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Reprinted from THE BRYOLOGIST, Vol. XXV, September, 1921.

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RECENT STUDIES ON CERTAIN SPECIES OF RICCIA*

ALEXANDER W. EVANS

The genus *Riccia*, as ordinarily understood, includes the two subgenera *Euriccia* and *Ricciella*. In typical *Euriccia* the air chambers are very narrow and clearly extend in a single layer from the compact ventral tissue of the thallus to the upper surface; in typical *Ricciella* the chambers are much broader and seem to be arranged in two or more layers when cross sections of the thallus are examined. Largely on the basis of these differences *Ricciella* has sometimes been considered a distinct genus. In all probability, however, its broad chambers are really in a single layer, and the superimposed arrangement which they seem to show is due to the obliquity of their course. This being the case the distinction in the chambers become reduced to a difference in width, and even this distinction has been proved inconstant as a differential character. Juel (**5**) has shown, for example, that *R. Bischoffii* Hüben., a widely distributed species of the Old World has narrow chambers in the median portion of the thallus and broad chambers toward the margin; and Von Gaisberg (**4**, p. 264) has made similar observations in the case of *R. Gougetiana* var. *armatissima* Lev., a Mediterranean form. The latter author cites in addition certain species of *Ricciella* in which some of the air spaces are almost as narrow as those of typical *Euriccia*. In view of these transitional forms connecting *Euriccia* and *Ricciella*, it seems wisest to follow the usual custom and consider the groups subdivisions of a single genus.

Until a few years ago *Riccia fluitans* L. was universally regarded as a clearly defined species of *Ricciella* with a wide geographical distribution. It was said to occur in two distinct states or forms: an aquatic form without rhizoids, which never produced sexual organs and sporophytes; and a terrestrial form with rhizoids, which produced sporophytes with some degree of frequency. The fertile terrestrial form was said to develop when the aquatic form was deposited on the mud, upon the evaporation of the surrounding water, while the aquatic form was said to develop when the terrestrial form was flooded. Most writers considered that the aquatic form, in spite of its sterility, represented the typical condition of the species, and the terrestrial form was often separated as the variety *canaliculata* (Hoffm.) Lindenb., in spite of the apparent ease with which one form could be converted into the other. *R. fluitans*, moreover, was regarded as the only member of the subgenus *Ricciella* that was able to live indefinitely

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*Contribution from the Osborn Botanical Laboratory.

as an aquatic, unattached plant. At the same time several closely related species that grow on soft mud along the borders of ponds or streams, but not in the water itself, have been described. Two such species, *R. Huebeneriana* Lindenb. and *R. pseudo-Frostii* Schiffn., appear in recent European manuals; in North America *R. Huebeneriana* has likewise been reported, but *R. pseudo-Frostii* is replaced by *R. Sullivantii* Aust. Another more distantly related species, *R. Frostii* Aust., may be mentioned in this connection; this grows in similar localities and has a wide distribution on both sides of the Atlantic.

Recently, especially in Europe, the opinion is becoming more and more widely held that some of these other species of *Ricciella* may live as aquatic plants too, giving rise to states or forms which resemble the aquatic form of "*R. fluitans*" in a marked degree. The advocates of this opinion hold that these various aquatic forms have been included in the old conception of "*R. fluitans*" and that the latter is, in consequence, not the aquatic form of a definite species but merely an aggregation of the aquatic forms of various distinct species.

One of the earliest papers bearing on these points was published by Torka (7) in 1906 and dealt with *R. Huebeneriana*, which he discovered near Schwiebus in eastern Germany, growing as a terrestrial plant on mud. He placed some of this mud, which bore rosettes of the *Riccia*, in a glass receptacle and flooded it with water. After a while the tips of the thalli began to elongate and fork, but instead of clinging to the mud these new growths failed to develop rhizoids and often became detached, floating freely on the surface of the water. Here they remained green for some time but eventually perished unless the water was drawn off. If this was done the floating fragments would be left on the mud and would renew their growth, giving rise to attached plants of a fairly normal appearance. The part that had previously floated, however, failed to develop rhizoids and assumed a brownish color, apparently indicating a disintegration of the tissues.

On the basis of these results Torka concluded that *R. Huebeneriana* would be able to maintain itself as an aquatic plant in the open, if the places where it grew were flooded. In his opinion floating plants of this character would be the only ones to survive the winter, attaching themselves to the substratum and developing normally after the water had sunk to its usual level in the spring. He thus ascribed to *R. Huebeneriana* an amphibious habit, comparable with that of *R. fluitans*.

Five years later (8. p. 205) he announced the discovery of aquatic plants of *R. Huebeneriana* near Nakel and Zablocie in Poland and described them as a new variety under the name *Ricciella Hübeneriana* var. *natans*. In his description he notes the lack of rhizoids and the tendency of large mats of thalli to break up into small mats as the older parts die. As a result of this process the surface of the water becomes closely covered with innumerable plants in the late summer and early autumn. At the edge of the water some of these floating fragments attach themselves to decaying plants or to the moist earth, where they develop rhizoids as they continue their growth, showing a tendency to develop into a more robust terrestrial form, just as the floating fragments did in his culture experiments. Torka does not state whether these plants produced sporophytes or not. In 1914 he distributed excellent specimens of his var. *natans* (**9**, No. 51) from the Zablocie locality. These present the appearance of a slender aquatic *R. fluitans*, as this species is usually understood.

It is unfortunate that Torka's evidence is not more conclusive. Although, in his cultures, the tips of the thalli often detached themselves and floated on the water, nothing is said about their growing while in this condition. It is implied, in fact, that the floating fragments carried on a very precarious existence unless they came in contact with some firm substratum. The mere fact that they remained green for a while would hardly show that they represented a true aquatic form of *R. Huebeneriana*. In order to prove that such a form had been produced it should have been shown that the plants in question were capable of continuing their growth and development in their new environment. With regard to the Polish specimens of his var. *natans* the evidence is lacking that these actually represent *R. Huebeneriana*. The only way in which this could be proved would be by means of morphological characters either in the thallus or in the spores. No such characters are given, and, although the attached plants are said to resemble the attached fragments of *R. Huebeneriana* in the water cultures, these fragments (as represented by Torka's figure) are hardly representative of *R. Huebeneriana* as it normally appears. The case is further weakened by the fact that he does not report the normal terrestrial *R. Huebeneriana* in the vicinity of the var. *natans*, although he cites a single station for it at a somewhat distant Polish locality.

In 1916 Donaghy (**1**) published a series of interesting field observations on *R. fluitans*, as it occurs in Indiana. He reports that the so-called terrestrial form is uncommon in his region but notes its occasional appearance "on mud flats and wet fields during the autumn." This form produces sporophytes in abundance. The aquatic form is abundant around Angola, Fort Wayne, and Terre Haute, where "during the summer and autumn mats . . . . can be found floating in ponds and sluggish streams," sinking to the bottom in the winter and remaining there until spring. Although plants beneath the ice remain uninjured, those "frozen in the ice are much winter-killed, the apical ends alone remaining green." During "spring these plants make rapid growth, and by summer patches of thalli again dot the ponds and streams." When, owing to evaporation, the water becomes low, "mats of plants are" often "washed upon the wet edges of the ponds," and "in favored places the thalli coming in contact with the wet soil develop rhizoids . . . . and open air-chambers." Whether such plants ever develop sexual organs and sporophytes remained uncertain, Donaghy's evidence on this point being wholly negative. He reports a case where plants "remained alive in wet shaded places . . . . in contact with the earth sufficiently long to fruit," and yet "no sporophytes were formed."

In Donaghy's opinion these sterile terrestrial plants, derived from the aquatic plants, were distinct from the so-called terrestrial form of *R. fluitans*, and he failed to find the latter on the mud of ponds where the aquatic form was growing. He concludes from his observations that "it seems very doubtful if the aquatic form ever changes into the terrestrial form or fruits" or "if the so-called terrestrial *R. fluitans* and the aquatic *R. fluitans* belong to the same species." Here again, it would be interesting to know just how the two terrestrial plants differed from each other, but no distinguishing morphological characters are given. It is stated, however, that the reticulate spores of the so-called terrestrial *R. fluitans* measure 75–90 μ in diameter, and this would seem to show that the material had been correctly determined and had not been confused with the closely related *R. Huebeneriana* or *R. Sullivantii*, the spores of which are smaller.

Although Donaghy's observations throw doubt on the present delimitation of *R. fluitans*, he evidently considers that the so-called aquatic form of the species is something definite. The contrary opinion is clearly expressed by Familler (**3**, p. 12), and he presents certain morphological distinctions to support his views. According to his statements it has now been definitely established that *Riccia fluitans* consists of at least two or three aquatic forms of various *Ricciae*. He therefore does not accept "*R. fluitans*" as a species but ascribes specific rank instead to what most writers regard as the fertile terrestrial form of *R. fluitans*. For this he takes up the old name *R. canaliculata* Hoffm. (as some of his predecessors have done) and calls the aquatic form of this species forma *fluitans* (L.) Fam. Under *R. Huebeneriana* he includes Torka's var. *natans*, as *Riccia Huebeneriana* forma *natans* (Torka) Fam., and he recognizes further an aquatic form of *R. pseudo-Frostii*. Since, however, he regards this species as a variety of *R. Huebeneriana* its aquatic form receives the name *Riccia Huebeneriana* var. *pseudo-Frostii* forma *natans* Fam. He implies that other species of *Riccia* may likewise have aquatic forms and suggests that a Mexican specimen, collected by W. Schaffner many years ago and determined by A. Braun as *Ricciella fluitans*, may be the aquatic state of *R. Frostii*, but he does not give this plant a formal name.

In separating the aquatic form of *R. canaliculata* from those of *R. Huebeneriana*, he assigns to the first very long air-spaces and to the second shorter and more crowded air spaces; in separating the aquatic form of the var. *pseudo-Frostii* from that of the ordinary *R. Huebeneriana*, he assigns to the first marginal air spaces about as long as wide and a clearly defined median band and to the second marginal air spaces about twice as long as wide and an indistinct median band. These differences are shown on *pl. 1* and *2;* the figures give the impression that the morphological distinctions between the various aquatic forms are based on variable characters and that careful culture studies would be necessary before the taxonomic value of these characters could be accurately estimated. Of course, if it could be proved that an aquatic form with long air spaces gave rise to typical *R. canaliculata* and that a form with short spaces gave rise to *R. Huebeneriana*, the differences in the air-spaces would at once assume a greater importance. Unfortunately proof of this character is lacking, and some of Von Gaisberg's culture experiments, to be mentioned below, have yielded contradictory results.

Von Gaisberg's studies on *Riccia* (**4**), carried on in Goebel's laboratory at Munich, throw an interesting light on some of the questions here discussed.

Evidence is first presented to show that an aquatic form of *Riccia* is not necessarily sterile, even in Europe. In old specimens collected by A. Braun at Tempelhof near Berlin and labeled by him *R. "fluitans fructifera"* archegonia are present in abundance. These specimens lack rhizoids and present every appearance of having been aquatic in habit. Wherever archegonia are situated the thallus is distinctly broader, and where the archegonia are separated from one another by sterile tracts the thallus shows a series of marginal lobes on each side, indicating the position of the archegonia. Von Gaisberg compares the Tempelhof *Riccia* with the African *R. Dinteri* Steph. (apparently a manuscript species), which was found on stones in a spring. Here too the position of the archegonia is marked by marginal lobes. Unfortunately he gives us no data regarding the spores in either case. It should be mentioned in this connection that Familler (**2**, p. 166) had already noted the occurence of fruit in the aquatic form of "*R. fluitans*", before he had developed his later ideas regarding the species. His specimens came from Bavaria, but he tells us nothing about their structural features.

In his experimental work Von Gaisberg first utilized an aquatic form of "*R. fluitans*" growing in the university greenhouse at Munich. When this was transferred to soil it gave rise to what he called a "broad form," but even in this condition remained perfectly sterile, so that it was impossible to assign it to any known species on the basis of characters derived from the spores. He then turned his attention to an aquatic *Riccia* which he found in the vicinity of Starnberg in Bavaria. This plant was determined by Familler, presumably on the basis of its morphological features, as *R. Huebeneriana*; but when it was cultivated on soil it gave rise to a "broad form" essentially like that derived from the greenhouse material. Von Gaisberg expresses the opinion that this "broad form" is distinct from "*R. fluitans* f. *canaliculata*" and also from *R. Huebeneriana*. Although he thus differs from Familler, so far as the latter's determination of the Starnberg material is concerned, he agrees with him in considering "*R. fluitans*" a composite species and cites, in further defense of this view, the wide variation in width exhibited by herbarium specimens bearing this name.

In the brief description of the "broad form" it is noted that the air chambers are more or less polygonal; in cross section the thallus is bounded on each side by a single large chamber but elsewhere the chambers appear to be in two layers or sometimes, in the median portion, in three. Although these features might serve to distinguish the plant from *R. Huebeneriana*, as this species is usually described, they would hardly distinguish it from the "forma *canaliculata*"; and it is unfortunate that no other differential characters are indicated.

The work here reviewed shows that our knowledge concerning "*R. fluitans*" and certain terrestrial forms or species of the subgenus *Ricciella* is still far from complete. It shows further that additional culture experiments and accurate morphological comparisons will be necessary before satisfactory conclusions can be reached. The species of this subgenus are exceedingly variable and react to slight environmental differences. *R. Huebeneriana*, for example, although seemingly very distinct from *R. pseudo-Frostii* in size, in color and in the shape of the cross section of the thallus, is not so in reality. Familler (**3**, p 14) has shown that typical *R. pseudo-Frostii*, in some of his cultures, became directly transformed into *R. Huebeneriana*, and Nicholson (**6**, p. 202) has confirmed these results by careful observations in the field. There is every reason to suppose that *R. fluitans* is fully as variable as *R. Huebeneriana*. The so-called "broad form" of Von Gaisberg and the terrestrial form obtained by Donaghy in his study of the aquatic *R. fluitans* should therefore be subjected to a more rigid scrutiny than they have yet received, in order to determine whether their distinctive features are constant or inconstant in character. Until this is done their status must remain uncertain. Renewed search should likewise be made for the aquatic form of *R. fluitans* in fruiting condition, in order to determine whether or not the marginal lobing of the Tempelhof specimens represents a constant feature and also to compare the spores with those of the terrestrial form.

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POLLEN AND POLLEN ENZYMES

I. THE THEORETICAL AND PRACTICAL ASPECTS OF THE OCCURRENCE OF POLLEN ENZYMES

JULIA BAYLES PATON

Reprinted from the AMERICAN JOURNAL OF BOTANY, VOL. VIII, No. 10, December, 1921.

[Reprinted from the AMERICAN JOURNAL OF BOTANY 9: 471–501. January. 1922.]

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POLLEN AND POLLEN ENZYMES

JULIA BAYLES PATON

(Received for publication March 28, 1921)

I. THE THEORETICAL AND PRACTICAL ASPECTS OF THE OCCURRENCE OF POLLEN ENZYMES

Reasons for Undertaking the Investigation

A review of the literature shows very few complete or satisfactory reports of experiments in regard to either the general chemistry or the enzymes of pollen. Our knowledge of the subject seems to be very fragmentary. It is conspicuous by its omission from the textbooks of botany. Aside from the few references given later, up to the present time no mention of any important work has been found.

