraphis pellucida Hedw.

Tetraphidaceae

Plants in dense to loose tufts, yellowish green; protonema not filamentous; stems erect, 1-3 cm. long, densely radiculose at base, barren shoots with terminal gemmiferous cups containing lenticular, stalked gemmae; leaves ovate to ovate lanceolate, slightly concave, subdecurrent, costa wide, ending below apex, apices mostly acute, margins entire.

Autoicous; calyptra whitish, conical, acute, solid and rough at apex, enclosing the entire capsule; seta yellowish to reddish or brown, erect, 1-1.5 cm. long; capsule reddish, erect to ascending; operculum lustrous, acutely conical, cleft on one side; urn green when young, bright reddish brown when ripe, usually symmetrical, narrowly cylindrical, persistent; annulus none.

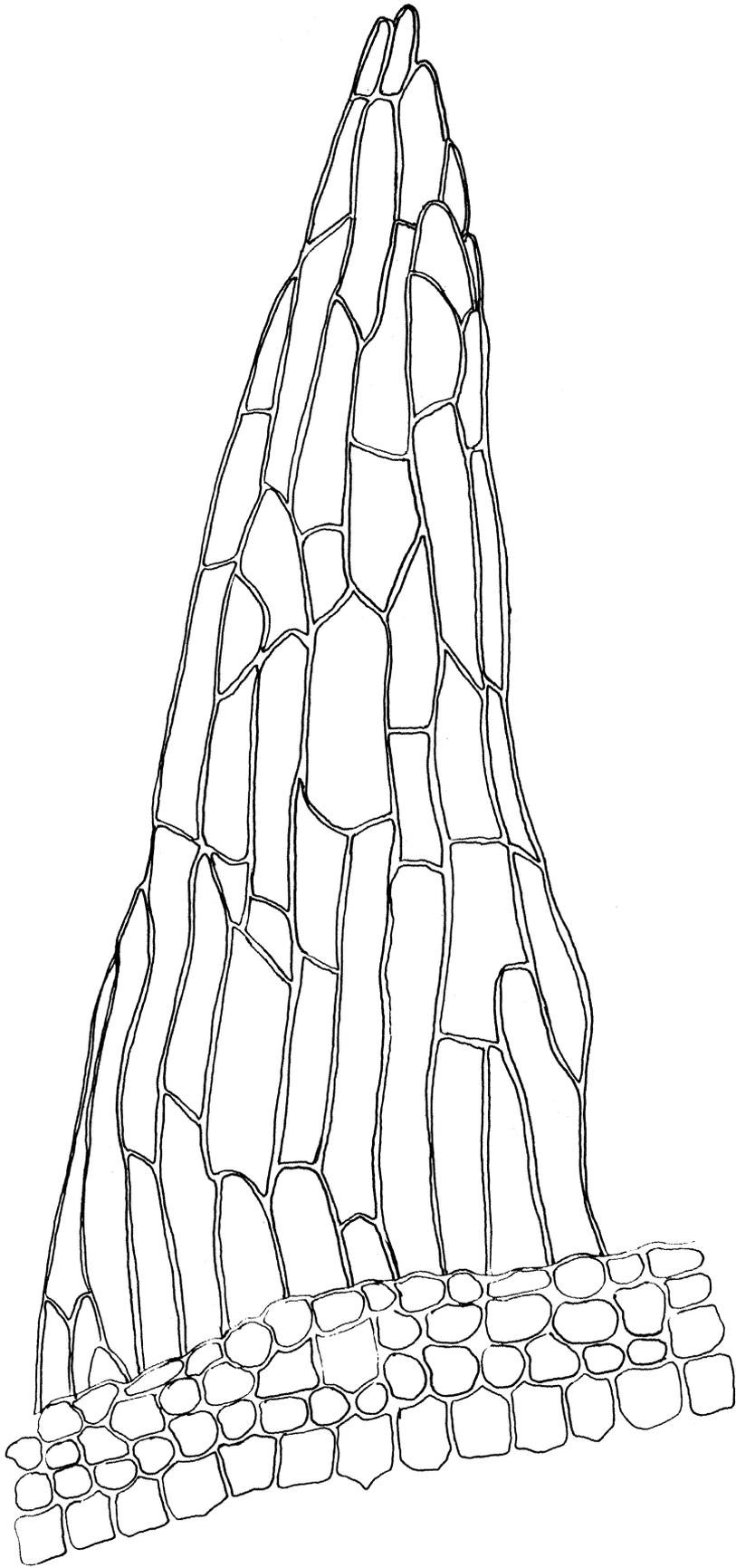
Spores slightly papillose, 8-12 microns in diameter, mature in spring to late fall.

Peristome Characteristics

Plate 1

Peristome reddish to brownish, single, teeth 4, linear-triangular, 3-4 cells thick, approximately 1/5 length of capsule, 570 microns long, 150 microns wide, inserted somewhat below the mouth of the capsule.

Plate 1



Atrichum angustatum (Brid.) B.S.G

Polytrichaceae

Plants growing in clusters or tufts, dark green; stems erect, single, 1-5 cm. long; upper leaves crisped when dry, erect to erect spreading when moist, linear-lanceolate, costa subpercurrent to percurrent, lamellae on upper surface of costa, 4-8, costa and lamellae together composing $1/4$ - $1/3$ width of blade, lamellae 6-9 cells high, blades bordered with two rows of cells, margins serrate along upper $1/2$ - $1/3$.

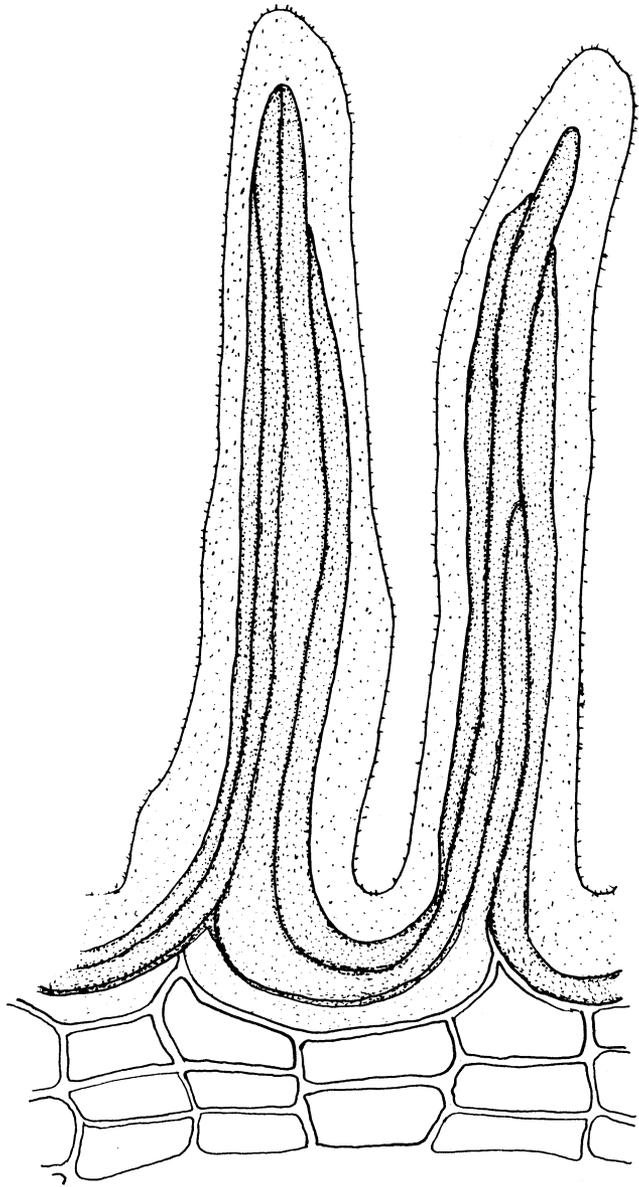
Dioicous; calyptra cucullate, slenderly rostrate, split $1/3$ of its length; seta castaneous, erect, 1-3.5 cm. long; capsule castaneous, almost erect; operculum hemispheric, slenderly rostrate, approximately $1/2$ length of urn; urn narrowly cylindrical, straight, 2.5-6 mm. long; annulus none.

Spores spherical, pale green to reddish yellow, pellucid, smooth to minutely roughened, 10-18 microns in diameter, mature late fall to winter.

Peristome Characteristics

Plate 2

Peristome single, teeth 32, linear-lanceolate, obtuse, 145-300 microns long, minutely papillose, axis yellowish brown, border pellucid, basal membrane about 50 microns high.



Pogonatum pensilvanicum (Hedw.) Paris

Polytrichaceae

Plants in clusters, forming thin sods, on a green felt-like persistent protonema; stems erect, very short, 1-2 mm. long, simple, with rhizoids at base; lower leaves bract-like, lanceolate-subulate, costa percurrent, with 10-15 lamellae on upper surface, apices long acuminate, serrulate, margins plane to erect, entire below, serrate above.

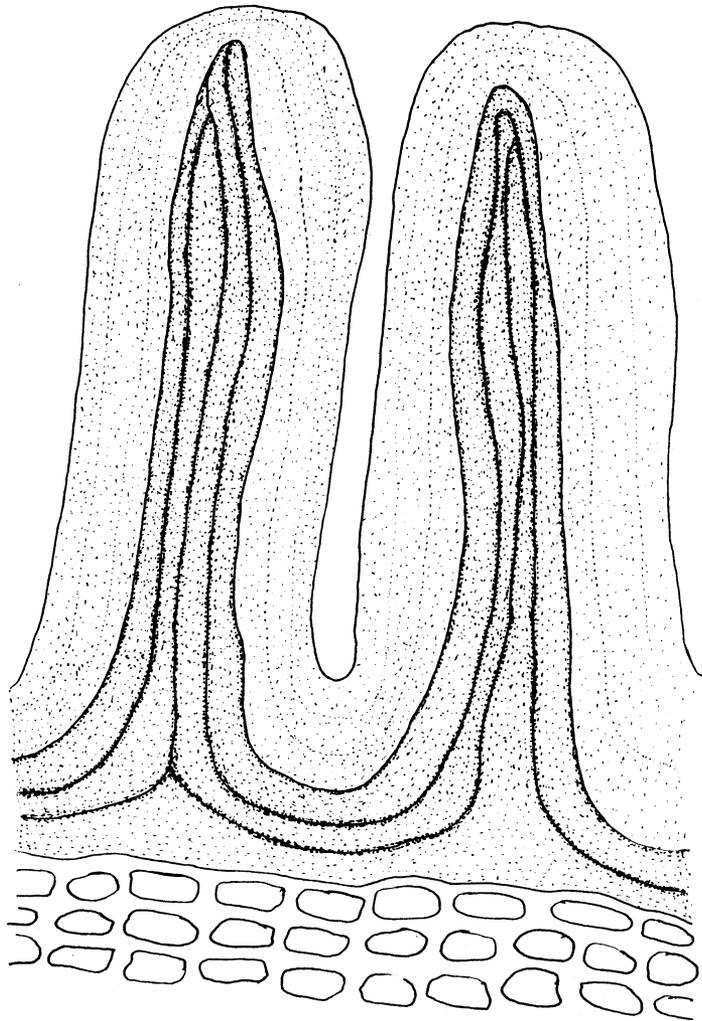
Dioicous; calyptra cucullate, extending well below capsule, densely hairy, light yellow or gray; seta yellowish to reddish, solitary, erect, 1-2.5 cm. long; capsule erect to slightly inclined, yellowish to reddish, operculum short conic, the beak slightly curved; urn cylindrical, symmetrical; without stomata; annulus none.

Spores yellowish brown, 8-12 microns in diameter, smooth, mature in late fall.

Peristome Characteristics

Plate 3

Peristome single, teeth 32, approximately 200 microns long, 50-70 microns wide, basal membrane about 50 microns high, axis brightly reddish orange, border pellucid, basal membrane light reddish, thick-walled.



Polytrichum ohioense Ren. and Card.

Polytrichaceae

Plants in loose tufts or sods, bluish green, olive green to reddish brown; stems chestnut brown, erect, rigid, 2.5-5 cm. long, up to 8 cm., usually simple, rhizoids at base of stem; leaves appressed to erect-spreading, somewhat contorted when dry, linear lanceolate, costa excurrent, with 32-50 lamellae along upper surface, lamellae 4-6 cells high, apices acuminate, ending in serrate arista, margins serrate nearly to sheath.

