THE EVOLUTIONARY SIGNIFICANCE OF VENTRAL SCALES IN THE MARCHANTIALES

by

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INTRODUCTION

The ventral scales in the Marchantiales, as a separate entity, have received little attention except as tools of systematics. In the course of preliminary investigation of these structures in Marchantia polymorpha, to find a satisfying answer to its place in the evolution story in the Hepaticae, it became apparent ventral scales in this species had characters of distinct value. From this point, an expanded investigation into other genera and species of the order, seemed indicated. Limited by the availability of material for study, twenty two genera were decided upon for enlarging the scope of the first, small and tentative study. Certain intermediate steps were essential if there were to be adequate data for consideration of the evolution theories, progressive and regressive. These steps included: (1) compilation of existing data on ventral scales in the literature; (2) direct observation and enumeration of findings not hitherto appearing in the literature; (3) acceptance of the previous taxonomic approach to these structures, and an evaluation of both types of data collected leading toward a more easily utilized body of taxonomic criteria, especially in the case of sterile specimens; (4) synthesis or integration of this body of information, and application of it brought to bear upon to the evolution story as it exists, and as it might be further expanded.

The few previous works have been concerned with the origin of scales, the general characteristics of mature scales, and the use of ventral scales in taxonomic procedures. Some mention has been made of their evolutionary significance, from the standpoint of homology with the leaves of the Acrogynae. Pigments, oil bodies, "rhizoidal initials", functions of the various parts of the scale have all had more specific attention by certain authors. This information is considerably scattered, except in a few morphological and taxonomic monographs, and general works. It is understandable that the primary concern of earlier studies was to discover how scales develop, and what morphological information could be obtained from them, significant in taxonomy. Ventral scales came under the classification of accessory data. Even today, the scales emphasized as of taxonomic importance are those associated with reproductive organs.

Naturally, concentrating on a single, ventral appendage of the thallus has led to new and startling facts and observations. It is hoped that the additional new findings on ventral scales with the other known characters of the gametophyte, will make more accurate and complete the means of identifying sterile specimens. The author is certainly of the opinion that a much more critical knowledge of and use of insertion patterns, and of young uneroded scales will clear up much of the fragmentary information in the literature. By this, he does not mean to imply that the information is incorrect, but that it varies so much as to be misleading. Such information has included description of eroded ventral scales, of parts and of half-scales of those species whose scales split into fragments midway in their ontogeny. If descriptions are made of scales whose apical portions have just emerged out of the apical notch of the thallus, a comparatively accurate picture can be obtained of the scale characteristics of the species. This again does not mean that description of fragments or of older intact scales is not useful, but that description of mature uneroded scales would tend to standardize our information on many species of thalloid liverworts.

The emphasis then, among other pertinent points concerning ventral scales, in this investigation is on: scale insertions; the exact number of rows of scales on the ventral surface of the thallus based on insertions; the development of scales; the record of changes taking place during the ontogeny of the scale; the types of development; the erosion of the scale; the development and character of laminar scales versus appendicular scales; and finally, the evolutionary tendencies of ventral scales in the Marchantiales.

MATERIALS AND METHODS

Plant material selected for study consisted of dry herbarium specimens and fresh living plants. Specimens were obtained from widely distributed locations and a wide range of ecological situations where study of the species indicated the need. For some of the less common forms there was no choice since they were often forms known from but one type of habitat. Attention was centered primarily on sterile specimens and more specifically on sterile dichotomies in which the sequence of scale development and arrangement had not been interrupted, or by the formation of groups of initials involved in the origin of new dichotomies (ventral branches and reproductive branches such as gametophores). When possible the dichotomies used were ones that had had a minimal contact with soil and usually represented vigorous young growth with a reduced possibility for any appreciable amount of erosion of the scales themselves.

In order to facilitate the study of ventral structures, two dyes were used. A 1% aqueous solution of bismarck brown, to which was added a crystal of thymol, was found fairly useful in the early stages of this study. This dye had a tendency to color the ventral cells of the thallus proper and consequently was eventually discarded. The dye that gave the best results was Toludine blue used as a 1% solution in 70% ethyl alcohol. Toludine blue has a high affinity for the wall materials in the rhizoids of liverworts, a moderate affinity for cell walls of the ventral scales and still less affinity for the ventral cells of the thallus. This proved to be a very convenient circumstance since quite a period of time was required, before the ventral cells of the thallus itself absorbed the dye. Since the rhizoids absorbed the dye so strongly the preparation of the thallus was facilitated. The exact relationship of the rhizoids to the ventral scales was revealed at all times, especially with reference to the insertion of these two structures. Toludine blue was used by Czaja (1936) who employed it to the alkaline-membrane effect of absorptive tissues. He found in Marchantia polymorpha that the cell walls of the rhizoids absorbed the dye tenaciously and ventral cells of the thallus remained practically unstained. The findings of this investigator have been in accord, and in fact have shown such differential staining to be the general rule for all species of liverworts studied. The tuberculate rhizoids were the structures displaying the highest affinity. McConaha (1939) also used the same dye in her studies on Conocephalum conicum. She found that the absorption of the dye was limited to the ventral appendages of the thallus.

Toludine blue was also found to be very useful in studying the developmental phases of the scale. While meristematic tissue has a very high affinity for this dye, some idea of cell lineage could be ascertained from stained dissections. Chromatic structures and figures could be seen without any difficulty. Another advantage in the use of this dye became evident in the observation of slime cells, oil bodies and slime papillae. These structures absorbed the dye greatest of any structure found on the ventral side of the thallus or, it might be said, they absorbed the dye to the same intensity as the rhizoids if not a little more so.

Because of such differential staining, the author was able to see the outline of scales and to detect rows of scales heretofore not reported for certain species in the literature. In most cases in which scales are normally colorless and very adherent to either the ventral side of the thallus or to the lamina of the appendiculate scales, detection was made easy because of the dark-staining slime papillae on their margin. In every case, the flux of slime produced by a scale with numerous slime papillae was of considerable magnitude and served as the chief adhesive agent.

The preparation of dried herbarium material, for both dissections and sectioning, posed no problem at all though some workers in the past especially taxonomists, have frequently voiced opinions to the contrary. The material was selected for the characteristics previously mentioned and placed in distilled water for twenty-four hours. Part of this time the capsule jars containing the specimens, were placed on top of a standard paraffin oven where the water became lukewarm for a few hours at a time. They were then placed in a solution of 5 ml. of formalin, 5 ml. of proprionic acid and 90 ml. of 70% ethyl alcohol to which was added 10 ml. of commercial glycerin to every 100 ml. of solution. The proportions of this FPA solution were made up exactly as for FAA fixations, long used in the preparation of materials for sectioning. The specimens were retained in capsule jars having an approximate capacity of 50 ml. in the FPAG solution for study. The specimens were allowed to stand in this solution for a week or two before a critical examination of ventral structures was made. It was found by taking this procedure, that the specimens cleared very well. Most of the chlorenchyma tissue of the thallus turned almost white. The only color that was retained was that of the anthocyanins in the cell walls of the ventral cells of the thallus and in the cell walls of the scales themselves. Another advantage of this procedure was that upon removal of the specimens from the FPAG solution, the glycerin was retained by the thallus tissue even when the specimens were rinsed in distilled water prior to staining. The rinsing removed most the the glycerin from the ventral appendages of the thallus. Thus, when stained in Toludine blue an even higher differentiation between the ventral appendage and thallus tissue was obtained, due to the retardation of the dye penetration by the glycerin retained in the generalized thallus tissue. Of course, in such genera as Plagiochasma, Reboulia, Mannia and Targionia no staining was necessary since the scales of these genera are deeply colored by anthocyanin pigments, often blood-red in color. Even in these genera, the stain was employed to demarcate the insertions of rhizoids and the young scales lying under the scales and scale-appendages at the apex of the thallus. All the young scales are colorless and do not become impregnated with anthocyanins until they are exposed consistently to higher light intensities.

The tools of dissection, consisted of dissecting needles fashioned from "minuten" insect pins, whose tips were bent to a variety of shapes. For a little larger dissecting needle, standard insect pins were used. These were two to three times the diameter of "minuten" insect pins. One of the most useful instruments devised was a micro-scythe, heated and tempered in oil. With this, it was possible to cut away the masses of rhizoids as well as to excise the ventral scales from the ventral tissue of the thallus.

In this latter use it proved the solution of one of the problems in studying ventral scales; the problem of whether an entire scale had been removed or whether part of it had been left adhering to the ventral side of the thallus. With this micro-scythe, it was possible to remove a narrow portion of the ventral thallus tissue along with the scale so that no damage resulted from the process of removing it.

It was possible to dissect a developmental series of scales with the "minuten", dissecting down to scales only 100 microns long. Of course, in those genera with extremely membraneous scales, it was difficult to dissect a scale from the ventral surface of the thallus even with these handy dissection tools.

Once the scale was removed, it was stained in Toludine blue, rinsed in distilled water and mounted on a slide. Drawings of scales were made with the aid of a camera-lucida on a standard compound research microscope. It was impossible to keep all drawings of ventral scales to the same magnification, due to the tremendous variation in size and character of scales. Details of the smaller scales could only be shown by drawing them to a greater magnification.

Another medium used in the preparation of illustrations, was that of photomicrography. Here, a deviation from usual methods was taken. Instead of using Kodak "M" plate or 5 x 7 film, the usual emulsion prescribed for this work, 5 x 7 Kodabromide, F. No. 3 and F. No. 4 paper was used. This had several advantages and few disadvantages. A 5 x 7 negative was made using a standard Bausch and Lomb Photo-micrograph instrument. The only disadvantage was the limitation to a 5 x 7 negative, from which enlargements and reduction in size could not be made. Contact prints are readily made, however, and the presence of the paper itself proved most advantageous. In making the contact print, the diffusing properties of the paper backing to the emulsion, had an effect of eliminating small imperfections in the negative, and to some degree the effects of small bits of debris that appeared with the mounted scale. Certain advantages were also found in masking out objectionable details in the background with the Ansco dye "Coccine", manufactured by Ansco Photographic Laboratories. In this procedure, any degree of "black out" from absolute to any intensity of gray could be obtained by dilution of the dye. Another advantage lies in the low cost of the method. The use of Kodabromide projection paper is obviously much cheaper than using cut film or plate. A standard printer was used with a sheet of double-weight, opal glass over the top.

A piece of plate glass, a little larger than a 5 x 7 sheet of photographic paper, was used to empress perfect contact between the paper negative and the positive printing paper. Azo and Velox No. F2 and F3, were used in making the positive contact prints.

All material was killed in Kraft III fixative as prescribed by Sass (1940). The preparation of microscopic sections of thalli for this study, followed standard procedure according to Johansen's (1940) Safranin and Fast Green staining methods. Microtome sections of the material were especially useful in determining how consistent as to thickness the scales of the Marchantiales might be. They were of especial value in learning detail of the base and of the insertion of a scale, and the number of cells involved in its thickness. Transverse, longitudinal and parasections were made of the various thalli.

Specimens were obtained from several sources: Mr. Ronald McGregor gave and loaned specimens from his own herbarium and that of the University of Kansas. As Director of the Hepatic Exchange of the American Bryological Society, he exchanged specimens collected by the author for those from other parts of the United States and countries outside it. Dr. Rufus H. Thompson contributed specimens from time to time. Dr. Dwight M. Moore, University of Arkansas, provided several from Arkansas. The New York Botanical Garden Herbarium loaned specimens in the genera, *Sauteria*, *Corsinia*, *Peltolepis*, *Bucegia*, *Cryptomitrium* and *Marchantia chenopoda*. The author's own herbarium, largely of Arkansas and Mexican specimens was heavily drawn upon. The list of all specimens used may be found in Appendix 1.

Generally speaking the specimens studied were selected because of their availability from the several sources indicated above. Twenty-two genera have been included to provide for a reasonable coverage of genera within the order, *Marchantiales*. *Exormotheca* and *Monoclea* unobserved by the author but drawn upon from accounts in the literature, was included to round out the concept of evolution in the *Marchantiales*.

REVIEW OF THE LITERATURE

One of the earliest, definite references to ventral scales in a genus of the Marchantiales, is found in the work of John Parkinson (1640)[1]; this was in relation to

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[1]Probably one of the earliest indications, concerning ventral scales in the Marchantiales, is found in the work of Fabius Columna, Rome 1616. According to Howe (1894) this marks the beginning of the written history of three species, Conocephalus conicus, Targionia hypophylla and Pellia. Columna writes of Targionia, "In place of a flower preceding the fruit, it has on the lower part of the leaf, while it is yet small, cartilages on either side, purple, then black, set opposite to each other after the manner of ribs or valves. These you can raise with the edge of a knife. They differ from the leaf in that the latter is green." In the interpretation of this, there is question in the raising of these structures "with the edge of a knife" of his confusing the involucre as developing from ventral scales. Noting that the structures were set opposite each other, "after the manner of ribs" suggests that he might have been observing a young thallus and these structures were then undoubtedly ventral scales. The author has himself observed thalli of this species, whose ventral scales are apparently opposite on older portions of the thallus, 5 or 6 mm. from the apex. This entire interpretation may be subject to dispute.

Targionia hypophylla. He listed this species under the name Lichen petraeus minimum acaulis, "The smallest Liverwort without stalkes." Of scales, he commented "this hath certaine sad purplish skins set on both sides of the lower part of the leafe, before any flowers appear, but when the leafe groweth greater, it waxeth of a sad purplish colour like the skins."

Dumortier (1823) stated that while the ancients recognized the characteristics of various genera, and Ruppius was the founder of various generic names, in use in his time, Vailant was the first who thought the differences between thalloid and leafy Hepaticae were sufficient to divide them under two headings: he gave the name Hepatica, to the thalloids and Hepaticoides to the leafy liverworts. Later, Micheli (1729) gave the name Jungermannia to frondose or thalloid forms and that of Muscoides to the leafy forms. Next, Linnaeus (1753) revived the name Jungermannia for a genus of the leafy hepatics, but combined these and the thalloids under the heading, Algae. Further, according to Dumortier (1823), Hooker established the name Jongermannes for all Hepaticae. In this same work, the thalloids were placed under a third division, Cephalotheceae.

Dumortier himself recognized scales on the lower surface of the thalloids and pointed out their position in reference to the midrib, comparing them to the leaves of the Acrogynae. In so doing, he referred to them as phyllariums, the term proposed for the basal, medial lobes of the leaves in the Acrogynae, and drew an analogy between the ventral scales of the thalloids and these structures.

Corda (1828), as far as ventral scales were concerned referred solely to the growth of rhizoids from scales in his general discussion, did identify ventral scales on the underside of the thallus in *Corsinia*.

Lindenberg (1829) only referred to the scales of *Lunularia*, *Fimbriaria nana* and *Oxymitra*.

Mirbel (1835) was particularly concerned with the scales that cover and surround the young, developing archegoniophore, and compared them to the skin of an onion. In correspondence with Griffith, he stated that the latter observed the deep, violet scales in *Targionia*, and that they were to the left and right of the midrib, covering the base of the rhizoids. Mirbel illustrated the ventral surface of the thalli of *Marchantia polymorpha* (Plate VI, fig. 48), but only figured this surface as having marginal scales.

Taylor (1836) described the scales of *Marchantia polymorpha*, *M. paleacea*, *Preissia quadrata*, *Conocephalum conicum*, *Asterella tenella*, *A. ludwigii*, *Lunularia cruciata* and *Dumortiera hirsuta*. He illustrated in Plate XII, fig. 2 of his work, a portion of the appendiculate scale and appendage of *Marchantia chenopoda*. In Plate XIII, figures 3 and 4, he illustrated the scales of *Asterella ludwigii* and *A. nepalensis*.

Gottsche, Lindenberg and Nees (1844), referred to scales by describing the color, shape and under surface of the thallus of numerous genera.

Griffith (1849) described the scales of Marchantia as over-lapping the rhizoidal bundles and wondered about the enlargement of the scales themselves, by apical growth. He noticed their arrangement in the genus Plagiochasma. He prepared meticulous legends for plates, that do not however, appear in the volume; this is to be regretted since there are several figures specifically on scales.

Kny (1867) discovered the origin and manner of growth of ventral scales in the genus Riccia. He also regarded the thallus as a fusion of stem and leaves.

Mitten (1870) in erecting the genus Exormotheca, described the new species E. pustulosa and its ventral scales.

Dumortier (1874) indicated a recognition of scale characteristics in Plagiochasma, Clevea, Asterella, Oxymitra, and three species of Riccia.

Leitgeb (1880) dealt with the genus Dumortiera, noting that the scales eroded very quickly because of the disorganization and death of their cells. He called them lamellae and expressed the opinion that they were homologous with ventral scales. Leitgeb (1881), in a long series of researches on liverworts, described the origin and development of scales in a number of genera, doing most of his work with free-hand sections.

Lindberg (1882) published a monograph on the genera, Peltolepis, Sauteria and Clevea, noting the presence of scales in these genera.

Levier (1894) gave a very complete account of the scales of several species of Riccia; he included R. sorocarpa, R. Michelii, R. bifurca and R. nigrella, commenting upon the descriptions of Lindenberg and Nees von Esenbeck in Synopsis Hepaticarum. Levier (1894) in another work discussed in detail the scales of Riccia Henriquesii. Goebel (1898) devoted several pages to ventral scales, under the heading, Appendages. He first took up mucilage -hairs and scales, discussing these structures in both the Jungermanniaceae and the Marchantiaceae. He then took up the subject of leaves, distinguishing between these structures and scales of the Marchantiaceae. Leaves of thallose forms, now classified in the Metzgeriales series, were also discussed with numerous examples.

Solms-Laubach (1899) reviewed the genera Clevea, Sauteria and Peltolepis in relation to their distribution, stating that in all three species the scales are colorless, are provided with slime papillae sparingly, and have a certain form. He added nothing significant on ventral scales, but concerned himself primarily with scales around the carpocephalum and at the base of branches.

Stephani (1896) identified scales in the Ricciaceae as being largely protective of the reproductive organs, insisting that they were always present even if hard to find and playing a role with the rhizoids in capillarity. Again in 1900 he described all the genera and species of the *Marchantiales*, known to his time. The descriptions are detailed and meticulous but the accounts, as may be expected, differ from what is now found especially in the numerous variations of appendages. In the scope of a work of this kind, however, to describe the numerous variations of scales found in some species, is impracticable. Most interesting is his account of the scales in *Marchantia polymorpha*, though it was brief; he made note of the appendages in the genus *Marchantia* and how important they were in the taxonomy of this genus. This is emphasized by the fact that for almost every *Marchantia* species, the greater portion of the account is of the appendage.

Warnstorf (1901) published one of the few articles, specifically on ventral scales; he illustrated and described what he thought were rhizoidal-initials in ventral scales, listing a number of genera and species in which he found them.

Quelle (1902) wrote on "rhizoidal initials", criticizing or commenting upon the previously mentioned article by Warnstorf (1901); he pointed out that many of these structures termed "rhizoidal initials" were in reality, oil bodies.

Cavers (1903) in a series of articles, discussed at length the origin and development of the ventral scales in Fegatella conica, as well as giving descriptions and ecological accounts of scales in a number of other genera in the Marchantiales. Cavers (1904) in a paper on Reboulia hemisphaerica not only described the scale arrangement and the young and the mature scale, but also the function of oil bodies, their odor, the advantages of these structures to the liverworts themselves, and makes special reference to the work of Pfeffer (1874) on oil bodies in general. He also reviewed again the ecological implications of ventral scales in this species.

Schiffner (1908), in studying the structure and life history of Bucegia romanica referred to Radian's brief description of the ventral scale, and takes issue with the exact description of Muller on ventral scales. He agreed with Muller that oil bodies are missing. Schiffner (1908), writing on Grimaldia and Neesiella in Hedwigia, illustrated the ventral side of the thallus of three species of Grimaldia, accurately figuring the ventral scales of each species.

Lotsy (1909) published a tremendous volume on botanical phylogeny, in which he systematically takes up the relationships and description of plant organisms, including every phase of ventral scales. He discussed ventral scales of the Marchantiales, illustrating in some cases, genera not previously figured. One of these in particular, is the ventral scale arrangement in Plagiochasma rupestre. With regard to other genera, this work reviews the findings on scales of other authors, up to his time.

Goebel (1910), in his archegonial studies, took up the development of ventral scales in both gemmalings and mature thalli and included illustrations of a few stages.

Cavers (1911) noted that in the Ricciaceae, ventral scales are usually present but never appendiculate; he observed that in Oxymitra, the ventral scales arise in two independent series as in other genera of the Marchantiales. He also noticed the appendage of Corsinia and the scattered arrangement of the scales on the ventral surface of the thallus. For Boschia, now Funicularia, he mentioned the behavior of the ventral scales in dry periods, when they fold up over the narrow thallus. He commented briefly upon the absence of scales in Monoclea and compared the genus with other reduced forms including the genus Monoselenium.

Massalongo (1912) wrote on the Italian Ricciaceae, describing and commenting upon the ventral scales of over thirty species of Riccia, in addition to Oxymitra and Ricciocarpus. Deutsch (1912), investigating both Cyathodium and Targionia, showed that in both genera ventral scales took origin from a single, cuneate, apical cell.

Macvicar (1912), in a manual on British Hepatics, included excellent descriptions of the scales of thalloid genera found there. He also stated in his introduction, that the broad thallus in the Marchantiales is an expanded axis having lateral appendages which arise in a regular manner as leaves, "and which in reality are leaves".

Kashyap (1914) described in detail the ventral scales of little known genera, species and varieties of liverworts from the Himalayas: Aitchinsoniella, Stephensoniella, Targionia hypophylla var. integerrima, Cyathodium tuberosum, Athalamia, Plagiochasma appendiculatum and Exormotheca tuberifera. Kashyap (1929) illustrates ventral scales, enumerates their distinctive characteristics, and his meticulous and clear summary on each genus and species cited from the Panjab region, make this paper one of the most important on ventral scales in the Marchantiales.

A year later, Evans (1915) published a monograph on the North American species of Plagiochasma; in the morphological portion of this paper, he described the ventral scales, their arrangement, and the range of variation found in the appendage. One can obtain a graphic picture of variation in the ventral scales of this genus from his numerous illustrations and from his meticulous descriptions of the scales of each species which leave no doubt as to the characteristics of scales pertaining to each species.

Kashyap (1916) in further speculation on the evolutionary relationships of genera at hand, described new forms of known species and new species from the Western Himalayas and Panjab. This work included detail on the ventral scales of

Fimbriaria pathankotensis, Grimaldia indica, Sauchia spongiosa, Athalmia dioica, Riccia robusta, R. robusta, R. pathankotensis, R. himalayensis and R. sanguinea.

Massalongo (1916) though excluding the Ricciaceae in this later article, included systematic descriptions of other genera in the Marchantiales with notations on ventral scales. The chief value of this work lies in the copius illustrations of scales, and the ventral aspect of the thallus showing scale arrangement; twenty-seven plates in all thoroughly illustrate the European genera and species that he covers.

Writing on the American species of Marchantia, Evans (1917) devoted considerable space to the morphology, taxonomic description, and variation of appendages of the scales in this genus. Likewise one notes that much pertinent information on Marchantia had been gathered, analyzed and tabulated. Three years later, when reviewing and investigating the taxonomic status of Asterella in North America, Evans (1920) described in detail the range in variation in this genus and the characteristics of the ventral scales in fifteen species, and in a few doubtful species.

Casares -Gil (1919) in a comprehensive work on Spanish Hepaticae gave emphasis to the ventral scale, in discussing its role on the thallus and in frequent illustrations of note.

R. Douin (1921) compared scale development in the

Ricciaceae with that in the Marchantiaceae, but most of his paper is devoted to a severe criticism of Underwood's (1894) The Evolution of the Hepaticae.

C. Douin (1923) gave detailed notes on the activity of apical initials, especially in the species Marchantia polymorpha, Reboulia hemisphaerica and Plagiochasma rupestre. He gave a long and specific discussion of the difficulty in not being able to observe the median, non-appendaged scales in Marchantia polymorpha, which had been observed by a few previous authors. Much of his discussion of segmentation in these genera, and other genera taken up, is somewhat hard to follow. C. Douin (1925), writing on the genera Peltolepis, Lunularia and Fegatella devoted his attention to the character of the ventral scale arrangement and scale migration back on the ventral surface of the thallus, in relation to segmentation, differentiation and maturation of the gametophyte.

Herzog (1925) gave a general description of the anatomy of ventral scales in the Marchantiaceae in relation to the homology of these structures with the leaves of the Acrogynae.

Gyorrfy (1926) in one of several papers from Hungarian writers on the genus Oxymitra, suggested the ventral scales were protective in function.

Patterson (1933) in a developmental study of Dumortiera hirsuta referred to the appendage of the ventral scale as "a limb".

Pande (1933), in writing of Riccia robusta, took pains to point out the difficulty for the investigator in removing scales for study or chemical treatment, or in failing to see these structures at all.

Buch (1935) at the International Botanical Congress, set forth his ideas on the ontogeny and phylogeny of leaves and leaf-like structures in liverworts; he stated that the homology of ventral scales and leaves of the Jungermanniales apparently has no basis.

Frye and Clark (1937) largely reproducing illustrations on ventral scales from writers prior to their time, amplified in some instances, the critique or description of the scales accompanied these plates and figures.

Schiffner (1938, 1939) explored the genus Cyathodium in a monograph synonomizing many previous species; he placed little emphasis on scales, indicating their scarcity and small size.

Voth (1940) in regard to nutrient supply and photoperiodism responses in Marchantia polymorpha in which he reported that cultures, deficient in phosphorus and nitrogen, had ventral scales intensely colored, a condition which did not appear with other element deficiencies.

In a monograph by Schiffner (1942) on the genus Exormotheca, whose species were new to him, he illustrated ventral scale characters that presented a striking reduction series.

Trabut (1942), recounting the Hepatic flora of North Africa utilized ventral scale characters in a key to Riccia and Oxymitra with descriptions of ventral scales in Clevea, Plagiochasma and Fimbriaria.

Grout (1947) added, to his Mosses With a Handlens, a section on Hepaticae utilizing the same method of ventral scale characters in keys, notably on Riccia, and suggested these structures be used as part of the recognition tools for other genera in the field.

Pande and Bhardwaj (1949) in further studies in Indian Hepaticae, described ventral scales as well as illustrating them in Conocephalum supradecompositum.

The latest edition of Rabenhorst's Krytogamen Flora on the liverworts of Europe by Muller (1952) presents a well organized tabulation and accounting of scale information on the many species covered.

Finally, in addition to Pande, Shrivastava and Khan's (1953) study on Asterella Khasiana, there is Schuster's (1953) work that offers the ecological implications of scales, noted in his discussion of the ecology of species occurring in Minnesota and adjacent regions.

In considering the evolutionary aspect of this work, and the literature on this phase of Hepaticology, it seemed advisable to list the principle works of this nature, and these chief exponents of the regressive and progressive evolutionary theories, apart from the general literature on ventral scales per se. Substantial contributions on evolution have been made by Leitgeb (1878), Underwood (1894), Wettstein (1903, 1908), Bower (1908, 1935), Goebel (1900, 1930), Cavers (1911), Kashyap (1914, 1919), Church (1919), Fritsch (1935), Chamberlain (1935), Campbell (1936), Eames (1936), Evans (1936), Frye and Clark (1937), Smith (1938), Chadefaud (1940), Burgeff (1943), Berry (1945), Mahabale and Bhate (1945), Castle (1946), Fulford (1948) and Jovet-Ast (1950). Some of the most prominent advocators of the progressive theory are Bower (1908, 1935), Campbell (1936), Frye and Clark (1937) and Smith (1938). The individual, most strongly advocating the regressive theory, recognizing wholesale reduction in liverworts, was Goebel (1910, 1930). Kashyap (1914, 1919), Church (1919), Evans (1939) and Castle (1946) also contribute much, while modifying the trend in certain ways, toward this idea.

CLASSIFICATION AND TERMINOLOGY APPLIED TO VENTRAL SCALES IN THE MARCHANTIALES

Ventral scales, occurring on the lower surface of the thalloid forms, are not all alike, as has been noted many times in the literature. The most striking kind of scale, especially in the more primitive genera such as Marchantia, Preissia or Bucegia, is the median appendiculate scale. (Plate IV, figs. 7, 8; Plate V, fig. 1; Plate I, Plate XI, fig. 4). The other type that is almost never median, except in some species in the section Ricciella of the genus Riccia, is the laminar scale which is devoid of an appendage. (Plate V, figs. 2, 3; Plate XVII, fig. 4). Appendiculate scales can be further classified as euappendaged and pseudoappendaged scales. (Plates I and II). Examples of the former can be found in the genera Marchantia, Preissia, Bucegia, Targionia, Conocephalum, Dumortiera, Lunularia, Asterella, Plagiochasma, Mannia, Monoselenium, Exormotheca, Reboulia, Wiesnerella, Peltolepis, Cryptomitrium and Corsinia. The pseudoappendaged scales are principally found in Oxymitra, Sauteria, Clevea, and Exormotheca. Laminar scales are present in Riccia, Ricciocarpus, Preissia, Bucegia and Marchantia. Because of their extremely reduced nature, two additional types of scales can also be designated. These are the filamentous and plate-type, as found in the genus Cyathodium. The last type to be considered, if one adheres to the homology of apical slime papillae with the ventral scale, is the slime, papillate hair, found in the genus Monoclea.

In the terminology applied to ventral scales and their parts the appendiculate scale has long been regarded as having two principle subdivisions. These are the appendage and the laminar portion. The author's proposal here involves three subdivisions as follows: (1) the appendage that is attached to the anterior margin of the scale; (2) the lamina which is the broad portion of the scale, arching away from the median axis of the midrib region, whose posterior margin is often two cells thick, and is inserted on both the midrib and the wing of the thallus; (3) that which the author has chosen to term the "eperon". The eperon can be defined as that portion of the scale, which is most posterior, acute to acuminate in form, and which forms an attenuated or short process of the scale. In the genus Oxymitra, the insertion of the lamina is almost parallel to the median linear axis of the thallus, having been rotated 90 degrees so that it is no longer more or less perpendicular to this axis, as is true in most other genera. The eperon, therefore, is the most anterior portion of the scale in reference to the apical region of the thallus in this genus as can be seen in Plate XVII, figure 1. The author feels justified in adding the term eperon to the terminology pertaining to scales for the following reasons:

(1) the cells in this region of the scale in many genera, are of a different form than in the lamina; (2) the eperon itself, is very distinct in form in many scales; (3) with the one exception, Oxymitra, it is always directed posteriorally; (4) when schizogenous splitting of the scale occurs, this process is often restricted to just the eperon - Cryptomitrium, Oxymitra and Corsinia; (5) it is most distinct and expanded, and has even been interpreted as a separate median scale in the species, Marchantia polymorpha, Massalongo (1916), Muller (1905), Frye and Clark (1937); (6) it is just as applicable a term as many others used in the literature, for parts of organs or of plants that merge into each other.

The word "eperon" in French means spur. It was chosen over certain Latin terms that seemed more cumbersome. In many scales, the eperon can be distinguished from the laminar portion, by its extremely long and narrow cells, compared to much shorter cells of rectangular form in the latter. Appendiculate as well as laminar scales possess eperons and in some genera, in both types of scales, it may be entirely absent. The total absence of this structure can be found in some species of Mannia, Exormotheca, Sauteria, Ricciocarpus, Wiesnerella, Cyathodium and Monoclea. Ventral scales may be extremely delicate and membraneous, hyaline, translucent or highly colored to black; they may be tough and very resistent to erosion or brittle; they may possess a heavy, waxey cuticulum; they may be closely imbricated or distantly inserted. The range of insertion--pattern variation can be noted in the Plates of this work, and be found to occur completely across the ventral surface of the thallus, or restricted to the marginal or axial region of the midrib.

SCALE DEVELOPMENT

In order to secure a better knowledge of scale development, the dissection method, cited above, was adopted in addition to the sectioning of thalli. Many accounts in the literature deal with observations of thallus sections for this phase of study of ventral scales.

Gottsche (1866) described the structure of young and old scales and their general nature in Clevea and Sauteria, but mentioned little concerning development. Kny (1867) discovered the origin and manner of development of ventral scales in the Ricciaceae. Leitgeb (1879) showed that the walls separating air chambers in the genus Ricciocarpus were homologous to ventral scales in their origin and development. He also noted that the numerous scales, in alternating rows in the aquatic form, originate independently of each other, and possess a long and continued basal growth. Leitgeb (1881) also discussed and illustrated some of the stages in the ontogeny of the ventral scale for Reboulia, Conocephalum, Lunularia, Preissia, Dumortiera, Targionia, and Cyathodium. He described at length the ventral scales of Marchantia polymorpha and reiterated Taylor's (1836) differentiation of three types of scales in this species. Leitgeb's work was by far the most important to this time on this phase of ventral scales. Solms-Laubach (1899) when reviewing the literature found few papers dealing with ventral scales specifically. He discussed and compared the origin of scales in three genera namely: Sauteria, Peltolepis and Clevea. He compared the structure of the mature scales, their color, and their arrangement on the ventral surface of the thallus. Cavers' (1903) work on Fegatella conica stands out as one of the more complete investigations on the development of the appendiculate scale in this species. Bolleter (1905) described the development of the ventral scale in the same species but was mainly concerned with the mature scale. He completely ignored Cavers' (1903) paper on Fegatella conica. Schiffner (1908) criticized Radian (1903) and Muller (1905) for their brief accounts on the scales of the genus Bucegia, but added little information concerning the development of the ventral scale. Pietsch (1911) reviewed Leitgeb's (1879) work on the origin of various structures of the thallus, and ventral thallus appendages in the genus Riccia. He used modern microtechnical methods and found that Leitgeb's (1879) contentions about the morphological development of ventral scales and air chambers, were correct. He illustrated and discussed the origin of the two latter structures with precision.