Although it is generally assumed, and is stated in our textbooks, that the pollen tube digests its way through the tissues of the pistil and the ovule, yet there seems to be no experimental evidence as to the exact nature of this enzyme action. Besides this, pollen enzymes must be very important in rendering the food stored in the grain available when the pollen germinates, in nourishing the tube during its passage through the style, and in stimulating the development of the embryo and the maturing of the ovary.

Moreover, pollen anaphylaxis is now regarded as the cause of so-called hay fever and other forms of pollen poisoning. Pollen enzymes may be concerned in these reactions, and the proteolytic enzymes may affect the stability of the pollen-protein solutions used in pollen vaccination.

In view, therefore, of the apparent meagerness of our knowledge of pollen enzymes and of the possible practical value of any contribution to this subject, it has seemed worth while to study the matter and to present the results.

The Literature of Pollen Enzymes

Few original, systematic experiments have been reported. Erlenmeyer (1874) found amylase, or diastase, in pine pollen. Van Tieghem (1869) reported invertase, or invertin, in the pollen of hyacinth, narcissus, wallflower, and violet. Czapek (1905, p. 393) quotes Strasburger's statement

[The Journal for November (8: 425–470) was issued December 19, 1921.]

that the pollen tubes of *Agrostemma Githago* bore through the membrane of the stigma papillae as evidence for a cytase in pollen. Czapek also refers to the investigations of Rittinghaus (1886, pp. 105–122) as confirming the opinion of Strasburger. The observations of Rittinghaus may, however, be interpreted quite differently, and point quite as definitely to the presence of a pectinase, as of a cytase. Rittinghaus examined numerous flowers, including Ipomoea, Convolvulus, Alisma, Agrostemma, Lychnis, Phlox, and Silene. He writes (p. 111):

> Die Verschmelzung zwischen der Cuticula der Papille und der Cellulosemembran des Schlauches ist ganz deutlich zu erkennen, und es leuchtet ein, dass die Lücke in der Cuticula ihre Entstehung nur einer unmittelbaren Einwirkung der Pollenschlauchspitze verdankt. Das lösende Agens ist somit nur im Plasma des Pollenschlauches zu suchen. Über die Natur desselben ist einstweilen leider nichts zu eruiren, zumal das einzige uns bekannte Cuticula-lösende Reagens kochende Kalilauge ist. Vielleicht wird man später die Erscheinung durch die Gegenwart eines besonderen Enzymes aufklären können.

J. R. Green (1891) noted amylase in pollen tubes. Green's later researches in 1894 are by far the most careful and complete experiments on pollen enzymes which have so far been reported. They will be briefly reviewed on a later page. Strasburger (1886) mentions diastase and invertin as present in pollen grains prior to germination. Sandsten (1909) reports invertase and diastase. Later, Kammann (1904) found protease, diastase, catalase, and lipase in rye pollen but does not give details of his experiments.

In the investigations of Green (1894, pp. 385–409) the pollen was powdered with glass and the powder suspended either in glycerine, or in a 5 percent solution of NaCl, to which 2 percent of potassium cyanide was added as an antiseptic. In other cases chloroform (a few drops) or oil of cinnamon was used as an antiseptic. The 5 percent NaCl solution proved preferable to glycerine. Diastase was found in the pollen of Gladiolus, Anemone, Antirrhinum, Tropaeolum, Pelargonium, Crocus, Brownea, Helleborus, Alnus, Tulipa, and Clivia; also in that of Zamia after germination begins. Experiments failed to show any sufficient evidence for diastase in the resting pollen grain of Zamia, and starch makes its appearance in these pollen grains only on germination. Diastase was absent from the pollen of Lupinus, Lathyrus, Eucharis, Richardia, and Narcissus. The diastase, according to Green, dissolves the starch without corroding the grains. The pollens tested for invertase were those of *Eucharis grandiflora*, *Narcissus papyraceus albus*, *N. Pseudo-Narcissus*, Helleborus, Richardia, *Lilium pardalinum*, and *Zamia Skinneri*. It was found in these, but was absent from the pollen of Alnus and of Clivia. He reports that

> A few experiments were made with a view to determining the existence of a cytolyst and a proteolyst, but in no case could either be found.

In the case of *Eucharis grandiflora*, tested for invertase, Green says that

> Only the contents of three or four anthers were used, yet a workable quantity of invertase was extracted.

In summarizing he says:

> The enzymes present in the resting pollen grains are, therefore, chiefly diastase and invertase, but their distribution is irregular, some containing one, some the other, and some both. At the onset of germination usually the amount of both diastase and invertase is considerably increased. . . . When the grain has lost the power of germinating the quantity of diastase is materially decreased.

The conclusions, as will be noted later, are not entirely in accordance with the results of the present experiments.

The Significance of Pollen to the Living Plant, and the Probable Rôle of the Pollen Enzymes

A medium-sized Indian-corn plant produces about 50,000,000 pollen grains. Cat tails (Typha), which produce about 60,000 flowers to the average spike, shed enormous quantities of pollen. A near relative, the elephant grass (*Typha elephantina*) of East India and New Zealand, yields enough for the natives to use as a flour in bread- and cake-making. The dense cloud of pollen from a pine tree has been photographed, and many a camper has noticed the yellow powder staining the canvas of his tent when dampness has moistened the grains. Liefmann (1904, p. 163) found 2,500,000 grains of grass pollen in one square meter. Yet so tiny and light are these pollen grains that a small amount represents millions of grains. Ulrich (1914) estimated 172,800,000 grains in one gram of ragweed pollen, and Kammann (1912) estimated 20,000,000 in one gram of timothy pollen. Pollen grains are nearly omnipresent during the flowering season. One would suppose from these figures that it is an easy matter to collect large quantities of pollen, but it is really not easy. The winged grains of pine pollen are blown away by the slightest breeze. Ragweed pollen cannot be collected easily after nine o'clock in the morning. The grain of pollen is surrounded by an oily envelope containing air. When this air is heated by the sun it causes the floating away of the pollen, or the so-called "smoking" of the ragweed. It is not easy to get enough for an experiment. The fact that during three fourths of the year we have pollen grains always with us makes it evident that if they have active enzyme action their importance cannot be lightly overlooked.

Pollen grains present many types of configuration. The commonest forms are oval or spherical, but an extreme variation is seen in the extraordinary filamentous pollen grains of eel grass (Zostera) and of another water plant, Halophila. Although the grains differ greatly in shape and in surface markings or finish, in internal structure they are very uniform. They usually consist in the Angiosperms of two cells. One cell is purely vegetative and gives rise to the pollen tube; the other is the generative cell.

Pollen grains vary considerably in size. A very extensive list of both measurements and descriptions of the pollen grains of many species and families is given by Hansgirg (1897, pp. 17–76).

The pollen grains are very resistant to excessive heat, cold, or dryness, and certain kinds retain their viability for many years. The pollen of the date palm tested by Popenoe at the Mecca experiment station was kept seven years and still retained its power of germination. Goodale (1916) found that dry pollen could retain its active poisonous properties for twenty-five to thirty years. It is evident that pollen is an interesting physiological unit, and our knowledge of its composition should be more complete.

Since one cell of the pollen grain is vegetative and gives rise to the pollen tube, food must be stored in the grain and at the time of germination rendered available. We should expect therefore to find enzymes suitable for the digestion of the materials stored in the grain, and perhaps capable of also digesting the inner pectin membrane (Mangin, 1893, p. 655) which envelops the grain. It is one aim of the experiments reported to determine whether such a correlation exists.

The distance that the pollen tubes have to traverse varies greatly. Where a style is absent and the stigmatic surface is just above the ovary, as in Vitis and Actaea, the tube has only a little way to penetrate. In flowers with long tubular corollas and slender filamentous styles, such as Crocus, Oenothera, and *Zea Mays*, the tubes attain a relatively great length. The time required for them to reach the ovule also varies greatly. In some flowers the tube reaches its full development in a few hours, while in the pine, following pollination in the spring, the grains put forth short tubes which do not complete their growth for a year (Kerner, 1895, **2**: 420). In certain oaks thirteen months elapse between pollination and fertilization. In regard to the Taxaceae, Coulter (1910, p. 268) writes:

> The tube may advance directly toward the archegonia or it may pursue a devious route, in some cases not reaching the archegonia until during the second season.

Other instances are cited by Coulter and Chamberlain (1903, p. 147). Why this long delay? An interesting physiological and chemical problem is waiting to be solved. The 13-inch pollen tube of *Colchicum autumnale* needs only twelve hours to reach its goal, and the 9-inch tube of *Cereus grandiflorus* completes its growth in a few hours (Schleiden, 1849, p. 407). In *Iris versicolor* the male nuclei were observed in the embryo sac 79 hours after fertilization and the tubes were 14 mm. long (Sawyer, 1917, p. 163). Surely an intruding, growing tissue of such size and duration must during its period of development, profoundly affect the cells with which it comes in contact, or which are adjacent to it, in its passage through the style. It has long been customary to liken the pollen tubes to the haustoria of parasitic fungi, for they closely resemble the latter in many respects. In Pinus, according to Mottier (1904), the tube serves both as a conducting passage for the male gamete and as an absorber of nutriment. The haustorial habit seems to be the more primitive condition, and we have survivals of it in certain Angiosperms, as in *Iris versicolor* (Sawyer, 1917), hazel, oak, elm, hickory, and certain mallows (Kerner, 1895), where the tube branches frequently and serves apparently as both haustorium and directing channel. (See also Coulter and Chamberlain, 1903, p. 148.) The nature of the tube has been dwelt upon here at such length in order to emphasize the fact that we ought to know more fully how these tubular filaments make their way through the tissues of the style and ovary. We assume that they digest their way. One author of a recent textbook even states positively:

> Very soon after pollination, the tube cell begins to develop a pollen tube, *which secretes an enzyme that dissolves the cell walls* and contents of the nucellar tissue, thus facilitating the passage of the delicate tube.

Is this true? Can we prove the existence of a cytase which digests the cell wall? Is one enzyme sufficient to account for the varied needs of the pollen tube in the course of its life history?

There are several conditions which the pollen tubes may encounter before they reach the embryo sac. These are as follows:

(1) *An open stylar canal.* In such cases the germinating tubes may force apart the cells of the stigma and soon enter the open space of the style without having to penetrate any cells, at least not until they reach the ovule. The middle lamella is usually composed of pectin compounds (Frémy, Mangin, Allen, and others). A pectin-digesting enzyme might therefore be required to dissolve the middle lamellae of the stigmatic cells, but afterwards the tube has a clear course. Examples of this sort are seen in violet, mignonette, lily, rhododendron, Hypericum, Cistus, *Atropa belladonna*, and iris. According to Kirkwood (1906), in the Cucurbitaceae

> The tubes pass chiefly over the surface of the conducting tissue lining the stylar canal and covering the placenta lobes, and this is rich in starch.

The suggestion is made that the tube is directed in its course by nutrient substances secreted by the conducting tissue. This would imply the presence of a diastase to digest the starch. Even if there is actually no tissue to be digested, it seems reasonable to suppose that the tubes may derive nourishment from the cells lining the stylar canal. Negative aërotropism, positive hydrotropism, and positive chemotropism, which have been frequently demonstrated in pollen tubes, direct their course so that they penetrate the stigma. These same responses tend in many cases to keep the tubes closely appressed to the cells lining the canal. Considering the length of time it often takes a tube to reach the ovule and its considerable growth, enzymes along with other factors in nutrition must play an important part. Frequently, as in Anagallis, the channel is only a narrow space almost completely filled with a mucilaginous substance, supposed to be secreted by the cells lining the canal. It may be pointed out here that the mucilages are closely related to the pectins. If this material is utilized by the tubes during their passage through it, we should expect a suitable enzyme to be present.

(2) *A mass of loose, conducting tissue in the style.* The cells in the interior

of the style frequently are loosely connected, elongated, and sometimes mucilaginous. The pollen tubes, according to most histological reports, penetrate the middle lamellae of these cells. This is the condition most frequently met with. The pollen tubes follow the middle lamellae of the cells throughout their course. The lamellae are, as has already been stated, composed either of pectin or of closely related mucilaginous substances. Here again the necessity for a pectin-digesting enzyme is evident. It has been sought for in the experiments reported later. Since this condition is the most common, many examples could be cited. It may be well seen in members of the grass family and in Salvia (Bower, 1919, p. 269). Histological evidence seems to indicate that the cells of the style often remain intact. Shreve (1906, p. 115) says in regard to the pitcher plant (*Sarracenia purpurea*):

> The pollen tubes grow between the cells of the stigmatic surface and their entire passage is between the cells of the conducting tissue and never through them.

Gow (1907, p. 136), describing the fertilization of skunk cabbage (*Spathyema foetida*), writes:

> The central portion of the style consists of a loose mass of thin-walled cells through which the pollen tube readily forces its way to the upper end of the ovary.

Miller's account of the growth of the pollen tube of corn through the silk or style is interesting (1919, p. 264):

> Each silk has two fibro-vascular bundles. These bundles are surrounded by sheath cells which are characterized by their dense contents and large flattened nuclei. It is *between* these cells that the pollen tube travels down the silk. Arriving at the base of the silk the pollen tube works its way *between* the sheath-like cells that extend from the fibro-vascular bundles of the silk to the cavity of the ovary. The tube enters the ovary and twists and coils in its passage along the ovule coat until it reaches the micropyle. The pollen tube then pushes *between* the cells of the ovule until it reaches the embryo sac.

Again, in another part of his account, he says:

> The end of the pollen tube is greatly enlarged as it pushes its way between the sheath cells of the bundle. In its passage down the silk the *tube causes but little disturbance in the position of the cells, so that after the tube disappears the cells quickly return to their normal form and position.* [The emphasis here is my own.] The pollen tube so far as I have observed does not extend the full length of the silk at any time. It is difficult to locate it a short distance back of its growing region. It appears that the older portions of the tube are absorbed by the surrounding cells, while the growing part of the tube is apparently nourished by the dense sheath cells.

Land (1907, p. 276), in explaining the fertilization of *Ephedra trifurca*, notes that the pollen tubes force their way between the neck cells of the archegonium, rarely destroying them in their passage. Only in two instances were the lower neck cells destroyed.