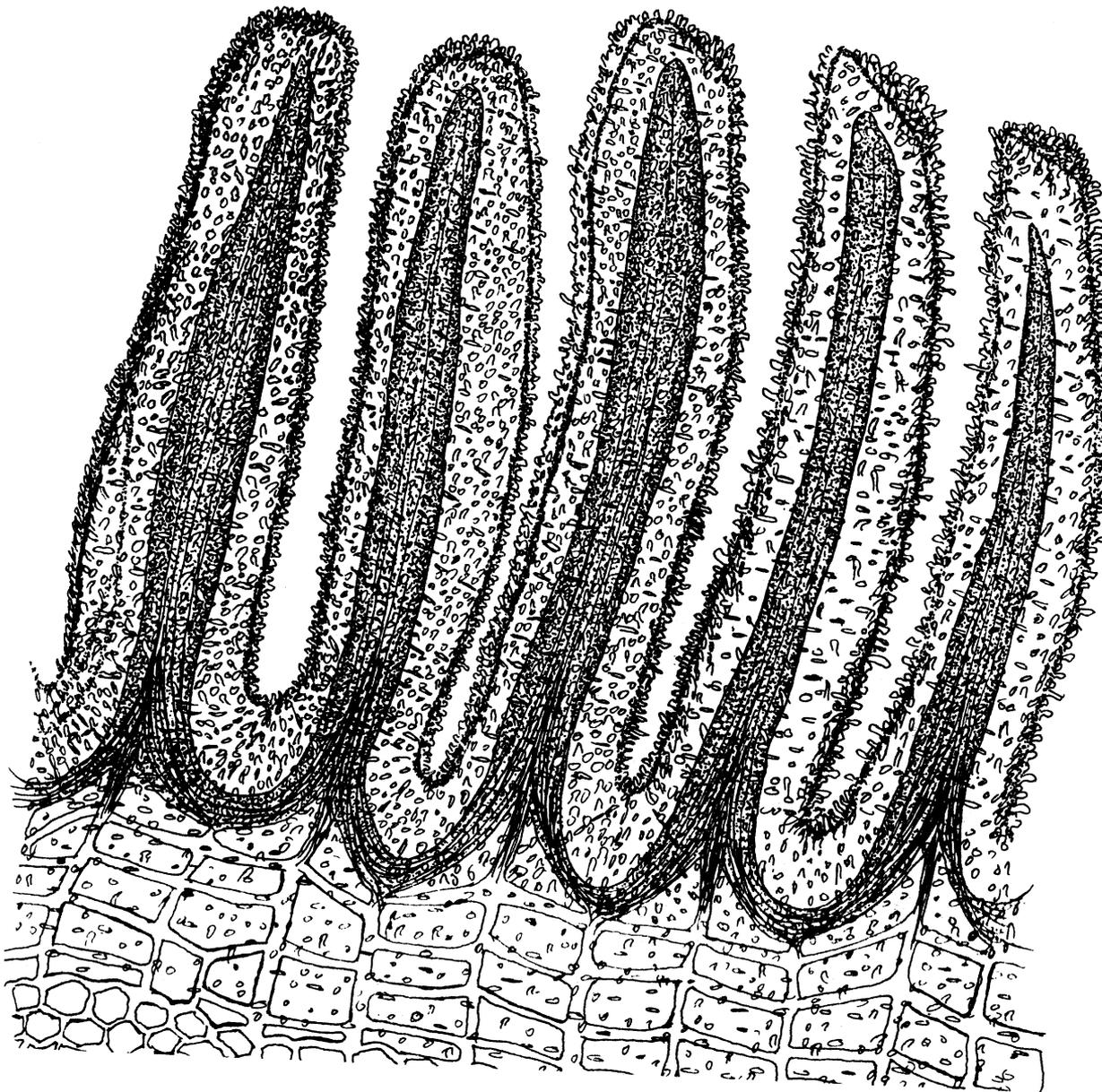
Dioicous; calyptra light yellowish brown, densely hairy, shorter than capsule; seta dark below, yellowish brown above, erect to horizontal or pendant; operculum depressed conic, beak curved; urn oblong, acutely 4-5 angled, 3-6 mm. long, narrowed toward base; annulus none.

Spores spherical, yellowish white, 8-17 microns in diameter, finely punctate, mature in midsummer.

Peristome Characteristics

Plate 4

Peristome single, teeth 64, pale yellow with darker brown axis, regular, 90-200 microns long, 35-50 microns wide, densely papillose; basal membrane cell walls dark red, regular.



Dicranella heteromella (Hedw.) Schimp.

Dicranaceae

Plants small, glossy, yellowish to dark green; stems erect to ascending, frequently branched; leaves numerous, generally falcate-secund, ovate-lanceolate to lanceolate, upper part of blade subulate, broadest at base and gradually narrowing to a filiform, channelled, rough awn, costa percurrent to excurrent, broad, usually with narrow margin of lamina, margins plane, entire below, sharply denticulate above.

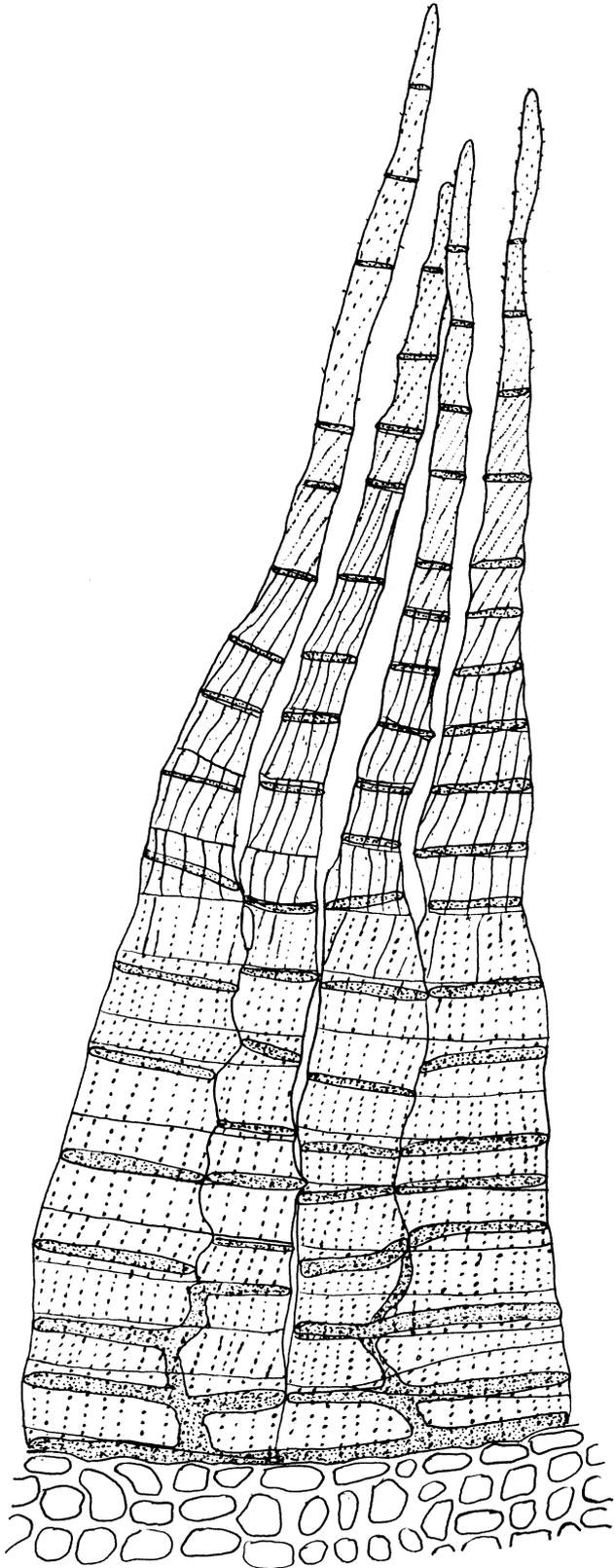
Dioicous; calyptra cucullate; seta usually greenish yellow, sometimes dark red with great age, erect to curved, .5-3 cm. long; capsule more or less inclined; operculum long and obliquely rostrate, beak curved downward; urn castaneous to dark brown, glossy, unsymmetric, ovoid to oblong-cylindric, strongly sulcate when dry, contracted strongly below mouth on lower side producing an oblique mouth; annulus poorly developed.

Spores yellowish, 10-15 microns in diameter, smooth, mature in autumn to winter.

Peristome Characteristics

Plate 5

Peristome single, teeth 16, approximately 500 microns long, 100 microns wide at base, dark red, mostly pellucid in upper 1/4, 2-3 cleft to middle or below, strongly to mostly striate below the subulate divisions, papillose.



Dicranum scoparium (L.) Hedw.

Dicranaceae

Plants large, 2-10 cm. high, glossy yellowish green, growing in tufts; leaves falcate secund, not undulate, strongly serrate, ending in a long narrow acumen; costa flattened, bearing four projecting lamellae on back, ending in apex or briefly excurrent, apices long, narrowly subulate.

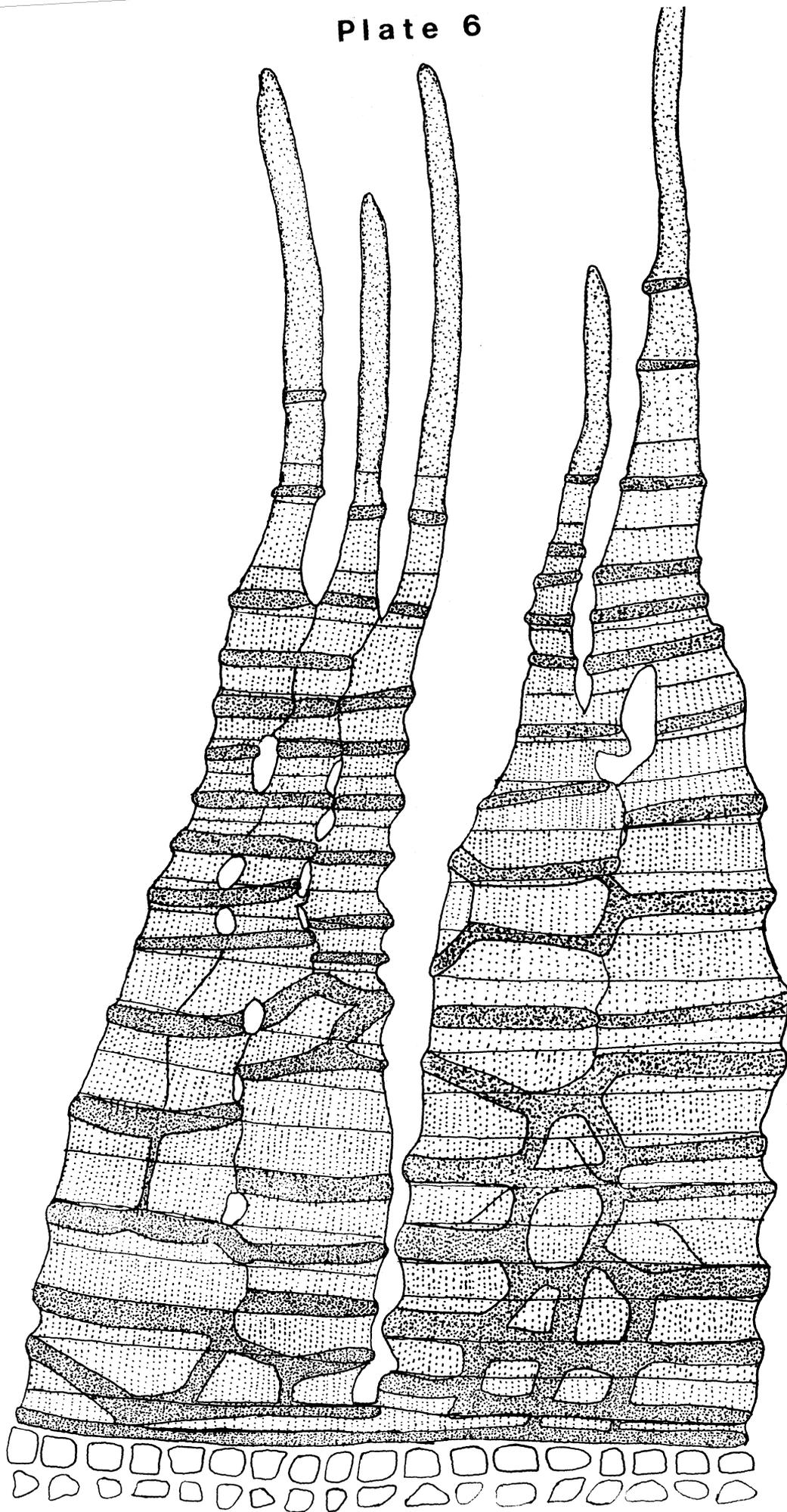
Dioicous; calyptra cucullate, conic rostrate; seta yellowish to reddish brown, erect, solitary 2.5-4 cm. long; operculum low conic, long rostrate; urn cylindrical, not contracted below mouth, 3-4 mm. long, usually smooth, neck distinct, short; annulus none.

Spores spherical, slightly rough, 20-24 microns in diameter, mature late summer to autumn.

Peristome Characteristics

Plate 6

Peristome single, teeth 16, reddish brown, cleft from apices to middle into 2, rarely 3, papillose divisions, papillae forming longitudinal striae in lower 2/3, approximately 600 microns long, 120 microns wide.



Ditrichum pallidum (Hedw.) Hampe

Ditrichaceae

Plants small, green or yellow-green; stems erect or nearly so, short, about .5 mm. long, usually simple; leaves slightly contorted when dry, long linear-subulate from a lanceolate or ovate base, concave below, channeled above, costa strong, long excurrent, serrulate toward apex.