A continued search of the literature yielded little concerning the overall development of ventral scales versus the comparative morphological origin of their principal parts or subdivisions. This was also true in regard to elongation, enlargement and maturation of these subdivisions.

The development of appendiculate ventral scales can be outlined in the following manner: (1) the origin of the scale; (2) the development and maturation of the appendage; (3) the development and maturation of the lamina of the scale; (4) the development and maturation of the eperon.

The first point above, can be further divided into three principle origins of scales: (1) origin by means of a primary slime papilla or unicellular slime hair; (2) origin by a primary papillate cell of the meristematic ventral epidermis of the thallus; (3) origin by a transverse row of papillate cells whose lateral walls are in contact with each other as in the genus Riccia.

For a critical review of the development of an appendiculate ventral scale, involving a slime papilla in its origin, the species Preissia quadrata was selected. The appendiculate median scale, here, has a single appendage, and therefore little confusion arises in distinguishing the linear series of successively older scales from the two alternating series of laminar scales that have no appendage. The laminar scales remain consistently smaller in size in this developmental series, until the appendages of the median scales are well on their way toward maturity. The laminar scales then elongate, enlarge and mature at a fairly rapid rate concurrently with the general enlargement and maturation of the lamina of the appendiculate scales.

The origin of the appendiculate scale in Preissia quadrata is usually initiated by the enlargement of a secondary segment or derivative cut off from a single, cuneate, apical cell Haupt (1926). This type of apical cell was also observed in sections prepared by the author but Cavers (1904) contended that a row of initials occupied the youngest apical portion of the thallus. The meristematic epidermal cell or scale initial, enlarges, producing quantities of slime at the base of the apical notch of the thallus. It attains a length of 40 to 50 microns, before an anticlinal division takes place in the basal portion. Successive anticlinal divisions occur in the basal cell and its subsequent daughter cells, to form a filamentous, slime-hair, primordial scale. Several oblique periclinal and parallel periclinal divisions next occur in all the cells of this filament except the apical two or three cells. This stage marks the morphological origin of the oblique lamina of the scale. When this area of the scale consists of 25 or more cells, one or two oblique divisions occur in the cell at the base of the apical slime papilla. These divisions result in the apical slime papilla being tilted to one side. Subsequent anticlinal divisions produce a filamentous appendage consisting of 5-12 cells. Plate I, figure 1. shows a young scale at the stage prior to the development of the filamentous appendage but minus the primary slime papilla. The author found it almost impossible to dissect the scale intact at this stage of development, without dislodging the primary slime papilla from its insertion. Plate I, figure 2. shows an appendage at the seven celled stage with a periclinal division having already occurred in the basal cell of the appendage. Also, behind the base of this appendage, there can be seen the large, off-set, primary slime papilla in a vertical position. One can also note in this figure, that the lamina of the scale consists of quite a number of cells with slime papillae already developing on its margin. Figure 3. of the same Plate depicts the further increase in size of the lamina, due primarily to additional cellular divisions, and an increase in the number of cells of the filamentous appendage. Figure 4. presents an interesting picture of the marginal slime papillae. Here, they are filamentous in nature and as far as the author could determine, they were gradually eroded down to the basal cell which is then transformed into a globular slime papilla that persists in the mature scale. In other words, the terminal cell of the hair-like slime filament functions as a slime cell for a time, becomes non-functional, and erodes away. The next cell in the filament then develops into a globose slime cell, functions as such for a while and erodes. This continues in basipetal succession. Another feature of figure 4, is the presence of a "split appendage". These were noticed from time to time, on mature scales and one is also shown in a much older scale in figure 7. The actual age or size of the scale when this division of the appendage takes place was not clearly determined by the author, but it apparently takes place early in the ontogency of the scale and remains "split" to maturity. In figure 5, it can be seen that by far the greatest number of periclinal divisions in the appendage occur in its first three or four basal cells. The apical two or three cells are devoid of periclinal walls, as is also evident in figure 6. In these two figures, the appendage almost equals the lamina in size, but the cells of these two structures are distinctly far apart, as far as the ontogeny of the individual cell is concerned. The lamina still consists almost entirely of meristematic cells while few if any additional cellular divisions will occur in the appendage. In fact, figure 6 typifies the scale as it appears just before the appendage emerges from the apical notch of the thallus by the rapidly elongating cells of the ventral surface along the developing midrib region. In the mature scale, (Plate I, figure 8.) the appendage has already started eroding as have many of the slime papillae on its margins. This scale was dissected off the ventral side of the thallus about 6mm. from the apical notch. All scales more posterior to this one showed a varying degree of erosion of both the appendage and the lamina of the scale. The eperon of the scale is the last part of the scale to become eroded and this is due in part to the fact that it is the last portion of the scale to mature. One consistent factor concerning erosion of scales, that could be observed many times, was the strong resistance to erosion of meristematic scales or parts. This may be due in part to the high production in and around the meristematic area, of mucous or slime. The excessiveness of the slime made it extremely difficult in many cases to prepare scales for staining and dissection.

The eperon of the scale usually can be clearly distinguished at the median end of the lamina and in Plate II, figure 5, can be seen to be developing its typical attenuation. The eperon and the basal cells of the lamina proper, are the last areas of the scale to enlarge and mature. Maturation of the entire scale proceeds from the apex of the appendage basipetally through the lamina, then changes direction and proceeds from the anterior lateral and basal portion of the almina to the most posterior and medial portion of the eperon.

The mature scale of Preissia quadrata is quite a vividly colored structure especially in those thalli found in the most xeric situations that the species can tolerate. This color, a brilliant blood-red is confined to the cell walls of the scale. The slime papillae on the margin of the scale are quite distant, but often occur as scattered pairs. On young, rapidly growing dichotomies of the thallus, the appendiculate scale has an exceedingly large lamina. This is especially noticeable in comparing the size of such laminae

Plate I

The Development of the Appendiculate Ventral Scale of *Preissia quadrata*

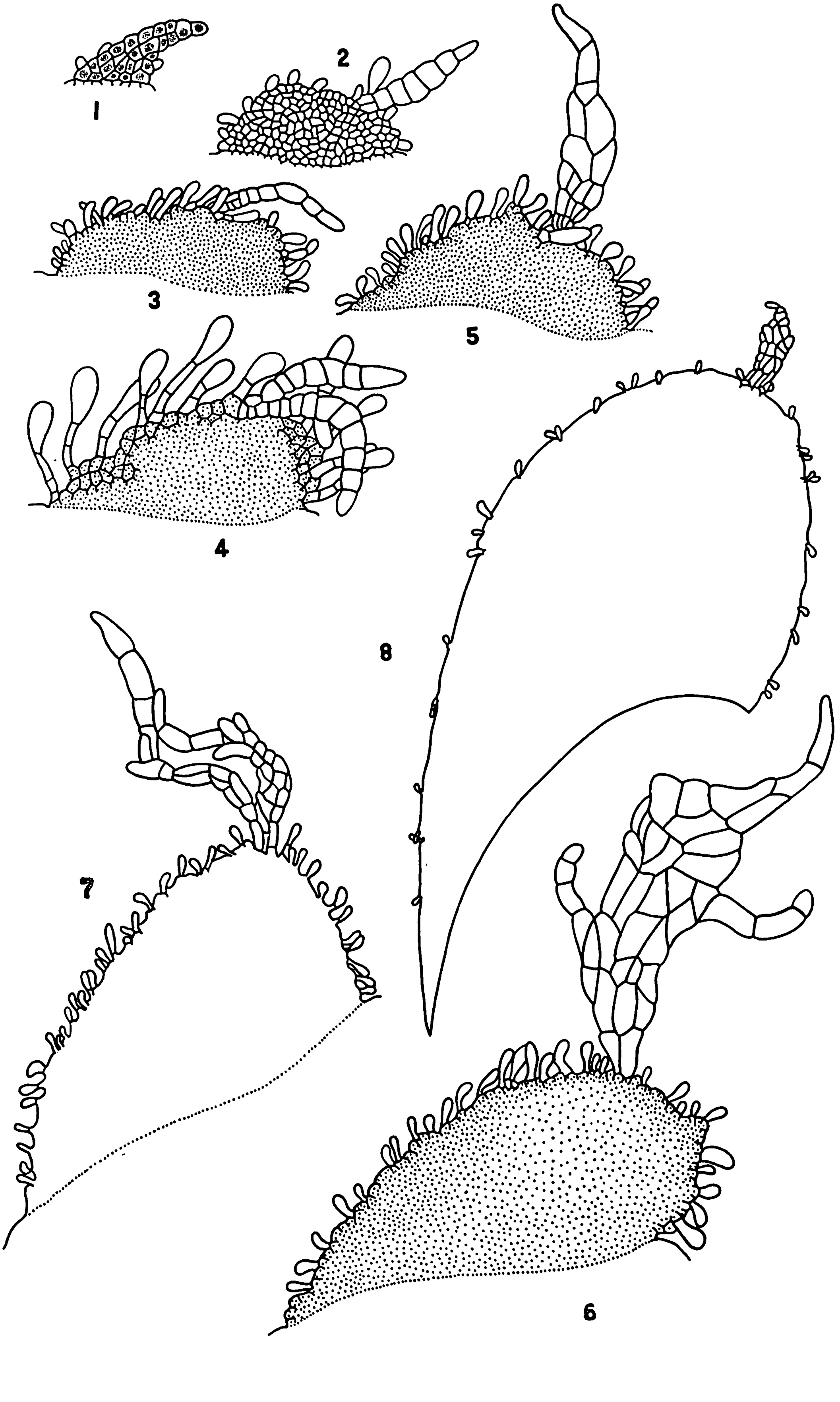
Fig. 1, Young appendiculate scale with lamina starting to broaden, X 443.

Fig. 2, Young appendiculate scale with a filamentous appendage and initial slime papilla at its base, X 224.

Figs. 3-4, Two older ventral scales, X 224.

Figs. 5-7, Three older scales showing the enlargement of the appendage and maturation of this structure, X 142.

Fig. 8, The mature ventral scale, X 25.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with those of scales on the older portion of a thallus that were produced at the end of the last favorable growing season. This is also true of the laminar scales studied in the various species noted earlier.

The second method, the development of an appendiculate scale not involving an initial slime papilla, is essentially the same as in the foregoing discussion. An example of this type of development is found in Targionia hypophylla. The primary, papillate, meristematic, epidermal cell, according to Campbell (1929) persists at the apex throughout the development of the scale. In his discussion of the two different origins of appendiculate scales, he does not differentiate between an initial slime papilla and an initial papillate cell. In Targionia, oblique cell divisions do not take place in the basal cell, for a time, below the persistent apical cell or primary papillate cell. Instead a series of successive anticlinal divisions results in a young filamentous appendage. Later cellular divisions follow essentially the same pattern as described for Preissia quadrata.

In concluding the discussion on the development of appendiculate, ventral scales, it might be well to point out that Cavers' (1903) interpretation, that the appendage of the scale originated and developed first, was most likely the result of a technique used in dissection. At least, this is the impression the reader secures when Cavers' account of the development of the scale in Fegatella conica is analyzed. The author found in dissecting and working a mass of meristematic tissue, cut out from around the apical cell, that it was necessary to roll this tissue back and forth under the cover slip, and then apply pressure just at the right moment in order to manipulate the appendage and the lamina of a scale into a horizontal plane beneath the cover slip. As has been noted in the account of the ventral appendiculate scale of Preissia quadrata, the development of the appendage and the lamina of the scale is concurrent, a fact that becomes obvious when the entire early ontogeny of the scale can be observed. Goebel (1908) said that the mature appendages overlap each other in the apical notch of the thallus like the leaves in a book. It can be said also that the transparent meristematic, laminae overlap in the same manner and appear to be merely part of the apical meristematic thallus tissue, even after being stained with Toludine blue. In fact, this is about the only disadvantage in using this dye, for its affinity toward meristematic tissue is extremely high. Another interesting and very useful fact concerning the marginal slime papillae was learned in this study. They can be used as an indicator of the relative development of the lamina of appendiculate scales. As can be seen in Plate I, figures 3, 4, 5, 6 and 7, the younger the scale, the closer and more numerous the slime papillae on its margin. When maturation begins, however, and the cells of the lamina begin to lose their isodiametric form, and enlargement proceeds toward maturity, the slime papillae become quite distant, even before much erosion of them has taken place. Figure 8 of a mature scale shows the result of both the enlargement of cells of the lamina and erosion of marginal slime papillae.

Oxymitra paleacea was selected for the development of a ventral scale that is not truly appendiculate, as it is frequently termed in the literature, or for what might be termed a pseudoappendaged scale (Plate II). It was found in this type of scale that the apical portion develops in all essential features like an appendage. In other words, the apical portion is homologous to the appendage in the appendiculate scale. As can be seen in Figure 1, this scale is initiated by a papillate cell that is cut off early from an epidermal derivative after a minimum amount of enlargement of the derivative. The epidermal derivatives here are cut off from a single, cuneate, apical cell of the thallus, and from its ventral face. The first division of this papilla is anticlinal (Plate II, figure 2). The young scale develops first into a uniseriate then into a biseriate filamentous structure. In Figures 3 and 4, two aspects of this young scale are shown, each illustration in both figures, representing a rotation of ninety degrees in relation to the other. Figure 5 shows the young scale developing a very definite lamina and represents the maximum development of the lamina of all scales observed at this stage. The apical cell remains undivided throughout the development of the scale, but the cell just beneath it and its derivatives, give rise to the portion of the scale corresponding to a true appendage.

As growth proceeds, the portion of the scale homologous to an appendage soon consists of mature cells about equal in area to the meristematic laminal portion. Also, as in truly appendiculate scales, the progressive maturation and dying of cells is initiated at the apex of the pseudo-appendage. Maturation proceeds basipetally and finally proceeds through the eperon of the scale. The eperon of the scale here is very narrow and composed of isodiametric cells. Those at the base of the eperon, remain capable of division for a long time. The eperon continually cuts off fragments until most of the laminar portion of the scale consists of hardly a living cell. These fragments begin to be cut off just after the first general enlargement of laminar portion takes place. Most of such fragments contain one or two rows of meristematic cells at their bases, which continue to enlarge the fragment as it is displaced across the ventral surface of the thallus toward the median axis (Plate II, figures 14 and 15) (Plate XVII, figure 1). As an indication of the gradual increase in number of eperon segments cut off at the apical end of the thallus to older portions on the ventral side of the thallus, a triangular area, devoid of

Plate II

The Development of the Ventral Scale

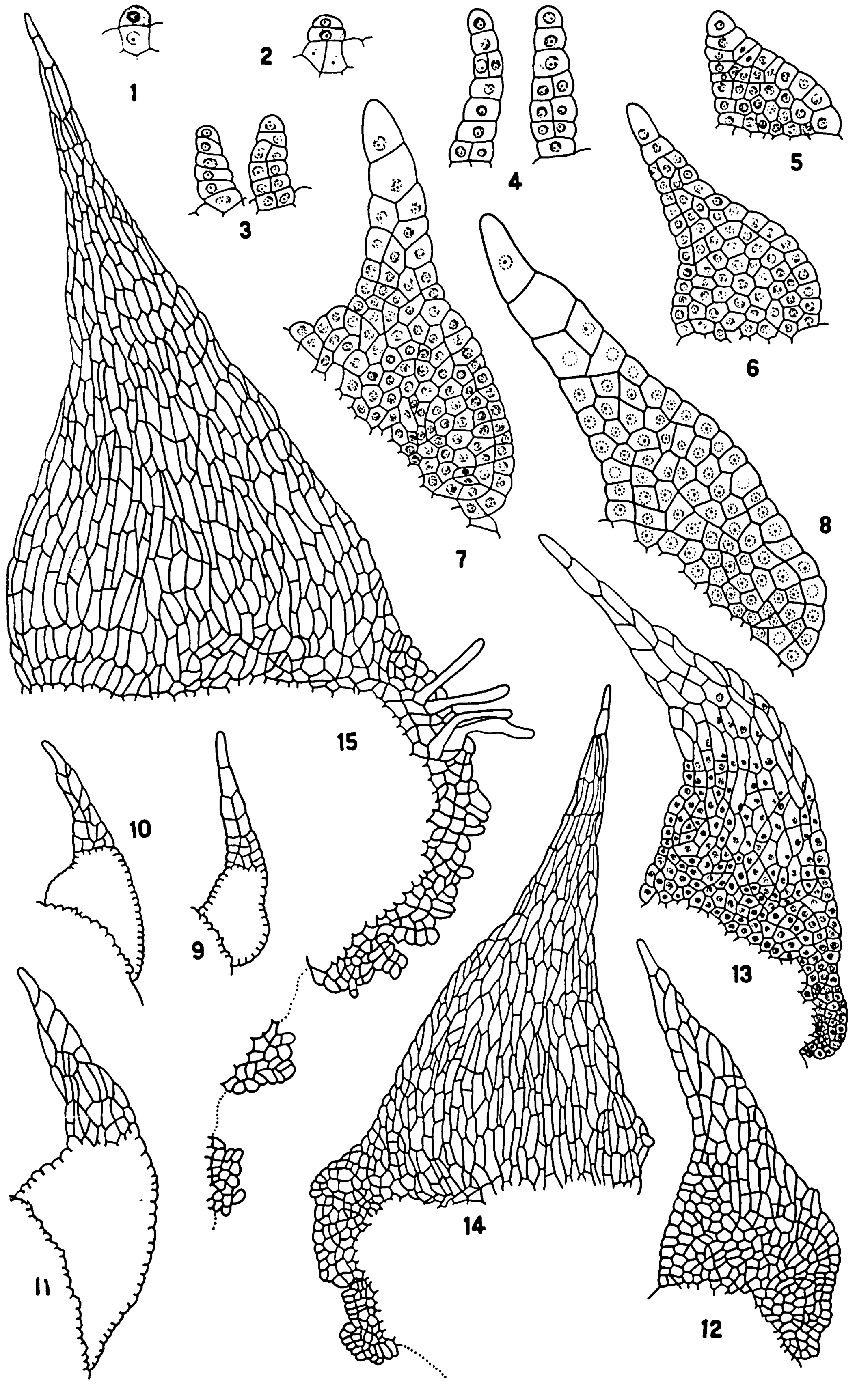
of <u>Oxymitra paleacea</u>

Figs. 1-8, Early stages in the development of the ventral scale and differeniation of the appendiculate apical portion of the scale, X 231.

Figs. 9-13, Stages in development of the ventral scale showing maturation of the appendiculate portion of the scale and differeniation of the eperon, X 82.

Fig. 14, Nearly mature ventral scale showing a fragment being cut off from the eperon, X 39.

Fig. 15, Mature ventral scale showing the long eperon with two fragments cut off from the eperon, X 51.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eperon fragments, can be noted in Plate XVII, figure 1, of the insertion pattern in this species. To the knowledge of the author, no descriptions of the development of this type of scale exists in the literature, for any species of liverwort.

The meristematic and schizogenous activities of the eperon in Oxymitra paleacea are interesting by the fact they are not common to this genus alone, but also occur in several of the genera which have been described in the literature as having a scattered scale arrangement. These two processes are primarily responsible for a scattered scale arrangement as has been noted above, in the enumeration of genera studied.

The third type of scale origin gives rise to a shield-shaped scale and scoop-like in structure. Papillae originate from secondary segments derived from a row of apical initials of the thallus. Their vertical cell walls do not separate from each other and together they give rise to a median ventral scale. The scale enlarges by cell divisions in all directions horizontally and by continued meristematic activity of cells in the basal portion of the lamina. During growth, the scale may split into, the two half-scales, being displaced by enlargement of the thallus forming two rows on each side of the longitudinal axis of the thallus as in Riccia lamellosa (Plate XVII, fig. 6). The ventral scale may remain intact and be displaced along the median line of the thallus and retain its shield-shape form as in *Riccia rhenana* (Plate XVII, figures 3 and 4).

ANALYSIS OF RECORDED DATA ON VENTRAL SCALES STUDIED

This section comprises the author's new findings on, and a critique of some previous records of, the ventral scales in those genera and species under study. According to their effectiveness, these data from sources other than our own are either interpolated into the discussion or summarized. Some of the findings at variance with those described in the literature are due in part to the techniques applied. Illustrations of the ventral aspect of the thallus in the plates may not necessarily always represent typical variations in species. For emphasis and clarity, some figures portray extremes in ventral scale arrangement and characteristics.

I. *Marchantia* *polymorpha* L.

The thalli selected for this species came rather close to *M. polymorpha*, var. *alpestris* and var. *aquatica*. These were from almost xeric to mesic situations at 10,000 feet; mesic and aquatic situations just above and below 4,000 feet, and aquatic and mesic situations below 1,000 feet. The ventral surface of the thallus of those specimens corresponding to var. *alpestris*, was small in area compared to the number of scales present; that is, there was a much greater number of scales for the area, than for any of the other forms. Those specimens typifying var. *aquatica* possessed much fewer scales for the ventral surface area.

Marchantia polymorpha is illustrated in Plate III, fig. 1 and M. polymorpha var. aquatica in Figure 2 of the same plate. Here one can see that the scale arrangement on the ventral surface of the thallus is exactly the same. The only difference to be seen in these Figures is that M. polymorpha typica has much more robust scales and more closely imbricated ones. The configuration of scales drawn for var. aquatica was typical for specimens found growing in situations almost completely aquatic in nature, or with a continuous year-round flow of water. The M. polymorpha illustrations typify the thalli growing in moist situations but with an intermittent water supply. Of course, in M. polymorpha var. aquatica thalli the scale arrangement was easily observed because of their distant placement and few rhizoids had to be removed before this arrangement could be observed. This was not the case in M. polymorpha var. alpestris as the rhizoids usually completely obscured the arrangement. Most of these rhizoids had to be entirely removed, or in the case of M. polymorpha var. alpestris the apical portion of the scale had to be cut away with scissors before the insertion pattern was revealed.

On M. polymorpha the appendages took five forms, falling into two general outlines, cordate and orbiculate. The latter form had a crenate finely dentate margin; the cordate form had a crenate, finely-dentate to a very coarse dentate, to almost a serrate margin. In some collections containing more than one plant from the same restricted area, four of the five types of appendage were found. In M. polymorpha var. aquatica all of these types were to be seen, and in addition, a sixth one that was orbicular in form with an entire margin. The marginal cells of this type of appendage had their longitudinal axes oriented here and there parallel to the margin of the scale, while in all other forms of the appendage, the longitudinal axes of the marginal cells were perpendicular to the margin of the scale. The entire-margined appendages had very thin walls, were usually light in color, and membraneous. The eperons were usually poorly developed and very light in color. Laminar scales were long and attenuated, but retained, in the rows other than the marginal row, the typical anterior notch of the lamina. Marginal scales were few in number compared to those in M. polymorpha and M. polymorpha var. alpestris. In In M. polymorpha var. aquatica, appendiculate scales frequently attained a length of 7-8 mm., such as are figured in Plate IV, fig. 7.

In the particular thallus from which this scale was dissected, the eperon happened to be darkly pigmented. The dark portion of the scale at the base of the lamina, is that portion of the lamina that is 2-3 cells thick. This scale was removed from the thallus about 2 cm. posterior to the apical region of the thallus. The rhizoidal bundle, compared to that in the two varieties, was usually rather loose in organization, and contained many fewer rhizoids. Another feature observed in this species and its two varieties, was that the insertion of the laminar scales gradually decreased in length from that of the median ones toward the marginal ones, which have the shortest insertions. The marginal scales on all thalli observed, appeared, at first, to have transverse insertions, but this was entirely due to pigmentation of the scale itself. As can be seen in Plate IV, figs. 1 and 2, a basal triangular portion is almost colorless, and the insertion of these scales is oblique as is that of all the other laminar scales. All the laminar scales including the marginal ones, have tuberculate rhizoids arising from the broader portions of the lamina. The eperon is destitute of rhizoids in all cases. In all scales, including the appendiculate, numerous tuberculate rhizoids arise at the base of the scale, from thallus tissue underneath the ventral scale. The eperon in all thalli of this species was observed to be less pigmented in the more aquatic habitats and progressively darker in the xeric to mesic habitats. This darkly pigmented eperon of the appendiculate scale has led investigators in the past, such as Muller (1905), Massalongo (1916) and Frye and Clark (1937), to describe it as a separate median scale. The eperon is actually expanded, and at its widest point, wider than some portions of the lamina of the scale.

Bischoff (1835) remarked upon the descriptions and illustrations of Schmidel and Micheli on ventral scales; marginal on male and female plants of this species, and he himself outlined intramarginal scales on living material; the scales were said to be irregular, often prominent beyond the margin. He noted further that Martius (1817) had found them at the margin of the frons in *M. polymorpha* var. *domestica*. Based on the insertion of the scales themselves, 12 rows were found alternating with each other. This is at variance with findings in the literature. Goebel (1898), Stephani (1900), Massalongo (1916), Evans (1917) and Macvicar (1926), to mention a few, designated three rows of scales on one half of the ventral surface of the thallus. Frye and Clark (1937) designated 6 or more rows, but it is hard to make certain if they intended 6 or more rows over the entire surface of the thallus, or merely a half of it. Kashyap (1929) stated that in the genus *Marchantia*, scales were in 2 or 3 rows on each side of the midrib, inner ones (median) large appendiculate; middle (laminar) without appendage, small, more or less ligulate; outer ones (marginal) near the margin, without appendage, small and more or less ligulate. Tuberculate rhizoids are given off from the surface of all the scales in addition to those arising in strands from the midrib. These 12 rows found by the author, are somewhat regularly arranged in rows parallel to the longitudinal axis of the thallus. Plate III, figs. 1 and 2, illustrating one half of the ventral surface of the thallus of M. polymorpha and M. polymorpha var. aquatica respectively, shows 6 rows of scales, each scale being numbered to show its relation to a given row. If we designate as No. 1 the marginal scales and proceed medianly toward the midrib, the appendiculate scale is the 6th scale. It can be observed from these figures, that No. 5 laminar scale is always found with its eperon extending medianly between the appendiculate scales. Just above or below the No. 5 laminar scale, the attenuated lamina of No. 3 scale can be seen to be just lateral to and sometimes extending medianly past the lateral margin of No. 5 scale. Likewise for scale No. 4, the posterior portion of the eperon is very near to the apical end of the appendiculate scale, almost in line with the insertion of the appendiculate scale. Laterally beyond the lateral margin of scale No. 4, and a little more irregular in position, can be found a No. 2 scale. The No. 3 scales, while they may be more or less in line and lateral to No. 5 scale, can also be seen alternating with No. 4 and No. 5 scale. The No. 1 scales, appearing alternately with No. 2 scales in M. polymorpha typica, seemed to be in pairs on some thalli but when their insertions are analyzed, they are usually found to be just lateral in most cases to the lateral margin of a No. 3 scale.

Toward the apex of the thallus, where the lamina of the ventral scale is still in the meristematic condition, the young laminar scales can be seen between the large

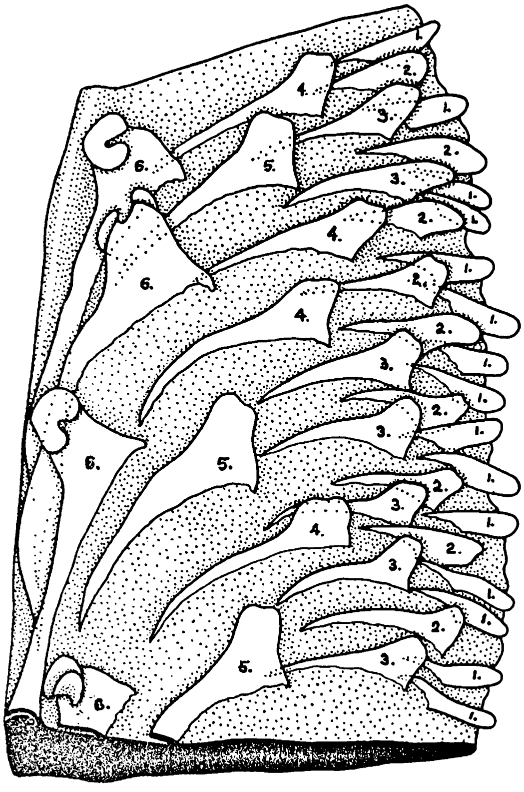
Plate III

Fig. 1, Ventral surface of the thallus of *Marchantia polymorpha* showing the ventral scale arrangement, X 13.

Fig. 2, Ventral surface of the thallus of *Marchantia polymorpha* var. *aquatica* showing ventral scale arrangement, X 13.

Fig. 3, Ventral aspect of the *Marchantia paleacea*, X 13.

Fig. 4, Ventral aspect of the thallus of *Marchantia domingensis*, X 13.



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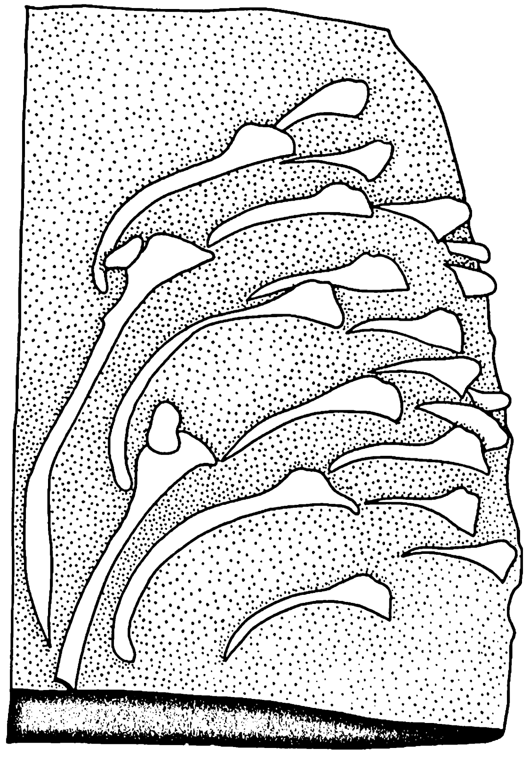

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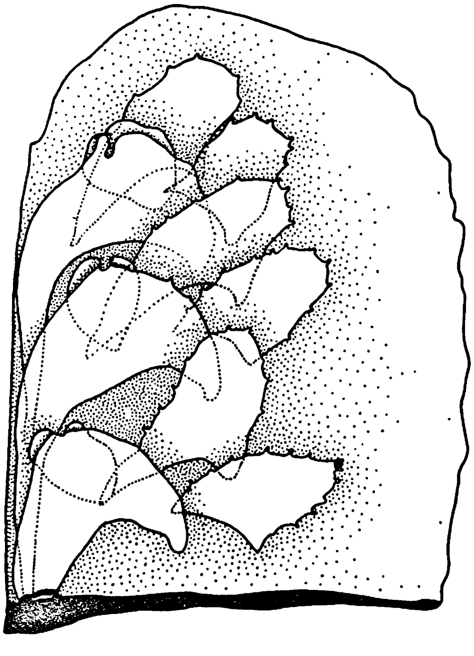

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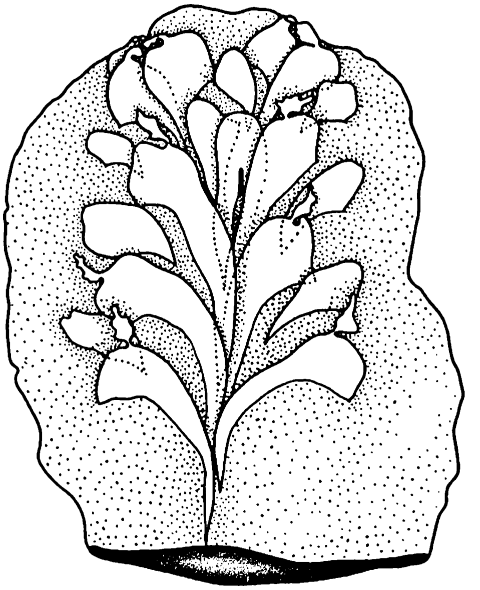

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meristematic laminae of the appendiculate scale. This is especially true at this stage of development when the appendages of the appendiculate scales have not yet emerged from the apical notch. As was also observed by Burgeff (1943), these laminar scales are separate and do not adhere together, nor are their insertions in line with each other. As the ventral surface of the thallus elongates and matures, these developing laminar scales are gradually displaced backwards and laterally from the apex of the thallus, and out from between the laminae of the appendiculate scales, as has already been noted in Plate III, figs. 1 and 2. The only scale or portions thereof remaining between the appendiculate scales is the No. 5 laminar scale. This is to be expected since, from the observations of meristematic scales at the apex of the thallus, one sees that the No. 5 scale is located most medial of all laminar scales.

All scales on the ventral side of the thallus possess oil bodies. This is true of the appendage as well as of the lamina of the scale. Usually the eperon was found destitute of oil bodies. On the whole one might expect to find more oil bodies in both the appendages and scales of thalli growing in habitats near-xeric for the species. In general fewer oil bodies were found in the appendages in the latter situation, a much greater number in the appendages from mesic habitats. On the other hand, a profusion of oil bodies were found in the laminae from all habitats. Slime papillae on the margins of the scale was general throughout, near-xeric forms in many cases revealing a greater number. In Plate VIII, fig. 11, for M. polymorpha and its two major varieties, is illustrated a typical meristematic laminar scale on whose margin can be seen many large and robust slime papillae. The slime flux in the apical notch of the thallus was considerable in amount, with numerous bacteria, fungi and other organisms living within it. The slime papillae on young appendiculate scales were also just as large and profuse. This slime flux serves not only in the retention of moisture around the meristematic region of the thallus, but also protects the developing scales from erosion. One of the greatest difficulties of this study was the elimination of this slime flux in the dissection of young scales. As long as much of it remained adhering to the scales it was very hard to stain the scale properly with Toludine blue.