(3) *Cell walls penetrated by pollen tubes.* According to most investigators this condition occurs only rarely. Perhaps it will be found more frequent if more observations are made. The classic illustration is corn cockle,

Agrostemma. Strasburger's illustration of the tubes actually penetrating and half filling the papillar cells of the stigma has been frequently copied. Mallow pollen tubes do the same. Recently Knight (1918, entry 964) has reported that in the apple there is no stylar canal. "Pollen tubes make their way through the tissue. There is a decomposition of the cells along this path with the extrusion of mucilage." This is interesting to compare with the opinion of Grieg Smith that mucilages are decomposition products of cellulose, and with Wiesner's statement that all gums are produced by a diastatic ferment acting on cellulose. The writer regrets that it has been impossible to secure corn cockle and mallow pollen so as to determine whether their enzyme action is different from that of other pollens. Apple pollen has shown some differences. In histological studies of fertilization little attention seems to have been paid to the question of how much the pollen tube disorganizes the neighboring cells. It seems that it would be worth while to examine material again with this thought in mind. Many of the drawings of the passage of the pollen tubes appear very diagrammatic. In this connection it is interesting to note Kerner's observation (1895, p. 392) that the pollen tubes of *Lamium amplexicaule*

> Perforate the walls of the anther and grow in the direction of the stigma until they reach it.

Pollen Grains as Carriers of Bacteria and Molds

Nine varieties of pollen were tested to see if any contained a rennin-like enzyme, such as is found in the juices of a number of plants. Thymol had been added to the unheated and autoclaved pollen extracts, but the milk had not been sterilized. It was observed that both the unheated ragweed pollen and the autoclaved dock pollen control had strongly coagulated the milk over night at room temperature. Repetition of the test with highest grade milk (Fairlea Farm) showed that unheated corn, Easter lily, and dock pollens caused clotting, as did even the autoclaved dock pollen. The strong "youghourt" or fermented milk odor, and the behavior of dock pollen made the reaction seem more like bacterial than like enzymatic action. Apparently the single period of heating in the autoclave had not destroyed all bacteria on dock pollen. Accordingly a number of tests were made employing the usual bacteriological methods. These tests showed that pollen grains harbor a varied flora of both bacteria and molds. It had been taken for granted that excess of toluol or of thymol was sufficient to inhibit bacteria and molds. Do the results of these tests with milk mean that in other instances it is the enzymes of bacteria and molds rather than those of pollen grains which cause the change? The writer believes that this is not true for the following reasons:

a. The results were constant with the same pollen regardless of its source. Corn, pine, maple, and goldenrod pollen were collected both in New Haven, and, owing to the difference in seasons, a few weeks later on the hills of Vermont, six miles from a town. When this possible source of error was suspected, ragweed pollen was purposely obtained from Michigan, from two parts of New York state, and from Connecticut. It does not seem probable that the bacteria and molds carried by pollen can be so constant as to cause similar enzyme action in each instance.

b. The reactions are too rapid to be due to bacteria. With the inhibiting action of antiseptics the time required for bacteria to develop in sufficient numbers to produce similar changes would be much longer. All the enzyme reactions recorded have occurred within 24 hours, and several have been almost instantaneous.

c. Slices of wood in water over night are not in any degree sterile, yet bacteria which have free access do not destroy the middle lamellae, but pollen grains do. Pollen grains taken from unopened anthers and put into sterile Petri dishes are not likely to have peculiar bacteria, absent from the immediate environment. Besides, examination of the pollen contamination showed only a few omnipresent common forms of bacteria.

d. Pollen solutions filtered through a Berkefeld filter gave the enzyme action of diastase on starch, and blood fibrin digestion.

e. It is probable that the ground pollen added something to the milk which stimulated the growth of bacteria already in the milk, and that it was these which caused coagulation rather than the bacteria introduced by the pollen. The reason for this belief is that in all the plates poured from milk to which pollen had been added *Bacillus fluorescens liquefaciens* was the dominant type. The plates after standing a few days were a bright apple-green from the fluorescent growth.

On other plates poured later from the pollen extracts only, not once did this form appear. In the latter it was often not until the third or fourth day that colonies of molds occurred. Doubtless there are resistant forms of spores on the pollen which endure the heat of the autoclave and develop under favorable conditions on the agar plates, but these can hardly account for digestions which occur during twenty-four hours.

The Chemistry of Pollen

While many kinds of pollen have been examined for certain special constituents such as starch, nitrogen, phosphoric acid, etc., only eight kinds of pollen, as far as I have been able to ascertain, have been analyzed with any degree of completeness. Czapek (1905) discusses topically the occurrence and distribution of the principal constituents of plants; if a substance has been reported present in pollen he mentions the fact. These scattered references afford a valuable index to the original literature of the earlier analyses.

According to Heyl (1919 *a*, p. 672) the walls of the pollen grain constitute 65 percent of the structure. Biourge (1892, p. 75) distinguishes four substances in the wall or envelope of pollen grains: cutin, cellulose, pectic substances, and callose. Sometimes one, or more than one, of the four materials are present in the same grain. These substances are indicated by characteristic solubility tests and by color reactions. He examined the pollen of 19 species of monocotyledons and 26 species of dicotyledons. His plates give over a hundred illustrations of the pollen grain coats and their sculpturing, showing details brought out by staining methods and chemical treatment. Mangin (1888, p. 144) states that the membrane is formed of pectin.

Water makes up a large but variable part of the grain. Thus Koessler (1918, p. 420) found 10.5 percent of moisture in ragweed pollen, while Heyl (1917, p. 1470) reports 5.2 percent for the same kind of pollen. Braconnot (1829, p. 104) found 47 percent of water in cat-tail pollen. Lidforss (1899, p. 292) examined a number of species and found the average moisture content to be about 10 percent.

The colors of pollen differ greatly. It is deep yellow in Easter lily, dark red in tiger lily, salmon in cypress, and white in petunia. Even in the same flower the color may vary, as is noted by Plimmer (1912, p. 51) in *Lythrum salicaria*, which has yellow pollen in the short stamens and bluish green pollen in the long stamens. Heyl (1919 *b*, p. 1285) states that the yellow pigment of ragweed is entirely glucosidic and about 0.6 percent of the pollen. He finds a quercitin glucoside which on melting yields a cherry-red oil; and a glucoside isorhamnetin which has beautiful characteristic crystals in the form of hexagonal prisms. So far, no other analysis of the pigments of pollen has been located in the literature.

Starch has been found present in some kinds of pollen and absent in others. Molisch tested 110 varieties and found starch abundant in 45, only a trace in 9 varieties, and absent from 46. That is, about half the kinds tested contained starch. Lidforss (1899, pp. 294–298) examined 150 wind-pollinated flowers of 72 genera and 29 families of native or naturalized Scandinavian plants, and found the pollen of all rich in starch. On the other hand, he tested the pollens of a few wind-pollinated tropical plants and found them starch-free. He also calls attention to the fact that Nägeli found the pollens of *Alnus glutinosa* and *Plantago lanceolata*, collected in Germany, starch-free, while pollens of the same species collected by himself in a more northerly region contained starch. Similarly, Nägeli found the pollen of juniper on Swedish mountains to be rich in starch, while Molisch found little in that of the Austrian juniper. Further, Molisch states that the pollen of *Antirrhinum tortuosum* is completely starch-free in summer, but in November he finds grains of three sorts, those which are normal but starch-free, little empty grains, and normal starch-containing grains. Tischler (1909, pp. 219–242), however, does not find this correlation between climate, or temperature, and the starch content of pollen. He examined a large number of tropical plants at Buitenzorg and reports that the plants growing under relatively unfavorable conditions of assimilation, for example on mountains 3,000 m. high and in the desert, showed no higher percentage of pollen with starch than the plants growing under the favorable climatic conditions of the tropical rain forest. He does, however, observe that there is frequently a difference in starch content between mature and immature grains.

Lidforss (1899, p. 306) reports the analysis of sixteen varieties of pollen for nitrogen and P_2O_5. Of these, 11 were from anemophilous, and 5 from entomophilous flowers. He found the average nitrogen content of the wind-carried pollen to be 4.63 percent, while that of the insect-carried pollen was 7.49 percent. The P_2O_5 showed a similar difference; the average for the former pollen being 1.76 percent, and for the latter 3.03 percent. Whether or not this represents a real correlation must be established by further observations.

The relative amounts of protein, fat, sugar, ash, etc., can best be seen by comparison of tables 1–7. It is interesting to note, from Stift's analyses of the pollen of three varieties of *Beta vulgaris*, that the different constituents may vary considerably in the pollen of one species (Stift, 1896, p. 43; 1901, pp. 105–106).

TABLE 1. *Comparison of Pollen Analyses (figures indicate percentages)*

Kind of Pollen	Authority	Protein	Fat	Ash	Carbohydrates	
Date palm . .	Vauquelin, 1802			$Ca_3(PO_4)_2$ $Mg_3(PO_4)_2$		
Cat tail	Braconnot, 1829		3.60		Starch	Sugar
Cypress	Church, 1875	8.67	1.87	3.70	85.76	
Hazel	Planta, 1885	30.06	4.20	3.81	5.26	14.7
						Saccharose
Pine	Planta, 1885	16.56	10.63	3.30	7.06	11.24
Pine	Kressling, 1891	15.87	10.00	5.50	7.40	12.075
						Pentosans
Beet	Stift, 1896,	16.90	3.52	9.18	0.89	12.26
	1901	16.68	5.47	7.13	0.89	7.27
Rye	Kammann, 1912	40.00	3.00	3.40	25	
					Dextrin	Sugars
Ragweed . . .	Heyl, 1917	24.40	10.80	5.39	2.10	2.10
						Pentosans
						7.26
Ragweed . . .	Koessler, 1918	8.25(?)	10.30	10.60		6.89

Stoklasa (1896, p. 631) analyzed the pollen as well as various other organs of apple, horse chestnut, and beet, and concludes:

> Das lecithinreichste Organ der ganzen Pflanze aber ist entschieden das Pollenkorn.

He found in apple pollen 5.86, in that of horse chestnut 5.16, and in that of beet 6.04 percent of lecithin. Heyl (1919 *a*, p. 672) discusses the chemical "building stones" from which the substance of pollen sperm nuclei may be built, if there is a parallelism with the chemical composition of animal sperms.

TABLE 2. *Analysis of Pine Pollen, Przybytek and Famintzin, 1885 (figures indicate percentages)*

Water	6.79
Ash	
Calcium oxid	35.23
Sodium oxid	3.62
Magnesia	7.00
Calcium	0.88
Iron and aluminum oxid	5.30
Phosphoric acid (anhydrous)	29.86
Sulphuric acid (anhydrous)	14.83
Chlorine	0.99
Manganese	a trace

TABLE 3. *Stift's Analyses of Pollen from a Cattle-fodder Beet and from two Varieties of Sugar Beet (figures indicate percentages)*

	Fodder Beet, 1895	Sugar Beet, 1895	Sugar Beet, 1900
Protein	15.25	16.90	16.68
Nitrogenous substances not protein	2.50	2.77	5.82
Fat (ether extract)	3.18	3.52	5.47
Starch and dextrin	0.80	0.89	0.89
Pentosan	11.06	12.26	7.27
Other nitrogen-free extractives	23.70	26.27	28.86
Crude fiber	25.45	28.21	27.95
Ash	8.28	9.18	7.13
Water	9.78		

TABLE 4. *Heyl's Analysis of Ragweed Pollen (1917)*

Alcohol-soluble (42.9 percent) contains (in percentages):

Moisture	5.28
Starch (diastase)	0.00
Crude fiber	12.20
Pentosans	7.26
Protein	24.40
Nitrogen in alcoholic extract	1.08
Ash	5.39
Dextrin	2.10
Fat	10.80
Lecithin	0.75
Ether-soluble, but not ligroin-soluble	1.75
Sucrose	0.40
Glucose	1.60
Resin	17.40
A nitrogenous base	trace

From the above review and from the analyses given in tables 1–7 it is clear that our knowledge of the chemistry of the pollen of the very numerous species of flowering plants is very limited. It is a discouraging problem because of the difficulty of getting large quantities of material, as Heyl points out when he estimates that it takes 610 million grains of ragweed pollen to make a gram.

TABLE 5. *Kammann's (1912) Analysis of Rye Pollen (figures indicate percentages)*

Inorganic substances		13.58
Water	10.18	
Ash	3.4	
Organic substances		86.42
Alcohol-ether-soluble	3.	
Carbohydrate	25.	
Non-protein nitrogen	18.	
Protein	40.	

TABLE 6. *Koessler's (1918) Analysis of Ragweed Pollen (figures indicate percentages)*

Inorganic substances		21.1
Moisture	10.5	
Ash	10.6	
Organic substances		78.9
Total reducing sugars after hydrolysis	6.89	
Ether-soluble lipoids	10.3	
Fatty acids after hydrolysis	4.75	
Phytosterol	0.34	
Insoluble in ether but soluble in 95 percent alcohol	12.5	
Extractives, etc., soluble in alcohol (resins) and water	11.5	
Insoluble residue (crude fiber, proteins, etc.)	37.71	

TABLE 7. *Purin Bases and Amino Acids in Pollen*

Kind of Pollen	Authority	Purin Bases	Percentage
Pine	Planta, 1885	Hypoxanthine Guanine	0.04
Hazel	Planta, 1885	Hypoxanthine Guanine	0.15
Pine	Kressling, 1891	Xanthine	0.015
		Guanine	0.021
		Hypoxanthine	0.085
		Amino Acids	
Ragweed	Heyl, 1917	Histidine	not given
		Arginine	"
		Lysine	"
		Agmantine	"
Ragweed	Koessler, 1918	Arginine	2.13
		Histidine	2.41
		Cystine	0.57
		Lysine	0.97

Other Physiological Aspects of Pollen in which Enzymes may Play a Part

In certain flowers there are two kinds of pollen grains, some of which produce tubes and others which do not. Müller (1883, p. 242) first distinguished these as "*Befruchtungs*"- and "*Beköstigungs*"-pollens, the former being the fertile, and the latter the sterile pollen which Müller thought served as the food of the pollinating insects. Tischler (1910, pp. 219–242) has studied this subject and has made the interesting discovery that in certain pollens, at least, the sterile grains may be stimulated to produce tubes by the addition to the culture medium of a trace of saliva or of diastase. The lack of a specific enzyme in these pollens seems thus to be the cause of sterility. It is quite possible that in other pollens the lack of pectinase, cytase, invertase, or of other enzymes may be equally important in inhibiting the growth of the tube. In some cases the deficiency may be made good by an enzyme secreted by the stigma. The whole question has a great deal of significance in problems of plant breeding.

Pollen enzymes may be concerned in the production of the characteristic odors of pollen which are probably factors in insect attraction. The emanations from moist pollen indicate the presence of fermentation products.

It also seems reasonable to suppose, as Erlenmeyer (1874, p. 206) has suggested, that pollen enzymes are co-workers with the enzymes from the body of the bee used in producing bee-bread.

Gardeners commonly believe that contact with pollen is frequently the cause of the discoloration and decomposition of the petals which is often a sequence of pollination.

II. Experiments in Regard to Pollen Enzymes

Plan of the Experiments

An effort has been made to collect a large variety of pollens, representing different families of plants, and including some of the so-called "hay-fever pollens." These pollens have been tested for twelve different enzymes. On account of the difficulties in collecting all the pollens at the start, the experiments have been made in two series. For the first the available pollens were those of (1) Easter lily, (2) *Lilium rubrum*, (3) red maple, (4) Norway maple, (5) Siberian crab-apple, (6) Austrian pine, (7) Scotch pine, (8) magnolia, and (9) dandelion. In the second series of experiments, in addition to some of the first nine pollens, those of the following plants were used: (10) corn, (11) daisy, (12) dock, (13) elm, (14) goldenrod, (15) ragweed, (16) rye, (17) tiger lily, (18) timothy. Not every one of the eighteen pollens has been used in every test, but an effort has been made to use as many as possible.