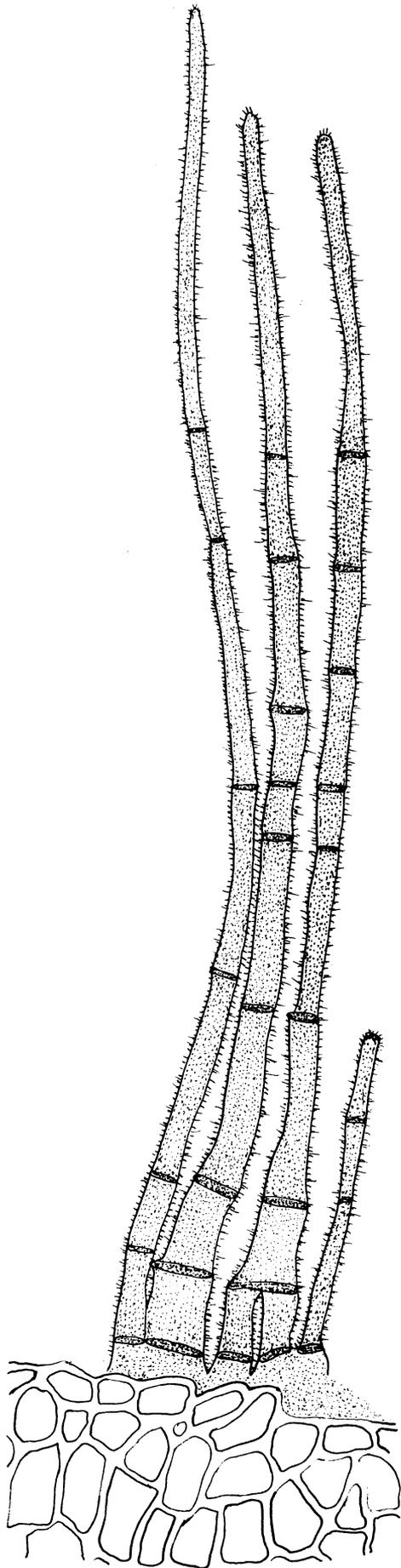
Paroicous; calyptra cucullate, slenderly rostrate, straight, smooth, up to 2.5 mm. long; seta bright yellow to orange, erect, slender, 1-4 cm. long; capsule light brown to yellow to yellowish red, ascending to inclined; operculum conic, obtuse; urn narrowed near mouth, subarcuate and irregularly sulcate when dry; annulus of 1-3 rows of cells.

Spores brownish or reddish pellucid, spherical, 14-18 microns in diameter, papillose to coarsely warty, mature in early spring.

Peristome Characteristics

Plate 7

Peristome single, teeth 16, reddish yellow, approximately 575 microns long, 10-15 microns wide, deeply bifid into filiform, spinose-papillose, nodose divisions, basal membrane very low, articulations small, few, widespread.



Grimmia apocarpa Hedw.

Grimmiaceae

Plants usually in small loose tufts, dark or olive green; stems erect or ascending; leaves imbricate when dry, erect spreading when moist, ovate-lanceolate, usually subcarinate to carinate, costa distinct, appearing as a ridge on back of leaf, disappearing in or below apex, apices subobtuse, hyaline, hair points usually short, margins narrowly recurved, entire throughout or serrate above.

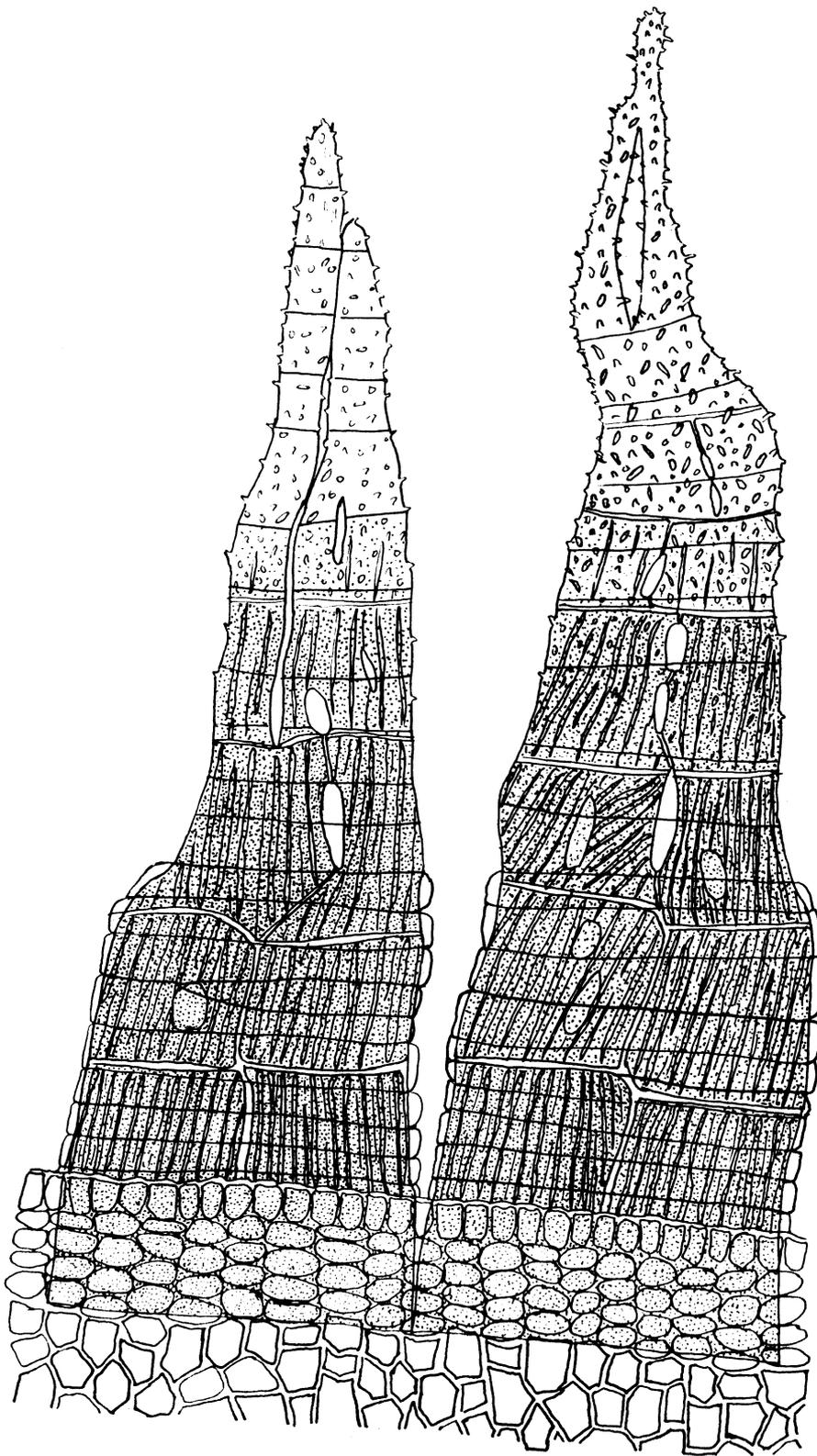
Autoicous; calyptra mitrate, lobed; seta erect, short; capsule immersed; operculum red, low conic, with short beak, columella attached to lid and falling with it; urn dark reddish brown, smooth, ovoid-ellipsoid, mouth wide when capsule empty.

Spores reddish brown, smooth, 8-18 microns in diameter, mature late spring to summer.

Peristome Characteristics

Plate 8

Peristome single, teeth 16, reddish orange to reddish brown, papillose above, strongly striate below, mostly cribose to sometimes entire, reflexed-revolute when dry, dorsal plates thicker than the ventral plates, 450 microns long, 125 microns wide, inserted below the mouth.



Leucobryum glaucum (L.) Schimp.

Leucobryaceae

Plants in dense cushions; leaves lanceolate, concave, almost entirely of costa, two kinds of cells, the outer large and empty, the inner ones small and chlorophyllose; margins entire except minutely denticulate at tip.

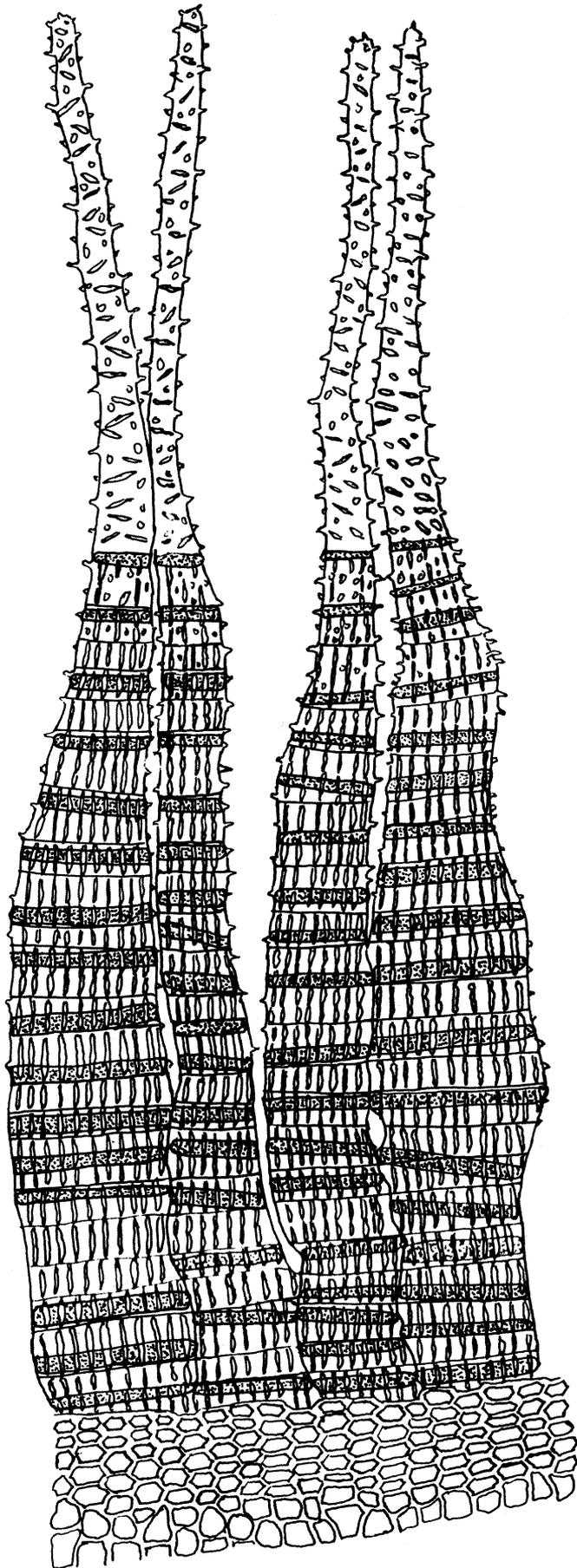
Dioicous; calyptra inflated, cucullate, longer than the capsule; seta erect, castaneous, about 1-2 cm. long; capsule inclined; operculum long rostrate; urn subarcuate to arcuate when dry, oblong to cylindrical, unsymmetric, usually distinctly strumose, with 8 ridges when dry.

Spores slightly roughened, 15-20 microns in diameter, mature in autumn.

Peristome Characteristics

Plate 9

Peristome single, teeth 16, 500 microns long, 200 microns wide, dark red to reddish brown, lanceolate, united at base into a tube, cleft from above to middle, into 2 lanceolate-subulate divisions, vertically striate and papillose.



Rhabdoweisia denticulata Brid.

Dicranaceae

Plants light to dark green; stems less than 1 cm. long; leaves oblong to linear-lanceolate, up to 2-3 mm. long, typically finely serrulate above, but often with teeth few and distant, keeled above, costa not quite percurrent, nearly or quite smooth on back.

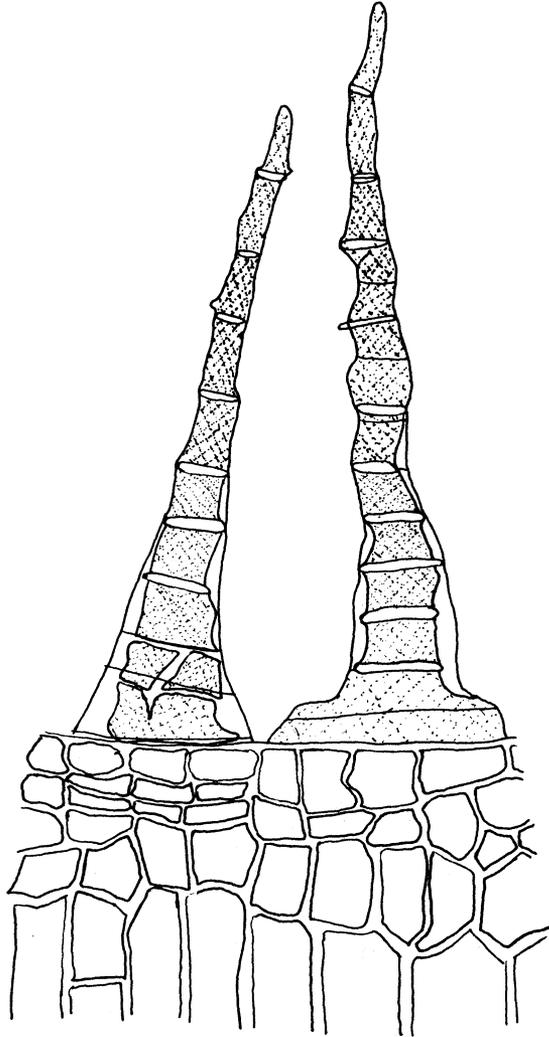
Calyptra cucullate, smooth, not fringed at base; seta erect, 2-5 mm. long; capsule erect, ovoid, deeply 8-plicate when dry, urn .5-1 mm. long; stomata few at base of urn; operculum with a long oblique beak; annulus lacking.

Spores approximately 17 microns in diameter, slightly roughened, mature in summer.

Peristome Characteristics

Plate 10

Peristome single, teeth orangish to reddish orange at base, linear from a lanceolate base, approximately 300 microns long, 50 microns wide at base, mostly smooth to slightly striate or papillose, almost a cross-hatch effect above from fine striations.



Weisia viridula Hedw.

Pottiaceae

Plants small, green to yellowish green; stems erect, occasionally up to 1 cm. long; leaves increasing in size from base of stem upward, erect spreading when moist, lanceolate, concave at base, costa strong, excurrent into a sharp subhyaline point, apices acute to acuminate; margins entire, strongly involute except at base.