With regard to appendages, the orbicular, thin-walled, entire-margined appendage illustrated in Plate IV, fig. 9, was found only in the aquatic habitat. The cordate appendage in figs. 12 and 13 of the same plate, was found in the aquatic habitat but is regarded by the author to be essentially the same type of appendage as the cordate-dentate or coarsely toothed appendage, found in all other habitats. The basis for this assumption is that on the margin of the appendage, in regular succession, were situated, long, delicate, papillae-like teeth composed of one cell, usually spaced 4 cells apart. Figure 10 of Plate IV represents the orbiculate appendage with the crenate margin, Figure 11 the finely dentate; orbicular appendage and Figure 15, an appendage of the same form partially dentate. Figure 14 illustrates a coarsely-toothed, cordate appendage that is typical of thalli growing at high altitudes, and at lower altitudes other than aquatic habitats. The margin gives in many instances the appearance of distinct serrations.

As has been noted above, Figs. 1 and 2 represent marginal laminar scales, and Figs. 3, 4, 5 and 6 are photomicrographs of No. 2, No. 3, No. 4, and No. 5 laminar scales as numbered in Plate III, figs. 1 and 2. In other words, in Plate IV, fig. 6 there is a No. 5 scale that is the most proximal scale to the median appendiculate scale, on the ventral surface of the thallus.

Burgeff's (1943) account is very clear on the origin of the appendiculate scale in this species, with regard to segments cut off from the apical cell, but is vague as regards the exact time that the scale initial arises from the derivatives of the apical cell. From the author's observations and microscopic sections, it appears that the apical slime papillae of the appendiculate scale arises from one of the derivatives twice removed from the apical cell. An anticlinal division in the base of this slime papilla separates it from the thallus tissue derivative of

Plate IV

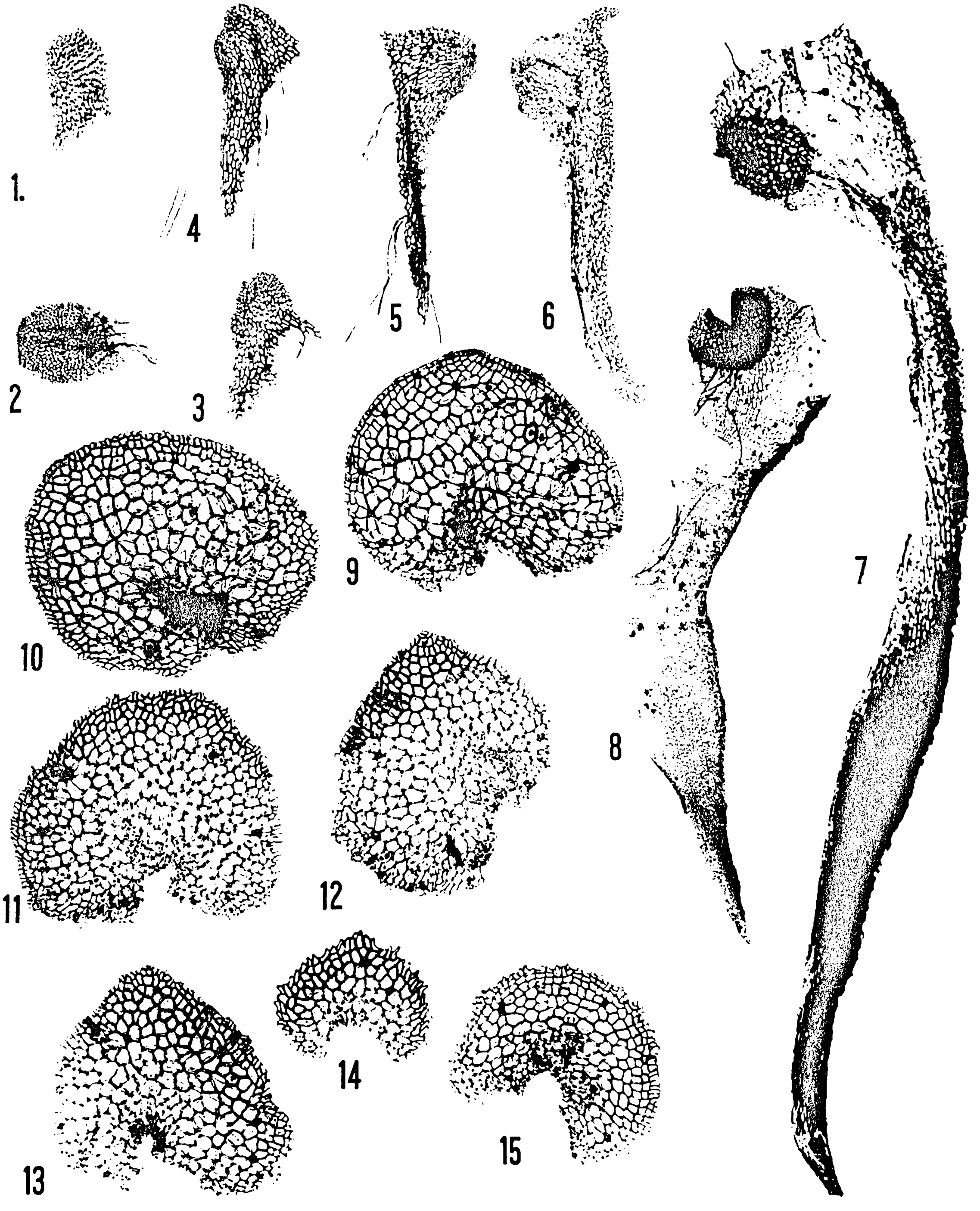
Photomicrographs of the ventral scales
and types of appendages found in
Marchantia polymorpha

Figs. 1-2, Marginal laminar scales, X 26.

Figs. 3-6, Intermediate laminar scales proceeding from outer row (fig. 3) to inner row (fig. 6), X 26.

Figs. 7-8, Mature partially eroded appendiculate scale and a younger appendiculate scale respectively, X 26.

Figs. 9-15, Various types of appendages of ventral scales found on thalli examined, X 61.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the apical cell; this cell quickly divides again by another anticlinal division and in effect the two basal cells represent the laminar initial and the appendicular initial of the scale. Further anticlinal divisions of the appendicular initial result in the development of a filamentous appendage which grows in an oblique fashion so that the slime papilla is pushed aside and is now found attached to the basal cell of the filamentous appendage. Divisions of the laminar initial result in a filamentous lamina made up of a very few cells before any periclinal divisions appear. The subsequent periclinal divisions in both the laminar portion and the appendiculate portion of the scale, result in a coincidental lateral broadening and expansion of both of these structures, with an early maturation of the appendage. The lamina of the scale, however, continues to enlarge by numerous cellular divisions in every direction and it remains meristematic until just before the mature appendage emerges from the apical notch of the thallus. As has been described in the development of the appendiculate scale of Preissia quadrata, this emergence is due to the rapid elongation of the ventral surface of the thallus at a higher rate than growth and maturation takes place in the lamina of the scale. In Plate IV, fig. 8 is a photomicrograph of a young appendiculate scale, removed from others, having their appendages still in the apical notch of the thallus. This scale was approximately 4 mm. long yet the eperon was still in a meristematic condition. Another feature concerning this scale is the presence of numerous tuberculate rhizoids attached to the lamina in the region of the appendage. Pigmentation of the eperon itself, however, has just been initiated.

The range of cell measurements for the appendage in this species, agree in all respects with those made by Evans (1917). It is curious to note that Goebel (1898), Massalongo (1916), Casares-Gil (1919) and Frye and Clark (1937) all illustrate the entire ventral surface of the species with six distinct rows of scales. It is curious to note that not one previous investigator has illustrated the complete appendiculate scale. They have been illustrated but only the anterior portion of the scale has been shown. Casares-Gil (1919) illustrated two laminar scales as well as the appendiculate scale.

Pearson (1902) indicated that scales in the Marchantiaceae were on each side, 2-5 seriate on the postical (ventral) face. In this species he noted them as numerous and brownish in color. Kashyap (1929) stated that the scales were in 3 rows, each side of the midrib; the median scales were largest, attached by a not very long base, appendage sub-rotund with an irregularly toothed margin; laminar scales more than half way from the midrib, without appendage, ligulate; marginal scales smallest, ligulate.

The range in scale color varied from almost colorless to an intense brownish red. The more intensely colored scales, according to Voth and Hammer (1940), at least in their culture studies, were found on thalli growing on substrates deficient in nitrogen and phosphorous. According to Voth (1943) thalli growing on substrates high in salt concentration, regardless of the salt involved, had thallus tissue as well as scales rendered colorless with progressive dying of the apical region of the thallus. The coloration of the scales was restricted to the impregnation of the cell walls of the scale by the pigment anthocyanin, as was previously noted by Mobius (1927).

II. Marchantia paleacea Bertol.

The specimens of this pale green Marchantia, selected for study, were collected primarily in Mexico and Arkansas. The basic scale arrangement (Plate V, fig. 3) indicates three rows of scales on one side of the thallus. The specimen, from which this figure was made, was secured at Fortin, Vera Cruz, Mexico, on a moist roadside bank at an elevation of 3,200 feet. This is mentioned because it was the only specimen studied in this species, that had all 6 rows of scales at their maximum development. Bischoff (1835) under the name M. tholophora described the scales on the underside of the frond as whitish, arranged in a series, prominent on either side of the midrib. Taylor (1836) stated that the number of rows of scales was two, on one-half of the thallus, as did many later authors including Evans (1917) who noted two very distinct rows. Previous to seeing them, the author was of the impression that this species was typified by having only four rows of scales on the ventral surface of the thallus. When it was necessary to prepare the four-rowed thalli for an illustration, the prepared specimen showed two additional outer rows, revealed by the Toludine blue technique. On these apparently four-rowed specimens, the scales found in the two additional rows were discovered to be quite reduced in many instances. They were usually colorless, weakly developed, and adhered tenaciously to the ventral surface of the thallus, so that the pigment in the ventral thallus cells showed through, and effectively masked them.

In Plate V, figs. 1, 2, and 3 illustrate the three types of ventral scales found. Evans (1917), noting that this species was first described by Micheli (1729) but without a description of scales, illustrated the anterior portions only of the appendiculate scale. To the knowledge of the author, no other worker but Casares -Gil (1919) has illustrated a complete appendiculate scale. Both he and Evans (1917) illustrated the laminar scales by outline only. It therefore seemed advisable to illustrate them by means of photomicrographs. All three scales show tuberculate rhizoids attached to the base of the lamina, as well as large slime papillae on the margins (Plate 5, figures 1, 2, and 3). It might be noted that in Massalongo's (1916) illustration

Plate II, fig. 9 and in Casares-Gil's (1919) Figure 163 c., d., there is an indication of slime papillae on both the laminar and appendicular scales.

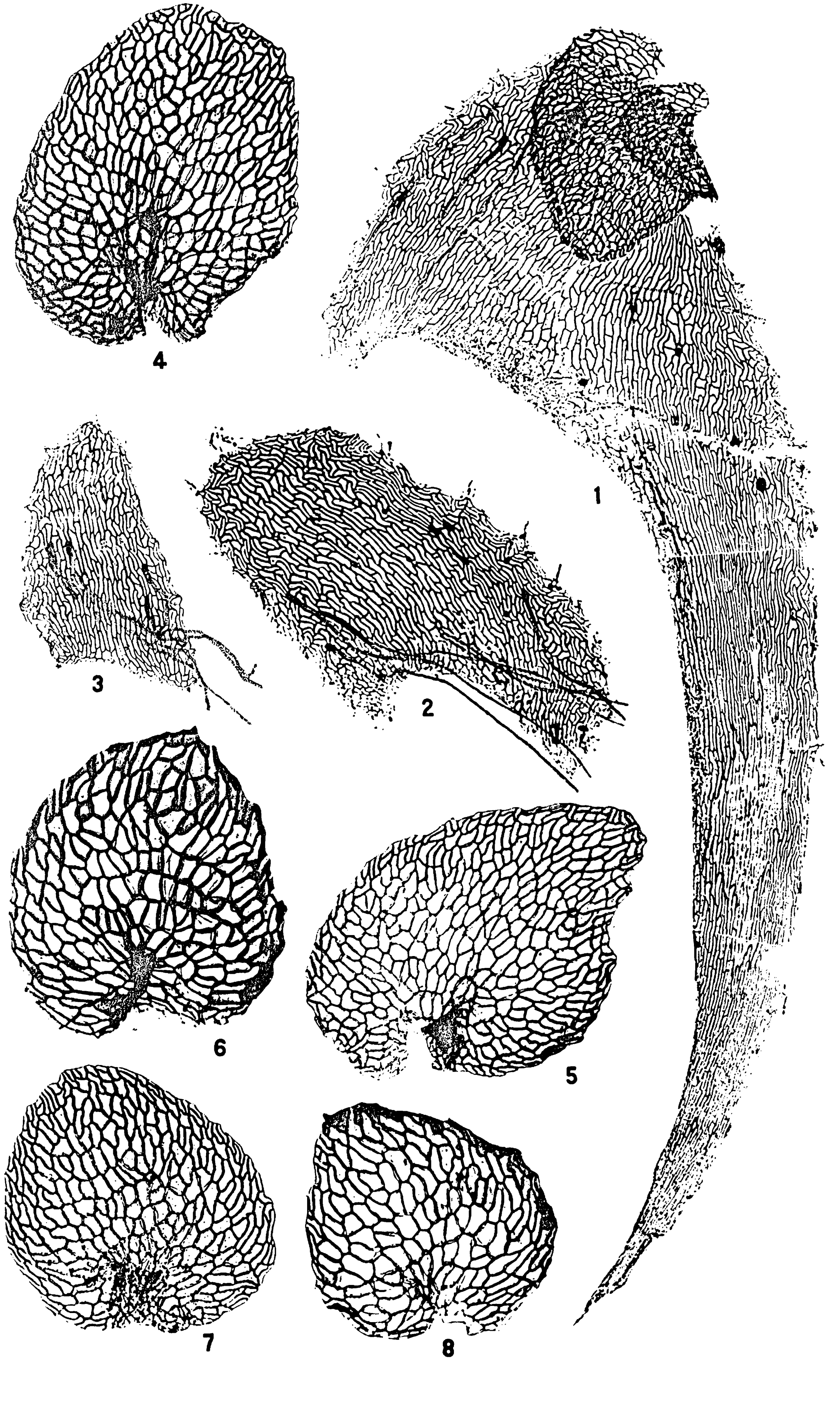
It is worthy of note, in Plate V, fig. 1, that the operon of the appendiculate scale is not enlarged or pigmented as was the case in Marchantia polymorpha. All three types of scale possess oil bodies in the lamina. Another consistent feature of the appendiculate scale is the rather large anterior and lateral, basal hook that is equally pronounced in Conocephalum conicum. Plate V, fig. 1 represents a scale typical of the median row on each side of the midrib; Fig. 2 shows a laminar scale of the row next to the median scale that has an oblique insertion, and Fig. 3 shows a laminar scale characteristic of the additional 2 rows first observed by the author. The observations for measurement and form of appendages were essentially the same as cited by Evans (1917).

In Plate V, figs, 4, 5, and 6 show three appendages representing the general form. In all cases the appendage was a little longer than it was broad, with a variation of lobes on the margin. A few appendages were found with a prominent apical tooth, consisting of 1-2 cells. Figure 6, 7, and 8 represent a series of appendages from the same apical notch. Figure 6 is the oldest of the series and was overlapping those of Figures 7 and 8, Figure 8 being the youngest. Both Stephani (1900) and Evans (1917) rely on the

Plate V

Photomicrographs of the Ventral Scales and appendages of *Marchantia paleacea*

Fig. 1,	Mature appendiculate ventral scale, X 43.
Figs. 2-3,	Laminar scales of inner and outer row respectively, X 43.
Figs. 4-5,	Appendages of appendiculate scale, X 83.
Figs. 6-8,	Appendages of appendiculate scales representing a series over an apical region of a given thallus, X 83.



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appendage in this species as a taxonomic point. It is also evident that Schiffner (1898), according to Evans, did not underrate their value. In many of the specimens examined, the appendages contained either none or very few oil bodies.

The scales are reddish-brown to reddish violet in color, especially the median appendiculate ones. The color of the laminar scales was usually lighter.

III. Marchantia domingensis Lehm. and Lindenb.

This species, first collected on Santo Domingo according to Evans (1917), has a similar insertion pattern to that of the previous species. It has four rows of scales but presents a much more irregular pattern. The most striking feature of the insertion pattern, (Plate III, fig. 4) is that in the rows of lamina scales. They are both widely spaced and vary greatly in size. They are usually oriented fairly close to the appendiculate scales and alternating with them. One feature of the appendiculate scale is the general outline of the lamina and the eperon, which is rather irregular. The appendages of these scales are somewhat reduced from those of the preceding species, and possess one or two-celled teeth on the margin which are most often separated by two or more cells. The laminar scales, (Plate VII, figs. 3 and 4), are found to be both large and small on older portions of the thallus and at the apex. As may be seen, large slime papillae are evident on the margins of these scales. Tuberculate rhizoids occur frequently on the face of the lamina, and a few of them can be barely seen in Figure 3 of this plate. A distinguishing feature of the species is the absence of oil bodies. In addition, the larger laminar scales have oblique insertions while the smaller ones have essentially transverse insertions. The development of scales in this species follows closely that of Marchantia polymorpha. In Plate IX, fig. 10, there is shown a very young appendiculate scale with an appendage about one-third of the way toward its full development; it has numerous slime papillae on the margin. Certainly in this species, a further reduction in the size of the appendage and a tendency toward reduction in the laminar scales distinguishes it from M. polymorpha and M. paleacea. While both types of scales possess slime papillae on their margins, scales back from the apex of the thallus, a centimeter's length, were completely devoid of slime papillae. In color the scale is reddish-brown to reddish purple.

Apparently only a few authors have concerned themselves with scales in this species. Several workers have contributed to accessory data on scales and data on distribution. Stephani (1900), concentrating his scale descriptions on the appendage, described the appendages of this species under its valid name and that of a number of synonyms: M. disjuncta, M. Elliottii, M. inflexa and M. linearis. He stated the appendage was large, ovate-oblong, pointed, irregularly crenate-dentate, margined with smaller cells; and, in the synonyms he added constriction of the appendage at its base, rotund and somewhat spiny. In our specimens, the appendages were consistent in having dentate margins but varied greatly in width. Cell sizes at the center of the appendage and the margin, agree closely with the findings of Evans (1917).

IV. Marchantia diptera Mont.

This Japanese species has essentially the same scale arrangement as M. paleacea, that is, two rows of prominent appendiculate scales on each side of the midrib and two lateral rows of alternating laminar scales. The appendages of this species has the same general form as in M. paleacea, except that their margins have a tendency to be undulate and mostly entire, compared to the large, tooth-like projections found in the previous species. When young but not mature appendages from each species were placed beside each other, they could not be distinguished. The differences in appendage in these two species, is more evident in those that have emerged from the apical notch of the thallus and are quite mature. Those of M. diptera have very thin-walled cells, giving the appendage a tendency to become easily creased and folded. This was not observed in M. paleacea. This feature, together with the characteristic margin was almost enough to tell the two species apart. A positive conclusion as to its validity, however cannot be drawn from one packet of specimens. Figures 5 and 6, Plate VII, represent two appendages of M. diptera. It can be easily seen that Fig. 6 is not too unlike the young appendages of *M. paleacea* figured in Plate V, figs. 7 and 8. Another feature that seems to show up more in the young appendages than in the older ones, is the consistent presence of quite a number of oil bodies. The color of the scales was observed to be a light fuschia red.

Gottsche, Lindenberg and Nees (1844) merely mentioned the scale in a description of the ventral surface of the thallus, indicating that the scales were pressed down and flattened in shape. Stephani (1900) described the appendage as cordate, rotund, subrotund and entire. Evans (1917) referred to the appendage briefly.

V. *Marchantia tosana* Steph.

This is also a Japanese species that was found to have two median rows of appendiculate and two rows of laminar scales. In just the single packet of material available, the appendage of the mature scales varied a great deal in size. The one consistent finding in these appendages was their elliptical, broadly lanceolate form. The smaller appendages usually measured about 200-300 microns long, and 100-200 microns wide. Larger appendages that were primarily elliptical in form, ran up to 375 microns long, and about 270 microns wide. The appendiculate scales themselves were almost entirely restricted to the midrib as far as their insertions were concerned. The laminar scales were rather uniform in outline and spaced much the same in relation to the appendiculate scale as was found in M. diptera and M. paleacea.

Stephani (1900) who named this species, described the appendage as being briefly acuminate, robustly and short-spined. These appendages are illustrated, in the large and small size in Plate VII, figs. 8 and 9. According to the author's opinion, the appendages possessed so many spine-like cells on their margins, that the margin appeared to be regularly serrate. This species is the only one in Marchantia, in which the author observed this characteristic. The appendages represent a definite reduction from those of M. chenopoda. The color of the scales was a light fuschia-red, and the scales appeared to be generally very delicate in form.

VI. Marchantia cuneiloba Steph.

This species had by far the most distinctive appendages, and the smallest scales, both laminar and appendiculate, of all the Marchantias studied. In Plate VII, figs. 1 and 2, are two typical appendages, and in Plate VI, fig. 1, is shown the arrangement of scales, typical of the specimens in one packet of material which included some twenty thalli. This species had the narrowest and most delicate eperon of any Marchantia species observed. The laminar scales are inserted very close to the basal portion of the lateral margin of the appendiculate scale. They were also very uniform in size and shape. The appendage itself possesses 4-6

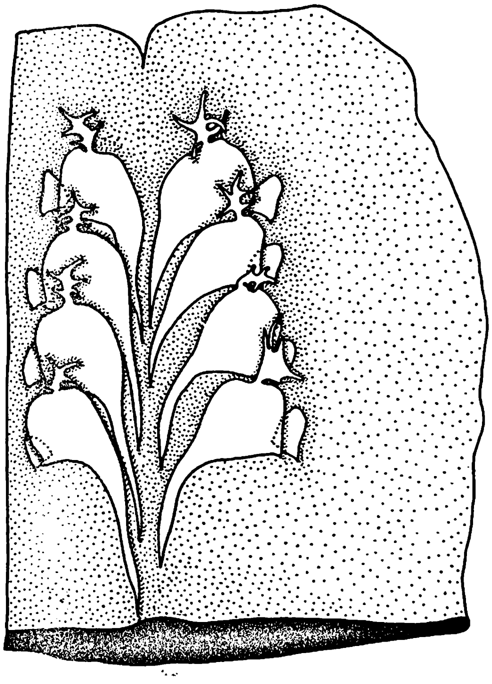
Plate VI

Fig. 1, Marchantia cuneiloba, ventral aspect, X 15.

Fig. 2, Wiesnerella denudata, ventral aspect, X 15.

Fig. 3, Targionia hypophylla, ventral aspect, X 21.

Fig. 4, Cyathodium smaragdinum, ventral aspect, X 40.



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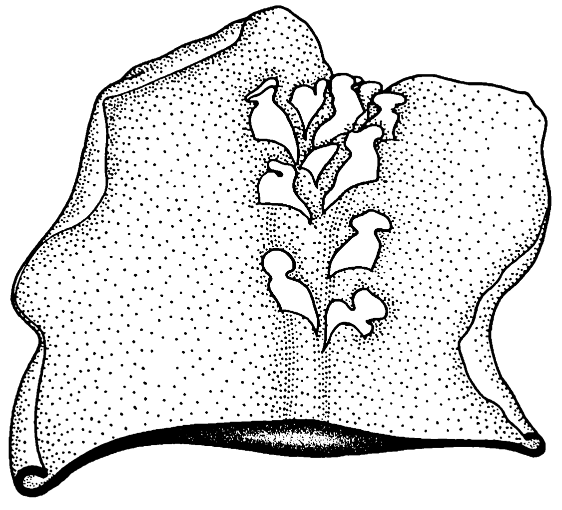

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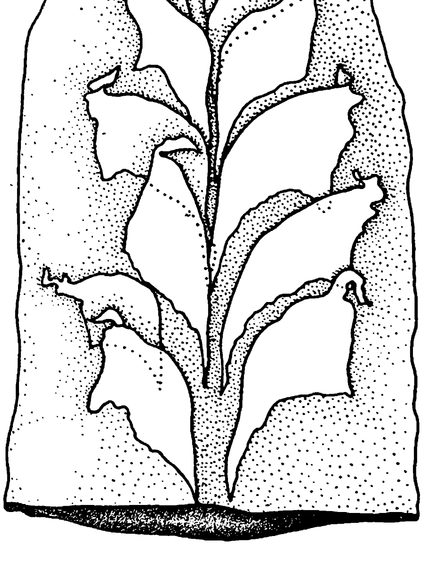

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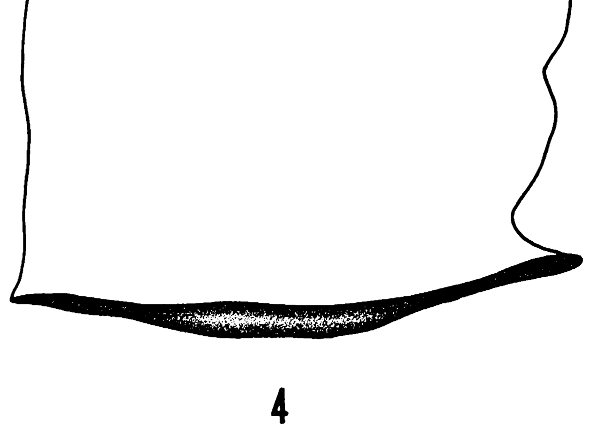

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filamentous teeth on its margins and the laminar portion of the appendage is at the most, never more than 4 or 5 cells wide. Here is a species in which we find a further reduction in the size and form of the appendage, and a reduction in the eperon to the point where it is almost functionless for the capillary conduction of water in connection with the rhizoidal bundles. Stephani (1900) described the appendage and noted that the filamentous teeth were of uniform size, and the color of the scales, purple. The specimens observed by the author were a dark magenta red.

VII. *Merchantia chenopoda* L.

This species was intermediate between *M. domingensis* and *M. tosana*, as far as characteristics of the appendage are concerned. These appendages have been thoroughly described and figured by Evans (1917). The author found essentially the same size of appendage, cell measurements, and characteristics of the margin in going over the same specimens from N. Y. Botanical Garden Herbarium that had been worked by Evans. The most striking characteristic of the appendiculate scales was the variation in form of the appendage. When the thalli had very narrow, long lanceolate appendages, it was quite easy to segregate the species, if these were the only type of appendage found. The other extreme in variation that made this judgment somewhat precarious, was the existence of broad, ovate appendages found on other thalli. A few thalli displayed moderation of the extremes in both kinds of appendage. The author believes, as Evans (1917, 1923) has indicated, that taking all characteristics of scales into consideration, with the range in variation in appendages, this species can be separated from all other American Marchantias.

One collection from Mexico showed a lateral displacement of the outer row of laminar scales toward the margin of the thallus. This species normally has 4 rows with an insertion pattern very similar to M. diptera, and show a retarded development of the outer row of laminar scales. These scales complete the later stages of their ontogeny after emergence from the apical notch of the thallus. Both of these variations found in the laminar scales were restricted to the more delicate forms observed. Plate VIII, fig. 7 represents an older scale consisting of a number of cells while figure 8 shows a scale on the same thallus a very short distance from the apical notch of the thallus. Both of these scales were from the same row on a given thallus. The scale color varied from an intense red violet to a light fuschia or magenta.

Evans (1917) reported that Plumier was the first to describe this species in 1705, but there is no mention of scales in Evans' report on Plumier. Taylor (1836) described the scale in this species as having an ovate base and a deep constriction separating this from the apical portion of the scale; he did not differentiate by name, the appendage and lamina of the scale.

Plate VII

Figs. 1-2, Appendages of appendiculate ventral scale of Marchantia cuneiloba, X 88.

Figs. 3-4, Laminar scales of Marchantia domingensis, X 80.

Figs. 5-6, Appendages of appendiculate scale of Marchantia diptera, X 62.

Fig. 7, Appendiculate ventral scale of Targionia hypophylla, X 38.

Figs. 8-9, Appendages of appendiculate scales of Marchantia tosana, X 130.

Fig. 10, Appendages of scales of Wiesnerella denudata, X 77.

Fig. 11, Appendiculate ventral scale of W. denudata, X 77.

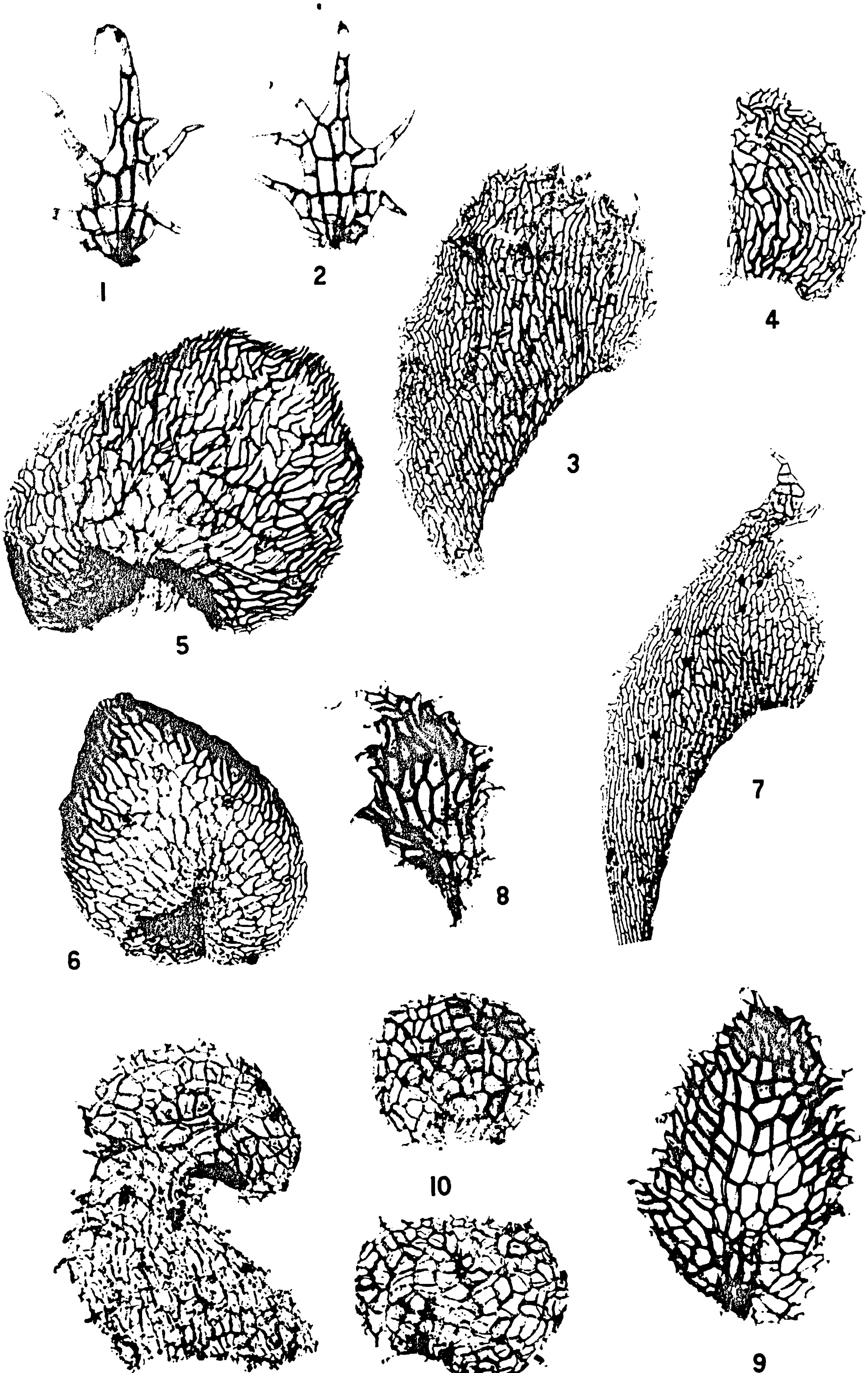

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Plate VIII

Figs. 1-4, Ventral scales of *Cyathodium smaragdinum*, X 454.