Methods of Collecting Pollen. Kinds of Pollen Used

The work was begun in February. At this time Easter lily pollen was available in the largest quantity. Since it is customary to remove the anthers as the flower opens, to prevent the pollen from staining the petals, it was easy to find an obliging florist who would place these anthers in a clean paper box. In this way surprisingly large quantities of pollen were secured. Care had to be taken to prevent molding. A paper box was found to be better for collection than glass jars, as the anthers dried more readily. It was also necessary to keep the anthers spread out, and to place them in a sulphuric-acid desiccator as soon as possible after collection.

When the anthers are dry, or partially dry, the large, sticky yellow pollen grains easily fall out. They can then be accumulated quickly by placing the anthers on one half of the bottom of a petri dish, moistening the other half with the finger tip, and then when the dish is covered and shaken in a horizontal plane the pollen adheres and heaps up on the moistened surface.

When it was necessary to remove adhering masses of pollen from a dish a glass brush was found better than a camel's hair brush, and for this purpose the glass brush from a Beegee ink eraser was excellent.

The easiest way of collecting the tiny pollen from many small flowers is by drying the blossoms on large sheets of paper and shaking them through a fine sieve. The anthers usually sift out and the pollen can be separated from the anthers by sifting again through fine silk bolting cloth. (Mimeograph typewriter diaphragm silk is convenient.) The microscope showed, in the case of red maple, that invisible hairs from the flower also sifted through, but the pollen from other plants appeared quite free from foreign particles.

Wodehouse (1916, p. 430) has suggested an excellent way of collecting large quantities of ragweed pollen.

> The flower heads just coming into bloom are crushed in a mortar with several volumes of carbon tetrachlorid. When strained through muslin the pollen passes through with the CCl_4 and can be separated by filtering on filter paper. The pollen is lighter yellow since the CCl_4 probably removed lecithin.

In collecting pine pollen it was found necessary to gather the staminate cones before they had opened, because later the slightest shaking of the branch scattered a cloud of pollen to the four winds. Cutting off the tassels of corn and allowing them to open indoors, over large sheets of paper, undisturbed by currents of air, gave the largest yield of corn pollen.

Preliminary Experiments

These experiments were in two parts: (1) Germination of the pollen grains, and (2) Comparison of the enzyme action of unground, ground, and germinated pollen. The results of these tests showed that the pollen ground with powdered glass was more effective in its enzyme action than either the unground or even the germinated pollen. The experiments were made as follows:

To secure vigorous growth of pollen tubes, Easter lily pollen was germinated (1) in tap water, (2) in 3, 5, and 16 percent sugar solution, (3) on agar, and (4) in Knop's solution and modifications. The stock agar recommended by Crabill and Reed (1915, p. 2) was used. This contains no carbon-containing nutrient and therefore does not favor bacterial and mold growths, which are exceedingly troublesome.

Formula for Stock Agar

Distilled water	1,000 cc.
Magnesium sulphate	0.5 g.
Di-potassium hydrogen phosphate	1.0 g.
Potassium chlorid	0.5 g.
Ferrous sulphate	0.1 g.
Agar	2.0 g.

The pollen tubes grew exceedingly well in the film of moisture formed on the surface of agar in petri dishes. The tubes were thicker, appeared more vigorous, and showed protoplasmic movement better than when grown in water or in dilute sugar solutions. This might be used as a method of showing variation in cell turgescence according to the density of the medium.

Formula for Knop's Solution

K_2SO_4	0.7 g. in 1 liter of water
$NaCl$	0.23 g.
$CaSO_4$	0.7 g.
$MgSO_4$	0.5 g.
Na_3PO_4	0.5 g.
NH_4NO_3	(solution 0.0649) 20 cc.

The tubes grew best in solutions from which the K_2SO_4 was omitted, and best of all in one in which the $CaSO_4$ was increased to 1.0 g. The K_2SO_4 seemed to cause disintegration of the tubes after 48 hours, but this evidence is of course very slight and more experiments must be tried to prove anything.

Of the four media used, tap water was selected as the best for Easter lily pollen. The grains germinated and produced long tubes in 24 hours, and the solution contained no foreign matter to be taken into consideration. After the tubes were well grown the pollen mass was filtered and dried in a desiccator. This dried germinated pollen was used both unground and ground with powdered glass.

Comparative quantitative determinations of the enzyme action of the unground, ground, and germinated pollen were made as follows: Having previously noted the marked invertase action of Easter lily pollen on cane sugar, the amount of copper precipitated from Fehling's solution by the reducing sugar formed was taken as an index of enzyme action.

The tests were made in five test tubes as follows: In each tube were placed 300 mg. of cane sugar, 15 cc. of distilled water (except in tube 4, where 10 cc. was used), and 8 drops of toluol. To tubes 1, 2, and 3 were added respectively 300 mg. each of unground, ground, and ground germinated pollen. To tube 4 was added 300 mg. of pollen boiled in 5 cc. of water, making the total quantity the same as in the other tubes. Tube 5 had no pollen added and served as a second control.

These tubes were allowed to stand in a warm room for 24 hours and were shaken occasionally. After this interval, 15 drops of each of the five suspensions was taken. To each portion 15 cc. of fresh Fehling's solution was added. The tubes were placed in a water bath and boiled an hour. The solutions were then filtered on desiccator-dried, weighed filter paper, and the copper precipitate was washed with hot water until free from the excess of Fehling's solution. The filter papers were then dried first in an oven and then in a desiccator and again weighed. The gain in weight represents the amount of reducing sugar present.

The weights of the papers are shown in table 8.

TABLE 8

	1st Weight	2d Weight	Gain
Unground pollen	824 mg.	857.05 mg.	33.05 mg.
Ground pollen	832 mg.	860.2 mg.	28.2 mg.
Ground germinated pollen	831.5 mg.	857 mg.	25.5 mg.
Boiled pollen	843 mg.	845.35 mg.	2.35 mg.
Sugar solution only	828 mg.	829.1 mg.	1.1 mg.

The gain in the unground pollen, which appears larger, is relatively less because in this test the 300 mg. was all pollen, while the 300 mg. in the other tests was partly powdered glass. From these figures and from several similar tests it seemed evident that in the case of Easter lily pollen invertase, at least, there was no advantage in previously germinating the pollen grains. Repetition of this type of experiment might show a wide range of variation both for kinds of pollen and for their enzymes.

The data obtained in testing for pectinase in Easter lily pollen confirmed the opinion that for this kind of pollen there was no gain in pectinase as a result of germination.

Tests for Amylase

The method used was to test a known quantity of starch paste with active pollen and an equal quantity with boiled pollen for a control. First, 10 cc. of 1 percent starch paste was used with 150 mg. of pollen. Later, 5 drops of 1 percent starch in 10 cc. of water was found to be a better dilution. Toluol was used as an antiseptic. The tubes were allowed to stand in a warm room for 24 hours and were shaken occasionally. Two portions of 15 drops each were then taken from each tube, and to one was added 2 drops of iodine to see if the starch had disappeared, and the other was heated with 15 drops of Fehling's solution to see if sugar had appeared. The results are seen in table 9.

In these tests, as in those already mentioned, the ground pollen was more active than the unground, but the germinated pollen did not appear to be more active than the ungerminated.

From table 10 it is seen that all kinds of pollen tested contained an amylase, but that this amylase was less active in the apple pollen (Siberian crab) and in that of the magnolia (cucumber tree) than in the other kinds.

In later tests with other kinds of pollen, Benedict's solution was used instead of Fehling's solution, as it is a more delicate test.

Table 9. *Tests for Amylase in Easter Lily Pollen*

	10 Cc. of 1 Percent Starch Solution + Toluol	5 Drops of 1 Percent Starch Solution in 10 Cc. H_2O + Toluol
Fresh (unground)	Slight digestion	Complete digestion
Fresh (unground)	Marked digestion but not complete	Complete digestion
Germinated	Marked digestion but not complete	Complete digestion
Germinated (ground)	Nearly complete digestion	Complete digestion
Boiled pollen	No digestion	No digestion

Table 10. *Tests for Amylase in Different Kinds of Pollen*

Pollen, 150 mg., added to 5 drops of 1 percent starch solution in 10 cc. of water to which toluol was added as an antiseptic.

Tests for starch: 15 drops of starch solution + pollen + 2 drops of iodine.

Kinds of Pollen	Active Pollen	Boiled Pollen
Easter lily	Rapid digestion	No digestion
Lilium rubrum	" "	" "
Red maple	" "	" "
Norway maple	" "	" "
Apple, Siberian crab	Slight digestion	" "
Austrian pine	Rapid digestion	" "
Scotch pine	" "	" "
Cucumber tree	" "	" "
Dandelion	Slow digestion	" "

Tests for sugar: 15 drops of starch solution + pollen, heated with 15 drops of Fehling's solution.

Kinds of Pollen	Active Pollen	Boiled Pollen
Easter lily	Rapid reduction	Some reduction
Lilium rubrum	" "	" "
Red maple	" "	" "
Norway maple	" "	" "
Apple, Siberian crab	Some reduction after ½ hr. heating	No reduction Cf. Table 8
Austrian pine	Rapid reduction	Some reduction
Scotch pine	" "	" "
Cucumber tree	" "	" "
Dandelion	" "	" "

Tests for Reducing Sugars

Since all the controls in the tests of amylase, except the boiled apple pollen, gave some reduction of Fehling's or of Benedict's solution, tests were made to determine the kind of sugar present in pollen. Filtered water extracts of the kinds of pollen listed above were heated with Fehling's solution. All except the apple pollen were found to contain reducing sugars, or some easily oxidized substance. When the apple-pollen extract was hydrolyzed with HCl and then neutralized with NaOH, it reduced the Fehling's solution, indicating the presence of a sucrose.

Tests for Starch

Solutions were treated first with chloral hydrate to render the grains transparent, and afterwards with iodine.

TABLE 11. *Tests for Starch in Different Kinds of Pollen*

1. Apple	−
2. Corn	+
3. Daisy	−
4. Dandelion	−
5. Dock	+
6. Elm	+
7. Goldenrod	−
8. Lily, Easter	−
9. Lily, tiger	−
10. Pine, Austrian	−
11. Pine, white	−
12. Ragweed	−
13. Rye	+
14. Timothy	+
15. Magnolia	−
16. Maple, Norway	−
17. *Lilium rubrum*	−
18. Maple, red	−

Tests for Zymase

The different kinds of pollen were tested with Pasteur's fluid, in Smith's fermentation tubes, for zymase. Toluol was added to inhibit bacterial action or molds. Apple pollen was the only one which showed any reaction, and since this was after standing 48 hours the result was doubtful. Since, however, apple pollen has been an exception in other instances, this test will be repeated when more pollen is available.

Tests for Invertase

Equal amounts of the different kinds of ground pollen (about 150 mg.) were added to 5 cc. of 3 percent cane sugar solution with 5 cc. of distilled water and 8 drops of toluol. Equal amounts of ground pollen were boiled with 5 cc. of distilled water and added to 5 cc. of the cane sugar with 8 drops of toluol solution for controls. The two sets of tubes were allowed to stand for 24 hours in a warm room. Then to 15 drops of each pollen solution were added 15 drops of Fehling's solution and the tubes were heated ½ hour to 1 hour in a boiling water bath, and the rate and amount of reduction in the different tubes were observed. Although this was not an exact quantitative test, as for the Easter lily pollen, yet the varying amounts of reduction in the different pollen solutions, and the differences between the active solutions and the controls, were strikingly noticeable. When the pollen was acid, producing a green color in Fehling's solution before heating, the tests were repeated, neutralizing the solution first. This was marked in red maple. Since the active pollen in every case caused more reduction than the boiled control, the reduction could not have been due merely to the reducing sugars of the pollen grains since the ruptured boiled grains would have yielded just as much sugar. The difference, therefore, may be due to the action of invertase. Moreover, apple pollen, which was found to contain sucrose, was extremely active in its invertase reaction. The results are shown in table 12.

Table 12. *Tests for Invertase*

Kinds of Pollen	Active Pollen	Control
Easter lily pollen.....	Rapid reduction	Slight reduction
Lilium rubrum.......	Slow "	" "
Red maple...........	Very rapid reduction	" "
Norway maple.......	Rapid reduction	" "
*Apple..............	Instant "	Some after 20 min. heating
Austrian pine........	Slow but marked	Slight reduction
Scotch pine..........	" " "	" "
Magnolia............	Very rapid	" "
Dandelion...........	Slow but marked	" "

Tests for Lipase

In the different methods used for testing for lipolytic enzymes the following substrates and testing reagents were used:

1. *Substrates.*

   (1) Ethyl butyrate.

   (2) Olive oil acidified with decinormal acetic acid and a little gum arabic added to make an emulsion.

   (3) Olive oil emulsion recommended by Zeller. 10 cc. of olive oil was dissolved in hot 100 percent alcohol. This was run through a hot separating funnel to which was attached a piece of glass tubing drawn out to a capillary jet. The stream of oil in alcohol was run into 100 cc. of cold distilled water which was stirred continually. The milky emulsion was then heated to drive off the alcohol and afterwards diluted with water.

   (4) Methyl acetate.

2. *Activator.* Approximately N/60 oxalic acid was used, partly because free acid is needed to counteract the slight alkalinity of the ground glass and more especially because free acid accelerates the activity of lipase.

3. *Alkali for titration.* Approximately N/10 sodium hydroxid solution was used to which a trace of barium hydroxid was added. To insure uniformity in readings, a 3-liter bottle was filled, and the solution was drawn off as needed through a connected graduated burette. Both the bottle and the burette had soda-lime bulbs at the inlet to absorb CO_2.

4. *Indicator.* Phenolphthalein was used in all titrations as an indicator.

5. *Antiseptic.* Toluol was added as an antiseptic. Controls of autoclaved pollen extract were run in each case, and the digestions were carried on in small stoppered Erlenmeyer flasks kept in an electric incubator at 36°–38° C. Samples were titrated at different time intervals. Methyl acetate was more strongly hydrolyzed than either ethyl butyrate or the olive oil preparations.

Austrian pine, dock, daisy, goldenrod, ragweed, rye, and timothy pollens were tested with the different substrates for lipase. The tests with ethyl butyrate were unsatisfactory. In the olive oil emulsion and methyl acetate media, Austrian pine, dock, ragweed, and rye pollens gave positive tests for lipase. The action on methyl acetate was especially marked with Austrian pine pollen, in which case the titrations showed nearly double the amount of acid with fresh pollen as compared with the boiled control.