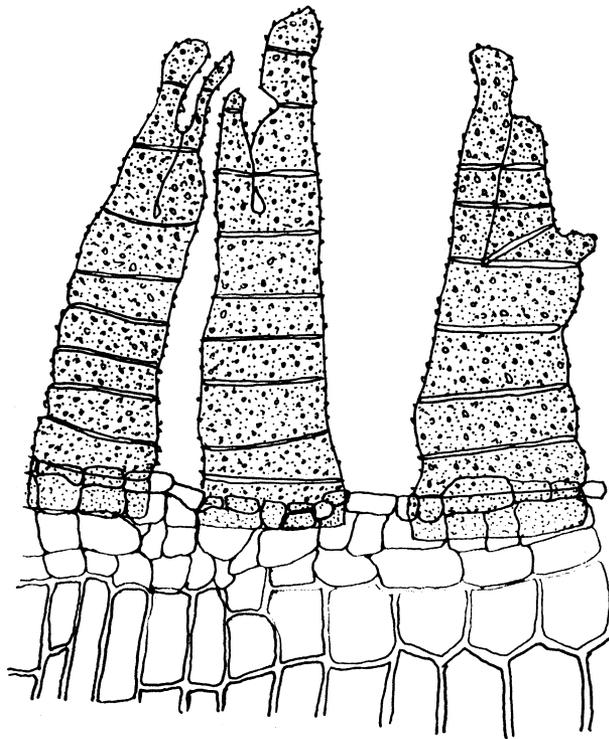
Autoicous; calyptra cucullate, covering 1/2-2/3 of capsule; seta yellow, reddish with age, lustrous, erect, 3-10 mm. long; capsule erect, symmetrical; operculum conic, long rostrate, beak usually oblique; capsule light to dark or reddish brown, often lustrous, ovoid to oblong-cylindric, smooth to plicate and slightly to not at all contracted beneath the mouth when dry; annulus narrow, persistent.

Spores pellucid, orange to brown, spherical, 12-19 microns in diameter, rather coarsely papillose, mature in spring.

Peristome Characteristics

Plate 11

Peristome single, teeth 16, orange to reddish, variable in length from almost lacking to 120 microns long, 50 microns wide, lanceolate and occasionally perforate to narrowly linear, often truncate, papillose.



Aulacomnium heterostichum (Hedw.) B.S.G.

Aulacomniaceae

Plants loosely tufted, 4-5 cm. high; leaves dense, erect, often inclined in one direction, not curled when dry, elongate-ovate, bases decurrent, costa stout at base, narrowing above, ending below apex, sometimes forked above, apices obtuse and apiculate to subacute, margins plane to slightly recurved, coarsely toothed in upper 1/2-2/3; pseudopodia sometimes present, up to 5 mm. long.

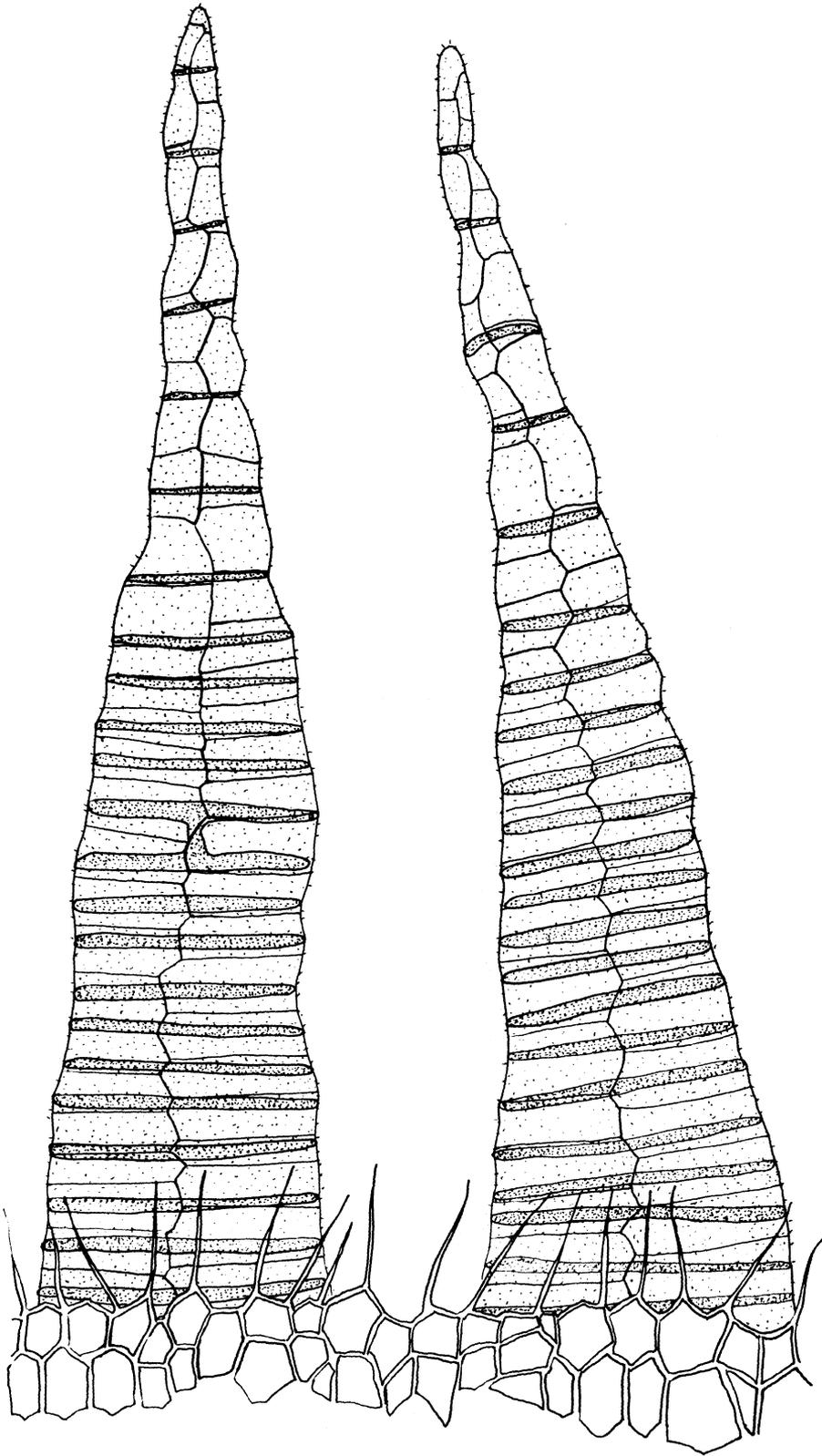
Autoicous; calyptra cucullate, long rostrate; seta reddish brown, erect, 6-15 mm. long; capsule reddish brown, inclined, slightly unsymmetric; operculum obtuse, short rostrate; urn oblong-cylindric, arcuate, 6-8 striate, tapering below into a short neck; annulus present.

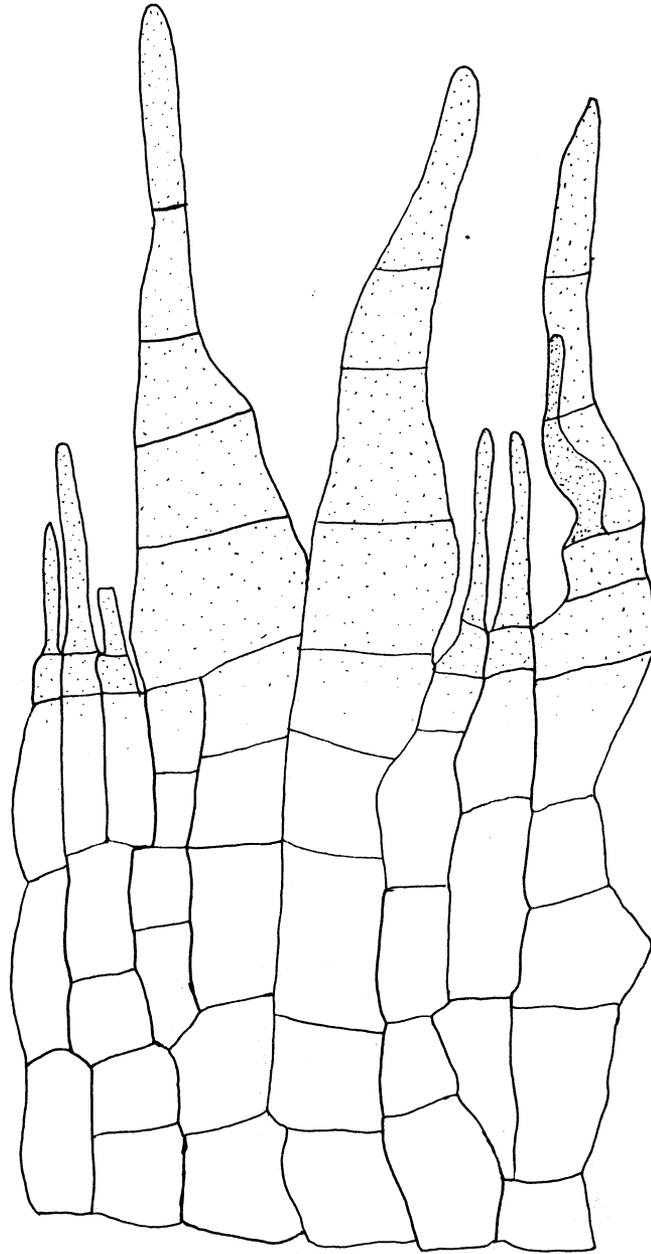
Spores slightly papillose, 9-12 microns in diameter, mature in early summer.

Peristome Characteristics

Plates 12, 13

Peristome double, teeth pale yellow to yellowish brown, 450 microns long, 100 microns wide, almost smooth in lower 2/3, hyaline and minutely papillose in upper 1/3, inner peristome minutely papillose at least above, hyaline, basal membrane 1/2 height of teeth, cilia 2-3 between the segments, shorter than the segments, the segments sometimes split above to the level of the basal membrane.





Bartramia pomiformis Hedw.

Bartramiaceae

Plants in tufts, green or yellowish green; stems erect, branched, 1.5-8 cm. long; leaves crowded, crisped when dry, spreading when moist, narrowly lanceolate to linear-lanceolate, canaliculate, base ovate or oblong, costa stout, prominent on lower surface of leaf, excurrent to a very spinulose, terete point, margins revolute, bistratose above, doubly serrate.

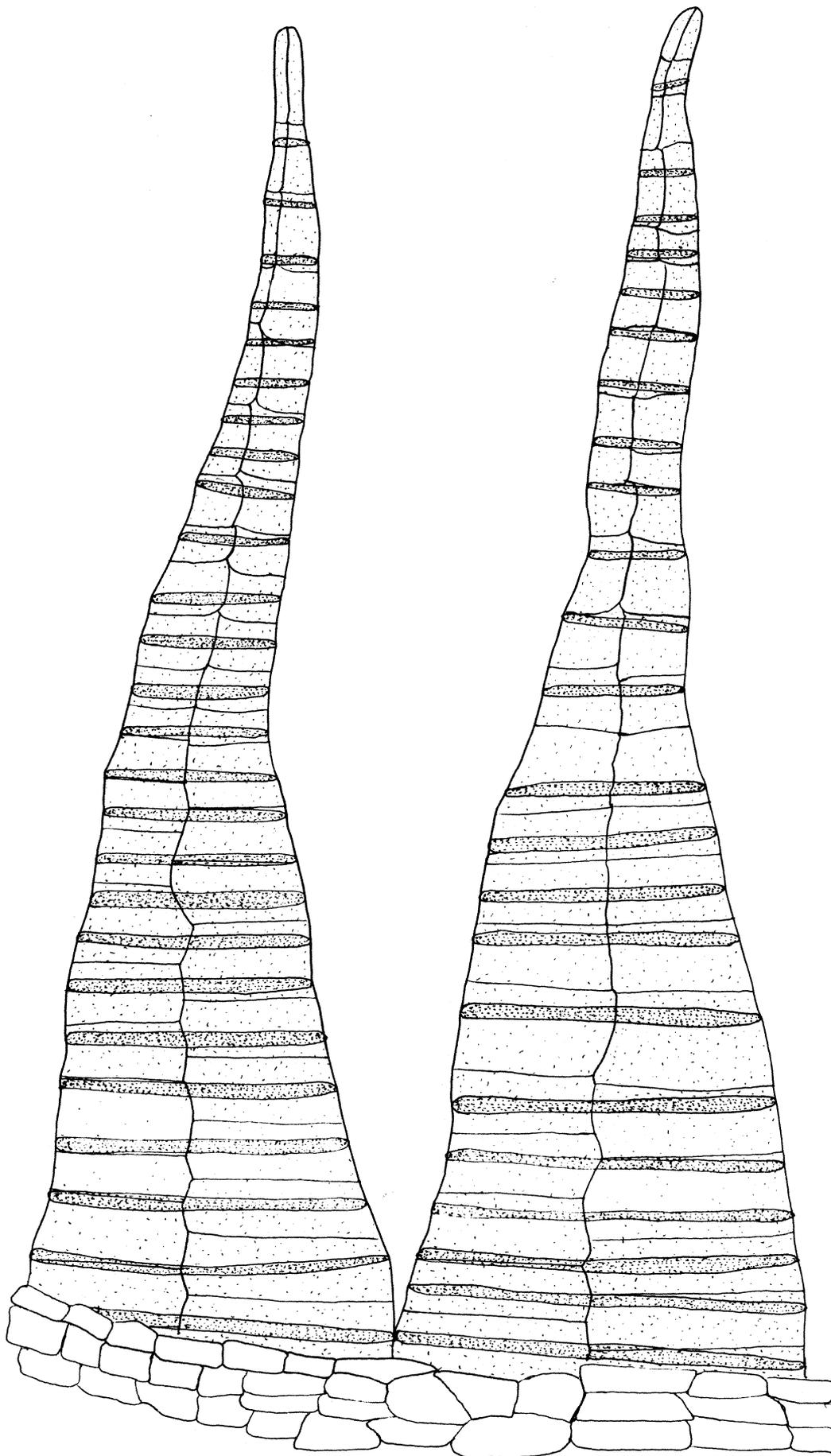
Autoicous to synoicous; calyptra narrowly cucullate, about 2 mm. long; seta reddish to chestnut-brown, erect up to 2 cm. long; capsule inclined or cernuous, unsymmetric, reddish to chestnut-brown; operculum short, convex; urn globose to ovoid, deeply furrowed when dry, approximately 1.5 mm. long and 1.5 mm. wide; annulus none or incomplete.