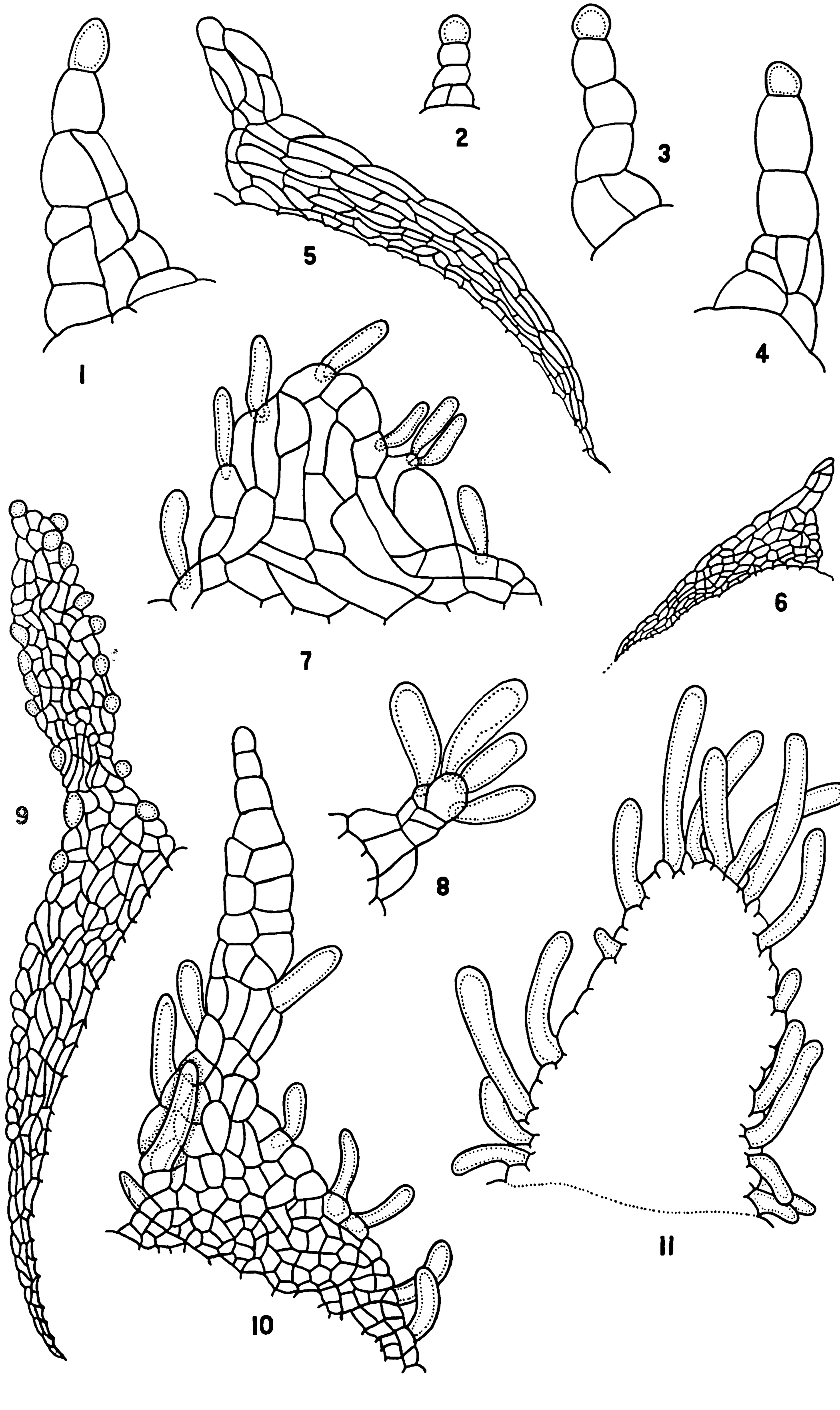
Figs. 5-6, Ventral appendiculate scales of *Dumortiera hirsuta*, X 76.

Figs. 7-8, Ventral laminar scales of delicate form of *Marchantia chenopoda*, X 300.

Fig. 9, Ventral appendiculate scale of *Monoselenium tenerum*, X 166.

Fig. 10, Young appendiculate scale of *Marchantia domingensis*, X 300.

Fig. 11, Young laminar scale of *Marchantia polymorpha*, X 245.



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VIII. Preissia quadrata (Scop.) Nees.

Taylor (1836) described this species under the name Marchantia androgyna and referred briefly to scales with no indication as to the number of rows of scales. Gottsche, Lindenberg and Nees (1844) made no reference to ventral scales but did describe those around the base of the gametophore. Stephani (1900) made no reference to the number of rows of scales, but described the scales as imbricate, broadly crescent-shaped, and purple in color. Pearson (1902) indicated that the thallus in this species as squamose on the postical (ventral) side, scales purplish-black, oblong acinaform. Cavers (1903) described the scales of Preissia and Reboulia as being large and deeply colored, usually extending on the lower surface of the thallus until they sometimes reached the thallus margins. He also compared the scale arrangement in this species to that found in Conocephalum conicum. Cavers (1911), in discussing the interrelationships of the Bryophyta, referred to Preissia briefly, and illustrated an almost complete scale under the name P. commutata, which showed slime papillae with rhizoids at the base of the lamina, and a broad-toothed appendage. Massalongo (1916) described the scales as subimbricate, subfalcate to ovate, appendage sublanceolate with the base constricted. He illustrated the thallus lower surface to show the scale arrangement. His Plate III, fig. 3 showed clearly two rows of scales median in position with one appendage attached to each scale. Casares-Gil (1919) described the scales as in one row on one side of the midrib, and purple to black. He illustrated in Figure 161 d. only a portion of a scale, with a rather large lanceolate appendage, bearing slime papillae on the margin. Evans (1923) noted the ventral scales as being lunulate, appendiculate in two longitudinal rows, appendages lanceolate to lanceolate-ovate, and coarsely to sparingly dentate. Macvicar (1926) indicated the scale arrangement was made up of one row on each side of the midrib, and consisting of semilunar scales with lance-shaped appendages. Haupt (1926) in a morphological study of this species, stated that the ventral surface bore two, longitudinal rows of purple scales along the median line. Grout (1927) merely referred to the scales as being purple in color. Kashyap (1929) described the ventral surface as reddish brown, scales imbricate, in one row on each side of the midrib, and semilunar with minute lanceolate appendages. Frye and Clark (1937) give a description of scale and appendage after other authors, but no indication of ventral scale arrangement except in an illustration of the ventral surface from Müller (1905); the scale illustration they used was after Massalongo (1916). Müller (1952) mentioned the scale color as purple, the size as large and the arrangement as in two longitudinal rows. Schuster (1953) added that the color was blackish-purple in specimens from the Minnesota region which was at variance with our observations of Preissia in most of the Arkansas locations. He also stated that the absence of oil bodies in the ventral scales was diagnostic for this species, in specimens of his region. Wittlake (1954) made his identification of this species in sterile specimens of Arkansas collections, solely on scale characteristics.

The insertion pattern as illustrated in Plate XI, fig. 2 is at variance with the findings of all previous authors. This figure is from a camera-lucida drawing that shows not only the two obvious and often reported median rows but also a row on each half of the thallus of small laminar scales that have previously been overlooked. The laminar scales are typical of those found in other species and genera in this order, many of them having transverse to slightly oblique insertions. Oil bodies were not observed in these scales nor in the appendicular scales. The laminar scales were very uniform in outline most of them at maturity being narrowly or broadly elliptical with numerous slime papillae on the margins, in both young and old scales. On a few laminar scales, tuberculate rhizoids appeared on the face of the lamina. Perhaps the non-detection of the laminar scales in the past, considering the large slime-flux produced by them, has been due to the fact they are often found adhering to the lamina of the appendiculate scales. They are generally inserted just between the lateral margins of the appendiculate scale, and a little posterior to the outer and lateral portions of the appendiculate scale. The discovery of these scales was due to the dark-staining slime papillae on their margins and other organisms in the slime flux. These scales are figured in Plate XII, figs. 8, 9 and 10. Figure 8 shows a young laminar scale near the apical region of the thallus, while No. 10 is an older scale, a little over a centimeter posterior to this region. It might be mentioned that the occurrence of tuberculate rhizoids on the face of these scales is not, however, the general rule, as most of them are destitute of rhizoids.

IX. *Bucegia romanica* Radian

The author had the opportunity of observing one packet of material from Rumania. Müller (1905) described the scale as light purple and lunate. Schiffner (1908) commented upon the large, half crescent-shaped, red violet scale with linear appendage and showing no oil bodies. These appendages were said to be 10 or more cells in breadth, possessing slime papillae on their margins, often with two near each other. These observations essentially agree with ours. Schiffner (1908) further illustrates the scale showing all these features but fails to show the narrow eperon in his illustration of the appendiculate scale. Haynes (1915) reported this species from British Columbia but made no reference to scales. The author saw tracings of Stephani's drawings, made by his daughter, in the collection of the N. Y. Botanical Garden Herbarium. The drawing was evidently made from a scale quite a way back on the thallus from the apical region, for, his illustration depicts a very linear appendage. The author quite frequently found such scales a centimeter or so back from the apical region. Two such appendiculate scales are illustrated in Plate XI, fig. 4, the most distant scales from the apical region of the thallus. Photomicrographs of the range in variation of appendages appear in Plate XII, figs. 4, 5, 6 and 7. Figure 6 represents an appendage, perhaps close in appearance to the one traced by Stephani's daughter. Massalongo (1916) illustrated the ventral surface of a thallus, showing two rows of appendiculate scales on each side of the midrib. This is again figured by Frye and Clark (1937) who do not state in their text the number of rows of ventral scales. Evans (1917) commented upon the scales in this species as "The ventral scales are in 2 rows, differing in this respect from <u>Marchantia</u>, but agreeing with <u>Preissia</u> and other <u>Compositae</u>. The scales have the usual semicircular or broadly lunulate form and each one bears a single lanceolate appendage." Later Evans (1943) added a little more to the details given in his previous paper. Casares-Gil (1919) briefly described the species but made no mention of scales, nor did he illustrate them. Müller (1952) described the appendiculate scale as having a lamella-like appendage, membraneous in texture, brown in color, and with slime papillae on the margin.

According to the author's findings on all thalli observed, the appendiculate row of scales had a tendency to become somewhat irregular. It might be stated that the detection of the two additional rows of laminar scales in this species was due primarily to the use of Toludine blue stain. The laminar scales in contrast to those found in Preissia quadrata, were extremely irregular in general outline as is shown in Plate XII, figs. 1, 2 and 3. Their insertions were transverse in every case. The greatest variation was found in the size of the scale. Plate XII, figs. 1 and 2 are at a much higher magnification than Figure 3 as can be seen by the size of the cells in each scale. Figure 3 shows a laminar scale that was equal in size to the lamina of the appendiculate scales if not larger. It is possible that these large laminar scales were overlooked in the past and thought to be merely appendiculate scales whose appendages had been eroded from the anterior margin of the lamina. Figure 1 represents a very young scale found just inside the apical notch, with numerous slime papillae on its margin, and with a few of them broken off and imbedded in the slime flux. The gray area surrounding the scale in this illustration, is a portion of the slime flux that adhered to the scale when the latter was mounted under a cover slip. The debris noted in this slime flux, consisted of colonies of bacteria and a unicellular Alga that was distributed here and there. A few tuberculate rhizoids, attached to the basal portion of the lamina, were found on only older laminar scales. All laminar scales usually showed slime papillae on their margins.

The color of scales was much the same as in Preissia quadrata. The exact position of the laminar scales was like that of Preissia. These laminar scales had a tendency to adhere to the lamina of the appendiculate scale, due to the production of large amounts of slime. Thus, Bucegia has four rows of scales; the two median rows appendiculate; and, the two lateral rows laminar.

X. Clevea hyalina (Sommerf.) Lindb.

In specimens of this species from a packet collected by Schuster No. 18004, the scale arrangement was essentially a scattered one. The species is repeatedly cited in the literature to have two irregular rows of ventral scales. In Plate XIII, fig. 1, it is quite apparent that the scales on the midrib are smaller than those found at its margins or on the wing of the thallus. There is no definite pattern of insertions, and the only nearly regular pattern may be found in those main fragments of the appendiculate scale which have the appendage attached. This arrangement is due primarily to an early, longitudinal splitting of the scale, and the subsequent displacement of the fragments some distance apart. Perhaps the illustration cited above represents an extreme in scale arrangement in this species, but the same arrangement appeared in the examination of more than 20 thalli in this particular packet. A typical uneroded scale can be seen in Plate XII, fig. 11, and shows an obliquely tapering scale, subtriangular in outline, and with an appendage three to four cells wide. Schuster (1953) stated that the scales were colorless or pale violet, and had tapering hyaline appendages that protruded beyond the margin of the thallus. He went on to say that the scales were not sharply appendiculate, and that they lacked oil bodies. The author found great variation in the distinction of the appendage from the lamina of the scale. The illustration in Plate XII, fig. 11 represents one of the more distinctive appendages. Other scales observed had tapered gradually and had much the same form as the scale found in Oxymitra paleacea. Because of the schizogenous splitting of the lamina of relatively young scales while still near the apical region or at the apical notch, one has to proceed with caution to learn whether the entire scale is present or not and particularly when examining ventral scales on older portions of the thallus.

Dumortier (1874) merely remarked upon the numerous scales on the ventral side of the thallus. Lindberg (1882) described the color of the ventral scales as hyaline, noting that they projected beyond the margin. Solms-Laubach (1899) discussed the scales at the base of carpocephala and on branches, briefly noting the shape and form of ventral scales, with slime papillae scattered on their margins. Stephani (1900) said the form of the scale was obliquely lunate with a long point ending in a filiform apex. Müller (1905) described them but added little to previous notes. Lotsy

(1909) stated that in the genus Clevea, slime papillae were missing near the apex of the scale, and were rudimentary at the base of the scale. Cavers (1911) merely mentioned the scales growing out from tissue below the archegonia when the stalk of the gametophore lengthened. Massalongo (1916) deviated somewhat from previous ideas, by describing the arrangement as two- four-seriate, and illustrated two ventral scales in Plate XVIII, fig. 11 of his paper. Evans (1914) noted that the scales formed a distinct cluster extending backward over the growing point of the thallus. Casares-Gil (1919) added one point to scale description by stating they were triangular in form. C. Douin (1923) stated that Clevea and Peltolepis had many rows of scales on each side of the median line. Evans (1923) expanded his earlier description by noting that there were two irregular rows of scales, colorless to purple, not truly appendiculate, and with margins bearing few or no slime papillae. Frye and Clark (1937) listed this species with a ventral scale description almost exactly that of Evans (1923). Müller (1940) illustrated three entire scales and an enlargement of a scale in this species in Figs. 2, 3, 4, 5, 6 of his work. These illustrations exhibited apical portions of the scale as wide, or wider and shorter than, any scales seen by the author. Trabut (1941, 1942) cited the scales but his description coincided with those of previous authors. Müller (1952) stated the appendages were lanceolate for scales in this species.

XI. Conocephalum conicum (L.) Dumort.

The author has figured a portion of the ventral surface of the thallus in this species in Plate XI, fig. 3 to show one of the more imbricated arrangements of the appendiculate ventral scales. There is little to be added to the observations of previous workers on ventral scales in this species. Mention should be made of the prominent, lateral, anterior hook of the lamina of the appendiculate scale. To our knowledge, Schuster (1953) has been the only writer to illustrate the outline of the complete scale in the species. Taylor (1836) described briefly the appendage as being terminal on the margin, and the scale somewhat lunulate in outline. Stephani (1900) described the lamina as being obliquely crescent-shaped, extending greatly into the costa; the appendage he added was small. Pearson (1902) described the thallus of this species as furnished on the Postical (ventral) side with numerous reniform or cordate scales of a purple color and delicate texture. Cavers (1903) outlined the origin of scales in this species as being initiated by a slime papilla, and indicated that the appendage was inserted by a narrow neck into the lamina. The lamina itself, he saw as long and narrow. He illustrated five stages in the development of the scale. In Plate VIII of his work, figures 12, 13, 14 and 15 showed the development of the appendage in relation to the initial slime papilla. Figure 16 illustrated only a portion of the mature scale with numerous rhizoids attached to its base. Bolleter (1905) without reference to Cavers recent work (1903) stated that the scales occurred in two rows on the midrib and illustrated the scales and appendage in detail. He pointed out that oil bodies occurred in the lamina of the scale. Maybrook (1914) deduced from her experiments in culture, that no scales or air chambers were seen in high moisture situations or very low intensities of light. Massalongo (1916) illustrated the scales and the ventral surface of the thallus in Plate VI, figs. 4 and 9 of his work. Evidently his scale illustrations present the anterior portion of the scale or a scale near the apical region of the thallus. His illustration of the ventral surface of the thallus was somewhat mystifying since the insertions of the scale appeared to be median and parallel to the axis of the thallus, rather than arching from the wing toward the midrib, and finally paralleling it. He described the appendage as being subrotund, and the scale hyaline to light violet in color. Lesage (1915) discussed briefly the relationship of rhizoids to the ventral scale. Casares-Gil (1919) duplicated much of the above data. R. Douin (1924) considered the action of environment on this species and quoted Ulmo (1913) as, "The form and appearance of the scales are independent of the physical environment". Macvicar (1926) described the variation in scale arrangement at the other extreme than that illustrated by the author in Plate XI, fig. 3. In his comments, the scales were said to be rather distant. C. Douin (1925) discussed the scales of the differentiated thallus extending beyond the androecium, that is, scale data was limited to those about the reproductive structures only. Kashyap (1929) described the ventral surface as pale green in color; the midrib as conspicuous, usually with tubes scattered in it; and, scales as distant, in one row on each side of the midrib, with a violet, reniform or orbiculate appendage. Frye and Clark (1937) described the scales as being membraneous, with slime papillae, as occurring in two rows and appendiculate, and with an appendage orbiculate to reniform in shape; all points already suggested by Evans (1923).

Previous authors suggested that the scales in this species were long and narrow; this can be clearly seen in our Plate XI, fig. 3 through the length of the lamina of one scale, marked by a dotted line. These particular scales on older portions of the thallus varied from 6.0--6.5mm. in length. As in other primitive species in the Marchantiales, a large rhizoidal bundle is enclosed the length of the midrib, and not only by the eperon, but by a good portion of the lamina of these scales as well. As noted in the literature, the margins of the scale have slime papillae present. It might be well to mention further that they are easily overlooked because of the narrowness of the scales, and because they are almost entirely restricted to the midrib, have numerous rhizoids and are very light in color. This opinion was also expressed by Casares-Gil (1919).

XII. Conocephalum supradecompositum (Lindb.) Steph.

The author observed specimens from two localities in Japan. This species has been reported from both Japan and the Himalayas of India. Pande and Bwardjai (1946) made a formal report of this species occurring in India, and followed this with a complete description (1949). They made note of numerous scales and rhizoids on the ventral surface of the thallus. The former were described as being "obliquely ligulate with a subrotund appendage" (illustrated in their Figures 9 and 10). These were said to occur "in two alternating rows on either side of the midrib, more numerous towards the apex, where they became crowded and overlapping". These findings do not vary from ours. One of the most striking points about the appendiculate scale is its subrotund appendage and the absence of a lateral hook to the lamina, which is found consistently in C. conicum. The midrib is prominent and the species is smaller than C. conicum, rarely attaining 2 cm. in width.

Lindberg (1884) in describing the species under the name, Sandea supradecompositum, described the scales as being quite uniform in size, ovate, acute and entire. Stephani (1900) compared it to C. conicum as well, and stated that it had an equally broad appendage, was dilute purple in color and had much larger cells than those found in the last mentioned species.

XIII. Lunularia cruciata (L.) Dumort.

The insertion pattern of the ventral scales of this species, a short distance back from the apex of the thallus, presents a different appearance than has been found in any other genus studied. The insertion of the appendiculate scale is almost perpendicular to the midrib of the thallus, with only the eperon of the scale bending abruptly parallel to the midrib. The eperon is very short, and the appendage distinctive because of the position it holds on the anterior margin of the lamina. Here, the appendage is inserted some distance from the lateral end of the lamina of the scale. The entire scale is very translucent to hyaline and the cell walls are so thin that little support is given to the scale itself. The scales do not erode away easily, however, so they can be found consistently on older portions of the thallus. The lamina of the scale contains oil bodies and the margins bear slime papillae. This species is illustrated in Plate XI, figure 1 where the general form of the appendage can be seen. The appendage may be broadly attached or very constricted at its base.

Bischoff (1835) termed the scales in this species as, scale-form little leaves, distinct, imbricate, membraneous, sublunulate, narrowing abruptly at the apex into a snail-like clump, then becoming distant, and concealed, making white cross-wise folds.

Descriptions of the scale by previous authors vary little from ours. Taylor (1836) calling them "stipulae" stated they were whitish, like scales of a fish. Stephani (1900) noted that the scales were four times as long as wide, with a slightly constricted appendage, that was rotund and with an entire margin. Pearson (1902) described the scales in this genus as imbricate, sublunulate, their apex abruptly contracted into a roundish cochleariform lobe. Of the species, he merely added that the postical (ventral side) was clothed with many scales. Massalongo (1916) illustrated two nearly complete scales, together with a view of the ventral surface of the thallus, showing scale arrangement, (Plate VII, figs. 5 and 9 of his work). Casares-Gil (1919) mentioned that the scales were arranged in two rows and that the insertions arched concavely toward the posterior of the thallus. He also illustrated both an appendiculate scale and the ventral surface of the thallus, showing the perpendicular pattern in reference to the midrib in Figure 156, c, and g. of his work. Evans (1923) cited the appendage of the scales as scarcely or not at all pigmented, orbicular to reniform in shape, and its margin entire to vaguely crenulate. Kashyap (1929) described the ventral surface as green, the scales in one row on each side of the midrib, thin, delicate, attached by a long semilunar base, appendage rotundate. Frye and Clark (1937) presented illustrations of this species after Massalongo, with the exception of Figure 1, Page 87, but no indication of scales were made. Müller's

(1952) description added little to that of workers prior to his paper. The sole reference and illustration of oil bodies of the scale of this species appeared in the work of Pfeffer (1874) in his Plate I, figure 12.

XIV. Dumortiera hirsuta (Sw.) Reinw.

This genus and species was found to possess very membraneous, translucent scales with distinct appendages. They are arranged in two longitudinal median rows. The appendage of the species consists of only a few cells as shown in Plate VIII, figures 5 and 6 of which illustrate both a young and a mature scale. The appendage of the scale in Figure 6 has not yet emerged from the apical notch of the thallus. Both Figures 5 and 6 are at the same magnification. These scales erode very quickly; those located posterior to the 5th or 6th scale from the apex of the thallus, are entirely destitute of lamina and appendage. All that remains just above the insertion of the scale is a portion, two-three cells in thickness, thus leaving only a ridge of cells arching from the midribregion anteriorly and laterally on the wing of the thallus. These ridges stain very readily with the technique already described. They continue to elongate as if the whole scale was intact. An illustration of the ventral side of the thallus can be seen in Plate IX, fig. 1.

Many contrasting statements can be found in the literature because of the early erosion of scales in this species.

Taylor (1836) used the name _Hygropyla irrigua_ for genus and species. He said scales were absent from the ventral surface of the thallus. Gottsche, Lindenberg and Nees (1844) noted that they were entirely absent or rarely covering the ventral side of the thallus. Leitgeb (1880) saw rudimentary lamellae on the ventral side of the thallus or just at the apex. He considered them as homologous with ventral scales, eroding early because of the disorganization and death of their cells. Stephani (1900) stated that the reduced ventral scales only serve as protection for the vegetative apical region. He described them as irregularly acuminate, lacerated with free elongated cells and early disappearing. Cavers (1903) stated that in _Dumortiera_ and _Cyathodium_, the scales were greatly reduced, consisting of a simple or branched row of cells. Ernst (1908) suggested that ventral scales were initiated on either side of the median, sagittal plane, that they overlapped each other and projected over the apex of the thallus. Massalongo (1916) further described these structures as minute, evanescent, and appearing only at the anterior extremity of the frond. In his illustration, Plate V, fig. 8, he showed rather large scales some distance from the apex of the thallus, extending across the thallus from the midrib region almost to the margin. Macvicar (1926) said the scales were evanescent on both sides of the midrib, and that ventral scales were not necessary to protect the rhizoids because of the hygrophilous

Plate IX

Fig. 1, *Dumortiera hirsuta*, ventral aspect, X 10.

Fig. 2, *Monoselenium tenerum*, ventral aspect, X 15.

Fig. 3, *Asterella echinella*, ventral aspect, X 15.

Fig. 4, *Asterella tenella*, ventral aspect, X 10.

Fig. 5, Ventral appendiculate scale of *A. tenella*, X 66.

Fig. 6-7, Two appendages of appendiculate scales of *A. tenella*, X 66.

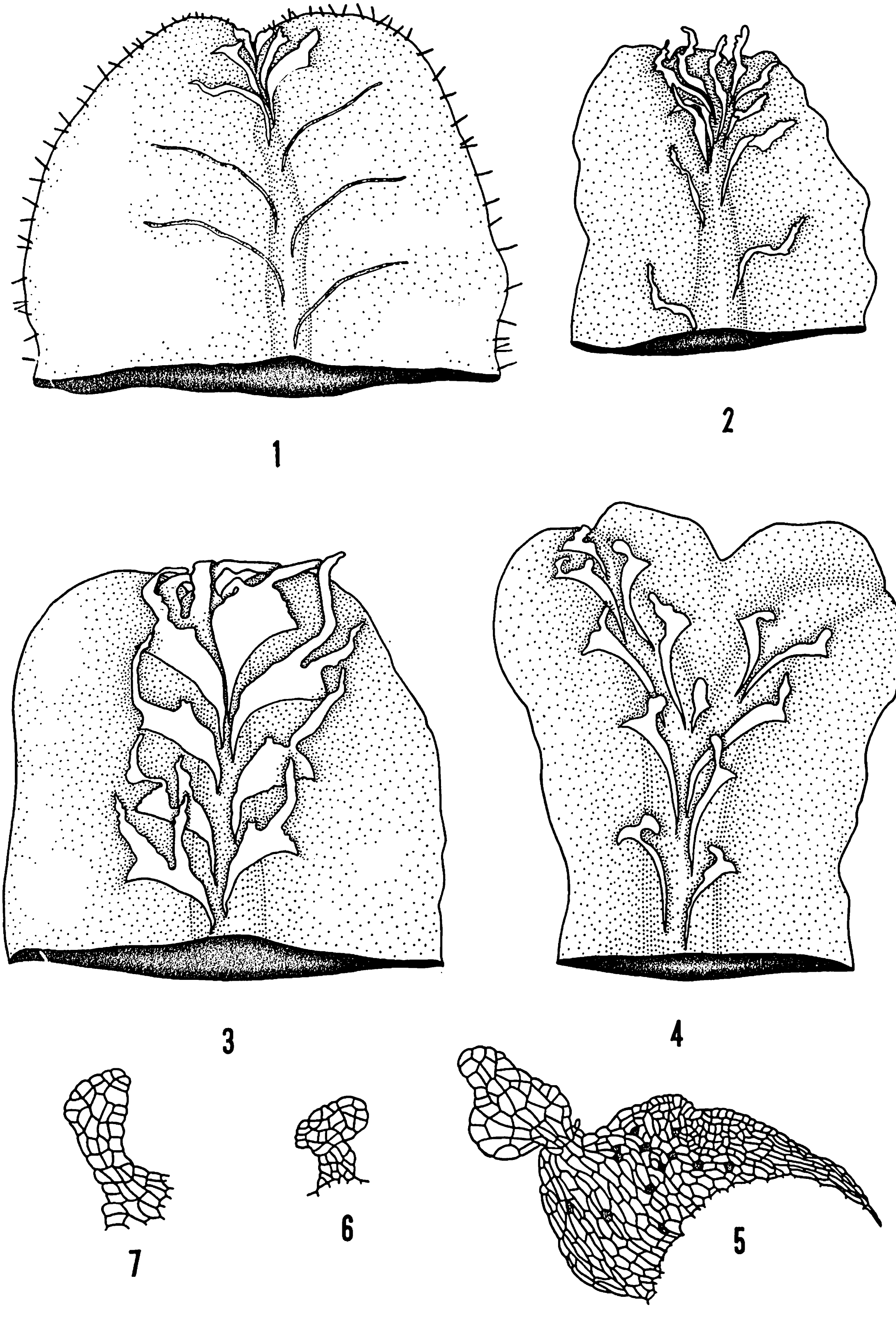
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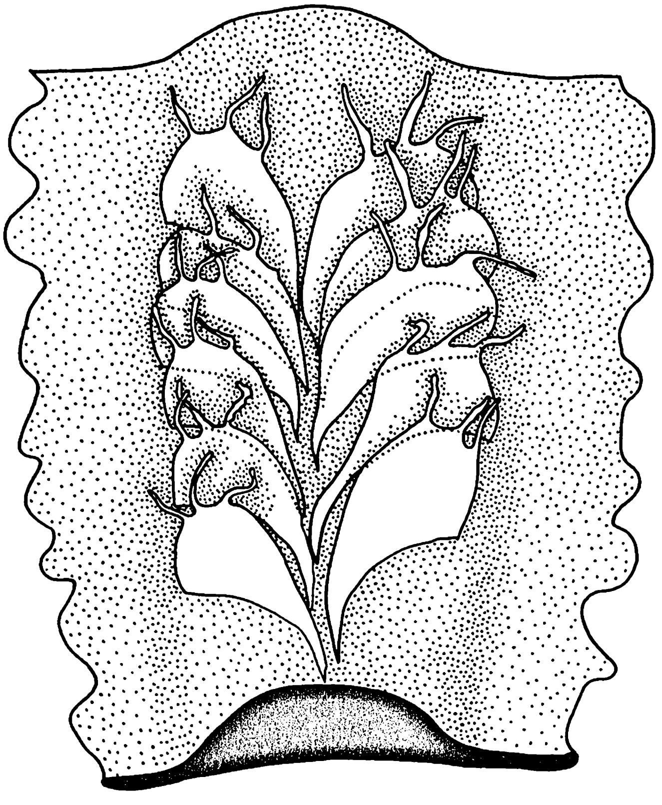
Plate X

Fig. 1, *Reboulia hemisphaerica*, ventral aspect, X 18.

Fig. 2, One half of the ventral surface of *Plagiochasma rupestre*, X 18.

Fig. 3, *Mannia fragrans*, ventral aspect, X 50.



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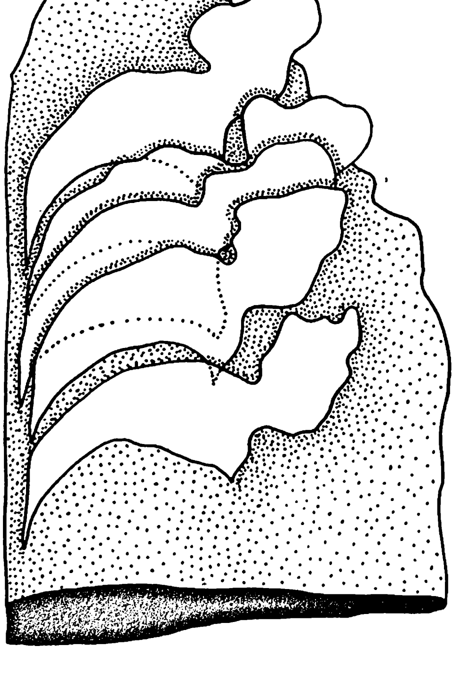

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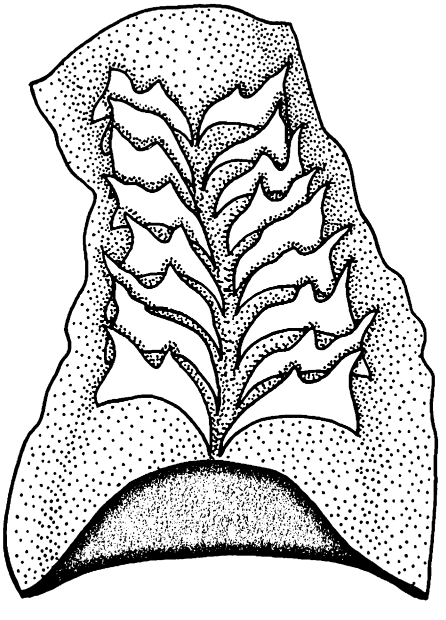

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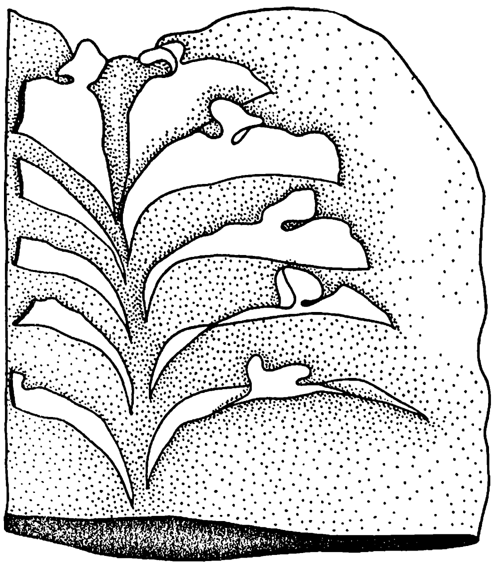
Plate XI

Fig. 1, *Lunularia cruciata*, three fourths of the ventral aspect, X 11.

Fig. 2, *Preissia quadrata*, ventral aspect, X 11.

Fig. 3, *Conocephalum conicum*, ventral aspect of midrib region, X 11.

Fig. 4, *Bucegia romanica*, ventral aspect, X 11.



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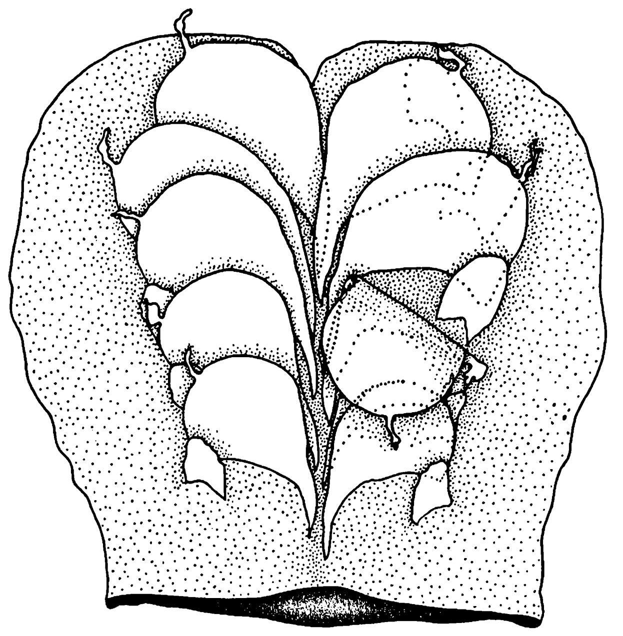

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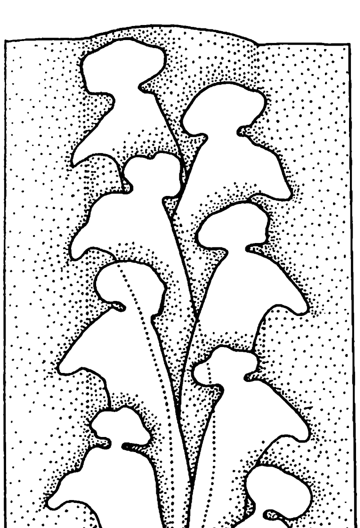

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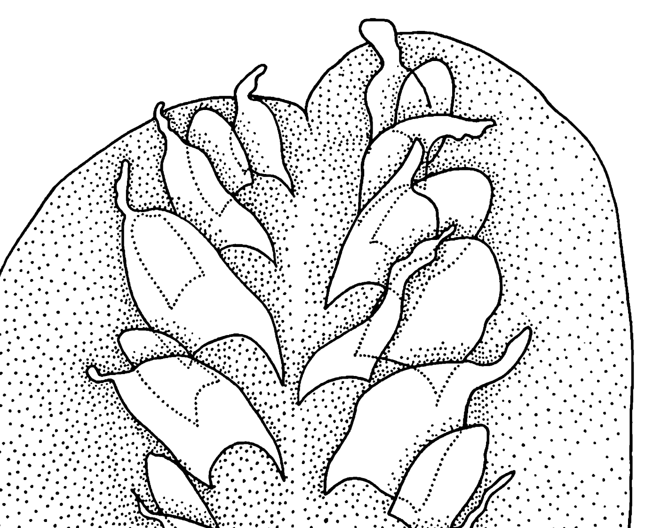

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Plate XII

Fig. 1, Very young laminar scale with its enclosing slime flux of *Bucegia romanica*, X 85.