Tests for Proteolytic Enzymes

Substrates for Proteolytic Enzymes

1. *Blood fibrin.* Fresh fibrin from pig's blood was obtained at the slaughter house, and was washed for several hours with a stream of cold water to remove corpuscles. Fairly uniform and compact strands of the fibrin were selected, and portions as nearly equal as possible were placed in test tubes with 10 cc. of distilled water, plugged with cotton, and sterilized for 20 minutes in an autoclave. Other portions were stained with 1 percent Congo red and the color was fixed by immersion in boiling water. The red color is liberated when the fibrin is digested. The colored fibrin was also sterilized.

TABLE 13. *Fermi's Gelatin Test*

5 cc. Fermi's gelatin, 5 cc. H_2O, 100 mg. pollen, 37° C. Degrees of liquefaction or failure to solidify, after standing in ice water 10 minutes, indicated by signs.

Kind of Pollen	Unheated Pollen		Autoclaved Pollen	
	24 Hrs.	48 Hrs.	24 Hrs.	48 Hrs.
1. Apple	+	++	−	−
2. Corn	+	+	−	−
3. Daisy	+	+	−	−
4. Dandelion	+	+	−	−
5. Dock	++	+++	−	−
6. Elm	+	++	−	−
7. Goldenrod	+	++	−	−
8. Lily, Easter	++	+++	−	−
9. Lily, tiger	++	++	−	−
10. Pine, Austrian	+	+++	−	−
11. Pine, white	+	++	−	−
12. Ragweed	+++	++++	−	−
13. Rye	++	++	−	−
14. Timothy	+	+	−	−
15. Magnolia	++	+++	−	−
16. Maple, Norway	+	+	−	−

2. *Fermi's gelatin.* The proportions used were those given by Dernby. 700 grams of gelatin were dissolved in 1,250 cc. of hot water over a water bath, strained through cheese cloth, and 2 grams of finely pulverized thymol were added. The solution was diluted to 2 liters and sterilized. Dernby diluted further before using, but this was not found necessary with the pollen extracts. When the gelatin was used it was melted over a bath and

to 5-cc. portions were added 5 cc. of distilled water and 100 mg. of pollen. For the control the pollen and water were first autoclaved. The tubes were incubated at 37° C. for 24 hours or longer (see table 13). The tubes were taken from the incubator and placed simultaneously in ice water, and the failure to solidify, or degree of congealing, during 10 minutes was noted.

Many investigators have used gelatin for detecting enzymes of the pepsin type, but the experiments of Malfitano, Mavrofannis, and Jordan, recently confirmed by Berman and Rettger, seem to indicate that liquefaction of gelatin by an organism is not proof of proteolytic activity. However, since pollen extracts, like pineapple juice, possess this power of liquefaction to a marked degree it has been considered worth while to record the observations.

Tests for Trypsin

Table 14

Congo red, blood fibrin, 2 cc. N/10 Na_2CO_3, 10 cc. pollen extract (50 mg. in 100 cc. distilled water, unheated and autoclaved), 1 mg. thymol in each tube.

Kind of Pollen	Test 24 Hrs.	Appearance of Solutions	
		Unheated	Autoclaved
1. Apple	−	No change	No change
2. Corn	++	Fibers disintegrated. Liquid very pink	Fibers unaltered Liquid pale yellow
3. Daisy	−	No change	No change
4. Dandelion	−	" "	" "
5. Dock	?	Fibers less firm. Liquid pinkish	No change
6. Elm	?	Liquid faint pink	" "
7. Goldenrod	++	Fibers disappeared. Liquid red-brown	Fibers unaltered Liquid yellow-brown
8. Lily, Easter	−	No change	No change
9. Lily, tiger	−	" "	" "
10. Pine, Austrian	+	Fibers partly disintegrated, liquid pink	No change
11. Pine, white	+	Fibers partly disintegrated, liquid pink	No change
12. Ragweed	+	Fibers partly disintegrated, liquid pink	No change
13. Rye	+	Fibers partly disintegrated, liquid pink	No change
14. Timothy	+	Fibers partly disintegrated, liquid pink	No change
15. Magnolia	++	Fibers disintegrated, liquid pink	No change
16. Maple, Norway	−	No change	" "

From tables 14–16 it may be seen that corn, goldenrod, Austrian pine, white pine, ragweed, rye, and timothy all gave positive results. Dock gave strongly positive results in the less alkaline medium, while magnolia and goldenrod were strongly positive in the more alkaline medium. Apple was negative with Na_2CO_3 added, but was positive without the addition of

Table 15

Same as shown in table 14, except that no Na_2CO_3 was added. Solutions slightly alkaline from the powdered glass. Thymol added to each tube.

Kinds of Pollen	Test 24 Hrs.	Appearance of Solutions	
		Unheated	Autoclaved
1. Apple	+	Fibers slightly disintegrated. Liquid pink	No change
2. Corn	++	Fibers completely disintegrated. Liquid pink	" "
3. Daisy	?	Fibrin darker, liquid milky	" "
4. Dandelion	–	No change	" "
5. Dock	++	Fibers completely disintegrated. Liquid pink	" "
6. Elm	?	Slight turbidity	" "
7. Goldenrod	+	Fibrin shrunken. Liquid dark brown	" "
8. Lily, Easter	–	" " " " "	" "
9. Lily, tiger	–	" " " " "	" "
10. Pine, Austrian	+	Disintegration, turbid, pink	" "
11. Pine, white	+	" " "	" "
12. Ragweed	+	" " "	" "
13. Rye	+	" " "	" "
14. Timothy	++	Complete disintegration. Liquid red	" "
15. Magnolia	–	No change	" "
16. Maple, Norway	?	Liquid turbid pinkish	" "

Tests for Pepsin

Table 16

Same as shown in table 14, except that 2 cc. of 0.2 percent HCl was added instead of Na_2CO_3.

Kind of Pollen	Test 24 Hrs.	Appearance of Solutions	
		Unheated	Autoclaved
1. Apple	–	No change	No change
2. Corn	+	Disintegration. Liquid pink	" "
3. Daisy	–	No change	" "
4. Dandelion	–	" "	" "
5. Dock	–	" "	" "
6. Elm	–	" "	" "
7. Goldenrod	–	" "	" "
8. Lily, Easter	–	" "	" "
9. Lily, tiger	–	" "	" "
10. Pine, Austrian	–	" "	" "
11. Pine, white	–	" "	" "
12. Ragweed	–	" "	" "
13. Rye	+	Disintegration. Liquid pink	" "
14. Timothy	+	" " "	" "
15. Magnolia	–	No change	" "
16. Maple, Norway	–	" "	" "

alkali. It may also be noted that in the digestion of fibrin in the presence of 0.2 percent HCl only the Gramineae showed activity. When Na $_2$ Co $_3$ was left out, apple, daisy (?), and dock were added to the list. These tests were repeated several times and gave consistent results. Toluol was substituted for thymol without any noticeable difference. In no case was there the slightest odor of putrefaction. The antiseptics were easily detected by their odor.

Tests for Erepsin

Solutions of Witte's peptone were used in the following proportions:

1. 10 cc. of 1 percent Witte's peptone, 2 cc. of N/10 sodium carbonate, 5 cc. of pollen extract 50 mg. in 10 cc. (unheated and autoclaved), 100 mg. of thymol.
2. 10 cc. of 1/10 per cent Witte's peptone, 1 cc. of N/10 sodium carbonate, 10 cc. of pollen extract (unheated and autoclaved), 100 mg. of thymol.
3. The above described solutions were used without adding sodium carbonate.

For testing, Gies's biuret reagent was used. This reagent consists of 10 percent KOH solution, to which 25 cc. of 3 percent $CuSO_4$ solution per liter is added. A large flask was filled with the reagent and connected with a graduated burette so that for each test the same strength of reagent should be used. In making the tests, 1 cc. of the solution to be tested was put with 20 cc. of biuret reagent in 25 cc. Nessler comparator tubes of uniform diameter and thickness. The color differences were read by looking down through the liquid at a white background. Solution 2 proved the best dilution. More than 1 cc. of the pollen-peptone solution did not give satisfactory results because of color interference and turbidity. In each test three tubes were compared: (1) 1 cc. peptone solution, or peptone plus Na_2CO_3, and thymol. (2) 1 cc. peptone, or peptone plus Na_2CO_3 plus unheated pollen, and thymol. (3) 1 cc. peptone, or peptone plus Na_2CO_3 plus autoclaved pollen.

The sixteen varieties of pollen previously listed were tested, but only apple and magnolia pollen gave positive results. Here the reaction of the unheated pollen with the biuret reagent gave a very faint pinkish tint as compared with the rose-violet tint of the controls.

Tests for Catalase

The decomposition of hydrogen peroxid in a fermentation tube was used as an indication of a catalase. All the kinds of pollen tested showed a marked reaction. Easter lily, magnolia, and apple pollen were exceedingly active. Maple pollen was the slowest but the action was evident. The boiled pollen extracts did not give the reaction.

Tests for Reductase or a Reducing Substance

The reduction of potassium permanganate solution by the different kinds of pollen was tested. All showed some reducing action; apple, Austrian pine, and magnolia were especially active. Apple pollen changed $KMnO_4$

at once to a pale amber. The boiled controls did not reduce the permanganate. This is not necessarily indicative of enzyme action. The reduction may be brought about by substances produced by the decomposition of the pollen grains.

Tests for Nuclease

Tests for phosphoric acid, which might indicate the splitting of nucleic acid, were made with ammonium molybdate on ground, unground, germinated, and boiled Easter lily pollen. All showed a strong phosphoric acid test so that no conclusions could be drawn.

Tests for Tyrosinase

A solution of tyrosin gave a negative reaction for all pollens of the first series tested.

Tests for Laccase

An alcoholic solution of gum guiacum, which was rapidly colored blue by freshly cut potato or orange peel, gave negative results with ten varieties of pollen.

Tests for Cytase

1. The method given by Crabill and Reed was used. Filter paper is dipped in manganese sulphate solution and then in potassium permanganate solution. The resulting manganic oxid colors the paper dark brown. Acids formed by the cellulose destruction combine with the manganic oxid to form light-colored salts which show by contrast on the brown background. Both ground and unground pollen placed on moistened sterilized strips of such paper caused no color change, although a subsequent growth of mold did so.

2. Cellulose was prepared from filter paper in the following manner. Schweitzer's reagent (ammoniacal cupric oxid) was used as a solvent. This was made by adding to a strong copper sulphate solution, first, ammonium chloride, and then an excess of sodium hydroxid. The blue-green precipitate thus formed was allowed to settle, the liquid decanted off, and the precipitate washed repeatedly with water on a Buchner funnel and filtered by suction. The precipitate was then dissolved in 0.92 percent ammonia. The resulting deep blue liquid readily dissolves strips of filter paper. When sufficient paper had been dissolved to make a thick, syrupy liquid, it was poured into dilute hydrochloric acid (1 : 5) and the cellulose was precipitated in small flecks. The precipitated cellulose was washed repeatedly with water on a Buchner funnel and filtered by suction, until the filtrate showed no trace of HCl when tested with $AgNO_3$. The pure white mass of cellulose was then boiled with distilled water to make a fine suspension and to sterilize it. The suspension was tested with both iodine and Benedict's solution to be sure that it was both starch- and sugar-free, as was the case. The tests were made as follows: 10 cc. of cellulose suspension, 100 mg. of ground

pollen, 30 cc. of distilled water, and 2 cc. of toluol were placed in small stoppered flasks. For the control the pollen and water were heated in the autoclave. The suspensions were incubated at 37° C., and shaken frequently. The solutions were tested for sugar at 24-, 48-, and 96-hour intervals, and then allowed to stand for several weeks at room temperature to see if there would be complete destruction of the cellulose. In no case has this occurred, although several preparations have been kept for three months (see table 17). In testing for sugar the flasks were well shaken. Then the cellulose was allowed to settle out and 2 cc. of the clear liquid was transferred to a test tube and 10 cc. of Benedict's solution was added. All the tubes, both the unboiled and the boiled pollen controls, were then heated simultaneously in a boiling water bath until reduction was complete. If there was a striking difference in the amount of precipitate in the unboiled and in the control the quantitative test was made, but if no difference could be detected the precipitates were weighed as described on a previous page. Pollens were selected which did not all contain starch, so that the resulting gain in sugar did not come from this source. Yet the diminution in the amount of cellulose in the flasks was so slight that it is difficult to interpret results.

Table 17

Kinds of Pollen	Unheated Pollen	Autoclaved Pollen
1. Apple	+	−
2. Corn	−	−
3. Daisy	−	−
4. Dandelion	−	−
5. Dock	+	−
6. Elm	−	−
7. Goldenrod	−	−
8. Lily, Easter	−	−
9. Lily, tiger	−	−
10. Pine, Austrian	+	−
11. Pine, white	+	−
12. Ragweed	−	−
13. Rye	+	−
14. Timothy	+	−
15. Magnolia	−	−
16. Maple, Norway	−	−

Tests for Pectinase

As has already been noted, special importance was attached to the possible occurrence of a pectinase as indicative that the pollen tube digests the inner lamella of pectin in the cell walls of the pistil. Three methods of testing for a pectinase were tried.

1. Pistils of Easter lily were placed in a tube with distilled water and freshly ground pollen, and a second set were similarly treated with boiled pollen. After 24 hours the pistils were examined for alteration of texture.

It was found that the pistils with the active pollen had noticeably softened and the styles could easily be teased apart with dissecting needles, while the pistils with boiled pollen were still firm. The longitudinal and cross sections of the pistil treated similarly showed the same results. Incidentally, the chemotropism of the pollen grain for the stigma was conspicuous in the active pollen tubes.

2. Equal amounts of desiccator-dried ground Easter lily pistil were treated with pollen, and tested quantitatively for sugar as in the invertase test already described.

	Dried Ground Pistil	Boiled Pollen	Water	Toluol
(*a*)	150 mg.	100 mg. in 5 cc. water	10 cc.	4 cc.
	"	100 mg. ungerminated	15 cc.	"
	"	100 mg. germinated	"	"
	"	100 mg. ground	"	"

(*b*) Solution 15 drops, alkaline to neutral.
Fehling's solution 15 drops.
Boil in water bath ½ hour.
Filter on weighed, desiccator-dried paper.
Dry in oven and desiccator.
Weigh again.

		1st Weight (mg.)	2d Weight (mg.)	Gain (mg.)
(*c*)	Boiled pollen	711	716.3	5.3
	Ungerminated	711.2	720.15	8.95
	Germinated	720.28	729.00	8.72
	Ground	827.00	839.00	12.00

3. The action of pollen on pectin was tested. The pectin used for the tests was prepared from the white inner skin of grape fruit, as follows:

Remove the white and boil in water.
Put through a meat chopper.
Leave in cold water 24 hours.
Boil from ½ to 1 hour.
Strain through cheesecloth.
Filter.
Concentrate by heating over a water bath.
Add 95 percent alcohol to precipitate.
Filter.
Wash with absolute alcohol.
Dry in a desiccator.

For the tests the following amounts were used:

(*a*) 3 cc. of pectin solution (300 mg. in 20 cc. of water), 300 mg. of pollen, 15 cc. of water, 8 drops of toluol.