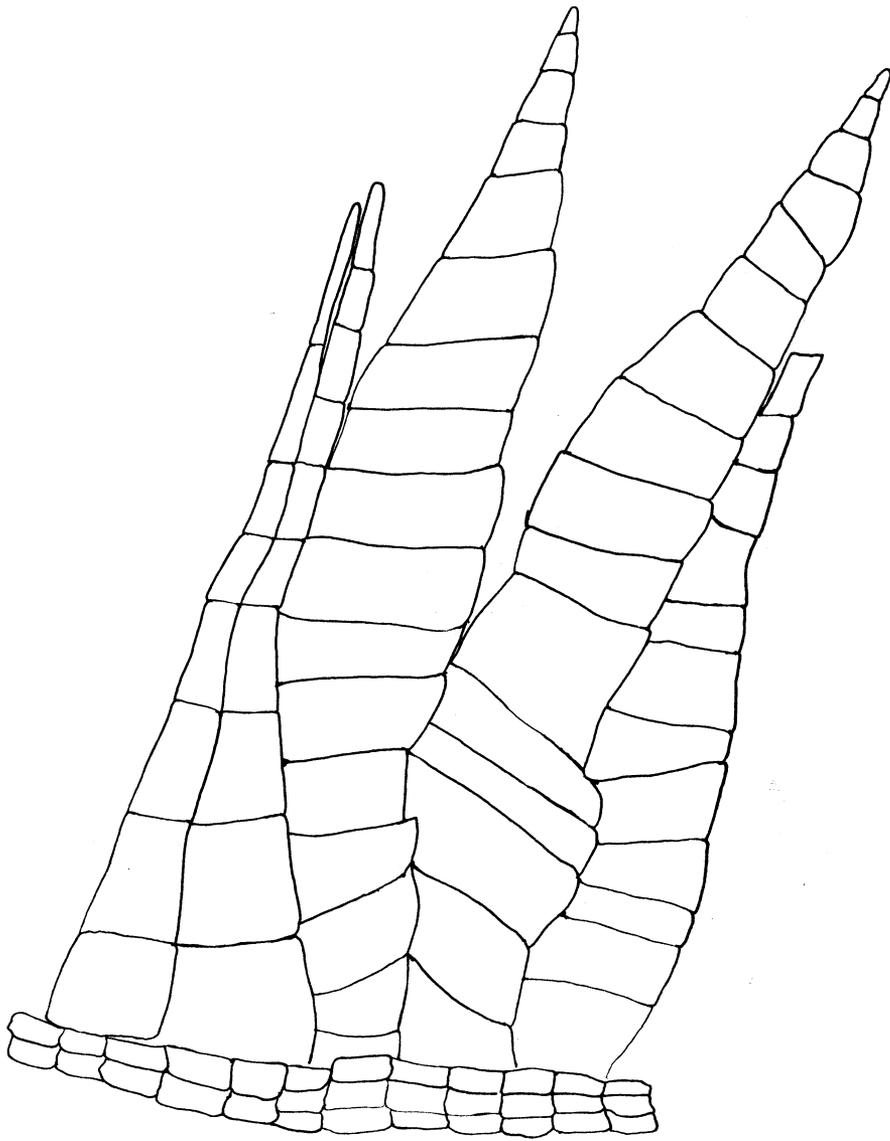
Spores reddish brown, spherical to reniform, coarsely papillose, 20-26 microns in diameter, mature May to June.

Peristome Characteristics

Plates 14, 15

Peristome double, teeth reddish, prominent bars on inside of teeth, lanceolate, their bases almost meeting, slightly papillose, approximately 390 microns long, 95 microns wide, inner segments pale yellowish from a high basal membrane, segments at first carinate later parted, basal membrane $\frac{2}{3}$ length of segments, cilia poorly developed or none.





Bryum argenteum L.

Bryaceae

Plants small, densely tufted, silvery or silvery-green; stems short, erect, branches terete, julaceous; leaves numerous, closely imbricate wet or dry, very concave, broadly ovate, costa slender, ending in upper 1/3 of leaf, margins plane or slightly reflexed.

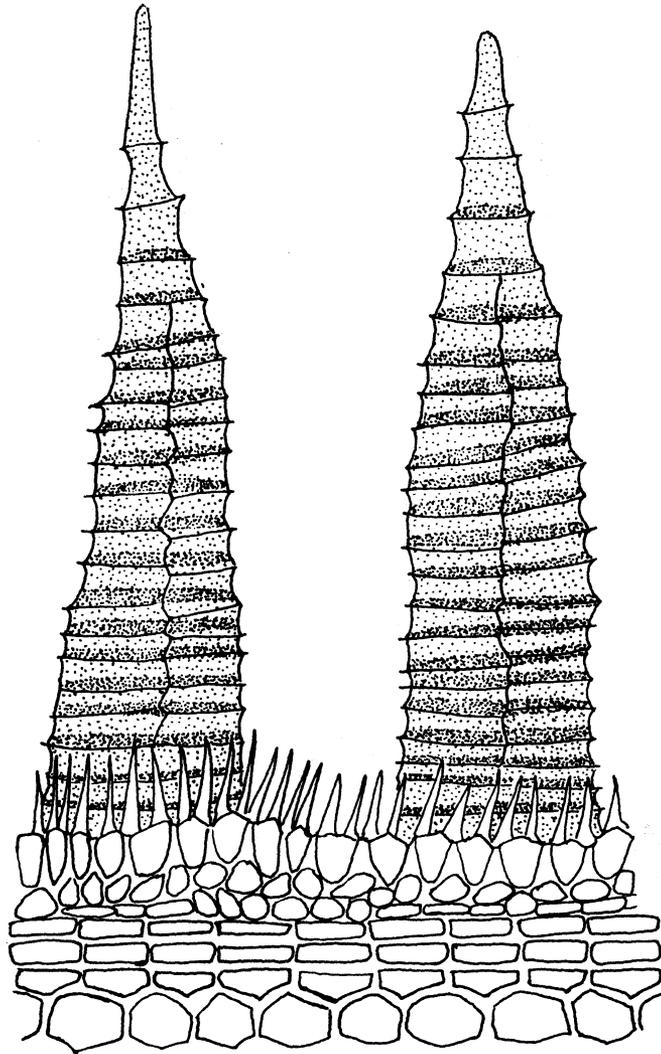
Dioicous; calyptra small, cucullate, fugacious; seta reddish or light to dark brown, pendant; operculum convex or low conic, apiculate; urn oblong, slightly contracted below mouth when dry; annulus of 3 rows of cells, deciduous.

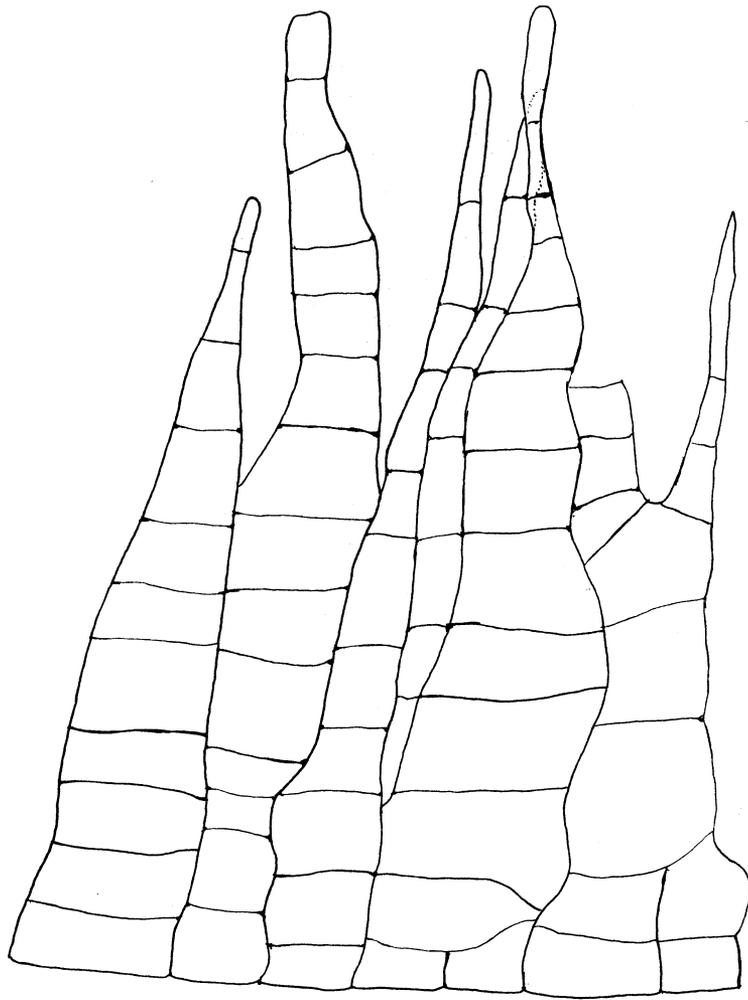
Spores yellowish, nearly smooth, 10-18 microns in diameter, mature in winter to early spring.

Peristome Characteristics

Plates 16, 17

Peristome double, teeth brownish yellow, orangish at base, approximately 330 microns long, 70 microns wide, linear-lanceolate, gradually tapering to slender hyaline tip, very finely papillose, inner peristome pellucid, finely papillose, segments nearly as long as teeth, rather broad, carinately split, basal membrane 1/2 height of teeth, cilia 3, appendiculate.





Diphyscium foliosum (Hedw.) Mohr

Buxbaumiaceae

Female plants densely clustered in mats; stems very short; leaves crisped when dry, subconcave, narrowly ligulate, costa broad and flattened, especially at base, ending just below apex of leaf, apices obtuse and cucullate, or bluntly acuminate, margins plane, crenulate, papillose, cells of leaves strongly papillose on both surfaces; the male plants minute, scattered; perichaetial leaves very large, gradually narrowing to long setaceous point.

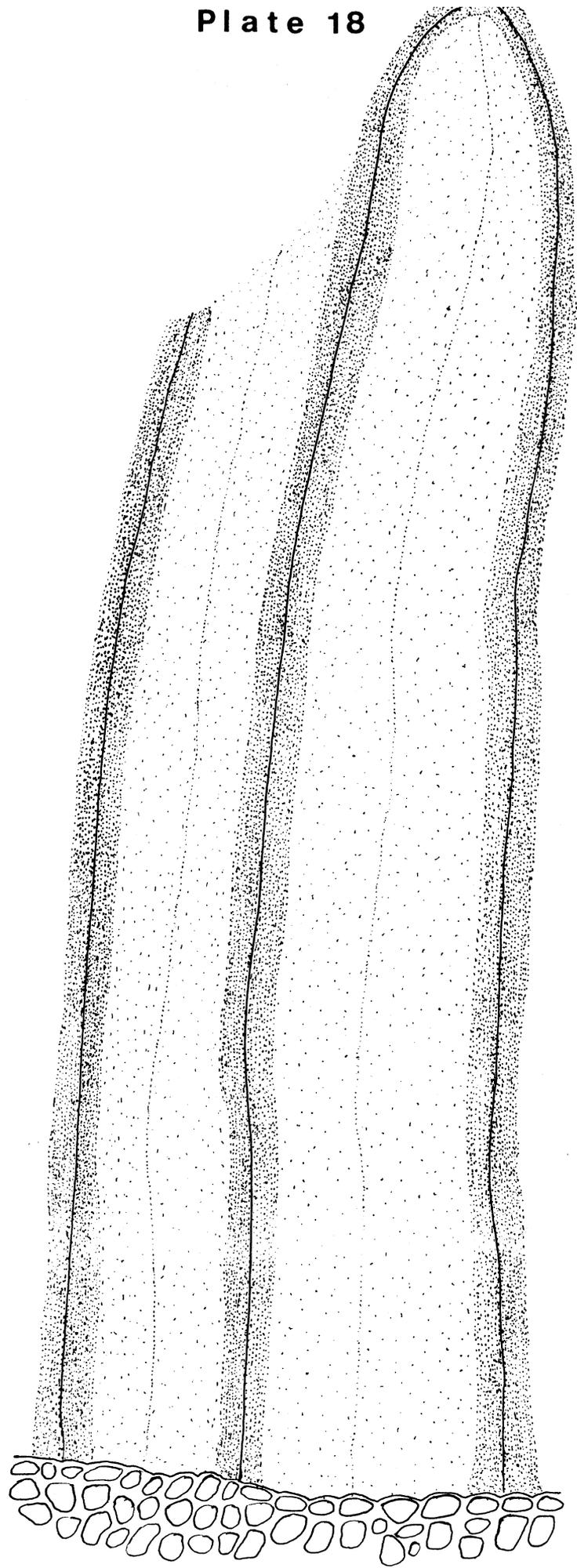
Dioicous; calyptra small, covering operculum; seta very short; capsule golden brown inclined, almost sessile, immersed or slightly emergent, resembling a grain of wheat in size and appearance; operculum acute, conic, curved; urn conic-ovoid, ventricose, very unsymmetric, 4-6 mm. long; annulus present, small.