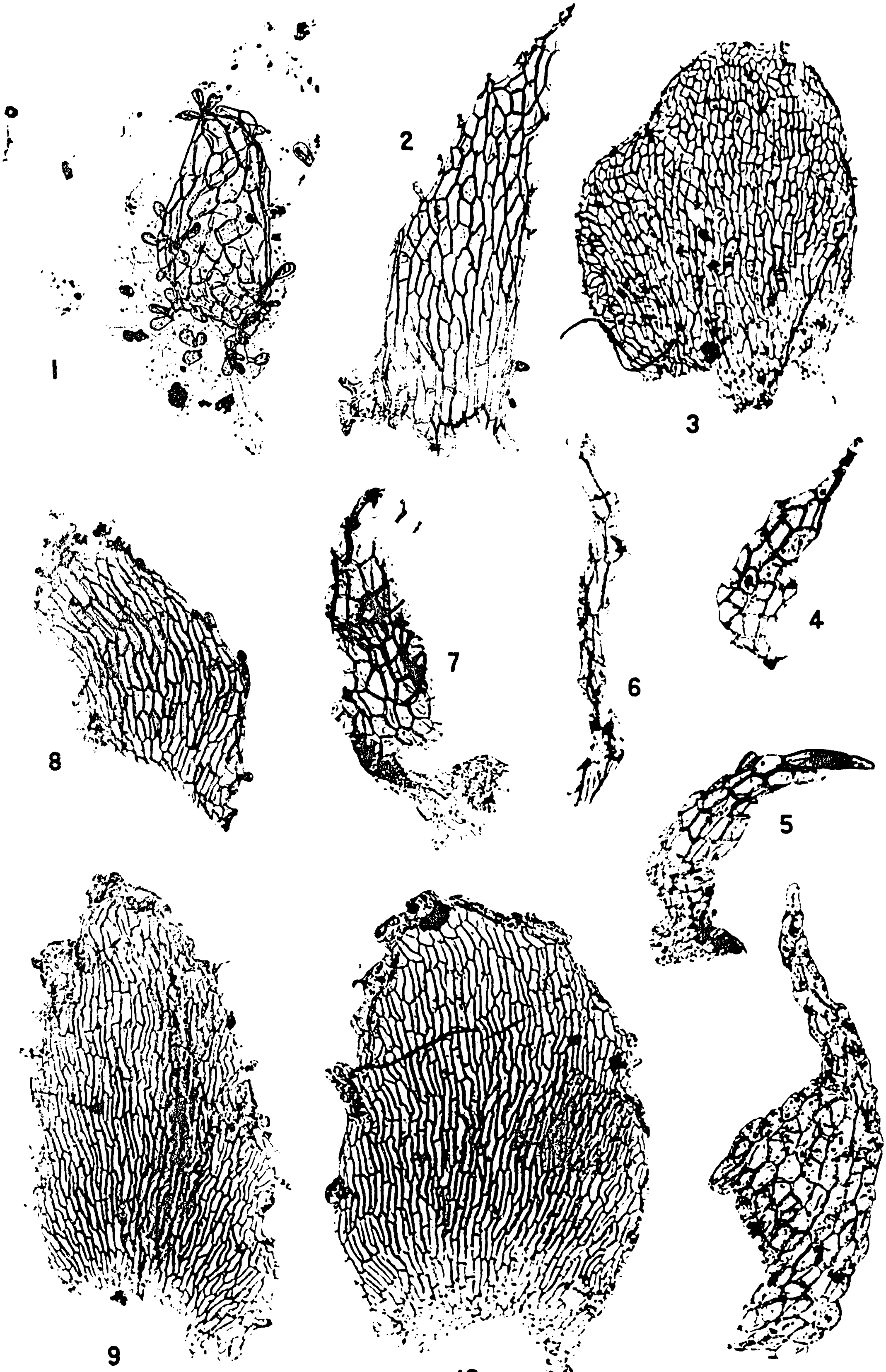
Fig. 2, Mature laminar scale of *B. romanica*, X 85.

Fig. 3, Mature laminar scale of *B. romanica*, X 30.

Figs. 4-7, Mature appendages of the appendiculate scale of *B. romanica*, X 85.

Figs. 8-10, Laminar scales of *Preissia quadrata*, X 85.

Fig. 11, Uneroded appendiculate ventral scale of *Clevea hyalina*, X 85.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nature of the plant. Evans (1923) added that the scales were hyaline and rudimentary, without distinct appendages. Kashyap (1929) described the ventral surface as green in color; scales as simple, hyaline, evanescent, in older parts as narrow, long, oblique ridges attached to the thallus along their entire length and occurring in one row on each side of the midrib. Patterson (1933) in his morphological study, described them as consisting of a short limb with two wings, each of which covered a rhizoidal bundle. O'Hanlon (1934) reported that <u>Dumortiera</u> had no ventral scales, despite the fact that she thought that these organs were characteristic of the <u>Marchantiaceae</u>. Frye and Clark (1937) repeated Evans' (1923) observations that the ventral scales had no distinct appendages.

As may readily be seen from the above data, there has long been a discussion about the presence or absence of ventral scales in this species. It is hoped that the illustrations, cited above may clarify the issue.

XV. <u>Reboulia</u> <u>hemisphaerica</u> (L.) Raddi.

This robust liverwort has a characteristically biseriate insertion pattern. <u>Reboulia</u>, <u>Bucegia</u> and <u>Preissia</u> all are consistent in the possession of a large and expanded lamina of the appendiculate scale. Bischoff (1835) illustrated in detail the ventral scales and scale arrangement in this species. Taylor (1836) described the scales as imbricate, purplish, pinnately arranged on each side of the midrib, and as rotund and bicorneate. Gottsche, Lindenberg and Nees (1844) stated that they were broadly ovate, purple in color, and two-horned (probably appendages). Stephani (1900) said the scales of the genus were obliquely lunulate with the appendage small to linear, basally constricted and with an acute apex. No specific data on scales in this species was recorded. Pearson (1902) described the thallus as squamose on the ventral side, scales dark purple, imbricate, quadrate-longate. Cavers (1903) compared the scales of <u>Preissia</u> and <u>Reboulia</u>, saying they were large, deeply colored, usually extending on the lower surface of the lateral wings or even reaching the margin of the thallus. Cavers (1904) further discussed the ventral scales of this species, noting that they were roughly semicircular in outline, with a narrow basal prolongation that extended inward to the middle line of the thallus (eperon). He went on to say that the free round margin in most cases bore two long narrow pointed appendages, frequently bore only one and occasionally there might be three of them present. He noted how the young scales curved upward and occupied the groove in which the row of initial cells rests. He stated that the cells of the young scale contained chloroplasts, protoplasm, and starch grains, and that the marginal cells frequently grew out into club-shaped mucilage hairs. He added that the mature scale lost its contents and acquired deep colored cell walls; that in the basal growth of these scales they possess many living cells capable of division which enable the scale to grow further in breadth. He said they had brown-colored oil bodies which were responsible for the characteristic odor of this species. Massalongo (1916) indicated the scale had one or two linear or lanceolate appendages that were basally constricted, as illustrated in Plate XIX, figures 4 and 4 A of his work. Casares-Gil (1919) suggested the scale to be decurrent, the appendage filiform; and, his Figure 150, c. indicated that the scale had two narrow linear appendages with oil cells in them. Haupt (1921) in a study of the gametophyte and sex organs of this species, concluded that the scales arose separately, were one cell thick except at the base, and were non-appendaged. Evans (1923) referred mainly to the scale appendage, stating there were two, rarely three present, and that they were composed of cells larger than those in the rest of the scale. Macvicar (1926) described the scales as imbricate, obliquely lunulate with two acute, linear appendages. Kashyap (1929) described the ventral surface as purple, with purple scales, imbricate, in one row on each side of the midrib, obliquely lunate, reaching halfway to the margin, and with two linear appendages. In addition he illustrated the ventral scale in Plate XV, fig. 5 of his text. Frye and Clark (1937) indicate the same findings as offered by authors prior to their work. Grout (1947) compared <u>Preissia</u> with <u>Reboulia</u> as to size and general appearance, stating that this species could be differentiated by the two-toothed purple scales, together with other characteristics. Müller (1952) remarked that the scales had mostly two appendages, sometimes three or four, hair-like in outline, and at the base of which lay a slime papilla. He illustrated a scale with four appendages in Figure 58, e. of this work. Schuster (1953) made no point of scales in this species except to include Reboulia under the section of his key containing linear appendages and oil bodies; he illustrated a scale in Plate 83, figure 7, showing two linear appendages.

The basic number of appendages on the thalli seen by the author, seemed to be three, each two-four cells wide. In every case where scales were found to have two appendages, either the third appendage was absolutely colorless and adhering to the lamina of the scale, or there was good evidence of its having been eroded away. Scales were found with only one appendage, but young scales bearing three linear appendages dissected from the apex of the thallus, suggests strongly that this is characteristic. Observation of Arkansas material, and that from widely distributed points showed those thalli, found in xeric conditions, possess scales that rotated toward the margin of the thallus, thus orienting the three appendages almost perpendicular to the margin. In Plate X, figure 1, there is the ventral surface of the thallus not showing the conditions described above. Here, the scales have rotated but little and the appendages are oriented essentially parallel to the midrib. In the specimens examined, the scales of this species were usually blood-red in color, and when dissections were in progress practically no staining of the scales themselves was required. The number of appendages for each scale, and the relative orientation of these appendages are the chief diagnostic points in the species.

XVI. Monoselenium tenerum Griff.

The ventral scale arrangement for this species can be seen in Plate IX, figure 2. The midrib of the thallus is not usually as pronounced as in this illustration. The complete scale, shown in Plate VIII, fig. 9, was dissected from the ventral surface of the thallus near the apical region and represents one of the most intect scales found on the thallus. Numerous slime cells, that can hardly be called papillae, can be seen on the margin of the appendage, and on a portion of the lamina. A few oil cells were also in the appendage, and are noticeable in this figure as two-three small cells in the lower half of the appendage. When the scales of this species were first noticed, there was such a profusion of slime around the apical region, that scales located essentially opposite each other, on each side of the longitudinal axis of the thallus, adhered together. Often it was only the apical portion of the appendages of two scales that adhered, and this seemed to indicate that both scales, perhaps, had a common origin. Further dissection revealed that they were separate from the first and only adhered to each other because of the slime involved. On older portions of the thallus the scales were quite distant and soon became very eroded. Goebel (1910) in a monograph on this genus, stated there were chloroplasts and colorless plastids in the cells of the scale, in addition to oil bodies, and slime papillae on the scale, both of which he illustrated. He further indicated that the tuberculate rhizoids arise directly from the ventral surface of the thallus. He illustrated two early stages of ventral scales of the sporeling in Figure 39, II and III of his work. Cavers (1911) said there were small ventral scales on the ventral surface of the thallus; he compared Monoselenium and Monoclea in their reduction of various organs to different degrees. He went on to say that the thallus in this species resembled that of Monoclea, and the ventral scales, instead of being reduced to unicellular, filamentous papillae, translucent to hyaline, as in Monoclea, resembled those of Dumortiera or Cyathodium.

XVII. Wiesnerella denudata (Mitten) St.

This species has scales very similar in texture to those of the preceding genus. The lamina is obliquely subtriangular with a large orbicular appendage, attached to its apex. (Plate VII, figs. 10, 11). The ventral surface of the thallus can be seen in Plate II, fig. 6, with the scales restricted to the central portion of the thallus. Schiffner

(1896) erected the genus on a liverwort, named by Mitten prior to his time. He described a new species *Wiesnerella javanica* in the same paper, and illustrated a scale from it that appears to be intermediate between *W. denudata* and *Dumortiera hirsuta* as far as size and character of the appendage is concerned, (Plate I, fig. 4 of his work). Stephani (1900), when first noting this species, stated no scales were present. Later, Stephani (1917) described the scale as follows: Ventral scales large, obliquely lunate, hyaline, uniseriate on both sides of the costa, with a large subrotund, constricted appendage with a margin sparsely-toothed and turning up. Again, Stephani (1917) in Volume VI, of *Species Hepaticarum* reduced *W. javanica*, formerly described by Schiffner (1896) to synonomy. Kashyap (1929) stated that the ventral surface was brownish; scales were oblique, lunate, large, hyaline, in one row on each side; and the appendage large, subrotund, and strongly constricted.

The dentate margin of the appendage, indicated by Stephani (1917) was so characterized because of slime papillae distantly located on its margin. These papillae stain very darkly with Toludine blue, and were thus easily discernible. Slime papillae were found to be numerous on the margin of the lamina. The color of the scale was translucent to hyaline.

XVIII. *Asterella tenella* (L.) Beauv.

This species is one of the most variable in the genus, as far as width and length of the thallus is concerned. The ventral aspect of the thallus and its scale insertion pattern is illustrated in Plate IX, fig. 4. It also gives indication of the variability of the eperon. Figures 5, 6, and 7 of the same plate illustrate a scale that was dissected about one cm. from the apical notch. There are two appendages. Oil bodies are scattered in the lamina of the scale and slime papillae are scattered on the margins. The appendage of the scale was usually ovate and entire on scales that were not eroded. From observations in the field, this species stands out for its sensitivity to slight changes in habitat. The resulting variations in thallus size and characteristics of the archegoniophore, and certainly variation in ventral scales need continued critical investigation.

Bischoff (1835) described the scales in this species as lying across the lower surface, arising from the midrib with hairy rhizoids, clearly not touching the margin of the frond, purple in color, not always covering over the entire surface. Taylor (1836) was one of the earliest writers to mention the scales in this species. He called them "stipulae" and described them as acuminate from a broad base. Gottsche, Lindenberg and Nees (1844) indicated there were a few lunulate, purple, solitary scales, furnished with a lanceolate unique tooth on either side. Stephani (1900) stated that the scales were large and purple in color, and the appendage obliquely triangular, acute and hyaline. Evans (1920) described them as ovate to lunulate, more or less pigmented, containing oil bodies (10 to few or scattered). The appendages, he added, were one or two in number, narrowly to broadly ovate, more or less dentate on the margin, and with a rounded apex.

XIX. Asterella echinella (Gottsche) Underw.

The scales of this species appeared to be very susceptible to erosion; a fact which was borne out from examination of many dichotomies. Plate IX, fig. 3 depicts the young scales at the apex as having long and ligulate appendages. They are two in number and have relatively large laminae for their total length. The smaller laminae appearing on the older portions of the thallus, and the irregularity of the appendages owe their origin to erosion. The scales at the apex are closely imbricated but essentially in an alternate arrangement. Here and there, some scales have only one appendage but the basal portion of the eroded appendage is evident. The eperon is very narrow, and varies from being distinct from the lamina to gradually tapering into it. The ventral scales are usually much less impregnated with anthocyanins, in this species, than in Marchantia, Mannia or Plagiochasma species. The appendages lose almost all of the red pigment as they mature. In some thalli examined, slime papillae were very evident on the margins of both the appendage and of the scale, but were much reduced on other thalli.

Stephani (1900) described the scales as small and purple; and the appendages as narrowly lanceolate and entire.

Evans (1920) defined the appendage as narrowly subulate, acuminate, entire or nearly so. His 1923 account is essentially the same. Frye and Clark (1937) followed the description of Evans (1920) in detail. The author found the scales on a few thalli to be completely colorless, and the greater part of the lamina to be a light, fuschia pink on other thalli. Those thalli from definitely xeric habitats, however had the most intensely colored scales.

XX. _Mannia fragrans_ (Balb.) Frye and Clark

This species, widely distributed according to Schuster (1953) in unglaciated regions and their borders, exhibited certain variations, most noticeably in the appendage. Very wide, wedge-shaped, highly colored appendages were found in those specimens from limestone situations with a high run-off of water. In specimens from other situations where surface water had a tendency to seep rather than run off, the appendages were hyaline on the older portions of the thallus and wedge-shaped. Thalli in the latter type of situation were apt to have three appendages to a scale. The insertions were found to be relatively short in this species and the one to follow. Longer insertions with a fair development of the eperon of the scale and a tendency toward dissection of the eperon were found in other species, such as _M. pilosa_. The thallus illustrated in Plate X, fig. 2 comes from a specimen from a high run-off habitat; it shows the most extreme development of the wide, wedge-shaped type of appendage.

The insertion pattern presents an alternating, biseriate arrangement, and the typical short scale insertion associated with a more xeric habitat for this species. The author disagrees, however, with Schuster (1953) that this species probably represents the most pronounced xerothermophyte in the Marchantiales. Oxymitra and more than one species of Riccia can equal this species in growth in xerophytic conditions such as those seen often in Arkansas and its surrounding area, and in the arid regions of Mexico.

DeNotaris (1839) stated this species differed from M. rupestris in its scales (paleae) that were narrow, long, silvery, very plentiful, so that the frond appeared quite bearded at the margin, toward the apex. He appeared to draw his description from Montagne (1837). Leitgeb (1881) noted the rise of ventral scales at the apex of the thallus. Stephani (1900) stated the scales were very large at the apex, imbricate, purple in color, with long double appendages that were hyaline in color, lanceolate, and entire in form and marginal characteristics. Massalongo (1916) added little more to scale description but illustrated two scales in his Plate XII, figs. 8 and 9, showing long, acuminate to narrowly lanceolate appendages on each scale. Casares-Gil (1919) again described the color as purple, with the appendage lanceolate, long and hyaline, and bending over the anterior margin of the frons. Evans (1923) noted the scales to be imbricate, lunulate, deep purple, with appendages occurring in two's, rarely as one or three. In fruiting plants he specified their much larger size, often more or less bleached, and forming a dense white cluster at the apex of the thallus. Müller (1952) described the appendages as limited to two, but occasionally three and distantly inserted. Schuster (1953) illustrated a scale in his Plate 78, Figure 4, which had a somewhat lanceolate appendage with clearly visible oil cells. He also indicated the area of the lamina of the scale that is clearly pigmented.

From the author's observations, all scales examined were deeply colored red violet, extremely brittle, and apparently covered with a heavy layer of cuticle. The color was so intense in some scales that they had to be bleached with a 50% clorox solution before all essential features of the lamina could be seen.

XXI. Mannia rupestris (Nees.) Frye and Clark

This species was worked because the material was at hand for study, and because it possessed scales very different from many of the common Mannias. The scale is rather wedge-shaped, obliquely triangular, with a single appendage that is distinct or indistinct. DeNotaris (1839) noted the scales in this species as "paleae", to be few, minute, fleeting before the naked eye, standing forth at the apex about the reproductive organs. Stephani (1900) described the scale as exceedingly variable and irregular, with the apex acuminate or bilobed. The author often found the lamina to be entirely colorless but with a pigmented appendage. Scales were arranged in two irregular rows on the ventral side of the thallus. Massalongo (1916) noted one to two appendages, that were evanescent, and compared the scales of this species to those of M. pilosa. Evans (1923) stated the scales were ovate, the appendages subulate, acute to acuminate and entire. Müller (1952) described the appendage as lanceolate, and as having oil bodies in the lamina. He illustrated two complete scales showing slime papillae on the margin, and a portion of a scale in which an enlarged slime papilla and oil bodies were present. (Fig. 67, c, d, e. of his work).

XXII. Plagiochasma rupestre (Forst.) Steph.

This species which has some 30 synonyms listed to the present time has been described in the literature almost as frequently, and with ventral scales coming in for their share of attention. A few noteworthy reports will be mentioned together with some observations.

One half of the ventral surface of the thallus is illustrated in Plate X, fig. 3; this includes the general insertion pattern and one of the types of appendage occurring in this species. The scales are deep violet red and are uniseriate on either side of the midrib, as are the scales in all other species of Plagiochasma. The genus contains species that are both xeric and mesic in nature. The xeric forms have scales that are intensely colored, usually greatly expanded, and forming a small cluster at the apex of the thallus. The margins generally inroll so completely that the dorsal surface of the thallus is completely obscured. In more mesic habitats, on cliff edges where an appreciable amount of soil remains, it grows in conjunction with Preissia quadrata, Reboulia hemisphaerica and some of the more mesic species of Asterella; the scales are much less conspicuous, often much lighter in color, and the margin of the thallus is much less inrolled. These conditions were observed in the field, at an altitude of 3,800 feet in the ectones between subtropical and neoarctic vegetation.

Gottsche, Lindenberg and Nees (1844) noted the scales were lanceolate and obsolete on older portions of the thallus. Leitgeb (1881) stated that the ventral scales were in two rows. Stephani (1900) described them as imbricate, purple in color, broadly crescent-shaped and abruptly appendiculate, with narrow lanceolate appendages with entire margins. Massalongo (1916) further added that the scales were subfalcate, slightly extended beyond the margin of the thallus, and with one to two appendages not constricted at the base. Casares-Gil (1919) ascribes to the scale, a reflective metallic color. He illustrated a portion of the ventral scale in his Figure 149, f. Evans (1915) noted that the scales were obliquely lunate to ovate, entire, with a few scattered cells containing oil bodies; appendages were one or two, rarely three, ovate to lanceolate, acute to acuminate at the apex. His 1923 paper has essentially the same data. Müller (1952) mentioned the presence of oil bodies in the appendages. The author's findings coincide with those of previous investigators.

XXIII. Cryptomitrium tenerum Aust.

This species, closely related to Mannia, has its ventral scales in two very irregular rows that are somewhat scattered over the ventral surface of the thallus. It is a species in which early schizogenous splitting of the lamina, or more often, of the eperon of the scale takes place. In figs. 2, 3 and 4 of Plate XIII there is one relatively uneroded scale, and two partially eroded cnes. The form of the cell in the laminae of these scales is nearly isodiametric. No obvious oil cells were seen in them. Small and very reduced slime papillae were observed on the margin of the lamina. Many of the filiform appendages were not uniseriate but were from two-four cells wide. The uniseriate appendages, either single, or in pairs on the anterior margin of the lamina, were observed on older parts of the thallus. Figure 5 of the same plate, illustrates the scattered arrangement of these scales and their fragments. Many of those occurring on the midrib of the thallus have developed their own "false appendages".

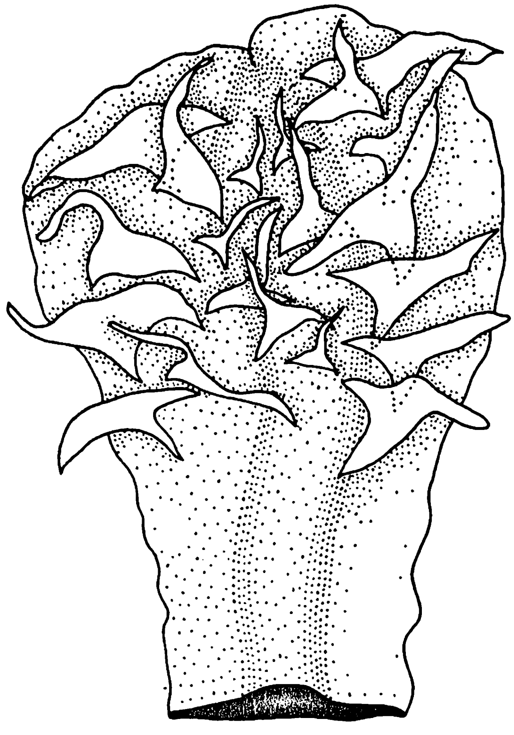
Gottsche, Lindenberg and Nees (1844) stated that the costal scales eroded early (an implication). Under a synonym of this species, they recorded that ventral scales were

Plate XIII

Fig. 1, *Clevea hyalina*, ventral aspect, X 26.

Figs. 2-4, Ventral scales of *Cryptomitrium tenerum*, X 72.

Fig. 5, Ventral aspect of *C. tenerum*, X 15.



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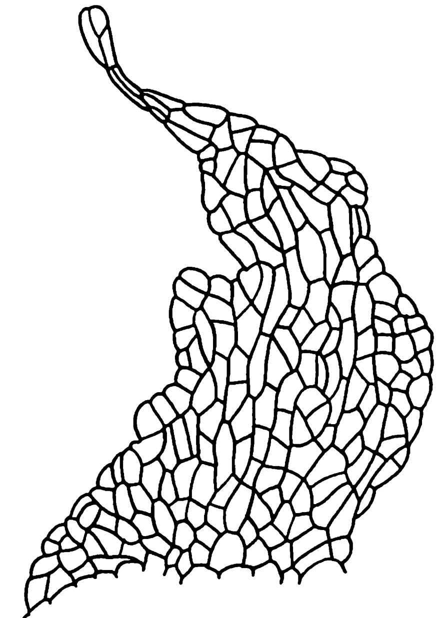

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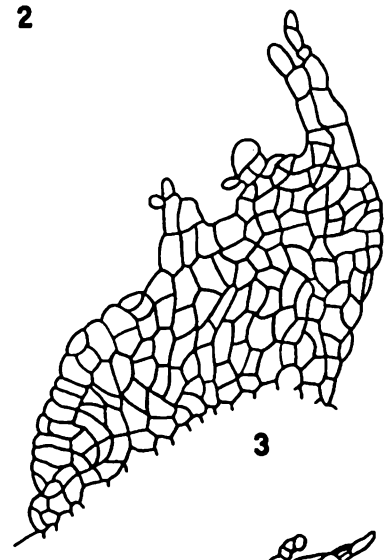

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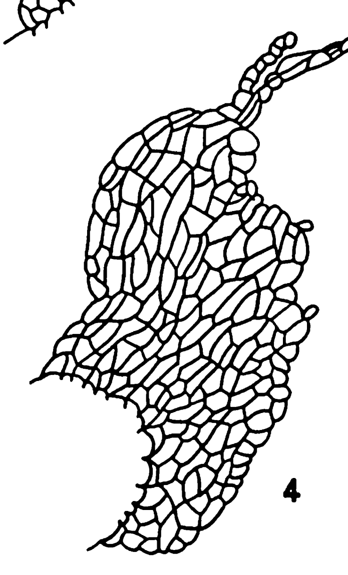

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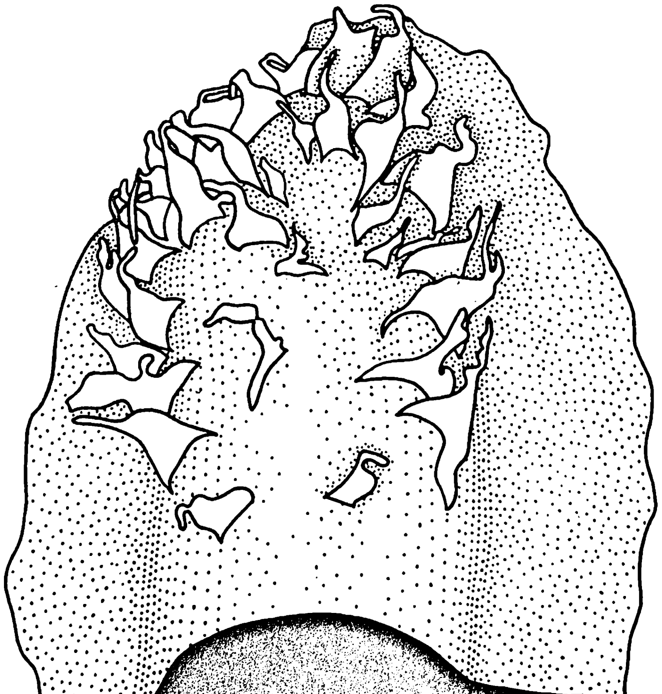

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rare. Stephani (1892) described the scales as biseriate in arrangement, with small, remote, filiform appendages, purple to violet in color, scales ovate in form and variously lobed. He added that the schizogenous splitting, that we note, was due to the irregular lobing of the scales; that the splitting, not infrequently down to the base, was responsible for the obscure biseriate arrangement. Stephani (1900) reported that the lobes of the scale that split and separate the farthest were furnished with filiform appendages, composed of eight superimposed cells. He added further that the various fragments attached to the thallus were distantly placed in relation to each other. Kashyap (1929) underlined these remarks by saying of the genus that the scales were small, distant, and in two rows.

XXIV. Peltolepis grandis Lindb.

Split and eroded scales, as well as uneroded ones showed small peg-like slime papillae on the margin. These papillae are very reduced, varying from 13-20 microns long. In many specimens they appear to be merely a marginal cell, but when they are stained in Toludine blue, their high concentration of cytoplasm is quickly revealed. The apical portion of old eroded scales on which a portion of a true appendage is still present has very isodiametric cells, while most of the laminae consist of asodiametric cells. The cells of the lamina varied in size from 20-50 microns wide to 65-200 microns long. The schizogenous splitting of the scales usually takes place very early in this species. Plate XV, fig. 9 shows the ventral surface of the thallus, representing the extreme of this process, as we have noted it. Plate XVI, figs. 1 and 7 depict two complete scales. Figure 1 represents the outline of an intact mature scale, one of the few found. Figure 7 represents a very young scale whose appendages were still inserted in the apical notch of the thallus. This young uneroded scale had slime papillae located at regular intervals on its margin. Slime papillae were found on both the ventral and dorsal face of these structures. The cells of the lamina were asodiametric for the most part, while those of the appendages were essentially isodiametric in form, (Plate XVI, fig. 7). No rhizoids were found inserted on the scale. All figures in Plate XVI, except Figs. 1 and 7, represent variations in schizogenous splitting and erosion of the main fragment of the ventral scale.

Lindberg (1882) mentioned the ventral scales as very few, and not reaching the margins. Stephani (1900) stated that the scales were hyaline, or purple at the base, large, abruptly appendiculate from a semicrescent-shaped base; and that appendages were lanceolate, rarely two or three acuminate, and furnished with key-like cells at the margin and the apex. It might be well to add here, that in every case where the author observed thalli with scales apparently having only one appendage, dissection of scales with their appendages still inserted in the apical notch of the thallus, revealed two appendages attached to the anterior margin of the meristematic lamina. Massalongo (1916) said the scales were hyaline or light red, subfalcate, with one to two appendages. He also illustrated the ventral surface of the thallus with four rows of scales in Plate XXI, fig. 10. Casares-Gil (1919) stated that the scales were semilunar, with a well differentiated appendage, lanceolate in form. Evans (1923) noted the scales to be small and inconspicuous, the appendages white to purplish; statements later adopted by Frye and Clark (1937). C. Douin (1923) attributed the fragments of scales, displaced after they are split off, to a secondary segmentation of meristematic cells at the apex of the thallus. He referred to these fragments as merophytes. He gives one the impression that the merophytes are separate entities having their own independent origin, rather than one by schizogenous splitting as we had observed them to be. Müller (1952) indicated that the appendages were broadly lanceolate with numerous slime papillae.

XXV. <u>Targionia</u> <u>hypophylla</u> L.

This species has one to several slime papillae on the margin of the appendage. A rather wide neck attaches the appendage to the lamina of the scale, and is only slightly less in width than the appendage itself. An apical process of the appendage consisted of two-four cells, and the distal end of this process was not a slime papilla. Often, another large tooth or process on the lateral margin of the appendage consisted of two-three cells. Oil bodies were chiefly confined to the lamina of the scale and were 8-14 in number. Occasionally, an oil body or two was found in the neck of the appendage. Cells of the lamina were generally rectangular in form and varied from 26-80 microns long, and 20-30 microns wide. At the base of the lamina, where the lamina is more than one cell in thickness, several tuberculate rhizoids are inserted. The eperon is usually distinctly delimited by its extremely long and narrow cells with thin walls. Slime papillae are located at irregular intervals on the margin of the lamina and of the eperon. They are very small, ranging in size from 10-15 microns in width, to 15-20 microns in length. Oil bodies vary in diameter from 10-30 microns. On the two surfaces of the appendage, the slime papillae are much larger than those on the margin, are from one to three in number, and are 50-60 microns long. The ventral surface of the thallus, showing the apparently opposite arrangement on each side of the longitudinal axis, is presented in Plate VI, fig. 3. Every thallus examined showed an appendiculate scale here and there out of line with the rest of the scales in a given row.

Gottsche, Lindenberg and Nees (1844) described the ventral surface of the thallus as being dense with imbricate, subtriangular, and tridentate scales. Under another synonym of the species, they spoke of the scales as rotund. Stephani

(1900) said the scales were purple in color, remote, obliquely triangular, and with entire to dentate margins. Pearson (1902) described the thallus of this species as "clothed on the postical (ventral) side with numerous, densely imbricate, broadly lanceolate, chocolate-purple scales." He illustrated two scales, and a portion of a third after Schiffner, Alliers and du Buysson. C. Douin (1906) said the ventral scales were in two rows. Lotsy (1909) illustrated a mature scale with numerous rhizoids at its base. (Figure 3, Page 112 of his work). Deutsch (1912) in contrast to some of our findings, stated that the scales were arranged in a wonderfully exact regular fashion, that the two rows of scales were separate from the first, and that they arose from young segments close to the apical cell. O'Keefe (1915), working on the structure and development of this species, illustrated a longitudinal section of the thallus that showed the scale papillae, arising one-two segments ventrally from the apical cell. Massalongo (1916) described them as violet in color, imbricate, obliquely ovate to subtriangular, with a crenate-dentate margin. He also illustrated the ventral surface of a fertile thallus and a mature scale in Plate XXV, figs. 3, 6 respectively. Casares-Gil (1919) merely indicated the location of scales on the thallus but illustrated a scale and the ventral surface of a fertile thallus in Figure 166, a, d. of his work. Evans (1923) noted the scales to be large but scarcely reaching the margin, and the appendage lanceolate, with its margin entire to sparingly and irregularly spinose-dentate. Macvicar (1926) described the ventral surface of the thallus as strongly convex; the scales purple-black in color, large, obliquely triangular and with a broad, awl-shaped appendage. Kashyap (1929) described the ventral thallus surface as purple; the scales as obliquely, broadly triangular, with a long subulate apex, and the margin as usually with projecting mucilage cells.