(*b*) 15 drops of the pollen-pectin solution, 15 drops of Fehling's solution, or Benedict's solution. Treat as stated above (2 *b*).

	1st Weight (mg.)	2d Weight (mg.)	Gain (mg.)
(*c*) Austrian pine (active)	767.5	789	21.5
" " (boiled)	779	785	6
Norway maple (active)	778	797	19
" " (boiled)	782	794	12
Magnolia (active)	814	835	21
" (boiled)	809	815	6
Apple (active)	795	805	10
" (boiled)	799	807	8

(*d*) In this test 150 mg. of pectin and 150 mg. of ground pollen and glass were used, and the entire amount precipitated with Fehling's solution.

	1st Weight (mg.)	2d Weight (mg.)	Gain (mg.)	Actual Gain (mg.)	
Apple pollen (active)	765	963	198(−150)	48	28
" " (boiled)	754	924	170(−150)	20	
Red maple (active)	767	969	202(−150)	72	·23
" " (boiled)	748	947	199(−150)	49	

(*e*) Later similar tests were made with seven other kinds of pollen, daisy, dock, goldenrod, white pine, ragweed, rye, and timothy. All gave positive results for the pectinase test.

Subtracting the constant 150 mg. of pollen and glass, the actual gain of sugar from pectin for the apple pollen, as compared with the control, is 28 mg. and for the red maple pollen 23 mg. This is larger than in the previous table, but larger quantities were used. Not only do the quantitative determinations show that pectin is converted into sugar by active pollen, but also in comparing the tests and their controls in the test tube it was very noticeable that the reduction of Fehling's solution was greater with unboiled pollen.

4. Another test which confirmed the presence of a pectinase was made for me by Mr. F. B. H. Brown, Yale University. Mr. Brown in his work on tropical woods, by a special method of technique, has succeeded in making sections one eighth as thick as are usually cut. When sections of dragon-tree wood (*Dracaena aurea*), *Tecoma obtusa*, and a species of roselle were floated on water with Easter lily pollen and allowed to remain from 24 to 48 hours, on examination with the microscope it could be plainly seen that in many places the middle lamellae of the cells had been completely digested. Permanent slides were prepared.

Tests for Bacteria and Molds on Pollen

1. One method was as follows: Extracts of nine different pollens were made, 50 mg. in 10 cc. of water. This extract was then diluted by the usual milk-testing method in sterile bottles to dilutions of 1 : 100 and 1 : 10,000. 1 cc. of this dilution was then placed in sterile petri dishes and agar plates were poured. The plates were then incubated at 37° for 24 hours, in an inverted position to prevent moisture from washing off cultures,

and the colonies were counted. Results from two of several tests are shown, giving the averages (see table 18).

2. 100 mg. of Easter lily pollen was ground well with sterile sand, then well shaken with 100 cc. of 0.85 percent NaCl and 100 mg. of thymol. 1 cc. of this suspension was diluted with 100 cc. sterilized water. Plates of agar were poured with 1 cc. of this dilution and incubated 24 hours at 30°. The average number of colonies on 4 plates was 3. The experiment was repeated, omitting thymol, and the average number on 4 plates was 12. Similar tests with corn, ragweed, and rye gave corresponding results. Thymol does exert an inhibiting action but does not prevent growth of bacteria introduced with the pollen.

3. One gram each of corn, ragweed, rye, and Easter lily pollen was ground with sterile sand and extracted 24 hours in the ice chest with 100 cc. of 0.85 percent NaCl. This solution was filtered through a small, thoroughly sterilized Berkefeld filter into a sterile side-neck flask. Care was taken to plug the side-neck with cotton before sterilizing so that no contamination could enter while filtering by suction. 1-cc. portions of each filtrate were removed with a sterile pipette and agar plates were poured, 4 of each kind of pollen. These were incubated at 37° for 48 hours. No colonies appeared. All the plates were sterile. Six days later one plate had a colony of mold, but this could easily have been later contamination. The sterile filtered extracts were then used for testing for diastase, liquefaction of gelatin, and digestion of fibrin. The diastatic action seemed as rapid as before filtration, but the gelatin liquefaction and fibrin digestion were decreased. The gelatin was completely liquefied after 48 hours, and the rye and ragweed extracts caused only slight digestion of the fibrin. Repetition with other samples confirmed the belief that the filter absorbed the enzyme to a considerable extent. If one could use separate filters for each kind of pollen and work with large quantities, this difficulty might be overcome by allowing the filter to become saturated with the extract.

TABLE 18. *Bacteria and Mold Colony Counts. Averages of Four Plates each. Dilutions 1 : 100 and 1 : 10,000. 37°, 24 Hours.*

Kind of Pollen	Unheated		Autoclaved	
	1 : 100	1 : 10,000	1 : 100	1 : 10,000
Corn	8	0	0	0
Daisy	17	0	0	0
Dock	72	2	14	1
Goldenrod	20	0	0	0
Lily, Easter	2	0	0	0
Pine, Austrian	11	0	0	0
Ragweed	43	1	0	0
Rye	31	2	0	0
Timothy	27	14	0	0

4. Washing the pollen before use was tried with corn, ragweed, and Easter lily. 1 gram of unground pollen was shaken vigorously with 300 cc. of distilled water in a liter cylinder, and then filtered into a sterile flask through a sterilized Buchner funnel and filter paper, and washed four times with sterile distilled water. Plates were poured from the last washing, dilution 1 : 100. Some plates were sterile and others from the same filtrate had from 1 to 19 colonies. The washed pollen when diluted and tested showed a similar lack of constancy, so that there seems to be no gain in washing, and this method may cause loss of enzymes.

Repetition with dock pollen failed to show that it always had a higher count. There was probably some initial contamination in preparing the extract.

Summary

Although it has been assumed that pollen tubes digest their way through the style, there is little experimental evidence as to the exact nature of this enzyme action. Histological examination shows that in most instances pollen tubes make their way between the walls of adjacent cells rather than penetrating them. We should expect therefore to find most frequently not a cytase- or cellulose-digesting enzyme, but rather a pectinase capable of digesting the pectin of the inner lamella. This has been proved in the writer's experiments to be the case.

Eighteen species of pollen have been used; these have been tested for thirteen kinds of enzymes. So far amylase, invertase, catalase, reductase, and pectinase have been found in all. Pepsin, trypsin, erepsin, and lipase have been demonstrated in some and not in others. Cytase was doubtfully identified in six of the eighteen. Tyrosinase and laccase have not been found in any, and zymase was found only in Siberian crab apple pollen.

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Reprinted from The Bryologist, Vol. XXV, May 1922.

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THE BRYOPHYTES OF MICHIGAN WITH PARTICULAR REFERENCE TO THE DOUGLAS LAKE REGION*

George E. Nichols

Our knowledge of the bryophyte flora of Michigan seems to be limited to five published lists, of which three are based on collections from Isle Royale, the extreme northern outpost of the state. Of these three, the first in order, by Holt[1], records 38 mosses; the second, by Cooper[2], raises the number of mosses to 104; the third, by Conklin[3], records 36 liverworts. Of the two remaining papers one by Kauffman[4], based in large measure on specimens collected in southern Michigan, records a total of 131 liverworts and mosses; the other by Praeger[5] records 10 species of *Sphagnum* from the vicinity of Douglas Lake.

The present paper, like Praeger's, is the outcome of investigations carried on at the University of Michigan Biological Station, situated on Douglas Lake, and is based primarily on collections made by the writer during the summers of 1920 and 1921. By far that larger number of records are from the immediate vicinity of Douglas and Burt Lakes, in Cheboygan County, but collections were also made in the vicinity of Pellston, Cecil Bay, and Big Stone Bay, in Emmet County, and on Mackinac Island, in Mackinac County. Cheboygan and Emmet Counties are the northernmost counties in the southern peninsula of Michigan, while Mackinac Island lies in the straits of Mackinac, between Lakes Michigan and Huron. A few scattered records are included from the southern shores of the northern peninsula of Michigan (Prentis Bay and Scotty Bay), based on collections by Dr. J. H. Ehlers, who is responsible also for a number of records from other localities.

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* Contribution from the Osborn Botanical Laboratory.

[1] Holt, W. P. Notes on the vegetation of Isle Royale, Michigan. In "An ecological survey of Isle Royale, Lake Superior", prepared under the direction of C. C. Adams. Lansing. 1908 (1909).

[2] Cooper, W. S. A list of mosses collected upon Isle Royale, Lake Superior. Bryologist **16**: 1-8. 1913.

[3] Conklin, G. H. A list of Hepaticae collected upon Isle Royale, Lake Superior. Bryologist **17**: 46-48, 52-55. 1914.

[4] Kauffman, C. H. A preliminary list of the bryophytes of Michigan. Mich. Acad. Sci. Rep. **17**: 217-223. 1915.

[5] Praeger, W. E. A collection of sphagnum from the Douglas Lake region, Cheboygan County, Michigan. Mich. Acad. Sci. Rep. **21**: 237, 238. 1919.

The March number of The Bryologist was published May 22, 1922.

Holt's Isle Royale list includes the following 8 mosses which are not known to have been found elsewhere in the state and which were not subsequently collected on that island by Cooper.

Dicranum longifolium Ehrh.
Grimmia unicolor Hook.
Ulota americana (Beauv.) Limpr.
Paludella squarrosa (L.) Brid.
Bryum pallens Sw.
Hygrohypnum polare (Lindb.) Broth.
Neckera oligocarpa Bruch
Dichelyma uncinatum Mitt.(?)

Cooper lists 12 additional mosses from Isle Royale which are not definitely known to occur elsewhere in the state, as follows:

Polytrichum alpinum L.
Cynodontium polycarpum (Ehrh.) Schimp.
Grimmia ovata Schwaegr.
Racomitrium canescens (Timm) Brid.
Encalypta procera Bruch
Anoectangium lapponicum Hedw.
Splachnum ampullaceum L.
Bryum inclinatum (Sw.) Bland.
Bryum Mühlenbeckii Br. & Sch.
Mnium subglobosum Br. & Sch.
Amblystegium fluviatile (Sw.) Br. & Sch.
Calliergon Richardsonii (Mitt.) Kindb.

Both Holt and Cooper list *Sphagnum subsecundum* Nees (as *S. platyphyllum* Sull.).

Conklin's list of Isle Royale liverworts includes the following 5 species not elsewhere recorded from Michigan.

Cephalozia bicuspidata (L.) Dumort.
Lophozia heterocolpa (Thed.) Howe
Lophozia longidens (Lindb.) Macoun
Lophozia Lyoni (Tayl.) Steph.
Sphenolobus minutus (Crantz) Steph.

Kauffman records 28 liverworts and mosses which appear on no other Michigan list (including the present one); viz.:

Ricciella fluitans (L.) A. Br.
Ricciocarpus natans (L.) Corda
Lunularia cruciata (L.) Dumort.
Reboulia hemisphaerica (L.) Raddi
Calypogeia suecica (Arn. & Pers.) Warnst. & Loeske
Porella pinnata L.
Pleuridium alternifolium (Dicks.) Rabenh.
Ditrichum pallidum (Schreb.) Hampe
Ditrichum tortile (Schrad.) Lindb.
Fissidens taxifolius (L.) Hedw.
Barbula fallax Hedw.
Barbula unguiculata (Huds.) Hedw.
Tortula subulata (L.) Hedw.
Orthotrichum Braunii Br. & Sch.
Orthotrichum ohioense Sull. & Lesq.
Physcomitrium turbinatum (Michx.) C. Müll.
Bryum affine (Bruch) Lindb.
Aulacomnium heterostichum (Hedw.) Br. & Sch.
Fontinalis antipyretica L.
Entodon cladorrhizans (Hedw.) C. Müll.
Entodon seductrix (Hedw.) C. Müll.
Leskea obscura Hedw.
Thelia asprella (Schimp.) Sull.
Brachythecium acuminatum (Hedw.) Kindb.
Brachythecium acutum (Mitt.) Sull.
Oxyrrhynchium praelongum hians (Hedw.) Warnst.
Rhynchostegium serrulatum (Hedw.) Jaeg.
Thamnium allegheniense (C. Müll.) Br. & Sch.

The lists of both Cooper and Kauffman include two additional bryophytes which have not been collected in the region covered by the present investigation, namely *Bryum intermedium* (Ludw.) Brid. and *Stereodon curvifolius* (Hedw.) E. G. Britton; while both Conklin and Kauffman list *Jungermannia lanceolata* L. and *Porella platyphylla* (L.) Lindb[1]. To these should be added, as not elsewhere recorded for Michigan, *Anacamptodon splachnoides* (Froel.) Brid. and *Elodium paludosum* (Sull.) Loeske, collected by the writer at Lakeside, Berrien County, in 1910.

Of the 261 species to be noted in the present paper as occurring in the Douglas Lake region, no less than 101 appear not to have been previously reported from the state. These species will be marked with a star (*).

For a country of moderately rolling topography with little rugged relief, a country of sands and gravels with almost no outcrops of bed rock (except at Mackinac Island), a country which has been almost completely lumbered and more or less extensively burned over, the comparative richness in species of the bryophyte flora in the Douglas Lake region, at first thought, seems almost incredible. But this diversity is at once explained by the surprising variety of habitats which this region, superficially so lacking in promise, reveals upon closer examination. The principal types of habitat, in so far as these are of bryological importance are as follows:

The Hardwoods.—The magnificent forests of beech, sugar maple and hemlock which, with white pine, formerly covered the uplands throughout this region are now represented only by occasional primeval stands and by somewhat-more frequent second-growth tracts of woodland.

The Aspens.—The prevailing type of vegetation on uplands today is dry open woodland, more or less densely populated by aspen, with a sprinkling of other trees.

The Lake Bluffs.—Steep embankments, usually of gravel and from three or four to more than fifty feet high, border the shores of Douglas and Burt Lakes in several localities, affording conditions favorable to many bryophytes which are found in no other type of habitat.

Sandy Lake Shores.—Sandy lake shores in general possess little of bryological interest. Certain species, however, appear to be restricted to the beaches, growing at about the level of winter high water mark, but for the most part only in places where the ground remains quite moist, even in summer.

Rocks and Cliffs.—Through most of this region the only rock substrata are afforded by the scattered to locally abundant glacial boulders; but Mackinac Island abounds in rocks and cliffs, here as elsewhere mainly limestone.

The Gorge.—One of the most striking physiographic features of the region

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[1] The majority of American specimens formerly referred to *P. platyphylla*, however, are now assigned to *P. platypyhlloidea* (Schwein.) Lindb., and only one apparently authentic Michigan record for the true *P. platyphylla* is known, viz., a specimen collected at Ann Arbor in 1907 by Dr. Conklin.

is this steep-flanked ravine, its floor from sixty to seventy feet lower than the surrounding upland and in which occur the "Big Springs", sources of Carp Creek. The Gorge is situated about a mile from the Biological Station.

The Streams.—There are a number of these, varying in size, in flow and swiftness, in temperature, and in character of banks, but all agree in having a sandy, gravelly or muddy floor, rocky stream beds being conspicuously lacking in this region.