Spores minute, 7-10 microns in diameter, mature in early summer to early fall.

Peristome Characteristics

Plate 18

Outer peristome lacking or rudimentary, the inner whitish, forming a 16 plicate, truncate cone, each division approximately 650 microns long, 85 microns wide, papillose evenly on the divisions, thickened and papillose on the ridges, with faint vertical line in middle of each division.



Funaria hygrometrica Hedw.

Funariaceae

Plants closely or loosely clustered, light green or pale yellowish green; stems erect, 3-10 mm. high, simple or branching at base; upper leaves erect to appressed, rather closely imbricate into bulb-like tuft, broadly oval, oblong, oblong-ovate, or obovate, concave, costa stout ending just below apex to briefly excurrent, apices acute to shortly acuminate, margins entire to crenate.

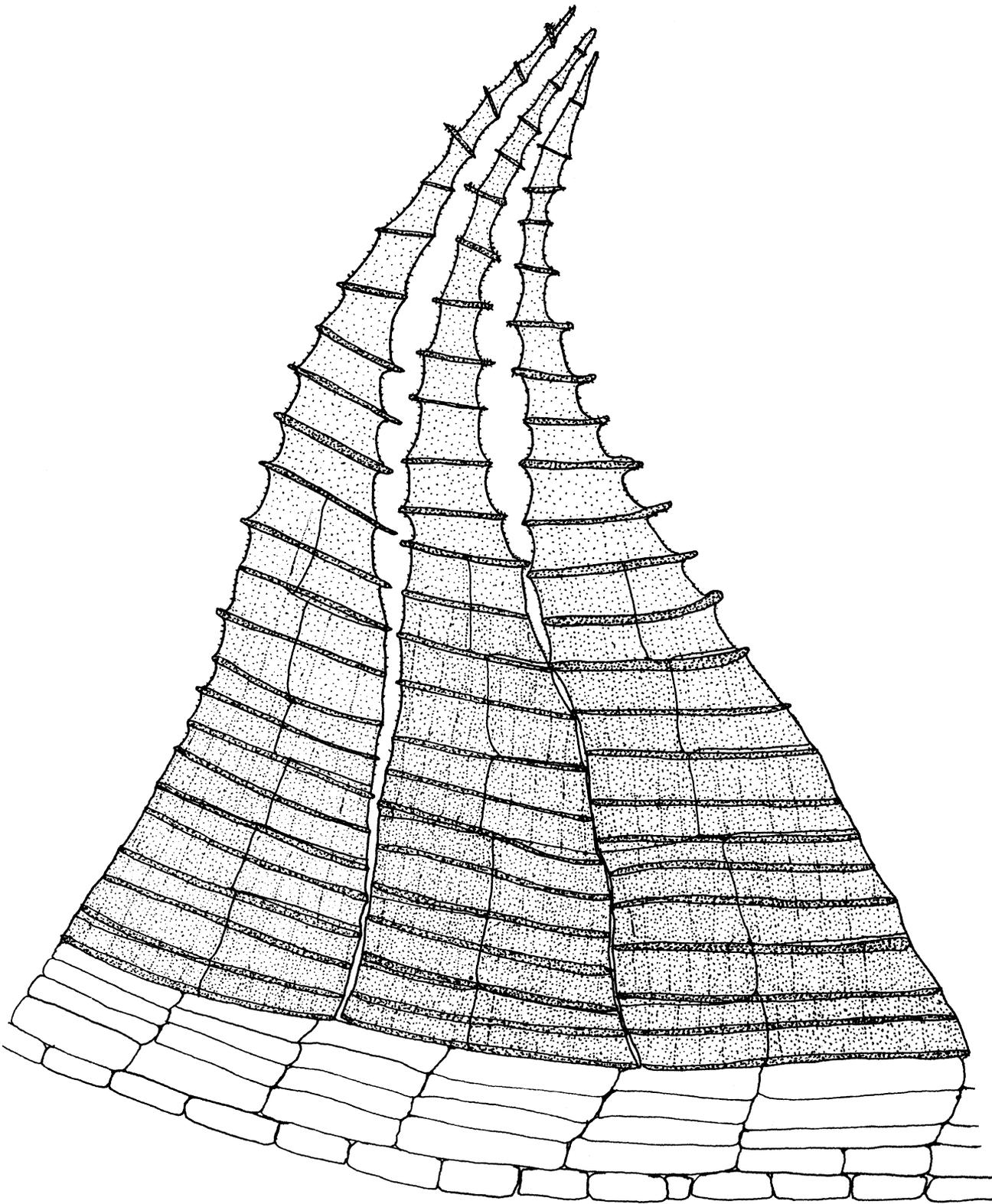
Autoicous; calyptra inflated, cucullate, long rostrate, early deciduous; seta erect, chestnut-brown, 2-5 cm. long, strongly twisted, upper part variously bent and curved when young and strongly hygroscopic when dry; capsule horizontal to pendent, greenish yellow when young, dark brown with age; operculum slightly convex; urn subpyriform, very unsymmetric, strongly arcuate, deeply sulcate when dry, mouth dark red, very oblique, often parallel with lower side of urn; annulus of 2-3 rows of large cells, deciduous.

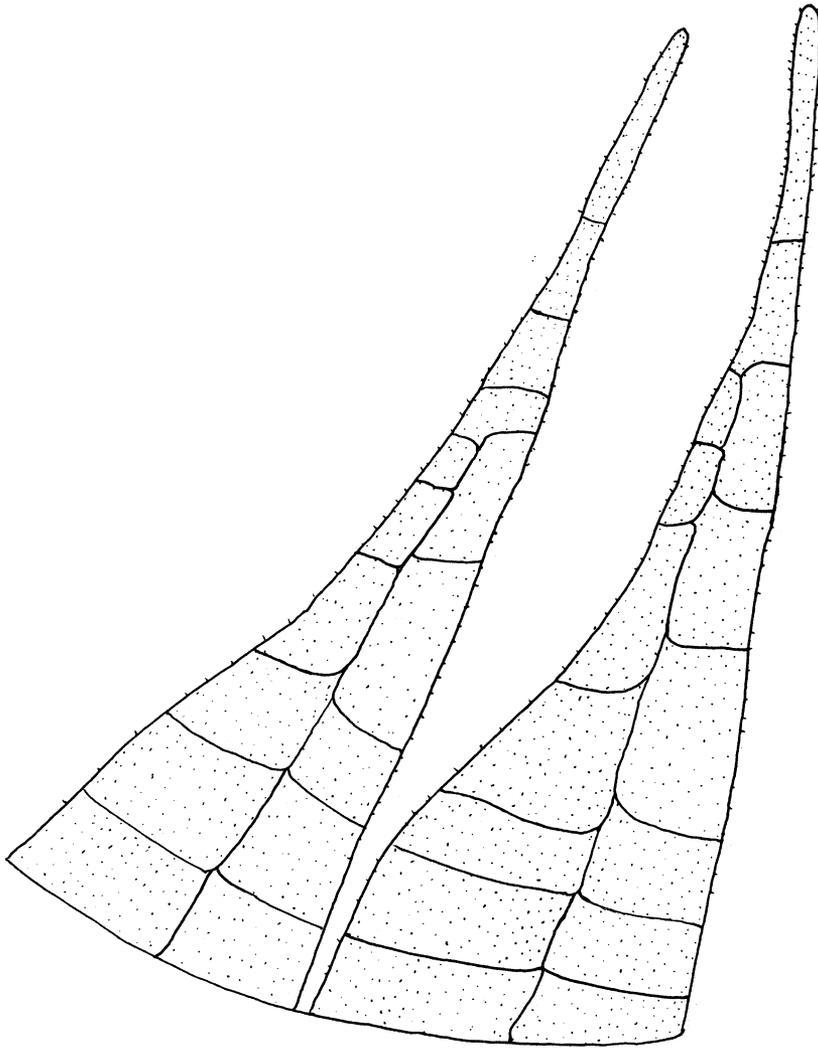
Spores 12-17 microns in diameter, smooth, mature in May or June.

Peristome Characteristics

Plates 19, 20

Peristome double, teeth 16, dark red to castaneous, about 425 microns long, up to 100 microns wide, spirally twisted, strongly papillose, with faint vertical striae below, subcylindric above with ciliate-fimbriate appendiculae, united by tips to small central disk, segments of inner somewhat shorter, their bases meeting lanceolate, with slender apices, papillose, lying opposite the outer teeth.





Mnium cuspidatum Hedw.

Mniaceae

Plants in large mats, light to yellow green; stems simple, erect to spreading; leaves few, becoming more numerous towards terminal rosette, crisped and distorted when dry, spreading when moist, obovate to oblong-oval, bases narrow, decurrent, costa rather strong, ending below apex, the apices acute, short or cuspidate, border unistatose, margins serrate in upper 1/2-2/3.

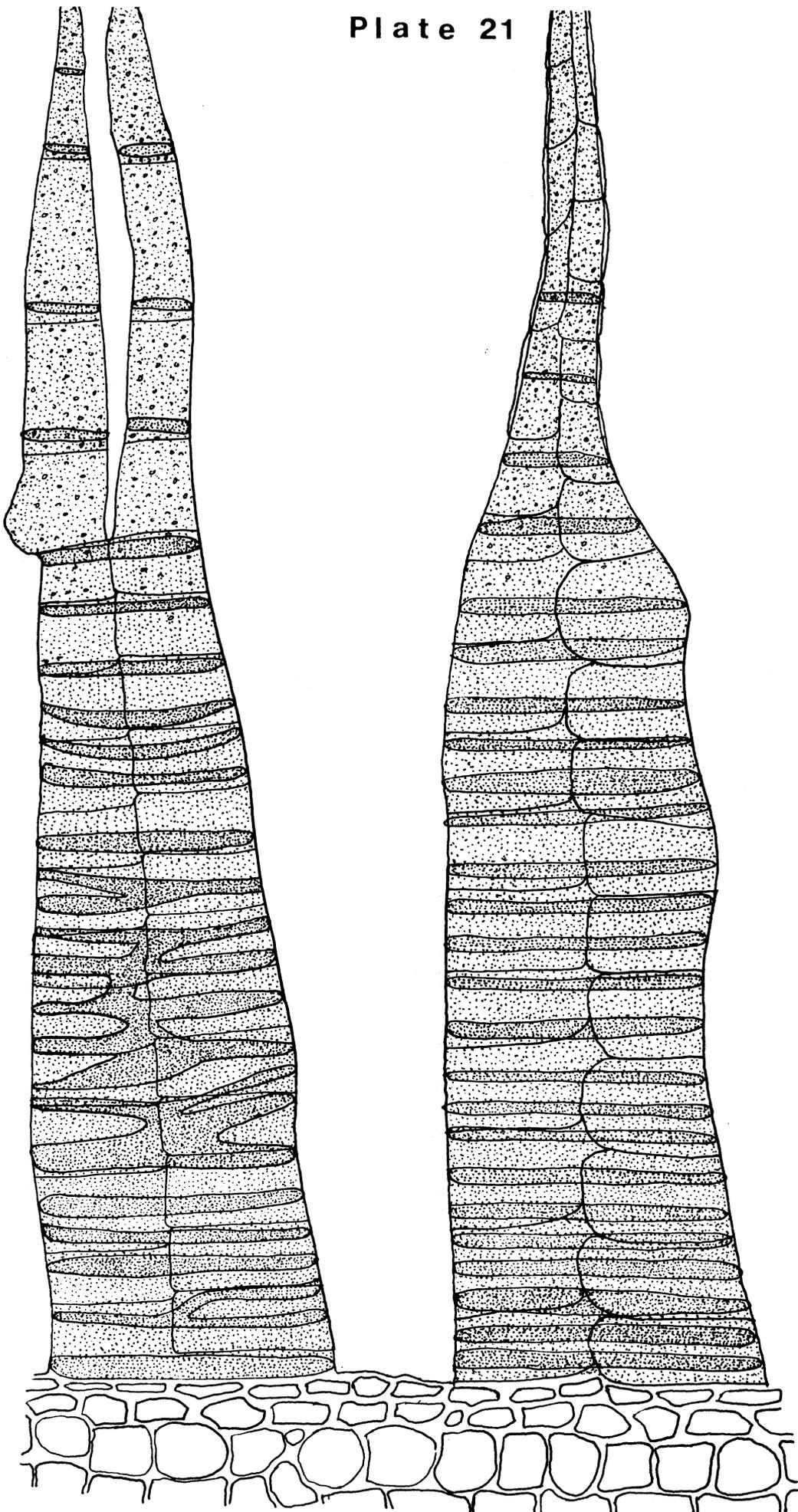
Synicous; calyptra cucullate, inconspicuous, fugacious; seta single, erect, slightly reddish yellow, up to 3 cm. long; capsule subpendulous to pendulous, yellow to brownish yellow; operculum rather large, conic, obtuse; urn oblong to oval, neck very short; annulus of 3-4 rows of cells.