XXVI. Cyathodium smaragdinum Schiff.

This species, illustrated in Plate VI, fig. 4, shows the ventral surface of the thallus with the small, filamentous, or minute plate-like scales clustered at the apex of a dichotomy. These scales are essentially like all others in Cyathodium except in C. foetidissimum. A series of scales is illustrated in Plate VIII, figs. 1, 2, 3 and 4. Figure 1 is the plate type of scale, the largest the author could find. In every case the apical cell of the scale is a slime cell. These scales are very delicate, and great care had to be exercised during dissection to keep them from collapsing. Toludine blue marked their location immediately upon its application.

Leitgeb (1881) wrote that the ventral scales appeared only on the apical portion of the thallus, that they were in two rows, though they might appear in one row; and that at the apex there was a small hyaline cell. Stephani (1900) described the scales of the genus as being minute or entirely wanting. Massalongo (1916) noted them as being three-four cells long and evanescent. Lang (1905) described the thallus ventral surface as not having a distinct midrib; and the ventral scales as very inconspicuous. Both observations were made on C. cavernarum, however. Kashyap (1929) apparently in accord with Stephani (1900) said of the ventral scales in the genus, that they were minute, either in two rows or wholly absent. Chavan (1937), in a morphological study of C. barodae, now a synonym of this species, described the ventral scales as filaments and small plates and illustrated them in Figs. 8-12 of his work. Schiffner (1938), in his monograph on the genus, placed the last mentioned species in synonomy with C. smaragdinum, and suggested that on the under side of the thallus and between the rhizoids there were a few rudimentary ventral scales. Our findings indicate that the scales are rather distantly located, and irregularly so on each side of the longitudinal axis of the thallus.

XXVII. Sauteria alpina Nees.

This species is often reported in the literature as having two irregular rows of scales on each side of the median longitudinal axis of the thallus. This configuration is represented in Plate XV, fig. 1. Observations were made of a few thalli that showed a scattered arrangement. This is another species in which longitudinal, schizogenous splitting of the lamina of the scale takes place early in the ontogeny of the scale. The later this process takes place, the more orderly is the resulting arrangement of scales in two rows. Pairs of long, narrow, young scales, that actually represent two separate fragments of one scale, can often be found at the apex of the thallus. These fragments have a tendency to develop their "false indistinct appendages". Fragments of scales, taken from older portions of the thallus, appear in Figures 3, 4, 5, 6, 7 and 8 of Plate XV. Figure 2 represents a young, uneroded scale, that had its apical portion over the end of the thallus. Most of the cells are isodiametric in form, and the slime papillae are very few on the margin, often hardly projecting beyond it. Most of the young scales dissected had this oblique triangular form. The scales were hyaline to light purple in color.

Gottsche, Lindenberg and Nees (1844) described scales as ovate to lanceolate, with an acuminate apex. Lindberg (1882) merely remarked that the underside of the thallus was scaly. Stephani (1900) stated the scales were imbricate, in four series, obliquely triangular from a broad base, with large irregular cells, and with margins irregularly dentate. Casares-Gil (1919) corroborates this opinion. Evans (1923) added that the scales scarcely extended to the margin and did not form a conspicuous apical cluster. Kashyap (1929) described them in detail: "Ventral scales imbricate, in four rows, hyaline, oblique from a broad base, formed of large irregular cells, apex gradually acuminate, upper half coarsely and irregularly dentate or sublaciniate with clavate cells." Frye and Clark (1937) described them in part, as translucent, long and narrow.

XXVIII. Corsinia coriandrina (Spreng.) Lindb.

This species is frequently reported in the literature as having a scattered arrangement of scales. The ventral surface of the thallus, depicted in Plate XIV, fig. 6, shows this arrangement. The author also observed several thalli that one could describe as having two irregular, longitudinal rows. The scales split most frequently in the eperon region; but, as can be seen in Figs. 4 and 5 of this plate, there are two fragments of scales with the biseriate type of appendage attached, separated by a splitting of the lamina. Figures 1 and 2 represent intact, uneroded scales with their typical filiform appendages, which in places are uniseriate as well as biseriate. Figure 2 shows the youngest scale in this plate. Figure 3 shows the eperon of a scale that was located about 2 mm. from the apical notch splitting off a fragment. Oil bodies are few, usually two-four per scale. Slime papillae are scattered on the margin, and somewhat irregular in form. Most of the cells of the entire scale are isodiametric in form.

Corda (1829) indicated scales or stipulae as he called them were present in this genus. Bischoff (1835) described the scales (palea) as very delicate, transparent, lanceolate-

Plate XIV

Figs. 1-2, Mature scales of *Corsinia coriandrina*, X 72.

Fig. 3, Mature ventral scale of *C. coriandrina* showing a fragment begin split off of its eperon, X 72.

Figs. 4-5, Two scale fragments with the true appendage attached of *C. coriandrina*, X 72.

Fig. 6, *C. coriandrina*, ventral aspect, X 18.

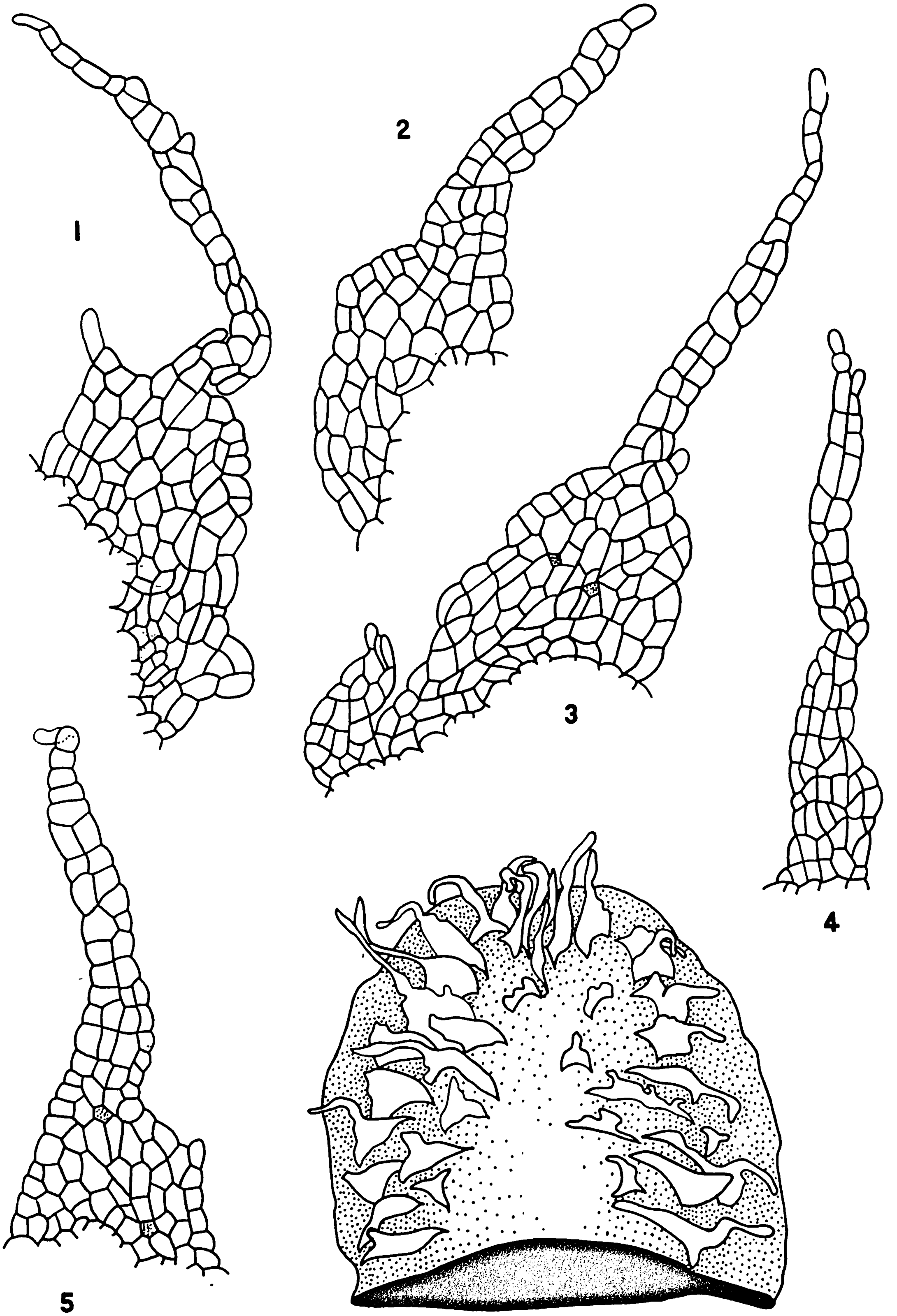

Plate XV

Fig. 1,	Sauteria alpina, ventral aspect, X 15.
Fig. 2,	S. alpina, mature ventral scale, X 68.
Figs. 3-8,	S. alpina, various ventral scales and fragments, X 28.
Fig. 9,	Peltolepis grandis, ventral aspect of a thallus, showing the extreme observed in the process of schizogenous splitting of the ventral scales, X 15.

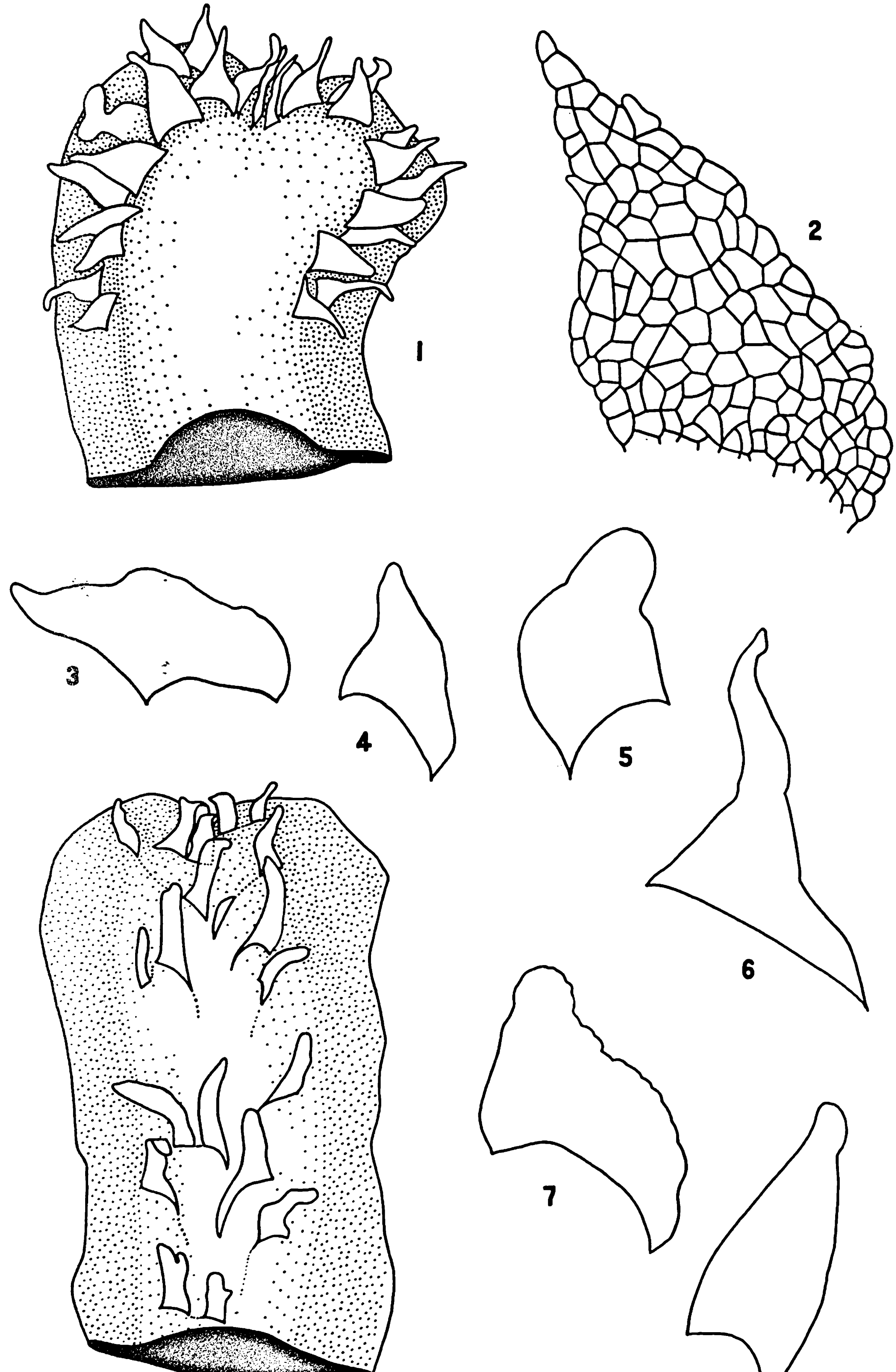
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Plate XVI

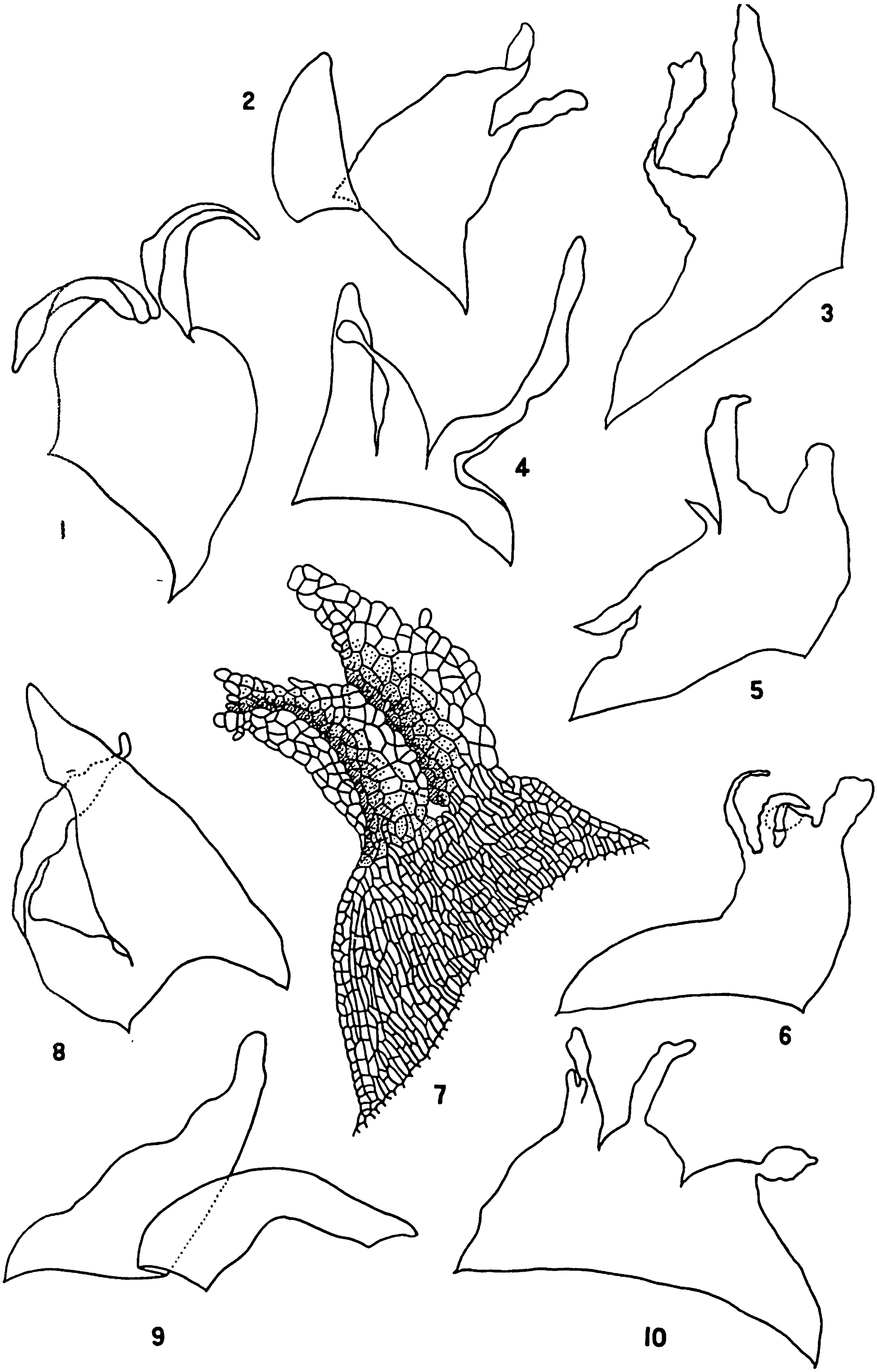
Fig. 1, *Peltolepis grandis*, outline of a mature ventral scale with its two appendages, X 28.

Figs. 2-6, *P. grandis*, various scales showing varying degrees of schizogenous splitting, X 28.

Fig. 7, *P. grandis*, young appendiculate scale with two almost mature appendages, X 64.

Figs. 8-9, *P. grandis*, ventral scales with almost complete splitting of the lamina, X 28.

Fig. 10, Ventral scale of *P. grandis*, showing both false and true appendages, X 28.



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subulate, a fact not many authors can discern, he added. Gottsche, Lindenberg and Nees (1844) stated that the thallus of this species either had scales or was sparsely supplied with them. Leitgeb (1881) stated that on the ventral side of the thallus there were not two, regular rows of leaves (scales) but across the whole thallus surface there were spread out, very small, but fairly long, colorless scales, and between them arose both kinds of rhizoids as well as on the midrib. Stephani (1900) described the scales as hyaline, conical in form, and putting forth uniseriate rhizoids from the base. Cavers (1911) stated that they were small, and scattered over the whole underside of the thallus; and that the appendages were reed-like and bent over the growing point. He emphasized that the appendages are characteristic of the development of the appendiculate ventral scales of the higher Marchantiales. Massalongo (1916) illustrated two mature scales with broad ovate bases and long filiform appendages in his Plate, XXVII, fig. 9. Evans (1919) suggested that they were ovate to lunulate, colorless, and gradually tapered into a filamentous appendage. His later account, (1923) was essentially the same except to describe the scale margin as entire. Müller (1952) stated that they were in two longitudinal rows and that the appendages eroded early.

XXIX. Oxymitra paleacea Bisch.

The characteristics of the scales of this species have already been explored in the section on scale development.

The findings in the literature are either in accord or disagree with those earlier data.

Lindenberg (1829) described the scale as long, pale to white, girdling the frons on both sides. Bischoff (1835) described the scales in this species as "paleae", arising on both sides of the midrib, close together, imbricate at the base, lanceolate-subulate, white, more or less concealed under the narrow attenuated margin of the frond, or else stretched out, causing the margin to appear hairy; this description was amplified with excellent plates. DeNotaris (1839) described the scales as "paleae", not exceeding the margin of the frond, but coming forth clearly from the margin, making it appear hairy. Gottsche, Lindenberg and Nees (1844) stated it was triangular in form, and somewhat keel-shaped. Leitgeb (1881) suggested that there were two long rows of leaves (scales) which are immediately independent in form from their point of origin, and that, they agreed essentially with the leaves in the Marchantiaceae. He added they had a long continuing basal growth. Levier (1894) described the scales as numerous, quite visible, white at the margin of the thallus, but medially always black or violet in color, rarely taking on a red tint. Stephani (1900) said they were triangular, large, densely imbricate and purple at the base; the apex free, hyaline, greatly cuspidate, surpassing the margin of the frons, and curving inward like a hook at the apex of the frons. Lotsy (1909) stated the scale arrangement was in two rows. Cavers (1911) added to this latter remark, that they had two independent rows. Casares-Gil (1919) described them as large, triangular and falcate, and illustrated a portion of a mature scale in his Fig. 138 d. Howe (1923) indicated that the lateral ventral scales were numerous and conspicuous, projecting far beyond the margins, 2-4 mm. long, in shape, long-lanceolate or ovate with acuminate or filiform apices, and reddish-brown in color at the base. Gyorrfy (1926), who was concerned with ventral scales in their protective role at the vegetative point, said they were robust, reddish, close together, hyaline, and ending in a spike at the apical end of the thallus. Frye and Clark (1937) illustrated, after Howe (1914), a rosette of thalli showing the apices of scales projecting beyond the margin. Müller (1952) stated there were no oil cells present, and illustrated a portion of a mature scale in his Fig. 94 f. Wittlake (1954) indicated the presence of ventral scales in Figs. 5 and 6, Page 306 of his report.

XXX. Ricciocarpus natans (L.) Corda

This genus has numerous rows of alternating scales on the ventral surface of the thallus. The insertions of the scales are represented in Plate XVII, fig. 2. The scale itself has been described and illustrated several times in the literature, so, the author merely illustrates the basal portion and its insertion in Figure 5 of the above plate. This view of the base of the scale, shows the face of the insertion, attached to the thallus, and indicates its variable width of from one-four cells.

Bischoff (1835) described the scales in this species as reddish violet "paleae" in a clump on both sides of the margin; to illustrate this he presented plates showing figures of a single scale, arrangement of scales, and origin of the scales. Leitgeb (1881) noted that the ventral scales were prominent on all sides, and a dingy brown in color in the aquatic form. When the species was cultivated on earth, he said, the scales were short and diminutive. He added that meristematic ventral segments at the apex of the thallus were in a horizontal row, as in the majority of Riccia species, and that each papilla of this row then grew out into a ventral scale. The scales he believed were in two-three rows, the bases near each other. A footnote completed the remarks, indicating that most often the scales in growing plants were found in four rows. Stephani (1900) stated that the scales were absent or else obliquely inserted in three rows on each side of the costa, and dentate with a free margin. Goebel (1905) said that the large water form has strongly developed ventral scales which contain chlorophyll. Lotsy (1909) described them as being in many rows distributed over the entire surface of the thallus. Cavers (1911) noted them as long and narrow, and as showing a long and continued growth in length owing to the basal cells remaining meristematic. He also mentioned that the land form, discovered by Lewis, (1906), had scales short and semilinar in shape. Massalongo (1916) varied the description by saying they were lamelliform, linear-lanceolate, violet or subviolet, with a margin remotely dentate to serrulate with highly colored teeth. Casares-Gil (1919) added that they were in three rows on each side of the costa, large, acuminate and denticulate on the margins, and violet in color. He illustrated a portion of a mature scale in his Figure 137 b. Howe (1923) summarized them as, lateral-ventral scales, usually large and conspicuous. Macvicar (1926) noted the presence of oil bodies in the scale lamina. Kashyap (1929) described the scales of the floating form as pendant, serrated and violet, and in the terrestrial form as violet, dentate. Frye and Clark (1937) emphasized the scale color in terming it reddish-violet or brownish-green, and stated that there were small or rudimentary scales only in the land form. Schuster (1949) gave an adequate description by calling them stiff and sword-like, and purple in color. In his 1952 work he elaborated this by adding that they are linear, spear-shaped, violet-purple, and form a conspicuous ventral mat.

XXXI. <u>Riccia lamellosa</u> Raddi.

DeNotaris (1839) described the scales of this species in detail. He stated that as whitish, hyaline, roughly textured, broad, short, rotund "lamellae", they stand out at the margin of the frond, thick in clusters, imbricate toward the apex of the frond edges, in dry condition they are brittle and curled up, and are destroyed quickly at the base of the frond. Gottsche, Lindenberg and Nees (1844) described the scales of this species, under the name R. Dufourii, as imbricate, rotund of margin, incurving and pale in color. Leitgeb (1881), in discussing several species of Riccia including R. lamellosa, indicated that on the ventral side of the thallus there was a row which later, because of lateral growth of the thallus, became split. This he ascribed to Kny as the first observer, though as he observed, the process was common to many Riccia species. Stephani (1900) described the scales as large, robust, exceeding the margin of the thallus, densely imbricate, and hyaline with a papillose-crenate or subdentate margin. Lotsy (1909), under the section heading of Ricciaceae, stated that one found on the under side of the thallus, one row of chlorophyll-containing ventral scales. Cavers (1911) mentioned that, in Riccia species, the ventral scales are generally present, but often small, and never showing differentiation of an appendage. Massalongo (1912) termed these scales as very large, subfalcate, somewhat entire and extended beyond the margin of the thallus. Howe (1923) suggested they were obtuse and undulate, patent or somewhat imbricate. Macvicar (1926) said, "ventral scales are originally in one row, in the middle of the lower surface, but by expansion of the growing thallus they become split into two rows, one on each side of the median line". This might be taken as a summary description of ventral scales in Riccia and their disposition on the ventral side of the thallus. Kashyap (1929) discussed the ventral scales in the genus as "Ventral scales usually in one row at the apex, but later, through rupturing in the median line, apparently two-rowed, well developed, rudimentary or sometimes absent, hyaline or colored. Schuster (1953) stated that the thallus was characterized by prominent, decolorate ventral scales which project slightly beyond the margin, when the segments are moist, for form a distinct fringe, but become very prominent when the thallus is dry.

The ventral surface of this species with attached scales, is figured in Plate XVII, fig. 6. The scales are closely imbricated with rhizoids, which are not shown, arising on the median margin of the scale. The pair of scales next to the apical scale, in this illustration, has very irregular median margins due to the recent splitting. The apical scale is essentially shield-shaped in outline. Other than this, our findings are in accord with those in the literature.

XXXII. Riccia rhenana Lorbeer

The scales of this species are not usually split in two at the apex of the thallus. They are very broad, membraneous, and composed of comparatively large cells for such a small structure, and are located distantly on the ventral longitudinal axis. In Plate XVII, figs. 3 and 4 show the ventral side of the thallus, the scale arrangement, and a mature ventral scale. This species has undoubtedly been described many times in the literature under the name of R. fluitans, but we hardly ever find the scale itself described in these accounts. Many taxonomists have merely referred to the scales in the R. fluitans complex as absent or rudimentary. In fresh thalli, their location can be easily detected by the appearance of colonies of Algae and other debris occurring in the pocket formed between the thallus and the scale. In this species the scale may be said to be shield-shape. Müller (1942) suggested that it was half moon-shaped. This would be so, if only the apical portion of the scale is considered, but the scale has a broad posterior median lamina, consisting of from 5-12 cells long and 8 cells wide. The anterior portion of the scale, which is extended and rounded, is entirely free; it has two small lateral projections consisting of a few cells each. The basal portion of these projections are inserted directly on the thallus.

This species was chosen because it represents one of the largest species in the R. fluitans complex, and characteristically possesses the same type of scale that is found in R. fluitans. Stephani (1901) stated that because of its aquatic habitat, scales would be entirely useless and would be found to be entirely absent in this species.

Plate XVII

Fig. 1, *Oxymitra paleacea*, ventral aspect, X 20.

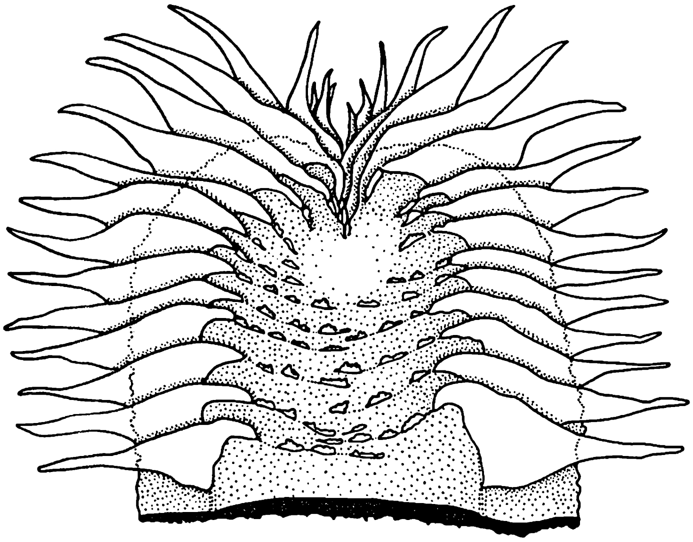
Fig. 2, *Ricciocarpus natans*, ventral aspect showing insertion pattern, X 8.

Fig. 3, *Riccia rhenana*, aquatic form ventral aspect, X 4.

Fig. 4, *R. rhenana* ventral scale X 83.

Fig. 5, *Ricciocarpus natans*, base of ventral scale showing face of insertion, X 70.

Fig. 6, *Riccia lamellosa*, ventral aspect, X 59.



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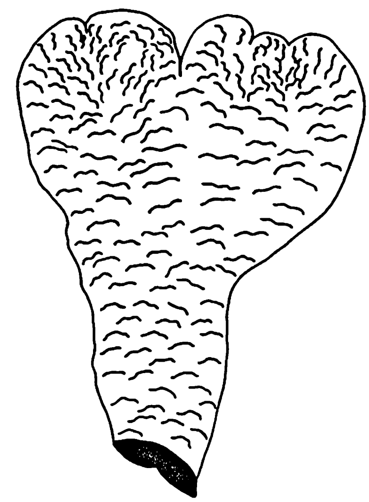

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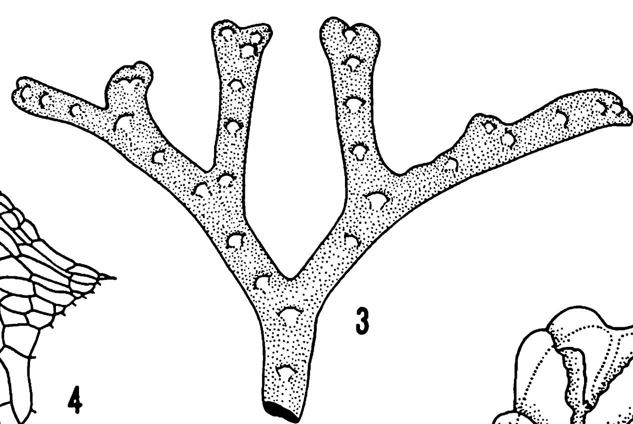

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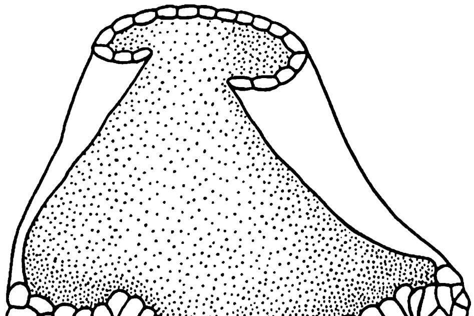

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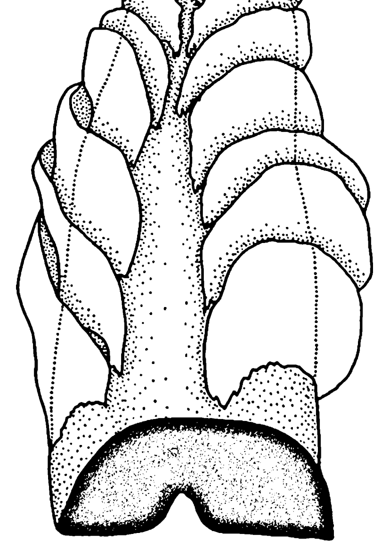

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THE EROSION OF VENTRAL SCALES

In the opinion of the author, erosion is the most pertinent process influencing the interpretation of scale form and size. In the genera, Peltolepis, Clevea and Sauteria the influence of erosion occurs early during elongation and maturation in the ontogeny of the scale. Here, total schizogenous splitting occurs from the apical portions of the lamina, basally to its insertion. If this comes early, as it usually does in these genera, the half-scales or smaller fractions of the scale migrate from each other to some distance. The migration is due to a differential elongation of cells of the ventral epidermis of the thallus, and the direction in which these elongations take place. Those cells in the central portion of the midrib, elongate parallel to the linear axis of the thallus, more than in any other direction. The young scales, however, are inserted on meristematic midrib and wing cells of the thallus. Those cells of the wing of the thallus, or on the margin of the midrib, elongate in a more lateral-direction. Thereafter the medial fragment of a scale or half-scale will be displaced posteriorly a much shorter distance, but will also move back on the thallus in a lateral direction, or toward the margin of the thallus. How far these fragments will move apart depends upon how early the splitting of the lamina occurs. In the genus Peltolepis some thalli were found in which such splitting occurred rather late in the maturation of the scale. When this happens, the scale has a tendency to remain near the marginal portion of the mid-rib region. The laminausually splits just between the two appendages, to its base, when the scale is mature. The thallus shown in Plate XV, fig. 9, exemplifies the extreme in this process where schizogenous splitting took place very early. In other genera, such as Corsinia, Oxymitra, and Cryptomitrium, splitting is restricted to the eperon. This again occurs early in the maturation of the scale, and the fragment, cut off from the eperon, may be oriented on an older portion of the thallus in an irregular fashion or in a regular linear way, as in the genus Oxymitra, (Plate XVII, fig. 1).

Erosion in scales other than in the above noted genera, is restricted to the process of actual tearing and stretching of cellular tissue of the scale. In some genera, cells can erode by the process of dying and becoming colorless, and by dropping out on the margin due to the breakdown of their middle lamellae. When this happens the margin of the scale, after a time, usually becomes restored in such a way that no indication is left of the location, along that margin, where the eroded cell disappeared. More often large areas of cells are torn out or eroded away by the above mentioned process, and this definitely alters the general outline of the scale.