Coniferous Forest Swamps.—Low wet grounds commonly are wooded mainly with white cedar and black spruce. A typical swamp of this kind is Reese's Bog, about a mile from the Station, which occupies a strip perhaps two miles long and up to half a mile wide along the northern shore of Burt Lake. The tamarack predominates locally in wooded swamps, more especially in areas that have been burned over.

Open Marshy Swamps.—These are characterized typically by the abundance of sedges and grasses and the scarcity of sphagnums. Commonly they are periodic swamps and the underlying mineral soil is but sparingly covered with organic debris.

Open Sphagnum Bogs.—These are of the familiar sort, characterized by the abundance of sphagnum mosses and ericaceous shrubs and by the presence of a deep peaty substratum.

In the detailed list which follows, generally speaking, the habitat relations of each species are indicated, together with its comparative frequency in the region under consideration. For the majority of species definite stations are cited, these stations being represented by specimens in the Herbarium of Yale University and most of them also by duplicate specimens in the Herbaria of the New York Botanical Garden and of the University of Michigan. For species recorded as "common", however, as well as for some of those recorded as "frequent", specific stations are not given: in all such cases a definite "Douglas Lake" station can be assumed. Except where otherwise noted, all records are based on the writer's collections. Of the localities mentioned, aside from those that can be found on any good map of this region or for which the name given is self-explanatory, Fontinalis Run, Reese's Bog, and Colonial Point adjoin Burt Lake; North and South Fishtail, Grapevine Point, Polypody Bluff, Bryant's, Fairy Island, and Pine Point border on Douglas Lake; while Lancaster, Munro, Vincent and Mud Lakes, together with the various "bogs", are all in this immediate vicinity.

For assistance in the determination of material grateful acknowledgment is made to Mrs. E. G. Britton, Dr. A. L. Andrews, Mons. G. Dismier, Dr. A. W. Evans, Dr. A. J. Grout, and Mr. R. S. Williams.

Marchantiaceae

CONOCEPHALUM CONICUM (L.) Dumort. Common along overhanging banks of streams in moist woods.

MARCHANTIA POLYMORPHA L. Common on wet ground in the open, but especially in swamps that have recently been burned over.

Preissia quadrata (Scop.) Nees. Frequent in wet open situations, on earth banks and logs. Carp Creek; Mackinac Island.

Metzgeriaceae

Pallavicinia Flotowiana (Nees) Lindb.* Locally abundant on wet sandy lakeshore at North Fishtail.

Pallavicinia Lyellii (Hook.) S. F. Gray. Locally abundant on wet sandy shores at Vincent Lake.

Pellia epiphylla (L.) Corda. Sandy roadside in swampy woods; rare in Reese's Bog

Pellia Fabroniana Raddi.* Shaded, overhanging stream banks and lake shores; frequent. North Fishtail; Big Stone Bay.

Pellia Neesiana (Gottsche)Limpr. Locally abundant along wet muddy shores of Maple River, west of Pellston.

Riccardia latifrons Lindb. On rotten logs; common in wet woods.

Riccardia multifida (L.) S. F. Gray. Swampy woods along Carp Creek; locally abundant.

Riccardia pinguis (L.) S. F. Gray. Floating in Smith's Bog; rare.

Jungermanniaceae

Bazzania trilobata (L.) S. F. Gray.* On ground, logs and stumps; common in moist woods.

Blepharostoma trichophyllum (L.) Dumort. On logs and ground in swampy woods; Reese's Bog.

Calypogeia Neesiana (Massal. & Carest.) C. Müll.* On logs, stumps and ground in moist woods; occasional. Reese's Bog; Mackinac Island.

Calypogeia paludosa Warnst.* On wet ground in an open bog; Mud Lake.

Calypogeia Trichomanis (L.) Corda. On shaded banks and earth in woods; frequent. Carp Creek; Colonial Point.

Cephalozia catenulata (Hüben.) Spruce.* On a rotten log in moist woods; Gorge.

Cephalozia connivens (Dicks.) Lindb.* On wet ground in Bryant's Bog.

Cephalozia curvifolia (Dicks.) Dumort. On logs; common in moist woods.

Cephalozia fluitans (Nees) Spruce.* On wet ground or floating; frequent in open bogs. Mud Lake; Bryant's Bog.

Cephalozia media Lindb. On logs and banks; frequent in moist woods. Reese's Bog; Vincent Lake.

Cephalozia pleniceps (Aust.) Lindb.* On logs in wet woods; occasional. Reese's Bog; Carp Creek.

Cephaloziella hampeana (Nees) Schiffn. On moist earth in wood road near North Fishtail.

Cephaloziella Sullivantii (Aust.) Evans.* Moist sandy bank in woods near Smith's Bog.

Chiloscyphus fragilis (Roth) Schiffn.* Floating in springs and cold brooks; locally abundant. Reese's Bog; Carp Creek; Scotty Bay Creek (Ehlers).

Chiloscyphus pallescens (Ehrh.) Dumort. On wet logs and ground in open swampy woods; frequent. Smith's Bog; Reese's Bog.

Frullania Asagrayana Mont. On trunk of tree in Reese's Bog.

Frulliana Brittoniae Evans.* On a tree near Douglas Lake (Mrs. E. W. Brown).

Frullania eboracensis Gottsche. Common on trunks of trees in open woods.

Geocalyx graveolens (Schrad.) Nees. On rotten logs and banks; occasional in moist woods. Reese's Bog; Mackinac Island.

Harpanthus scutatus (Web. f. & Mohr) Spruce. On rotten logs; frequent in moist woods.

Jamesoniella autumnalis (D. C.) Steph. On earth and rotten logs; common on lake bluffs and in moist woods.

Lepidozia reptans (L.) Dumort. On earth and logs; common in moist woods.

Lepidozia setacea (Web.) Mitt.* On wet ground in Mud Lake Bog (L. Blinks).

Lophocolea heterophylla (Schrad.) Dumort. Common on earth along lake bluffs and in moist woods.

Lophocolea minor Nees. Common on moist gravelly soil along lake bluffs.

Lophozia badensis (Gottsche) Schiffn.* On wet or moist shaded banks; common on Mackinac Island.

Lophozia barbata (Schreb.) Dumort. Moist gravelly lake bluffs; locally abundant at Douglas Lake.

Lophozia excisa (Dicks.) Dumort.* Gravelly lake bluff at south end of Burt Lake.

Lophozia incisa (Schrad.) Dumort. On shaded banks and rotten logs. Reese's Bog; Carp Creek; Douglas Lake.

Lophozia Kaurini (Limpr.) Steph. Local on wet sandy lake shore; North Fishtail.

Lophozia marchica (Nees) Steph.* On wet ground in Reese's Bog.

Lophozia porphyroleuca (Nees) Schiffn. On moist ground and logs in Reese's Bog.

Mylia anomala (Hook.) S. F. Gray.* Frequent in open sphagnum bogs.

Odontoschisma denudatum (Mart.) Dumort.* On a wet, rotten log in the Gorge.

Plagiochila asplenioides (L.) Dumort. Common on moist gravelly lake bluffs and on banks and logs in wet woods.

Porella platyphylloidea (Schwein.) Lindb. Common on trees in moist woods.

Ptilidium ciliare (L.) Nees. On a moist shaded bank; south end of Burt Lake

Ptilidium pulcherrimum (Web.) Hampe. Common on logs, stumps and tree trunks in wet or moist woods.

Radula complanata (L.) Dumort. Common on bark of trees in moist woods.

Scapania curta (Mart.) Dumort. On the ground along lake bluffs; local at Douglas Lake.

Scapania glaucocephala (Tayl.) Aust.* On logs in moist woods; occasional near Douglas Lake.

Scapania irrigua (Nees) Dumort.* Wet sandy ground; rare. Reese's bog; Vincent Lake.

Scapania nemorosa (L.) Dumort.* On earth and logs in wet woods and along lake shores; rare. Vincent Lake; Douglas Lake.

Sphenolobus exsectaeformis (Breidl.) Steph.* On rotten log in Reese's Bog; rare.

Sphenolobus Hellerianus (Nees) Steph.* On rotten log in Reese's Bog; rare.

Sphenolobus Michauxii (Web. f. & Mohr) Steph. On rotten log in Reese's Bog; rare.

Trichocolea tomentella (Ehrh.) Dumort. Common on the ground in swampy woods.

Anthocerotaceae

Anthoceros laevis L. On moist earth along a wood road in Reese's Bog.

Sphagnaceae

Sphagnum capillaceum (Weis) Schrank. Common in open bogs.

Sphagnum capillaceum tenellum (Schimp.) Andrews. Common in open bogs.

Sphagnum compactum DC.* Locally abundant in wet sandy depressions near Douglas Lake.

Sphagnum cuspidatum Ehrh. Common in wet depressions in open bogs.

Sphagnum Dusenii C. Jens. Common in wet open bogs.

Sphagnum fuscum (Schimp.) H. Klinggr. Common in bogs.

Sphagnum Girgensohnii Russow. Common in wooded bogs and swamps.

Sphagnum magellanicum Brid. Common in bogs and swamps.

Sphagnum palustre L. Frequent in wooded swamps. Ingleside; Vincent Lake.

Sphagnum papillosum Lindb. Locally abundant in Mud Lake Bog.

Sphagnum recurvum Beauv. Common in bogs.

Sphagnum recurvum tenue H. Klinggr. Frequent in Gleason's and Bryant's Bogs.

Sphagnum robustum (Russow) Röll. Locally abundant in Bryant's Bog.

Sphagnum squarrosum Crome. Frequent in swampy woods. Gorge; Reese's Bog; Big Stone Bay.

Sphagnum subbicolor Hampe.* Frequent in Bogs. Reese's Bog; Big Stone Bay.

Sphagnum teres (Schimp.) Aongstr. Locally abundant in Mud Lake Bog.

Sphagnum Warnstorfii Russow. In boggy, wooded swamp; Reese's Bog.

Sphagnum Wulfianum Girg. Locally abundant in boggy wooded swamps. Reese's Bog.

Dicranaceae

Ceratodon purpureus (L.) Brid. On earth and other substrata; very common in open situations and the most abundant moss in the aspens.

Dicranella Grevilleana (Brid.) Schimp.* Locally abundant on a moist clayey bank; Mackinac Island.

Dicranella heteromalla (L.) Schimp. On the ground; frequent in upland woods. Mud Lake Hardwoods; Lancaster Lake (Ehlers); Pellston; Colonial Point.

Dicranella rubra (Huds.) Kindb.* Locally abundant on a moist clayey bank; Mackinac Island.

Dicranella Schreberi (Sw.) Schimp. Locally common along a wet, sandy lake shore; North Fishtail.

Dicranum Bergeri Bland.* On the ground; occasional in bogs and wet woods. Mud Lake Bog; Big Stone Bay.

Dicranum Bonjeanii De Not.* On ground; frequent in open sandy woods Reese's Bog; Pine Point, Cecil Bay.

Dicranum condensatum Hedw.* On the ground; locally abundant in open sandy blueberry barrens near Big Stone Bay.

Dicranum Drummondii C. Mull.* On the ground, probably common in wet woods. Reese's Bog.

Dicranum flagellare Hedw. Rotten stumps and logs, and bases of trees; common in moist woods.

Dicranum fuscescens Turn. On the ground, logs, and stumps; frequent in moist woods. Reese's Bog; Big Stone Bay.

Dicranum montanum Hedw. On rotten logs and stumps; common in moist woods.

Dicranum Mühlenbeckii Br. & Sch.* On the ground in woods; Big Stone Bay.

Dicranum rugosum (Hoffm.) Brid. On logs, stumps, and the ground; common in moist or wet woods.

Dicranum scoparium (L.) Hedw. Logs, stumps and ground; common in woods.

Dicranum viride (Sull. & Lesq.) Lindb.* According to R. S. Williams *D. viride* is a synonym of *D. fulvum* Hook. On logs and trunks of trees; common in moist woods.

Ditrichum flexicaule (Schleich.) Hampe.* Locally abundant along an open gravelly roadside near the shore; Mackinac Island.

Oncophorus wahlenbergii Brid. On shaded logs; common but seldom abundant.

Saelania glaucescens (Hedw.) Broth. Rare on gravelly lake bluffs along shores of Douglas Lake.

Seligeria campylopoda Kindb.* On limestone boulders and stones in moist woods. Rare at Colonial Point; frequent on Mackinac Island.

Leucobryaceae

Leucobryum glaucum (L.) Schimp. On the ground in moist woods; frequent. Douglas Lake vicinity (Ehlers); Reese's Bog; Colonial Point.

Fissidentaceae

Fissidens adiantoides (L.) Hedw.* On the ground, logs, and tree bases; common in wet woods and along moist lake-shores.

Fissidens cristatus Wils. Frequent in the same sort of situations as the preceding species. Reese's Bog; Pellston Hardwoods.

Fissidens osmundioides (Sw.) Hedw. Occasional on tree bases in wet woods and on moist sandy lake shores. Douglas Lake; Reese's Bog.

Fissidens viridulus (Sw.) Wahl.* On ledges and stones in moist woods; common on Mackinac Island.

Pottiaceae

Barbula convoluta Hedw.* On moist gravelly or sandy banks; occasional. Fairy Island; Colonial Point; Big Stone Bay.

Didymodon luridus Hornsch.* Limestone cliffs and boulders; locally common along the lake shore at Mackinac Island.

Didymodon rubellus (Hoffm.) Br. & Sch.* Wet logs and rocks; locally common. Carp Creek; Mackinac Island.

Encalypta ciliata (Hedw.) Hoffm. Common on a moist gravelly lake bluff; Fairy Island.

Encalypta contorta (Wulf.) Lindb.* Lake bluffs, sand dunes, and earth; occasional. Bryant's; Cecil Bay; Mackinac Island.

Encalypta rhabdocarpa pilifera (Funck) Nees & Hornsch.* Very local on a moist gravelly lake bluff; Fairy Island.

Gymnostomum rupestre Schleich.* Moist shaded limestone ledges; occasional near the shore on Mackinac Island.

INSERT

The following entry should be inserted in The Bryologist 25: 49. May 1922, between lines six and seven:

Swartzia montana (Lamarck) Lindb. Moist shaded limestone ledges; local near the shore on Mackinac Island.

TORTULA RURALIS (L.) Ehrh. Open sandy or gravelly ground: locally abundant. Cecil Bay; Big Stone Bay; Mackinac Island.

WEISIA VIRIDULA (L.) Hedw. Gravelly lake bluff; Colonial Point.

Grimmiaceae

GRIMMIA APOCARPA (L.) Hedw.* On sunny rocks; local along shore of Burt Lake; common on Mackinac Island.

Orthotrichaceae

ORTHOTRICHUM AFFINE Schrad.* Trunks of hardwood trees in the woods; frequent. Several localities near Burt Lake; Big Stone Bay.

ORTHOTRICHUM ANOMALUM Hedw. Sunny limestone boulders. Rare at Big Stone Bay; common along shore at Mackinac Island.

ORTHOTRICHUM BRACHYTRICHUM Schimp.* On hardwood tree in woods adjoining Smith's Bog.