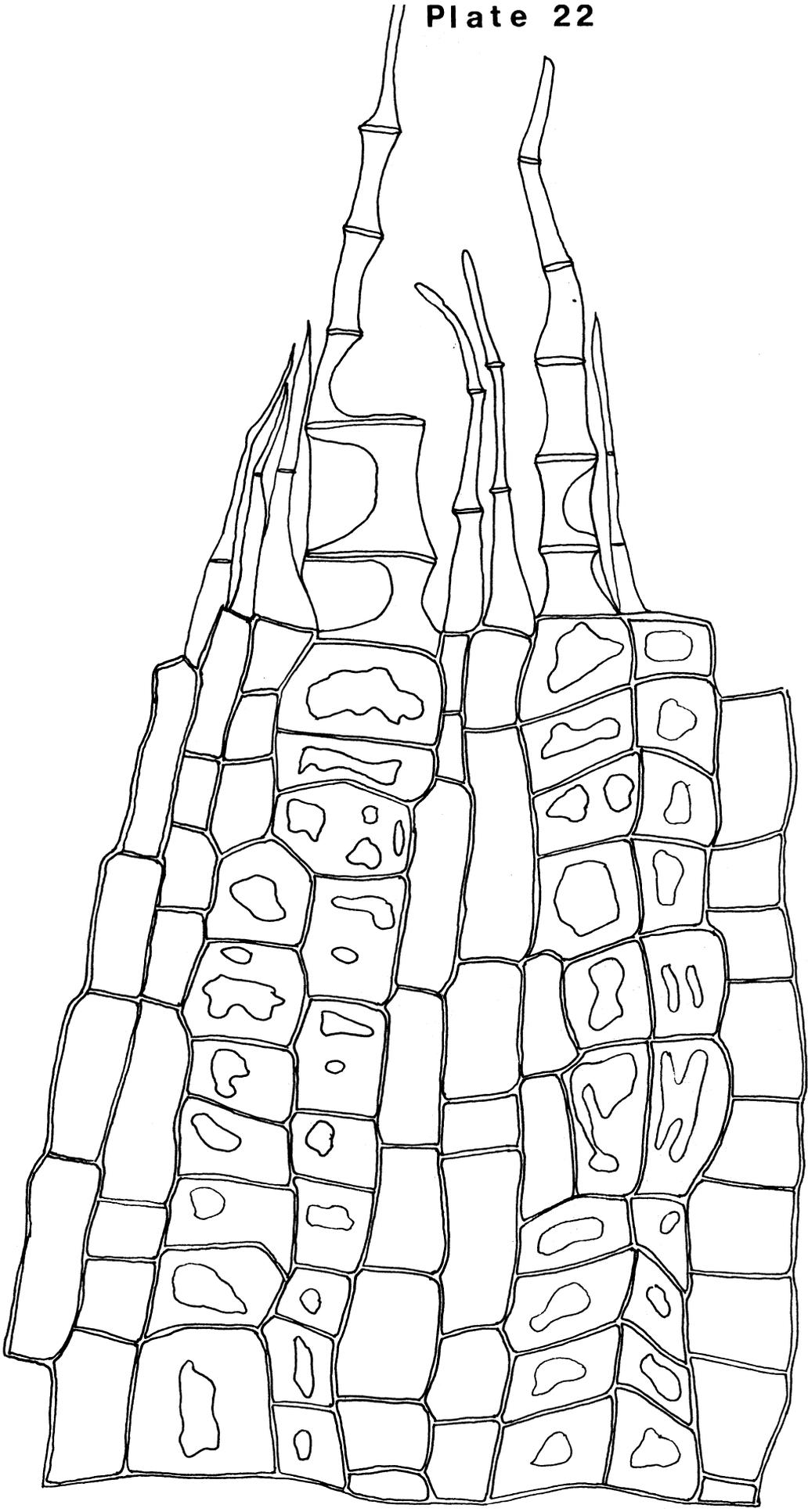
Spores yellow, faintly papillose, 20-28 microns in diameter, mature in April and May.

Peristome Characteristics

Plates 21, 22

Peristome double, teeth 16, linear lanceolate, up to 600 microns long, 100 microns wide, yellowish pellucid, papillose, inner peristome reddish yellow to brown, papillose, strongly perforate, segments carinate, ending in awn-like tip, same height as teeth, basal membrane 1/2 height of segments, cilia 3-4, prominently nodulose.





Mnium punctatum Hedw.

Mniaceae

Plants rather large, in loose tufts; stems erect, rigid, mostly simple, 2.5-7.5 cm. high; leaves distorted when dry, rounded ovate, the rosulate spreading, oval, broadly obovate, or obovate-spatulate, gradually narrowing to base, not decurrent to slightly so, costa strong below, percurrent, ending in apiculus, or ceasing just below the tip, the apices broadly rounded to slightly emarginate, border purplish brown or reddish.

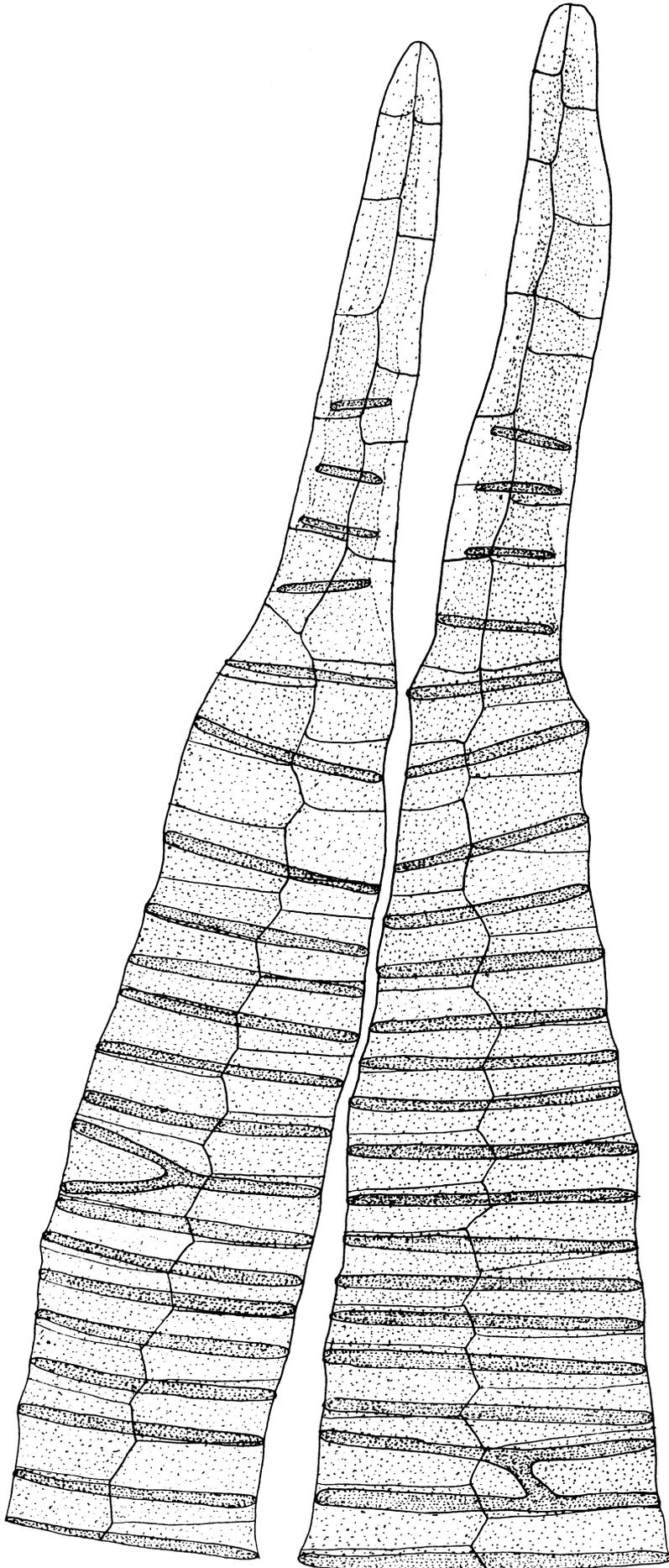
Dioicous or synoicous; calyptra cucullate, inconspicuous, fugacious; seta erect, purple-brown or reddish, rather glossy, 2-4 cm. long, 1-3 from same perichaetium; capsule horizontal to pendulous, yellowish or brownish with age; operculum conic, acutely rostrate; urn ovoid, oval-oblong, or oblong-cylindric; annulus of 1-3 rows of cells.

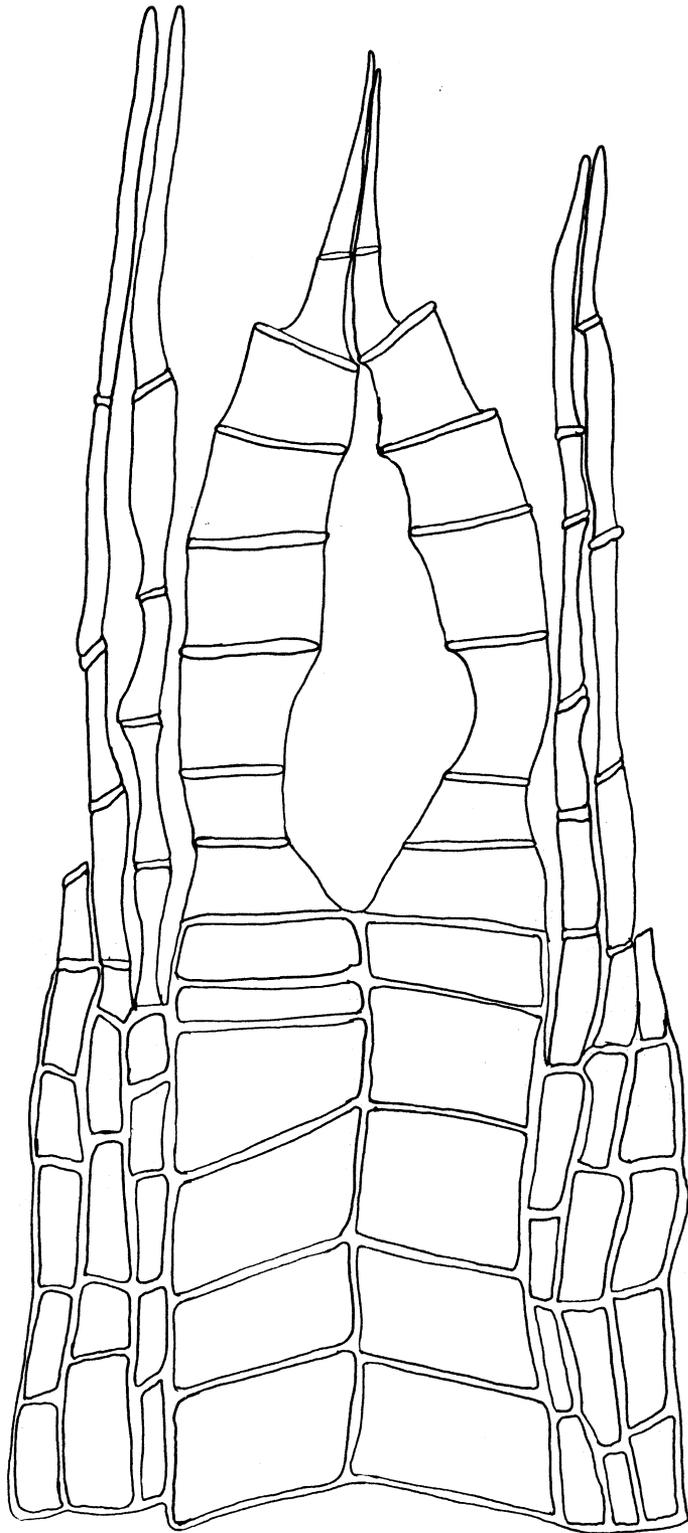
Spores brownish yellow, nearly smooth to roughened, 28-40 microns in diameter, mature winter or spring.

Peristome Characteristics

Plates 23, 24

Peristome double, teeth 16, yellowish brown, approximately 575 microns long, 105 microns wide at base, pellucid, papillose, the papillae sometimes appearing to be in longitudinal striae, inner peristome golden-yellow, pellucid, finely papillose, segments carinate fenestrate, narrow and gradually tapering to a slender apex, basal membrane up to 1/2 height of segments, cilia 2-3, somewhat nodulose, longer than the segments.





Orthotrichum pumilum Dicks.

Orthotrichaceae

Plants in close tufts, dark green; stems erect, up to 1 cm. long; leaves imbricate, not contorted when dry, erect spreading when moist, broadly to narrowly oblong-lanceolate, concave, costa strong, ending below apex, apices briefly acuminate to narrowly obtuse, usually with a single subhyaline cell at apex, margins revolute nearly to apex, entire.

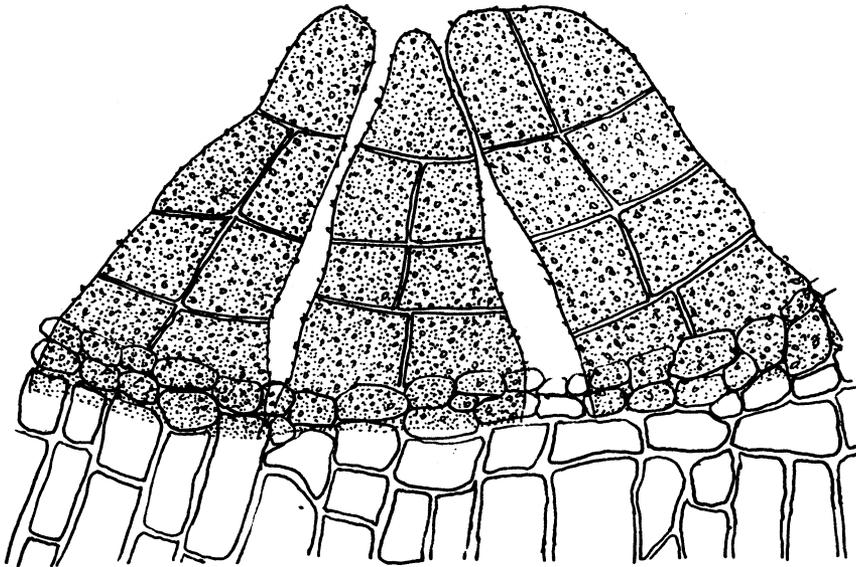
Autoicous; calyptra strongly plicate, usually with a few very short hairs at apex; seta short, .5 mm. long; capsule immersed to slightly emergent; operculum conic, apiculate; urn usually light colored, oblong to oblong-ovoid when moist, 8-ribbed and contracted below mouth when dry, abruptly narrowed to seta, neck distinct; stomata immersed; annulus present.