Young scales that have not begun the elongation and maturation of their laminae, are very resistant to erosion. This is usually due to the large amounts of mucous and slime that engulf or embed them. In those species that do not have slime papillae on the margins of their scales, slime cells of the ventral tissue provide the necessary mucous. This is very noticeable in the genus Oxymitra where slime cells in the ventral surface of the thallus are in regular rows next to the insertion of the scale, and in irregular rows a little distance from the insertion.

The general erosion of scales is, as might be expected, greater when a dichotomy of a thallus is growing over rather coarse soil. Fine alluvial soils cause little erosion to scales, and often times, when making this study, as has already been indicated, the selection of a particular thallus dichotomy was made of those not in contact with the soil at all. Massalongo (1916), in his illustration of the ventral scale arrangement in Peltolepis (Plate XXI, fig. 10), must have made this illustration from a culture specimen, or from one that had had little contact with the soil. In the material, examined by the author, there was failure to find any thalli of this genus, exhibiting such regularity of scale arrangement, or as complete an individual scale on the older portions of a thallus as he depicted. In Marchantia polymorpha the lamina frequently becomes completely eroded down to two or three tiers of cells in height at its basal insertion, and all that is left uneroded is the expanded, dark-colored, or black, eperon of the scale which covers the median rhizoidal bundle running the length of the thallus. This has been the chief reason for the interpretation, by some investigators in the past, of the eperon of this species as a separate median scale. Evans (1917) clearly stated, as did Muller (1952), that the median row of scales in this species is appendiculate.

Different genera vary a great deal in the susceptibility of their scales to erosion. One extreme instance of this, is that of Dumortiera whose scales become so quickly eroded, that intact scales exist only closely around the apical notch of the thallus. This has led some investigators, such as O'Hanlon (1934) and Evans (1923) to state that no scales exist on the ventral surface at all, or that they were without distinct appendages. As can be seen in Plate IX, fig. 1, the only remains of a ventral scale on older portions of the thallus, are the two- or three-celled, thick basal portions of the lamina, seen as ridges on its ventral surface. In Plate VIII, figs. 5, 6, can be seen an older and a young scale respectively, with distinct appendages, and at the same magnification. The young scale has its appendage still curved upward into the apical notch of the thallus. There also seems to be a correlation between the degree of erosion and the structure of the cells making up the lamina. In such genera, as Sauteria, Corsinia, Cryptomitrium and Clevea, that have isodiametric laminal cells, a high tendency toward erosion is the rule. On the other hand, those scales with asodiametric cells, such as in Marchantia, a much lower tendency is evident in the fact that perfectly intact scales can be found on older portions of the thallus. Again, Dumortiera, in which the scale lamina has essentially the same general kind of cell form as Marchantia, a high erosional tendency is exhibited.

THE FUNCTION OF THE VENTRAL SCALES

The interest in the part that ventral appendages play in the life of the thallus has been centered on their probable function in the conduction of water and their efficiency in this process. This particular function was first pointed out by Kny (1890) who compared the rhizoidal bundles as wick-like structures, which served as such in the conduction of external water on the ventral side of the thallus. Apparently it was Cavers (1904), who also mentioned ventral scales in this process as facilitating the process in conjunction with rhizoids. Bolleter (1905) also made observations on rhizoids and ventral scales which confirmed the opinions of previous authors.

Marchantia polymorpha has a very efficient system of rhizoidal bundles made up of rhizoids originating under each scale. The rhizoids converge under the scale into a median bundle, and where the bundle ends it is directed toward the next posterior median scale. In this way, a continuous system of rhizoidal bundles is formed from the margin of the thallus to the midrib. The many tuberculate rhizoids, which originate on the surface of the laminar scales themselves, can also be observed joining the rhizoidal bundles as they extend between scales and emanate from beneath them. In consequence, the scale contributes much to the external conduction of water in addition to covering the rhizoidal bundles, by forming the narrow capillary spaces between the scale and the ventral surface of the thallus.

At the apex of the thallus, however, the scales, rhizoids, and mucilagenous materials play a great part in the retention of water around the meristematic tissue in this region. Any excess of water, which is acquired in this area, is quickly transferred down the midrib rhizoidal bundle in Marchantia polymorpha and transferred laterally to the margin. The midrib area is all the more efficient in this respect in this species, because of the tremendous development of the posterior eperon of the appendiculate scale. This expanded eperon can be seen readily in Plate IV, figures 7 and 8. Figure 7 is of an old appendiculate scale whose eperon is quite long and has turned black in color. The entire insertion of the eperon is parallel to the axis of the midrib, and parallels portions of three or four eperons of scales, more apical in position. By this condition of successive extended eperon the median, rhizoidal bundle is completely enclosed for the full length of the thallus except in the proximal apical region. McConaha (1939) in an investigation pertaining to the external conduction of water, calculated that ventral scales are responsible in Conocephalum conicum for 380% increase in the ventral surface of the thallus and that rhizoids contributed 3,100%.

Another function, attributed to the ventral scale or its subdivisions, is the protection of the meristematic region around the apical cell by the numerous appendages in those species normally having appendiculate median scales. This is accomplished by the successive overlapping of the young to completely mature appendages. In species of *Marchantia* this overlapping of older appendages is clearly visible in the apical notch from the dorsal aspect of the thallus. The young appendage, as noted earlier in development, grows upward through the notch and enlarges in the later stages of elongation, almost completely covering those beneath it. Since the young scales are pulled out of the notch during the elongation and maturation of the ventral surface of the thallus, enlargement of the laminar portion takes place at a much slower pace. As Goebel (1905) has stated, when this happens, their chief function is finished. In contrast to this, however, the eperon, particularly in *Marchantia polymorpha*, still performs its function in relation to the central rhizoidal bundle long after the rest of the scale has eroded away entirely. It must be remembered, on the other hand, that perhaps the above discussion only pertains to those thalloid liverworts that have a problem of obtaining water because their ventral surface tissue is not absorptive; for, we find this arrangement of ventral appendages of the thallus in species living in aquatic to xeric situations.

In other genera, where scales are almost non-existant on the ventral surface, as in Cyathodium or Monoclea, and are limited to the apical notch, they have the sole function of retention of water in this area of the thallus by a production of slime. In genera like Peltolepis, Sauteria, Corsinia, Cryptomitium, and Clevea no rhizoidal bundle system exists, but rhizoids are present at the base of scales as well as on the ventral surface of the thallus. Here, in the many thalli examined, it appears that there is a general provision for the absorption of water over the entire ventral surface tissue of the thallus. In such species as Riccia fluitans and R. rhenana, the scales being median in position and shield-shape, obviously function only in the role of protector of the growing apical region of the thallus, where they are half the size than they are at maturity. Goebel (1905) and Stephani (1896) in relation to the Ricciaceae have attributed the functions of absorption and of giving the plant more stability in the water, to the ventral scale of the aquatic form of Ricciocarpus. Since they contain chlorophyll, he believed they were responsible for a certain amount of assimilation. Kashyap (1914) found chloroplasts in the young scales of Targionia hypophylla var. integerrima as did Goebel (1910) in the scales of Monoselenium tenerum. Cavers (1904) observed not only chloroplasts in the young scales of Reboulia hemispherica but also starch grains. Cavers (1904) also ascribed another protective function of scales; that due to the oil bodies they contain. The oils in these cells give off a pronounced odor, as in Conocephalum conicum, Mannia fragrans, and Reboulia hemispherica, and "they appear to play an important part in the economy of the plant, since, as shown by Stahl, they serve to protect the thallus against the attack of snails and other animals". Macvicar (1926) reiterated the function of rhizoids and scales in relation to the conduction of water and mentions that storage of water by the rhizoids is facilitated by the overlapping scales which obviously prevent large losses of water by evaporation.

Another role of ventral scales as protective structures, is their growth around and covering young adventitious ventral branches as in Targionia hypophylla, as noted by C. Douin (1906). Gyorrfy (1926) stated that the lateral ventral scales in Oxymitra paleacea protect the tender tissues of the thallus by over-arching it when required.

The author has no real information concerning the functions of scales beyond that of previous authors but did notice during this investigation the rapid conduction of the Toludine blue, when applied to the apical region, and its distribution through the rhizoidal bundles beneath the scales.

THE USE OF VENTRAL SCALES IN TAXONOMY

Ventral scales have been noted almost from the beginning of recorded observations on thalloid liverworts. Many early writers merely noticed their presence, and it was not until early in the nineteenth century that they acquired any significance in the taxonomy of Hepaticae. Here and there in recorded observations there was speculation as to what they might actually represent. By 1850, they were being used regularly in taxonomic descriptions. Gradually, from this time on, the characteristics of color, size, shape, texture, and arrangement on the ventral surface of the thallus began to receive attention. Yet this was essentially collateral and accessory information, that would identify a few species at hand. Later, attention was turned to the phylogenetic picture, general development and origin of scales, as well as on oil bodies, slime papillae and appendages. The use of this data is much the same today, still collateral and accessory.

Applying the characteristics of scales in taxonomic procedures, to species of thalloids the world over, offers many limitations; many times becoming a precarious use when the scale is the sole means of identification. Evans (1917) was quick to point out in his study on Marchantia, that he was prone to use characters of scales as diagnostic aids in certain species, especially those of the appendage; but, he found that variations in appendages, when a long series was examined, made this use untenable. He added that it was much more advisable to use the characteristics of scales in conjunction with one or more characters of other structures of the gametophyte. This problem always becomes more acute where genera contain many species. In monotypic genera, or genera with a few species, the scale characteristics can become diagnostic for the genus as well as for the species it contains. Examples of this may be seen in the following: Dumortiera, Wiesnerella, Conocephalum, Oxymitra, Ricciocarpus, Reboulia, Preissia, Bucegia, Monoselenium, Peltolepis and Lunularia. Since the author was limited to twenty-two genera of the Marchantiales, by the availability of material, and did not see all the species of every genus studied, or all the genera in the order, there may be other genera to be included in the above list. Of the genera and species studied for which descriptions are available in the literature, those that have scale characters of diagnostic value are: Marchantia, Cyathodium, Monoclea, Targionia and Riccia. Mannia, Plagiochasma, Exormotheca, Asterella, Clevea and Sauteria have species whose scale characteristics are different from any other liverwort, but due to the numerous variations within the genus, it is very difficult to formulate a classification on ventral scales without including these variations. A few examples of such species are: Exormotheca holstii, E. pustulosa, Plagiochasma cuneatum, Mannia rupestris and Asterella saccata. In Exormotheca holstii the apex of the scale is divided into one or two filamentous processes with branches. E. pustulosa has a scale with a very short insertion and no eperon, in combination with one filamentous appendage which is very evanescent. Plagiochasma cuneatum usually has more appendages, long and short, than any other liverwort studied, in combination with other characteristics of the scale. Mannia rupestris has a tapering scales like several other genera, arranged in two irregular rows, and with characteristic apices. Asterella saccata frequently has long or moderately short, narrowly acuminate appendages on the anterior margin of the lamina. It must be remembered that the above discussion is based on all available characteristics of the scale, not only the form and size of the scale and its appendage, but also texture, range in color, presence or absence of slime papillae, oil bodies, the eperon and its own character, and scale arrangement.

Evans (1917), in the genus Marchantia, took into consideration oil bodies, size of cells in the center of the appendage as well as size of those on its margin, the gradation of cell size between these two areas in the appendage, size and form of the appendage, relative position of appendiculate scale to the laminar scale, and finally the number of rows of scales on the ventral surface of the thallus. He did not take into consideration the following characteristics of the laminar scales: the type of insertion they possess; the relative size of the appendiculate scale; the occurrence of rhizoids on the surface of laminar scales; the exact insertion pattern of all the scales on the ventral surface of the thallus; the persistence of slime papillae on the margins of laminar scales; the variation in size of the laminar scale within one species, or on a given thallus of one species. If many of the above points were treated statistically, they would yield valuable data that could be utilized in the taxonomy of *Marchantia*. No attempt has been made in this study to do this, as it is merely our purpose to suggest additional data on the characteristics of ventral scales which might be added to the tools of identification, using *Marchantia* as an example.

The genera *Preissia* and *Bucegia* next come to our attention taxonomically because of the presence of two rows of laminar scales, not previously reported in the literature. In *Bucegia*, these laminar scales are so large, that undoubtedly in the past they have been taken for appendiculate scales. They could easily be interpreted as appendiculate scales, whose appendages have been eroded off the anterior margin of the scale, were it not for the type of insertion they possess. The appendiculate scale has an oblique insertion on the wing of the thallus that curves mediad and posteriorly, the eperon region of the scale becoming parallel to the median axis of the thallus. The insertion of the laminar scale is essentially transverse, and is found to be alternating with the appendiculate scale. Size and form of the laminar scale is also quite diverse in this genus, as is shown in Plate XII, figs. 1, 2, and 3.

In Preissia, the laminar scales are in the same relative position as those of Bucegia, but are much more regular in form. They do vary in size, however, (Plate XI, fig. 2) and (Plate XII, figs. 8-10). It is interesting to note that Preissia and Bucegia are believed to be phylogenetically very close to the genus Marchantia, in which, to the knowledge of the author, laminar scales are not absent in a single species. Consequently, the discovery of laminar scales in these two genera further strengthens the belief of phylogenetic relationship.

In genera, such as Clevea, Cryptomitrium, Peltolepis and Corsinia, thalli were observed, which had scattered arrangements of scales. In the literature, Corsinia is consistently reported to have this arrangement. Clevea and Sauteria frequently are noted as having either scattered scales, or two irregular rows on the ventral surface of the thallus. Cryptomitrium and Peltolepis are almost always cited as having two rows of ventral scales. It is apparent from the author's own observations and those in the literature, that all five of the above genera have, consistently, or at times, a scattered arrangement of scales. As described in other sections of this work, all these genera have a characteristic splitting of the lamina or the eperon, as well as the environmental conditions affecting them. Here, then, is a situation directly effecting scale arrangement in addition to the genetic tendency toward splitting, which the environment increases or diminishes.

An attempt has been made to develop a key to most of the genera, and some species, studied by the author. For some of these forms, identification by means of scales, is very convenient, and especially in the case of sterile specimens. In other cases this is not entirely so. One additional character of the gametophyte, such as pores, air chambers, growth habit, or habitat xeric or mesic, is often enough for a positive determination. The attempted key based primarily on scale characteristics appears on the following page.

Key to the Forms Studied
Based on Scale Characteristics

1. Appendiculate scales present .... 2.
   2. Only appendiculate ventral scales present....... 3.
      3. Ventral scales with one appendage............ 4.
         4. Appendage short, broad-lanceolate, orbicular or reniform, and entire to denticulate, hyaline or slightly to highly colored.................................. 5.
            5. Lamina of ventral scale broad, obliquely subtriangular, eperon short, acute, long or acuminate, oil cells present................................ 6.
               6. Appendage short, crenate-denticulate, none to many filamentous teeth on its margin, reddish-violet..............<u>Targionia</u> <u>hypophylla</u>
               6. Appendage orbicular, hyaline, distinct slime papillae on margin, margin entire, lamina extremely short.................<u>Wiesnerella</u> <u>denudata</u>.
            5. Lamina of ventral scale long, falcate, anterior hook present or absent, oil cells present......................... 7.

7. Appendage reniform to orbicular, inserted near apical end of lamina, cells small, neck constricted..... <u>Conocephalum conicum</u>.

7. Appendage reniform, hyaline, inserted some distance from apical end of lamina...<u>Lunularia cruciata</u>.

4. Appendage short, subulate not denticulate or long ligulate and crenulate, or filamentous-linear and uni or biseriate.................................... 8.

8. Lamina of ventral scale long and narrow, falcate, composed of asodiametric cells, hyaline.............. 9.

9. Appendage many celled, slime cells or papillae present..... ... <u>Monoselenium tenerum</u>.

9. Appendage several-celled, slime cells and papillae absent...... ..... <u>Dumortiera hirsuta</u>.

8. Lamina composed of isodiametric cells, eperon splitting fragments off schizogenously, oil cells present, colored or hyaline.............. 10.

10. Appendages long, uni to bi-
seriate, scales scattered over
ventral surface (fragments),
hyaline......... Corsinia coriandrina.

10. Appendages usually shorter, ir-
refularly seriate, scales usual-
ly in 2 rows, sometimes scatter-
ed, colored..... Cryptomitrium tenerum.

3. Ventral scales with one or more appendages..11.

11. Ventral scales, one or three appendages..12.

12. Ventral scale lamina regularly
splitting in two, or very brittle,
breaking easily on dissection....... 13.

13. Scales hyaline, whitish to
light purple, oil cells absent,
appendages two, broadly lanceo-
late, crenate on margin, slime
papillae present.. Peltolepis grandis.

13. Scales deep red to purple,
covered with heavy cuticle, oil
cells present their walls un-
colored; appendages lanceolate,
spatulate, acuminate or gradu-
ally tapering................. 14.

14. Appendages 1-3, if one it may be ovate to spatulate inserted closely, insertion of lamina short...... <u>Plagiochasma</u>.

14. Appendages inserted distantly, if one acuminate, if more than one narrow to broadly wedge-shape......................<u>Mannia</u>.

12. Ventral scales with lamina not splitting schizogenously; appendages usually 3................. 15.

15. Scales blood red to almost colorless, lamina large, broad for its length, oil cells present, slime papillae present, appendages linear, 2-3 in number ....<u>Reboulia hemisphaerica</u>.

15. Without above combination, but deeply colored.................... 16.

16. Appendages inserted on lamina close to each other, acuminate to lanceolate....... <u>Plagiochasma</u>.

16. Appendages inserted distantly acuminate to tapering, often bleached................. <u>Mannia</u>.

11. Ventral scales with 4 appendages
or 4 "false" ones........................ 17.
17. Scales closely imbricated, deep
red violet, insertion of append-
ages proximate, insertion of
lamina short covered with waxey
cuticle, oil cells present...Plagiochasma.
17. Scales light colored, oil cells
absent, "false" appendages pro-
duced by schizogenous splitting...
.......................Peltolepis grandis.
2. Appendiculate scales and laminar scales
present.. 18.
18. Ventral scales in 12 alternating rows,
eperon inflated, brown to black in
color.........................Marchantia polymorpha.
18. Ventral scales in 4-6 alternating rows..... 19.
19. Lamina of scale not sharply differ-
entiated from eperon; appendage
broad to lanceolate, color brown to
dull pink................... Marchantia species.
19. Lamina of appendiculate scale large
and very broad, almost orbicular,
eperon narrow, small or short, color
blood red to purple, oil cells absent,
rows of scales 4...................... 20.

20. Appendage one, small, denticulate, hardly noticeable on margina of lamina, neck usually constricted.............<u>Preissia quadrata</u>.

20. Appendage linear to broad, variable in form, large and evident, neck usually broad, not constricted............<u>Bucegia romanica</u>.

1. Appendiculate scales absent on under surface of thallus, or if present appendage fused with lamina..21.

21. Only laminar scales present, broad, ligulate, orbicular or tapering...........................22.

22. Scales tapering in outline obliquely, subtriangular to wedge-shaped...............23.

23. Scales with eperon anterior, splitting off fragments in a regular fashion, in a linear arrangement across ventral surface of the thallus........ <u>Oxymitra paleacea</u>.

23. Scales splitting lengthwise into equal or unequal fragments, eperon reduced or absent, in 2 irregular rows or scattered on ventral surface of thallus....................... 24.

24. Some scales distinctly appendiculate to slightly so, when present linear-filiform, 2-4 cells wide, eperon short but present, oil cells absent....... .... <u>Clevea hyalina</u>.

24. Scales obliquely triangular, fragments of various forms, linear apices never present, oil cells present.... <u>Sauteria alpina</u>.

22. Scales shield-shape, orbicular-crescent shaped, or narrowly ligulate in outline.

25. Scales ligulate, long with marginal teeth, scattered in alternating arrangement across ventral surface of thallus..............<u>Ricciocarpus natans</u>.

25. Scales orbicular, crescent or shield-shaped......................... 26.

26. Scales shield-shape confined to median longitudinal axis of thallus, distant............. <u>Riccia</u>.

26. Scales orbicular -crescent-shaped, margins entire to irregular, on ventral lateral margins of thallus, usually closely imbricated........<u>Riccia</u>.

21. Scales apparently entirely absent but found only in apical notch of thallus and on ventral surface bordering it........................ 27.

    27. Scales represented by a small plate of cells 12-20 or so, or by a filament of a few cells with frequently biseriate base............................ *Cyathodium*.

    27. Scales represented only by large hair-like slime papillae .... *Monoclea*.

Asterella, though represented in the study by two species, is not included in this key. From what can be derived from the literature, much more information is necessary on ventral scales and their variations within this genus, before an adequate analysis can be obtained. *Monoclea* was not studied but included in the above key because of the diagnostic apical slime papillae (scales).

THE EVOLUTIONARY IMPLICATIONS OF VENTRAL SCALES

The most frequently discussed point in the evolution of ventral scales is the question of their homology with the leaves of the Acrogynae. Buch (1935) and Schuster (1953) were reluctant to attribute any degree of homology with the latter structures. They regarded them as derived structures or enations. Schuster (1953) stated that in certain genera of the Metzgeriales as Blasia and Fossombronia, there is good reason to believe that they were derived from "leafy" erect forms. He further said, "there is direct evidence in the Anthocerotales and the Marchantiales pointing to possible derivation from free-enation types similar to Rhynia". Castle (1946) wrote, "the order represents an independent line of development in which no definite evidence of the primitive leafy condition remains". Church (1919), Evans (1939) and Chadefaud (1940) regarded the ancestral liverwort as having possessed the "leafy" form in both the gametophyte and the sporophyte. Church (1919) maintained that terrestrial plants were descendants of marine submerged aquatics, and that the leafless to a "leafy" life form had developed in diverse groups, even in the Algae themselves. Evans (1939) stated that, "the ventral scales found in the majority of the Marchantiales afford some evidence of descent from leafy forms. These scales agree with the leaves of most of the foliose hepatics in being one cell thick throughout and in being attached by a broad base." Other points of similarity lie in the fact that chloroplasts and starch grains are found in the scales of a few thalloid liverworts. Oil bodies are also found in these structures in both the Marchantiales and the Acrogynae. Several genera of the thalloids have scales two-three cells thick in the basal region as far as cell thickness in ventral scales is concerned.

If it is assumed that the thalloid hepatics descended from branched, green, aquatic thallophytes, certain possibilities present themselves in the modification of the submerged, branched form to the submerged foliose form. The first of these manifests itself in those forms whose branches were reduced to filamentous, uniseriate structures and whose cells had their longitudinal axes oriented perpendicular to the axis of the branch. Additional cell divisions, parallel to the longitudinal axis would result in a biseriate lateral appendage. Any difference in the division and elongation of the cells, as an activity in either row in this biseriate structure would lead to a bilobed, lateral appendage. (Plate XVIII, figs. 1, 2 and 3.) A shift of the potential for lateral appendage formation to the apical cell of the axis, accompanying this modification, seems indicated. These points would appear to offer one possibility in the modification of the ancestral green thallophyte toward the life form of the ancestral aquatic, "leafy" liverwort. Another possibility lies in the still further reduction of the lateral, uniseriate branch to a one or two-celled, papillate lateral appendage. The third modification in reduction of the lateral appendage might have been the total disappearance of this structure, but where the genetic potential for lateral appendage formation was retained.

I. The Modification of the Radially Symmetrical Axis

A definite change took place in the apical cell of the thallus, with the change from an erect, radially symmetrical axis to a flattened dorsal-ventral one. This change may not have affected the loss of lateral appendages along the axis. It involved a change from a cuneate apical cell with three cutting faces to one with four cutting faces. We can turn to the Metzgeriales, as a parallelism, whose members possess apical cells with two, three, and four cutting faces during the formation of a prostrate thallus. The sporeling phases in the Marchantiales possess an apical cell with two cutting faces; the adult thalli have one with four cutting faces. This apical cell with two cutting faces has the potential for the formation of ventral scales though no ventral scales are evident in sporeling phases. These are only produced when the cuneate cell with four cutting faces becomes established in the early ontogeny of the thallus.

Whether the evolutionary change in the axis from an erect, radially symmetry to a prostrate, dorsal-ventral symmetry was definitely prior to, concurrent with, or after a reduction of the lateral appendages remains an unsolved question. We find in species of Riccardia in the Metzgeriales, filamentous appendages over the entire ventral surface, but most of the forms of this genus are without these structures.

II. Scale Development and Evolution.

Scale development in the thalloids is similar to that of leaves in the Acrogynae. The ventral scale originates from one cell in a linear series of derivatives, twice removed from the apical cell, while leaves in the Acrogynae originate in one derivative, twice removed from the apical cell. After the one or several-celled appendage and lamina has been established, these two areas show a wide difference in cell division activity, and in the maturation process. This is true also in the development of the lateral appendage in the "leafy" liverworts. In these plants a differential growth results in the leaves becoming bilobed; but, if the rate of development remains the same in the two initial meristematic regions, the leaf is unlobed. Therefore, from an evolutionary standpoint, the appendage and the apical portions of the lamina in the thalloid scale, represent the lobes of a bilobed structure produced by the same process that resulted in a bilobed leaf in the Acrogynae.

III. Ventral Scale Insertion and Evolution.

An oblique insertion of lateral appendages is the rule in both the Marchantiales and the Acrogynae. There are few exceptions to this in both groups, and the oblique insertion is the result of the same process in both. In dorsiventral forms in the Acrogynae, this type of insertion is due to differences in growth of the axis relative to that of the meristematic leaves. Greater elongation of the dorsal surface of the stem or of its ventral surface results in oblique insertions tilted forward or backwards. The process, taking place in the thalloid, usually only involves a difference in the rate of elongation, and the direction of this enlargement of cells on the ventral surface of the midrib region and the wing of the thallus. All appendiculate ventral scales, which are the most primitive scales, have this type of insertion. Many laminar scales have this as well, though notable exceptions are to be found in Ricciocarpus natans and Cyathodium. The two types of insertions of a hypothetical ventral scale, are shown in Plate XVIII, figs. A and B. Figure B represents the beginning of the process that resulted in the posterior margin of the lamina being inserted, full length onto the ventral surface of the thallus. This is a strong possibility, if one considers the appendage and the lamina separate lobes of the lateral appendage.

IV. Examples of Regressive Evolution of Ventral Scales in Genera and Species.

One of the most clear-cut reduction series of any genus studied occurs in the genus Marchantia. This not only involves reduction in the number of rows of scales and reduction of the appendage, but reduction also in the size of both appendiculate and laminar scales. M. polymorpha has 12 rows of scales, broad appendages, and the largest appendiculate scales of any species examined. It possesses the largest laminar scales. Reduction of the laminar scale is evident from No. 5 scale to the No. 1 or marginal scale on a given thallus, (Plate V, figs. 1 and 2). M. paleacea has only six rows of scales and reduction of the outer two rows of laminar scales toward a vestigial condition, (Plate V, fig. 3). M. chenopoda has four rows of ventral scales with evidence, in the more delicate types of the outer two rows of laminar scales, of reduction to small groups of slime papillae, and to a lamina of three or four cells in width, (Plate IX, figs. 7 and 8). A reduction of the appendage occurs in this species in varying degree of form, from a broad dentate to a narrow lanceolate appendage. We have, then, in the genus Marchantia, a general reduction series from M. polymorpha to and including M. cuneiloba, (Plate XIX).

A general reduction in the number of appendages and the form of the ventral scale occurs in the genus Exormotheca. The tapering or subtriangular scale form has its apex further reduced to fine, filamentous divisions and branches. A reduction series proceeds to the most reduced ventral scale through the following species: E. gollani, E. pustulosa, E. fimbriata, E. algeriensis, E. welwitschii and E. holsteri.

Reduction is reflected in the nature of the appendage in Plagiochasma. P. rupestre has ventral scales with from one, or two, broad, ovate appendages, to three tapering acuminate appendages. P. cuneatum has appendages that are short or long, narrow and vaguely defined in many cases, and four in number, (Plate XIX).

There are further signs of reduction in the appendage in the genus Mannia. These vary, according to the species, from three narrow acuminate ones, to one in M. pilosa and a few others (Plate XIX).

Species of Wiesnerella show a reduction in the size of the scale, and change in its texture, from W. javanica to W. denudata.

Species of Cyathodium show a reduction in the number of cells in the ventral scale from those of C. foetidissimum to those of C. cavernarum and several others. One of the latter is C. smaragdinum (Plate IX, figs. 1, 2, 3, 4).

V. Trends in the Reduction of Ventral Scales in the Order as a Whole.

Five general regressive tendencies, formulated by considering characteristics of ventral scales alone, and disregarding true phylogenetic relationships are represented in Plate XIX.

The main tendency is dominated by the genus Marchantia. The primitive form M. polymorpha has 12 rows of scales across the ventral surface of the thallus. An obvious reduction in the number of rows of scales, takes place as one proceeds toward the more reduced form, Targionia. Characteristics shown by members of this tendency are: the membraneous texture of the scale; the presence of oil bodies and slime papillae in the lamina of the scale; the gradual reduction in the length of the oblique insertion; the gradual reduction of the appendage; and, the disappearance of oil bodies, slime papillae and appendage in the genus Riccia.

The tendency, based on Plagiochasma shows a steady reduction of the appendage to the point where it is fused with the lamina in Sauteria and Oxymitra. The most reduced genera, Ricciocarpus and Riccia have no appendage at all. The combination of characteristics which mark this tendency from the others includes: the short insertions; the change from deep violet colored to almost colorless scales; the schizogenous splitting of both lamina and eperon of the scale except in the genera Plagiochasma and Mannia; modification of the shape of the scale to the subtriangular form; and finally, the disappearance of slime papillae.

The tendency, based on Bucegia has the following combination of characteristics: the very definite broad and large, crescent-shaped lamina; the blood red color of the scales; a relatively small degree of reduction of the appendage to three filiform appendages in the genus Reboulia; and, a reduction in the laminar scales to the point where they totally disappear in Reboulia.

The tendency, based on Conocephalum is characterized by the following: the reduction of a long, narrow, falcate lamina to a short, almost transversely inserted lamina in Weisnerella; a retention of the orbicular, subrotund or reniform appendage with practically no reduction at all; a change in texture of the scale from membraneous and to a hyaline, flaccid scale; the retention of oil bodies and slime papillae throughout.

The tendency, based on Asterella presents the following characteristics: the change from a membraneous scale to a hyaline, flaccid scale, then reduced to a slime papilla in Monoclea; reduction of the appendage to its total disappearance in the genus Cyathodium and Monoclea; the change in position of the appendage from a subapical one to an apical, on the anterior margin of the lamina; and, the change from a moderately pigmented scale to a colorless scale.

It must be remembered that such tendencies as those above, represent five general trends in reduction, taking place in the genera of the Marchantiales from primitive members of the order, for the most part, to the reduced members of the order. The diagram in Plate XIX indicates the general nature of this reduction in ventral scales. Any application of phylogenetic relationships, taking all characteristics into consideration other than those of ventral scales, to this diagram, makes an interpretation of these tendencies absurd. The diagram was formulated by compiling all available data on characteristics of ventral scales from the deviates of each genera; then, on the basis of characteristics of the ventral scales, the five trends of reduction were arranged. It is obvious that various degrees of reduction would be scattered over a diagram, representing the phylogenetic relationships of the genera in the order. Therefore, this diagram may be said to represent the general nature of reduction in ventral scales, and only confirms the reduction tendencies, exhibited by other parts or organs of the gametophyte, that have been pointed out by numerous other workers. This is of course true only if one believes that the members of the order represent a regressive, evolutionary series of organisms.

The hypothetical, progressive, evolutionary process, in the history of the thalloids, probably ramified in many directions from the algal ancestral type, (Plate XVIII, fig. 1). Some stages in this process might have taken the course shown in Plate XVIII, fig. 2, 3 and 4. Figure 2 is an optical, transverse section of the green, aquatic thallophyte in which a reduction of the branch system has already begun. Figure 4 shows one hypothetical possibility, or the "dawn" leafy hepatic, in optical section. This "dawn" type implies a form from which our modern leafy liverworts might have arisen. Such a form had a bilobed, lateral appendage, which is the primitive condition in the leafy liverworts according to Castle (1946). Figures 4 and 5 are two possible forms, representing links in the chain of forms between radially symmetrical types, either completely reduced or partially reduced as to appendage, and the primitive type of thallus found in the modern genus, Marchantia. This genus is represented in Figure 6 of the same plate, and the 12 rows of scales on the underside have been pulled down perpendicular to the thallus itself. Marchantia is the termination of this progressive evolutionary trend. All other liverworts in the various families of the order show a reduction, in a gradual gradient, of structures in the gametophyte thallus form. One of these structures, then, is the ventral scale of the thallus. Figures 6-13 of Plate XVIII represent this regressive evolutionary process, in optical section. Several points of note may be seen in this series of diagrams as a whole: the reduction in the number of rows of ventral scales; the reduction and disappearance of the appendage; and finally, the change to a single ventral scale on the median line of the thallus. Other changes, accompanying the general regressive process have been enumerated under data for the five reduction trends of the scales themselves, and the description of genera and species.

Plate XVIII

Chart showing a few hypothetical forms that might have existed in the progressive evolutionary history of the Marchantiales and the regressive trend in living forms. All figures are optical transverse sections.

Fig. 1, The ancestral green thallophyte.