Spores 12-15 microns in diameter, mature in spring.

Peristome Characteristics

Plate 25

Peristome double, teeth 16, triangular-lanceolate, short, 130 microns long, up to 50 microns wide at base, usually united in pairs, reflexed when dry, finely papillose, dorsal plates thicker than ventral, segments of inner peristome 8, linear, of two vertical rows of cells at the base, sometimes not strongly developed.



Pohlia elongata Hedw.

Bryaceae

Plants erect, loosely tufted, with brown radicles below, 1-2 cm. long, green, without lustre; stem simple; leaves erect spreading, lanceolate, long acuminate, margins reflexed, upper part sharply denticulate, costa strong percurrent or slightly excurrent.

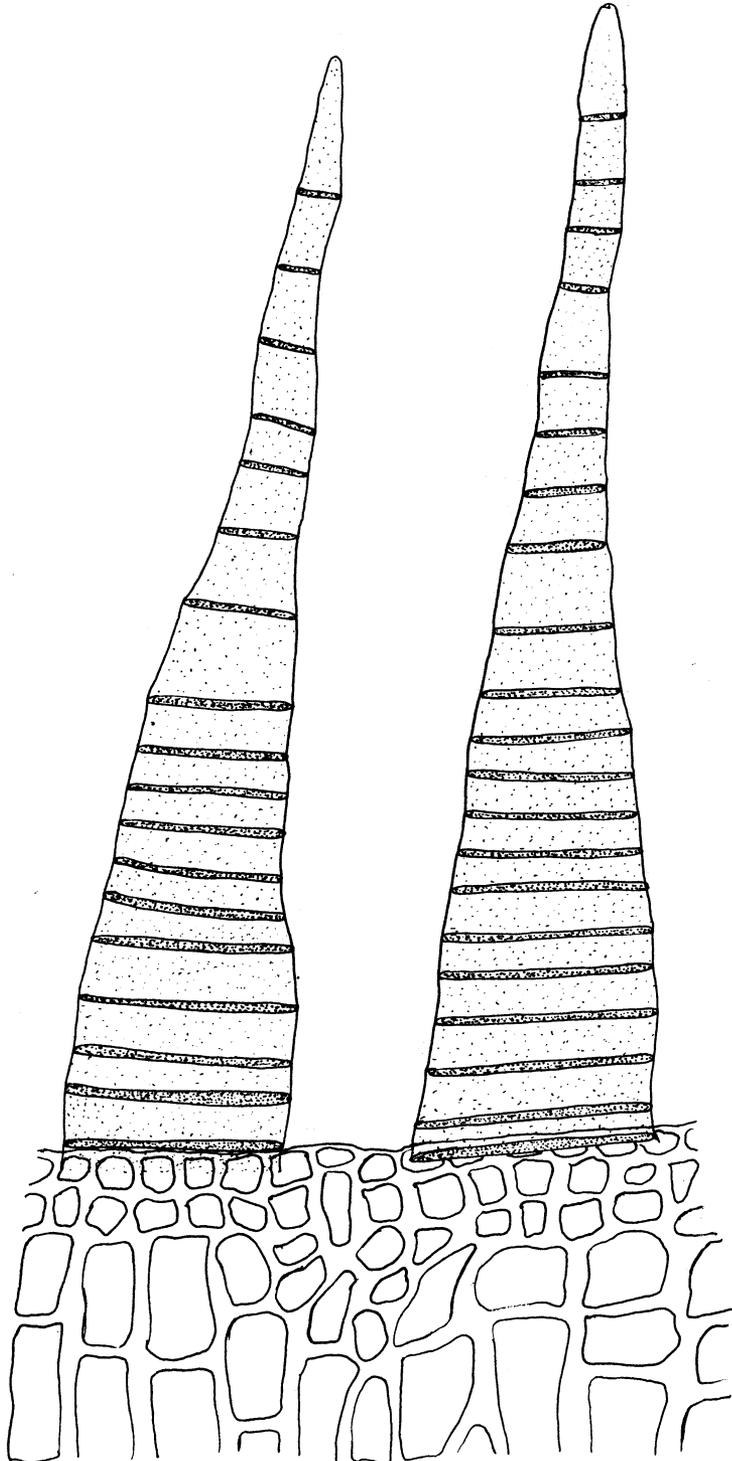
Paroicous; seta up to 3 cm. long, slender, reddish below, lighter above; capsule inclined to horizontal, very long and slender, up to 4-5 mm. long, cylindric or narrowly clavate, frequently somewhat curved and asymmetric, yellowish brown, becoming darker with age; neck narrow, of equal or greater length than rest of capsule; operculum conic, sharply apiculate; stomata phaneropore; annulus removeable.

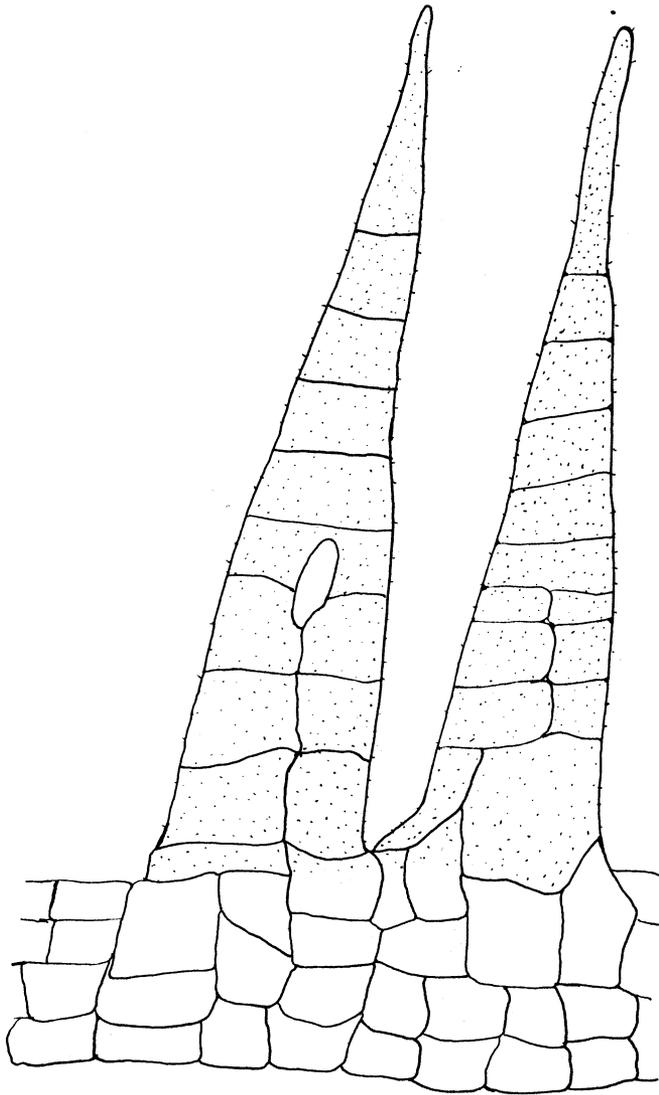
Spores brownish, 15-20 microns in diameter, papillose, mature late August or September.

Peristome Characteristics

Plates 26, 27

Peristome double, inserted near mouth of capsule, outer teeth yellow, fairly broad, papillose, narrowly bordered, approximately 360 microns long, 50 microns wide, inner peristome hyaline, papillose, with rather low basal membrane, segments of irregularly serrate outline, narrowly perforated or not, inner segments filling space between outer teeth, cilia lacking or 2-3, short, nodulose.





SUMMARY

In this study on peristome structure, an artificial grouping, Acrocarpi, was chosen as the Musci for morphological study and illustration. The Acrocarpi, or those mosses producing sporophytes terminally on the gametophyte, include species of nematodontous mosses and arthrodontous mosses. The arthrodontous Musci are usually further subdivided into the Haplolepidaceae and Diplolepidaceae.

The members of the Nematodontaceae which were included in this paper can be separated at the family level based on the comparative morphology of the mature peristomes.

The Tetraphidaceae produce the simplest type of nematodontous peristome. The single species studied was Tetraphis pellucida in which the tissue lying directly under the operculum splits almost equally into four sectors composed of three or four layers of whole dead cells. The peristome of a member of the Polytrichaceae is characteristically composed of short, pyramidal, solid teeth. Each tooth is made up of a central pillar of fiber-like cells surrounded by U-shaped cells that are more translucent. In this family Atrichum angustatum, Pogonatum pensilvanicum, and Polytrichum ohioense were the species closely examined. A third family of the Nematodontaceae was studied, the Buxbaumiaceae. This family was used by Philibert (1889) to tie together the Nematodontaceae and the Arthrodontaceae to a common ancestor. Its development is like that of a nematodontous moss, but the mature peristome resembles

an arthrodontous moss. In this family the peristome is formed from a broad zone, a characteristic of the Nematodontae, but the peristome is composed of only cell wall material, a characteristic of the Arthrodontae. The species studied and illustrated was Diphygium foliosum.

In the haplolepidous subdivision of the Arthrodontae five families were included. The family Dicranaceae was represented by three species, Dicranella heteromella, Dicranum scoparium, and Rhabdoweisia denticulata. In this family the peristome is generally single, reddish in color, generally cleft to below the middle, has a very low basal membrane, and is vertically striate. On preliminary examination the peristome of Rhabdoweisia seems not to fit in because of its lack of a cleft. It does, however, exhibit the other four characteristics and so seems to be more closely related to this family than other families of the Haplolepidae.

On the basis of peristome morphology the family Leucobryaceae seems to be closely related to the Dicranaceae. In this family the teeth are cleft to the middle or below, are reddish, united below in a tube, and are vertically striate and papillose. The only major difference between the families is the strongly papillose nature of the Leucobryaceae. The species included in this study was Leucobryum glaucum.

The Ditrichaceae, containing the species Ditrichum pallidum, also seem to be closely related to the Dicranaceae because of the reddish tint, the presence of a low basal membrane, and the deep cleft of the teeth. They can be separated, however, because of a lack of vertical orientation of the papillae and because of having only a few widespread articulations.

The Grimmiaceae, represented by Grimmia apocarpa, differs from the other Haplolepideae because in this family it is the dorsal plates that are thicker, which is the opposite of other Haplolepideae. It can be hypothesized that as the ancestors of this family lost the ability to produce an exostome the middle peristomial layer retained its propensity for producing a thick secondary cell wall. Instead of deposition on the outer tangential walls the thickening was laid down on the inner tangential walls. This is in contrast to other ancestors of the haplolepidous mosses, who as they lost the ability to produce an exostome also lost the ability to produce thick secondary cell walls on the middle peristomial layer.

Another family of the Haplolepideae studied was the Pottiaceae with a single species, Weisia viridula. It can be separated from the other haplolepidous mosses studied by observing its papillose nature. The papillae seem to be evenly distributed over the surface of the teeth without any hint of vertical orientation, which is a characteristic of the other families.

In the diplopidous subdivision of the Arthrodoneteae six families were studied and illustrated. Several of these families (Bryaceae, Mniaceae, and Aulocomniaceae) seem to be closely related but can be separated using characteristics of the peristome.

In the Aulocomniaceae, represented by Aulocomnium heterostichum, the peristome is double with an endostome consisting of a basal membrane that is one half the height of the teeth and is minutely papillose, at least above. Cilia vary from two to three and are shorter than the segments. The segments are sometimes split above to the level

of the basal membrane and delicate in structure. The outer teeth are pale yellowish in color, hyaline in the upper part.

The Bryaceae, represented by Bryum argenteum and Pohlia elongata, have outer teeth that are pale yellowish to yellowish brown and are minutely papillose. They are generally shorter than in other closely related families. The endostome in this family is variable, but is generally rather hyaline, delicate in structure, almost equal in length with the outer teeth, and has a basal membrane present. The segments alternate with the teeth of the exostome. The very delicate nature of the endostome and its nearly equal length separate this family from the other members of the Diplolepidae.

The teeth of the Mniaceae are larger than most of the other members of the Diplolepidae. Two species were studied, Mnium cuspidatum and Mnium punctatum. The endostomes of this family are usually quite well-developed, highly colored, and strongly carinate. This well-developed and highly colored endostome separates this family from the others. The species can be separated from each other because the endostome of Mnium punctatum is carinate-fenestrate, which means opening along the keels above, while Mnium cuspidatum is perforate on the segments nearly to the base.

The Funariaceae, represented by Funaria hygrometrica, is easily separated from all the other families because the segments of the endostome are all located exactly opposite the teeth of the exostome. It is the only family that has this unique feature.

The Bartramiaceae, represented by Bartramia pomiformis, can be separated from the others because the bases of the outer teeth meet or very nearly so. The teeth are also deeply red, strongly trabeculate,

and the trabeculae can be seen with a hand lens. The inner peristome is reduced and only about half the height of the outer teeth. Cilia, when present, are poorly developed. The segments are irregularly parted when fully mature, a characteristic found only in this family.

Hopefully it can be seen from this discussion that peristome morphology indicates close phylogenetic relationships between mosses with differing gametophytic characteristics. Furthermore, closely related families can be separated using peristome characteristics and many times separation can be carried down to the species level.

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