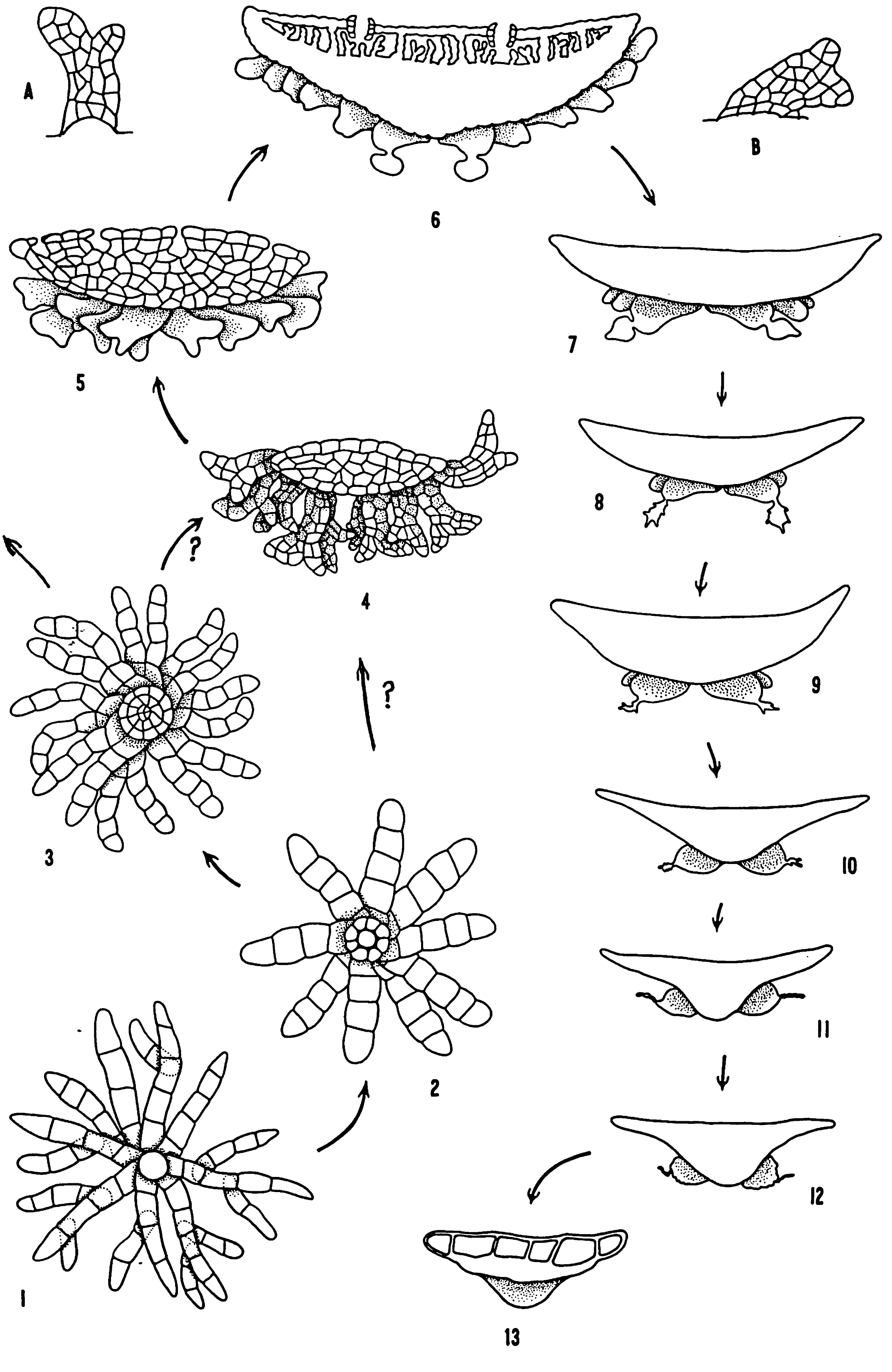
Fig. 2, Green aquatic thallophyte with reduced branches.

Fig. 3, Ancestral leafy thallophyte.

Figs. 4-5, Protomarchantia, two hypothetical forms between the radially symmetrical thallophyte and modern thalloids.

Fig. 6, Marchantia polymorpha.

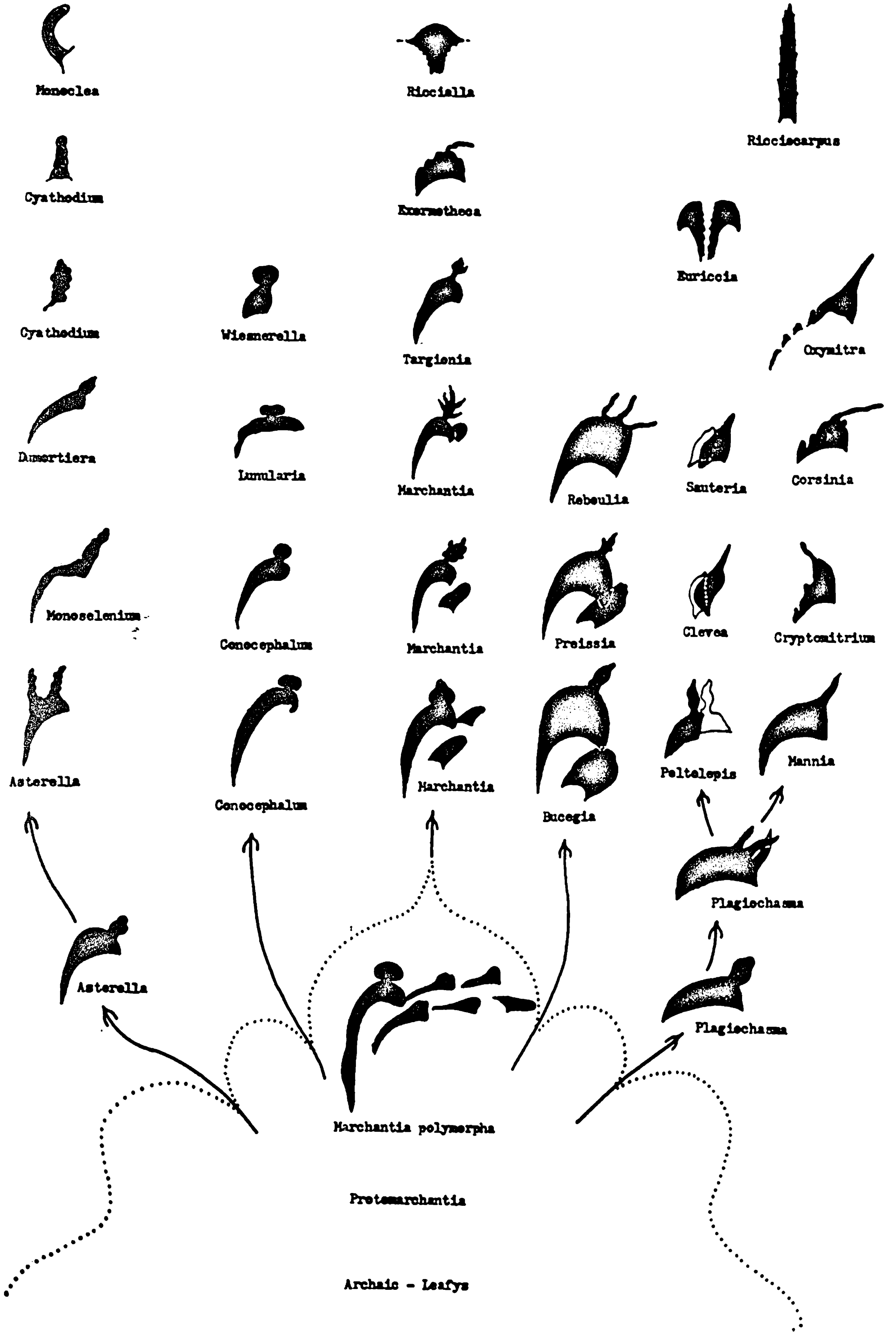
Figs. 7-13, Reduction series represented by living forms in the Marchantiales.



A
B
1
2
3
4
5
6
7
8
9
10
11
12
13
?
?

Plate XIX

Chart showing the five reductional trends of ventral scales based on the characteristics of the ventral scale in the Marchantiales, (not to be misconstrued to indicate a phylogenetic sequence).


Moneclea
Riocialla
Rioclocarpus
Cyathodium
Exormotheca
Buriccia
Cyathodium
Wiesnerella
Targionia
Oxymitra
Dumortiera
Lunularia
Marchantia
Rebeulia
Sauteria
Corsinia
Moneselenium
Conocephalum
Marchantia
Preissia
Clevea
Cryptomitrium
Asterella
Conocephalum
Marchantia
Bucegia
Peltolepis
Mannia
Plagiochasma
Asterella
Plagiochasma
Marchantia polymorpha
Protomarchantia
Archaic - Leafys

SUMMARY AND CONCLUSIONS

The evolutionary significance of ventral scales in the Marchantiales lies in their remote homology to the same processes of origin and development that occur in the formation of the leaf in the Acrogynae, especially of the amphigastrium. In the Marchantiales these processes result in a bilobed, ventral appendage, one lobe represented by the appendage of the ventral scale, the other by the lamina of the scale. Other noteworthy observations have been made in eleven of the thirty-two species studied. These findings are of morphological and taxonomic significance and are to be found in the genera Marchantia, Preissia, Bucegia, Peltolepis, Clevea, Sauteria, Corsinia, Cryptomitrium and Oxymitra. The work of Stephani (1900-1917) stands out above that of all others in faithful descriptions of ventral scales. To a lesser degree, the monographs of Evans (1915, 1917, 1920) and the works of Massalongo (1912, 1916), Casares-Gil (1919) and Kashyap (1929) represent the greatest concentration of information and illustration of ventral scales in the literature. Few illustrations of complete ventral scales exist in comparison with the number of works that refer to these structures. Multiplicity of color descriptions, presence or absence of ventral scales, differences in the number of appendages and the presence or absence of appendages exists for a given species in both early and more modern works.

The points of value on the morphology and taxonomy of ventral scales, secured from this investigation are as follows:

1. The species *Marchantia polymorpha* has 12 distinct rows of ventral scales across the lower surface of the thallus, as based on scale insertions.
2. All scales in *Marchantia polymorpha* have oblique insertions.
3. The genera, *Preissia* and *Bucegia* have four rows of of ventral scales based on scale insertions instead of the previously reported rows.
4. *Marchantia paleacea* has basically six rows of ventral scales on the lower surface of the thallus, instead of four rows reported in the literature.
5. *Marchantia chenopoda*, in the more delicate forms, has the outer two rows of laminar scales retarded in development and later stages in their development take place, on the ventral surface of the thallus itself, some distance posterior to the apical region of the thallus.
6. In the genera, *Peltolepis*, *Sauteria* and *Clevea*, regular schizogenous splitting takes place in the lamina of young scales, producing two irregular rows or a scattered ventral scale arrangement.
7. The genera *Cryptomitrium* and *Corsinia* regularly possess schizogenous splitting of their eperons,

and less frequently of their laminae.

8. The genus *Oxymitra* has an eperon that splits schizogenously, breaking off fragments that are displaced in linear fashion across the ventral surface of the thallus.
9. The complete development of the appendiculate scale of *Preissia quadrata* has been worked out beyond that of the younger stages which previously appeared in the literature.
10. The complete development of the type of scale whose appendage has become fused with the lamina, has been described and illustrated for *Oxymitra paleacea*.
11. The five reduction trends, exemplified by the ventral scales of the *Marchantiales*, confirm the evidence for reduction in the other parts of the gametophyte, already cited by previous authors.

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APPENDIX 1.

The collections cited and studied in this work are as follows:

1. Marchantia polymorpha (L.): 2 miles S.E. of Wolcott, Wyandotte County, Kansas, on moist, seepy, rocky, wooded hillside among several springs, Sept. 6, 1948, R. L. McGregor # 2420: Wolf Creek Pass, Colorado, at the Continental Divide, elevation 10,850 feet, on bank of small meadow brook, August 15, 1953, R. L. McGregor # 7474: Thornton, Cook County, Illinois, on burned-over area in acid flatwoods, May 10, 1941, Donald Richards, # 1134: 10 miles N.W. of Union Creek, Oregon, in cold spring water marsh on steep hillside in an old, cleared area, elevation 4,000 feet, June, 1953, W. V. Showalter, Wittlake # 2,000: 2 miles south of Wells, Ottawa County, Kansas, Ottawa County State Park, on moist sandstone outcrop, April 14, 1948, R. L. McGregor, # 1320: One mile NE of Neodesha, Wilson County, Kansas, sandy soil in blackberry thicket of an open oak woods on burned-over ground, May 1, 1948, R. L. McGregor, #1380: Mosca Pass, Colorado, on trail leading out of Great Sand Dune National Monument, on bank of small stream, mostly under flowing water, elevation 8,300 feet, August 13, 1953, R. L. McGregor, # 7468: Red Rock Falls, NE of Windon, Minnesota, on moist granitic ledge of small ravine, August 19, 1952, R. L. McGregor, # 5703: 22 miles SW of Tres Piedros, New

Mexico, on bank of Vallecito River, on soil below spring, elevation 9,200 feet, August 27, 1953, R. L. McGregor, # 7480 : Greer Spring, Oregon County, Missouri, July 19, 1953, L. J. Gier, # 6050: Roadside at Cisco Spring, Oregon County, Missouri, July 19, 1953, L. J. Gier, # 6070: In front of Library, University of Kansas Campus, Lawrence, Douglas County, Kansas, June 13, 1949, R. L. McGregor, # 3063: Thuringen Kr. Gotha : Georgenthal, June 20, 1944, Herbarium of K. Starcs, Nr. G. F 359: Banff National Park, Alberta, Canada, about three miles southward from the Athabasca-Saskatchewan Divide, along the Banff-Jasper Highway, on burnt soil, latitude 52° N, longtitude 117° W, July 9, 1940, T. C. Frye and E. M. Frye, # 2937 : Lake Kachess, Kittitas County, Washington, Sept. 30, 1931, Arthur Svihla, # 310 : Lake Kachess, Kittitas County, Washington, July 8, 1932, Arthur Svihla, # 361 : Blanchard Spring Creek, Stone County, Arkansas, on rocks amid stream, July, 1950, Wittlake, # 2001 : Martins Bluff, Benton County, Arkansas, on shale talus slope with continuous seepage water, April, 1948, D. M. Moore, Wittlake # 56: Fayetteville, Washington County, Arkansas, on ledges of a sandstone outcrop fed continuously by springs, May, 1948, Wittlake # 625: Robinson Mountain, Washington County, Arkansas, around spring on east-facing hillside May 1948, Wittlake # 623 : Dripping Springs, Hot Springs, Garland County, Arkansas, August, 1948, R. Whitmire, Wittlake, # 751 : Conway, Faulkner County, Arkansas, on moist soil, Sept. 1947, I. Hartsoe, Wittlake # 964: Ponca, Newton County, Arkansas, at base of ledge and among strewn boulders, April 1950, Wittlake # 1540 : Hewitt Spring, Washington County, Arkansas, July 1950, Wittlake # 1553 : 25 miles West of Ciudad Hidalgo, Michoacan, Mexico, on steep banks in a pine forest, elevation 8,900 feet, July 16, 1953, Wittlake # 2002.

2. Marchantia paleacea Bertolini : Tutla, Oaxaca, Mexico, elevation 6,550 feet, July 23, 1953, Rollin Baker, Wittlake # 2003: San Tanda, 30 miles NE of Jacala, Hidalgo, Mexico, elevation 4,000 feet, June 22, 1953, Wittlake # 2004: Fortin, Vera Cruz, Mexico, moist roadside bank, elevation 3,200 feet, Jan. 27, 1951, Rollin Baker : 9 miles SW of Tlalpacoyan, Vera Cruz, Mexico, elevation 3,500 feet, June 26, 1953, Wittlake # 2006 : 25 miles SW of Nuevo Morelos, Tamanlipas, Mexico, elevation 1,300 feet, June 19, 1953, Wittlake # 2007 : North Sylamore Creek near Blanchard Spring Recreation Area, Stone County, Arkansas, June 1951, D. M. Moore, Wittlake # 2008.

3. Marchantia domingensis Lehm. and Lindenb. : Melbourne, Izard County, Arkansas, on sandstone rock and soil above water's edge of spring-fed creek, September 4, 1952, Wittlake # 1965: 5 miles NW Texuitlan, Puebla, Mexico, growing epiphytically on large Lycopodium plants near their bases,

June 27, 1953, Wittlake # 2009: 5 miles SW of Tlalpocoyan, Vera Cruz, Mexico, elevation 2,700 feet, June 26, 1953, Wittlake # 2010 : El Salto Falls, San Luis Potosi, Mexico, at water's edge below falls around pools formed by travertine deposits, elevation 1,200 feet, June 18, 1953, Wittlake # 2011 : 5 miles SW of Hearne, Texas, on moist limestone outcrop of north-facing bluff along the Brazos River, plants very abundant, April 7, 1953, R. L. McGregor # 7148.

4. Marchantia diptera Mont. : Miyazaki, Sakatani, Japan, on rocky ledges, elevation 400 meters, June 8, 1953, S. Hattori and D. Shimizui, Wittlake # 2012.

5. Marchantia tosana Steph.: Miyozaki, Obi, Japan, on stone wall, elevation 10 meters, June 13, 1953, S. Hattori, Wittlake # 2013.

6. Marchantia cuneiloba St. : Kiushiu, Miyazaki, Obi, Japan, August 1946, Series 1946 of Hepaticae Japonicae, det. S. Hattori, leg. S. Hattori, Wittlake # 2014.

7. Marchantia chenopoda L. : 3 miles South of Tamazanchale, San Luis Potosi, Mexico, on moist ledge under dripping lime water spring, December 27, 1953, R. L. McGregor # 8043: Uruapan, Michoacan, Mexico, 10 kilometers South of Zararacua Falls, on dirt and rocks, January 9, 1941, Det.

Ruth Svihla, T. C. Frye and E. M. Frye # 3028 : Darien, Paca, Panama Canal and vicinity, elevation 2,000-6,500 feet, April 15, 1908, R. S. Williams, Det. by A. W. Evans, N.Y. Bot. Garden Herb. # 1084 : Jalapa, Vera Cruz, Mexico, November 1908, Barnes and Land, Det. A. W. Evans N.Y. Bot. Garden Herb. # 556 : Road from Ponce to Adjuntas, Puerto Rico, July 11, 1901, Coll. by L. M. Underwood, R. F. Griggs, U. S. Nat. Herb. # 732 : Calonia Perene, Dept. Junin, Peru, on bark, elevation 680 meters, June 14-25, 1929, Coll. by E. P. Killip, A. E. Smith, Det. by Herzog, U. S. Nat. Herb. # 24997 (From N. Y. Bot. Garden Herb.)

8. Preissia quadrata (Scop.) Nees. : Carp Creek, just above the Iron Bridge, R 3 W., T 36 N., Sec. 4, Cheboygan County, in dense, rather extensive mats on sand and humus accumulating on roots at edge of water, June 29, 1940, H. A. Gleason Jr., # 2570: Sowles Mills, Iowa County, Wisconsin, T 8 N, R 5 E, Sec. 23, moist wooded bank, September 6, 1953, R. L. McGregor # 7514 : Porfey's Glen Sauk County, Wisconsin, T 11 N., R 7 E, Sec. 23, on moist bank, September 5, 1953, R. L. McGregor # 7490 : Barkshed Springs, Stone County, Arkansas, along Sylamore Creek on ledges of limestone outcrop, on thin soil, August 5, 1953, Wittlake # 2019 : 2 miles SE of Pacific, Jefferson County, Missouri, on sandstone cliff along old course of Merimac River, November 15, 1941, F. G. Meyer, Det. by E. B. Wittlake,

105 : Bear Cave, Berrien County, Michigan, abundant on "Jufa Rock", July 3, 1940, D. Parker #336.

9. Bucegia romanica Radian. : Hungaria septentrionalis, Magas-Patra (= Patra-Magna), in valle locus Nesniardi Groldtio ad jara granitica, C 16-1700 ill, January 29, 1909, leg. Gyorrfy # VIII, (N.Y. Bot. Garden Herb.).

10. Clevea hyalina (Sommerf.) Lindb.: South of Wacouta, Goodhue County, Minnesota, over rather exposed moist soil near summit of bluff, May 15, 1950, Schuster # 18004.

11. Conocephalum conicum (L.) Dumort : 2 miles SE of Pacific, Jefferson County, Missouri, on sandstone cliff along old course of the Merimac River, November 15, 1941, F. G. Meyer, Det. by Margaret Fulford # 105 : Buffalo State Park, Baxter County, Arkansas, at base of cliffs near waterfall, April 15, 1952, Wittlake # 1919: Blanchard Spring Camp, Stone County, Arkansas, on high limestone ledges above camp, April 14, 1952, Wittlake # 1930: Ravender Springs, Randolph County, Arkansas, on rocks at base of canyon, June 20, 1948, Det. by R. L. McGregor, Delzie Demaree # 26809: St. Mary's College Campus, St. Joseph County, Indiana, on soil on bank of stream, September 27, 1941, D. Parker # 505: Bear Cave, Bearrien County, Michigan, abundant on "Jufa Rock", July 3, 1940, D. Parker # 336: Mittelfranken, Kr. Hersbruck,

Thachenstadt, Sclucht, (Flora Bavarica), June 8, 1947, K. Storcs # 1497: Petit-Jean State Park, Petit-Jean Mountain, Faulkner County, Arkansas, on shale talus at base of Cedar Creek Falls, April 17, 1952, Wittlake # 1902.

12. Conocephalum supradecompositum (Lindb.) Steph. : Hage-nura, Kachi-ken, Japan, on wet soil in shaded place, October 1, 1953, leg. M. Kamimura, Wittlake # 2029: Kiushiu, Miyazaki, Obi, Japan, elevation 100 meters, Series I, 1946, Det. S. Hattori, Wittlake # 2030.

13. Lunularia cruciata (L.) Dumort. : Pasadena, California, on the front lawn of Mrs. Michener, Dec. 11, 1953, Coll. by C. D. Michener, Det. by R. L. McGregor, Wittlake # 2026: Moulin Huet Bay, Island of Guernsey, March 17, 1953, (Bryophytes of the Channel Islands), on soil by waterfall Ex herbarium of A. C. Crundwell, # 25: San Franisquito Creek, near Chaucer Pope Street Bridge, Santa Clara County, California, January 31, 1938, Coll. by Ira L. Wiggins, Det. by R. L. McGregor, Wittlake # 2028.

14. Dumortiera hirsuta (Sw.) Nees. : North of Toccoa, Stephens County, Georgia, over dripping wet rocks below Toccoa Falls, August 15, 1952, R. M. Schuster # 2509: Miyazaki Prefecture, Obi, Japan, elevation 30 meters, on rocky ledges in damp, shaded places, May 30, 1952, Leg. and

Det. by S. Hattori, Wittlake # 2032: Hot Springs, Lake Side Hotel, Garland County, Arkansas, large spring, north-facing slope, July 25, 1948, Delzie Demaree # 27082 : 5 miles SW Tlalpacoyan, Vera Cruz, Mexico, June 26, 1953, Wittlake # 2033: Joplin, Montgomery County, Arkansas, April 1949, growing along creek bed, Wittlake # 455: Martins Bluff, Benton County, Arkansas, growing at base of perpendicular cliffs along White River, May 1948, Wittlake # 89: Mountain Pine, Garland County, Arkansas, growing along stream near water's edge, beneath underbrush, May 1948, Wittlake # 90.

15. Reboulia hemisphaerica (L.) Raddi : Petit-Jean State Park, Petit-Jean Mountain, Faulkner County, Arkansas, on path and on sandy soil of west-facing cliffs back of main lodge, April 17, 1952, Wittlake # 1891: Buffalo State Park, Baxter County, Arkansas, at base of cliffs near waterfall, April 15, 1952, Wittlake # 1920: Magazine Mountain, South of Paris, Logan County, Arkansas, on moist rocks, March 27, 1951, R. L. McGregor # 4767: South of Gretna, Sarpy County, Nebraska, on grassy slope of gully, elevation 1,100 feet, August 16, 1941, W. Kiener # 11066: Fly Gap, Franklin County, Arkansas, on banks of small stream, April 1949, Wittlake # 1477: Granite Mountain, Pulaski County, Arkansas, east-facing slope, March 1950, D. M. Moore, Wittlake # 1488: West Fork, Washington County, Arkansas, March 1950, R. French, Wittlake # 1523: Ponca, Newton County, Arkansas, found in

"Lost Valley", April 1950, Wittlake # 1541: Fincher Cave, Washington County, Arkansas, May 1950, Wittlake # 1586.

16. Monoselenium tenerum Griffith. : Miyazaki, Obi, Japan, elevation 10 meters, on shaded soil, June 13, 1953, S. Hattori, Wittlake # 2034.

17. Wiesnerella denudata (Mitt.) Steph. : Kumamoto, Hitoyoshi, Japan, elevation 110 meters, on moist rocks, March 30, 1949, K. Mayebora # 14920.

18. Asterella tenella (L.) Beauv. : 15-16 miles South of Oxford, Lafayette County, Mississippi, abundant in old field on northwest-facing slope, April 10, 1951, R. M. Schuster # M440 : Petit-Jean State Park, Petit-Jean Mountain, Faulkner County, Arkansas, back of main lodge on sandstone west-facing cliffs, April 17, 1952, Wittlake # 1890: Petit-Jean State Park, Petit-Jean Mountain, Faulkner County, Arkansas, on slopes of canyon below Cedar Creek Falls, April 17, 1952, # 1893: Bandmill, Izard County, Arkansas, on sandstone flat area among a grove of Junipers, April 13, 1952, Wittlake # 1952: Briggsville, Yell County, Arkansas, along roadside ditch in sandy soil, April 18, 1952, Wittlake # 1924: Little Red River, NE of Searcy, White County, Arkansas, on steep, shaded river bank, September 2, 1950, Wittlake # 2037.

19. Asterella echinella (Gottsche) Underw. : El Salto, San Luis Potosi, Mexico, just below waterfall on rocks and soil encrusted with lime, at edge of spray zone, January 1, 1952, R. L. McGregor # 5315: SE of Monterey, Nuevo Leon, Mexico, on moist rocks at Horsetail Falls, December 26, 1950, Det. by Lois Clark, R. L. McGregor # 4740: El Salto Falls, San Luis Potosi, Mexico, at water's edge below falls, elevation 1,200 feet, June 18, 1953, Wittlake # 2038.

20. Mannia fragrans (Balb.) Frye and Clark.: Near Ninemile Creek overlooking the Minnesota River, Hennepin County, Minnesota, over sandy exposed hillside terrace, May 1-8th, 1950, R. M. Schuster # 18020: Hole-in-the-Rock, West of Baldwin, Douglas County, Kansas, growing on flat south-facing ledges of a sandstone outcrop, April 1951, R. L. McGregor # 18856: Green Forest, Carroll County, Arkansas, at edge of oak forest, in rocky limestone meadow, November 1951, Wittlake # 1854.

21. Mannia rupestris (Nees.) Frye and Clark.: Buffalo River Ferry Landing, Marion County, Arkansas, on sandy soil on ledges growing among a small species of moss, April 1952, Wittlake # 1906: One mile North of Sylamore, on White River in Stone County, Arkansas, April 15, 1952, Wittlake # 1907: 3 miles North of Stillwater, Washington County, Minnesota, over calcareous, moist, shaded sandstone cliffs, June 11,

1950, R. M. Schuster # 18139.

22. Plagiochasma rupestre (Forst.) Steph. : South of Yates Center, Woodson County, Kansas, on soil at base of sandstone boulder in deep ravine, September 1952, Det. by R. L. McGregor, Wittlake # 2039: 19 miles South of Mante, Tamanlipas, Mexico, roadside deciduous tropical woods, elevation 1,300 feet, June 19, 1953, Wittlake # 2040.

23. Cryptomitrium tenerum (Hook.) Aust. : Pasadena, California, April 15, 1893, A. J. McClatchie, Lucien Underwood # 24, (N.Y. Bot. Garden Herb.) : Palm Canyon, Palm Springs, California, January 3, 1927, Caroline C. Haymes # 2645, (N.Y. Bot. Garden Herb.): Menlo Park, California, May 6, 1893, W. C. Blasdale, in Herb. of Marshall A. Howe, (N.Y. Bot. Garden Herb.)

24. Peltolepis grandis Lindb. : Helvetia, Bern Faulkorn, humicala in lapides, skiophila c. Fimbraria, elevation 2,300 meters, leg. et det. P. Culmann, August 1906, (N. 472 of Hepaticae Selectae et Criticae, edidit Fr. Verdoorn, Series X (1937), Cf. Ann. Bryologici, Vol. X.): Norge, Tramso arnt, Bordo, Stromali, March 8, 1891, H. W. Arnell (N.Y. Bot. Garden Herb.).

25. Targionia hypophylla L.: 23 miles S.E. of Nachixtlan,

Oaxaca, Mexico, in open clearings on rocks and soil in Pine-Oak forest, elevation 7,000 feet, July 5, 1953, Wittlake # 2041: 4 miles West of Rio Frio, D. F., Mexico, along roadside at base of boulders, elevation 9,800 feet, July 14, 1953, Wittlake # 2042: 13 miles West of Texmelucan, Puebla, Mexico, open sandy ground in old road cut, elevation 8,600 feet, July 14, 1953, Wittlake # 2043: 5 miles SW Tlalpacoyan, Vera Cruz, Mexico, open sandy ground, elevation 2,700 feet, June 26, 1953, Wittlake # 2044: 7 miles NE of Tapanatepec, Oaxaca, Mexico, elevation 1,300 feet, July 9, 1953, Wittlake # 2045: 32 miles, SE of Nochixtlan, Oaxaca, Mexico, on margins of Pine-oak forest, sandy soil, elevation 7,000 feet, July 5, 1953, Wittlake # 2046: 8 miles West of Mexico City, D. F., Mexico, elevation 9,100 feet, July 15, 1953, Wittlake # 2047: 29 miles NE of Copala, Sinaloa, Mexico, Pine woods in barranca country, elevation 6,000 feet, July 22, 1953, Wittlake # 2048: Surey County, England, on sandy hedge bank, August 26, 1953, Coll. by A.C.C., Det. by E. F. Warburg and A. C. Crundwell, Wittlake # 2049: Island of Guernsey, Lane Bank Talbot's Valley, England, March 24, 1953, A.C. Crundwell # 41: 16 miles NW of Ixtlan, Nayarit, Mexico, near lava field, on sandy banks of small depressions, elevation 2,800 feet, July 19, 1953, Wittlake # 2051.

26. <u>Cyathodium smaragdinum</u> Schiffner. : West Java, Bogor Botanical Garden, Archys, Indonesia, on wall in moist warehouse,

February 16, 1953, W. Meijer, Wittlake # 2036.

27. Sauteria alpina Nees. : St. Paul, Behring Sea, no specimen data, correspondence date November 13, 1897, of Trevor Kincaid to L. Underwood in Underwood's Herbarium, (N.Y. Bot. Garden Herb. 1907): Lahul, Himalaya, in wet places, elevation 14,000 feet, with Preissia quadrata, Walter Koelz # 1158, (Himalayan Research Institute, (N.Y. Bot. Garden Herb.): Lake Agnes, Canada, under rocks, elevation 7,000 feet, August 19, 1891, J. Macoun # 364, (Labelled as Clevea hyalina, annotated as Sauteria alpina, by Underwood, N. Y. Bot. Garden Herb.).

28. Corsinia coriandrina (Spreng.) Lindb. : Rabenhorst, Hepaticae Europae, No. 62, (Corsinia marchantioides Raddi), in collibus apricis, intra Borzoli et Panigalo prope Genuam, February 1857, Jac, Doria: On banks, road from Sorrento to Amalfi, Italy, March 1895, A. W. Evans: Texas, February 1915, F. M. McAllister: Last two specimens labelled also Corsinia marchantioides Raddi. All three specimens from N.Y. Botanical Garden Herbarium.

29. Oxymitra paleacea Bischoff.: Near Elk City, Montgomery County, Kansas, on east-facing wooded slope, April 4, 1942, R. H. Thompson: Three-fourths mile E. Fall River, Greenwood County, Kansas, sandy soil, clearing in Oak woods,

April 13, 1949, R. L. McGregor # 2670: 2 miles NW of Yates Center, Woodson County, Kansas, on sandy soil June 19, 1949, R. L. McGregor # 3200: 2 miles SE of Tecamachalco, Puebla, Mexico, rocky Agave-Cactus-Pepper Tree area, in open barren flats and found specifically at damp margins adjoining sandstone and limestone bedrock, July 2, 1953, Wittlake # 2052.

30. Ricciocarpus natans (L.) Corda: Loughton, Epping Forest, Essex, England, floating in pond, October 1948, Ex. Herb. F. A. Sowter # 16: 1½ miles NE of Lawrence, Douglas County, Kansas, swamp in Kansas River Valley, September 23, 1950, R. L. McGregor # 4676: Plumerville, Conway County, Arkansas, floating in Cypress swamp, April 1927, Delzie Demaree, Wittlake # 93: Grassy Lake, Hempstead County, Arkansas, floating at margins of Cypress swamp among duckweeds and Riccia rhenana, August 1950, Wittlake # 1649.

31. Riccia lamellosa Raddi. : Petit-Jean State Park, Petit-Jean Mountain, on shale talus at base of Cedar Creek Falls, April 17, 1952, Wittlake # 1899: Natural Dam, Crawford County, Arkansas, growing in pathway shaded by a plum thicket, March 1950, Wittlake # 1757: White River Narrows, Benton County, Arkansas, on margin of a typical flat, open sandstone area, April 1949, D. M. Moore, Wittlake # 424.

32. Riccia rhenana Lorbeer.: Plumerville, Conway County,

Arkansas, floating in a Cypress swamp, March 1950, D. M. Moore, Wittlake # 1852: Grassy Lake, Hempstead County, Arkansas, landform, found growing a few inches to a foot from water's edge on sand, August 1950, Wittlake # 2053; On edge of Hardy, Sharp County, Arkansas, growing in rapids of Spring River, September 1, 1952, Wittlake # 2054.