ORTHOTRICHUM OBTUSIFOLIUM Schrad. Bark of trees in woods; frequent. Reese's Bog; Smith's Bog.

ORTHOTRICHUM SORDIDUM Sull. & Lesq.* Trunks of hardwood trees; frequent on Mackinac Island.

ORTHOTRICHUM SPECIOSUM Nees. Trunks of trees in woods; frequent. Reese's Bog; Big Stone Bay; Mackinac Island.

ULOTA CRISPULA Bruch. On trunks of broadleaf trees; frequent in open woods. Reese's Bog; Carp Creek; Big Stone Bay.

ULOTA LUDWIGII Brid.* On bark of tree in hardwood forest west of Pellston.

ULOTA ULOPHYLLA (Ehrh.) Broth. On trunk of tree; Mackinac Island.

Funariaceae

FUNARIA HYGROMETRICA (L.) Schreb. Common on earth in open situations generally, but especially abundant in burnt-over places.

Bryaceae

BRYUM ARGENTEUM L. Locally abundant on earth in a door-yard; Colonial Point.

BRYUM BIMUM Schreb.* On the ground; common in swampy or wet woods.

BRYUM CAESPITICIUM L. Frequent on sandy or gravelly lake shores. Fairy Island; Colonial Point; Cecil Bay.

BRYUM CAPILLARE L. Sandy or gravelly ground; frequent in open woods.

BRYUM DUVALII Voit.* Locally abundant in wet open swamp; Reese's Bog.

BRYUM PALLESCENS Schleich.* Local along sandy shore of Lake Michigan near Big Stone Bay.

BRYUM PENDULUM (Hornsch.) Schimp. Frequent along sandy shore of Lake Michigan, near Big Stone Bay.

BRYUM VENTRICOSUM Dicks.* On ground in swampy woods. Reese's Bog; Cecil Bay.

Leptobryum pyriforme (L.) Wils. On earth; frequent in moist, open situations. Fairy Island; Smith's Bog; Gorge; Burt Lake Bluffs.

Mniobryum albicans (Wahl.) Limpr.* Open springy ground; locally common at northern end of Burt Lake.

Pohlia cruda (L.) Lindb. Common on a gravelly lake bluff; Douglas Lake.

Pohlia nutans (Schreb.) Lindb. On the ground and on stumps and logs in open situations; very common.

Pohlia pulchella (Hedw.) Lindb.* Locally abundant on a moist clayey bank; Mackinac Island.

Rhodobryum roseum (Weis) Limpr. On logs and the ground; occasional in moist woods. Burt Lake; Reese's Bog; Pellston Hardwoods; Big Stone Bay; Mackinac Island.

Mniaceae

Mnium affine Bland. On ground; common in wet woods.

Mnium ciliare (Grev.) Lindb. On ground in wet woods; probably frequent. Colonial Point.

Mnium cuspidatum (L.) Leyss. On logs and eartn; common in upland woods.

Mnium Drummondii Br. & Sch.* Swampy woods; rare. Reese's Bog.

Mnium marginatum (Dicks.) Beauv. On ground and logs; frequent to common in moist upland woods.

Mnium medium Br. & Sch. On the ground in moist woods; apparently rare. Colonial Point.

Mnium orthorrhynchum Br. & Sch. Moist earth and bases of trees; common on lake bluffs and in wet woods.

Mnium punctatum (L.) Schreb. Common in wet woods. Practically all material seen from this region is referable to the var. *elatum* Schimp.

Mnium rostratum Schrad.* Wet woods near Burt Lake; probably frequent.

Mnium rugicum Laur.* Springy roadside northeast of Burt Lake; also Douglas Lake vicinity. Local.

Mnium spinulosum Br. & Sch. Earth and logs in moist woods, but especially on lake bluffs; frequent. Fairy Island; Polypody Bluff; Reese's Bog; Big Stone Bay.

Mnium stellare Reich.* Frequent to common on moist, shaded banks, or on tree bases in wet woods.

Aulacomniaceae

Aulacomnium androgynum (L.) Schwaegr.* On moist, shaded banks; local. Vincent Lake; Carp Creek; Burt Lake Bluffs.

Aulacomnium palustre (L.) Schwaegr. On the ground; common and usually abundant in bogs, swamps, and wet woods.

Meesiaceae

Meesia triquetra (L.) Aongstr.* Local in open, sedgy bog at Mud Lake.

Bartramiaceae

Bartramia pomiformis (L.) Hedw. Locally abundant on a steep gravelly lake bank; Polypody Bluff.

Philonotis fontana (L.) Brid. Open springy places and along streams; frequent. Reese's Bog; Cecil Bay; Mackinac Island.

Philonotis marchica (Willd.) Brid.* Local on open, springy banks near shore of Burt Lake.

Plagiopus Oederi (Gunn.) Limpr.* Frequent on moist, shaded limestone ledges; Mackinac Island.

Timmiaceae

Timmia cucullata Michx. Moist shaded banks; rare. Reese's Bog; Mackinac Island.

Hedwigiaceae

Hedwigia albicans (Web.) Lindb. On sunny rocks; local. Colonial Point; Cecil Bay.

Fontinalaceae

Fontinalis Lescurii Sull.* On stones and logs in streams; rare. Fontinalis Run (Ehlers and L. Blinks); Scotty Bay Creek (Ehlers).

Fontinalis novae-angliae Sull.* In streams; occasional. Carp Creek; Maple River; Levering and Scotty Bay Creek (Ehlers).

Leucodontaceae

Leucodon sciuroides (L.) Schwaegr. On trunks of trees; common, especially in hardwood forests.

Neckeraceae

Neckera pennata (L.) Hedw. Trunks of trees; very common in moist woods.

Entodontaceae

Platygyrium repens (Brid.) Br. & Sch. Occasional on moist logs in woods, especially on bark of fallen birches. North Fishtail; Carp Creek; Colonial Point Hardwoods.

Pterigynandrum filiforme (Timm) Hedw. Occasional on roots of trees along a low lake bluff; Bryant's.

Pylaisia intricata (Hedw.) Br. & Sch. On the bark of a tree; Mackinac Island.

Pylaisia polyantha (Schreb.) Br. & Sch. On bark of trees; Reese's Bog.

Pylaisia Schimperi Card. On trunks of aspen and other trees; frequent in open woods.

Pylaisia subdenticulata Schimp.* On trunks of hardwood trees; frequent in open woods. Douglas Lake; Big Stone Bay.

Leskeaceae

ANOMODON APICULATUS Br. & Sch. On trunks of broadleaf trees; frequent in hardwood forests. Vicinity of Mud Lake and Pellston; Big Stone Bay.

ANOMODON ATTENUATUS (Schreb.) Hüben. On moist earth and bases of trees; occasional. Douglas Lake; Big Stone Bay; Mackinac Island.

ANOMODON MINOR (Beauv.) Fürn. On trunks of trees and logs; common in hardwood forests.

ANOMODON ROSTRATUS (Hedw.) Schimp. At the base of trees and on earth or rocks; occasional in upland woods. Fairy Island; Colonial Point; Big Stone Bay; Mackinac Island; Prentis Bay (Ehlers).

ANOMODON VITICULOSUS (L.) Hook. & Tayl.* On limestone rocks, or occasionally on trees; common on Mackinac Island.

ELODIUM LANATUM (Stroem) Broth.* On the ground in swamps; frequent. Reese's Bog; Gorge.

HAPLOCLADIUM MICROPHYLLUM (Sw.) Broth.* On rotten logs; occasional in wet woods. Smith's Bog; Colonial Point (Ehlers).

HETEROCLADIUM SQUARROSULUM (Voit) Lindb.* On the ground and at the bases of trees; rare in upland woods. Big Stone Bay.

LESKELLA NERVOSA (Schawegr.) Loeske. Bases of trees and rocks; common in woods.

LINDBERGIA AUSTINI (Sull.) Broth.* On trunks of hardwood trees in woods northeast of Burt Lake; very rare.

MYURELLA GRACILIS (Weinm.) Lindb.* Moist crevices of limestone rocks; frequent along the shore of Mackinac Island.

MYURELLA JULACEA (Vill.) Br. & Sch.* Rare on a gravelly lake bluff at Bryant's.

RAUIA SCITA (Beauv.) Aust.* On bark at the base of trees; occasional in upland woods. Mud Lake Hardwoods; Colonial Point; Pellston Hardwoods; Big Stone Bay.

THUIDIUM ABIETINUM (L.) Br. & Sch. Dry sand, gravel, and rocks in open situations; local. Shores of Douglas Lake; Cecil Bay; Big Stone Bay; Mackinac Island.

THUIDIUM DELICATULUM (L.) Br. & Sch. On logs and ground in moist woods. Frequent.

THUIDIUM RECOGNITUM (Hedw.) Lindb.* On logs and ground in moist or wet woods. Common.

Hypnaceae

ACROCLADIUM CUSPIDATUM (L.) Lindb.* On the ground in bogs and marshes; locally abundant. Mud Lake Bog; marsh south of Burt Lake; Alanson.

AMBLYSTEGIELLA CONFERVOIDES (Brid.) Loeske.* Limestone cliffs and boulders; common on Mackinac Island.

AMBLYSTEGIELLA SUBTILIS (Hedw.) Loeske.* On bark of broadleaf trees; common in upland woods.

Amblystegium compactum (C. Müll.) Aust. Local along springy lake bluff at Colonial Point.

Amblystegium irriguum (Wils.) Br. & Sch.* On wet banks, stones, and logs; common along streams, frequently growing in the water. Common.

Amblystegium irriguum spinifolium Schimp.* Scotty Bay Creek (Ehlers).

Amblystegium Juratzkanum Schimp. On earth and logs; not uncommon in moist woods.

Amblystegium Kochii Br. & Sch. On wet ground and in pools; occasional in swamps bordering Douglas and Burt Lakes.

Amblystegium orthocladon (Brid.) Card.* On base of tree along lake-shore at Polypody Bluff.

Amblystegium riparium (L.) Br. & Sch. Floating in the water or growing on roots, branches, logs, and ground subject to periodic inundation. Frequent to common in swamps and springs.

Amblystegium serpens (L.) Br. & Sch. On the roots and at the base of trees, and on earth; frequent. Polypody Bluff; Burt Lake Hardwoods; Colonial Point.

Amblystegium varium (Hedw.) Lindb. On earth and tree bases; frequent in moist woods.

Calliergon cordifolium (Hedw.) Kindb. Locally abundant on the ground in swamps and wet woods. Several localities in vicinity of Burt Lake.

Calliergon giganteum Schimp.* On the ground in bogs and swamps ; common and locally very abundant.

Calliergon stramineum (Dicks.) Kindb. On the ground in bogs; local. Bryant's, Gleason's, and Mud Lake Bogs.

Chrysohypnum chrysophyllum (Brid.) Loeske. Earth, rocks, roots, and stumps; frequent in wet woods. Reese's Bog; Big Stone Bay; Mackinac Island.

Chrysohypnum hispidulum (Brid.) G. Roth. On earth, roots of trees, and stumps; frequent in moist woods. Douglas Lake; Mackinac Island.

Chrysohypnum polygamum (Br. & Sch.) Loeske. Locally abundant on wet sandy lake shores and in marshes. Douglas Lake; marsh south of Burt Lake.

Chrysohypnum Sommerfeltii (Myr.) G. Roth.* Wet woods near Burt Lake.

Chrysohypnum stellatum (Schreb.) Loeske. Frequent in marshes and wet wooded swamps, growing on the ground. Pine Point; Carp Creek; Crooked River; Cecil Bay.

Drepanocladus aduncus (L.) Warnst. (*Hypnum uncinatum* Hedw.) Banks, rocks, logs, tree bases, and wet depressions; frequent in moist woods. Reese's Bog; Smith's Bog; Carp Creek; Cecil Bay; Big Stone Bay; Mackinac Island.

Drepanocladus fluitans (L.) Warnst. Locally abundant on periodically inundated ground; Smith's Bog.

Drepanocladus Kneiffii (Schimp.) Warnst. On the ground or floating in the water; common in bogs and swampy woods, on springy banks, and in wet situations generally. Under *D. Kneiffii* are here included a number of forms formerly referred to *Hypnum aduncum* Hedw., but more recently treated by various authors as distinct species. Some of these forms may indeed be specifically distinct, but their status in this respect seems altogether too uncertain to warrant attempting to separate them at the present time.

Drepanocladus revolvens (Sw.) Warnst.* Frequent in marshes and swamps, and along springy banks. Pine Point Bog; Cecil Bay; Big Stone Bay; Mackinac Island.

Drepanocladus scorpioides (L.) Warnst. Locally abundant in wet marshes. Pine Point; Cecil Bay.

Drepanocladus Sendtneri (Schimp.) Warnst.* Floating in pools in open swamps; locally abundant near Burt Lake.

Drepanocladus Sendtneri Wilsoni Warnst.* Smith's Bog.

Drepanocladus trifarius (Web. f. & Mohr.) Broth.* Wet sandy marshes; local at Pine Point and Cecil Bay.

Drepanocladus vernicosus (Lindb.) Warnst. Local in wet, open bog; Mud Lake.

Heterophyllon Haldanianum (Grev.) Kindb. On rotten logs and earth; common in moist woods.

Homomallium adnatum (Hedw.) Broth.* On tree bases and gravelly banks; occasional in open woods. Fontinalis Run (Ehlers); Colonial Point.

Hygroamblystegium filicinum (L.) Loeske.* Springy places and along streams; locally very abundant. Gorge; Mackinac Island.

Hygrohypnum palustre (Huds.) Loeske. On wave-washed logs and wet rocks; rare at Burt Lake Bluff and on Mackinac Island.

Hylocomium splendens (Hedw.) Br. & Sch. Common on the ground in moist woods.

Hypnum Schreberi Willd. On ground, logs, and stumps; one of the commonest mosses of moist woods.

Isopterygium elegans (Hook.) Lindb.* Moist woods, usually on earth or rocks; rare. Mud Lake Hardwoods and Carp Lake Hardwoods (Ehlers); Big Stone Bay.

Isopterygium turfaceum Lindb. Common in moist woods, usually on decaying logs.

Plagiothecium denticulatum (L.) Br. & Sch. Gravelly lake bluffs, and on the ground in wet woods; frequent.

Plagiothecium Roeseanum Br. & Sch.* Occasional on moist shaded banks. Polypody Bluff; Fairy Island; Burt Lake Hardwoods.

Plagiothecium striatellum (Brid.) Lindb. On the ground or logs; frequent in moist woods. Reese's Bog; Burt Lake Hardwoods.

Ptilium crista-castrensis (L.) De Not. On the ground, logs, and stumps; frequent in moist woods. Reese's Bog; Cecil Bay.

Rhytidiadelphus triquetrus (L.) Warnst. On the ground in moist woods; common.

STEREODON CUPRESSIFORMIS (L.) Lindb. Shaded logs and stumps; infrequent. Colonial Point (Ehlers); Mackinac Island.

STEREODON IMPONENS (Hedw.) Lindb. On logs and stumps in the woods; common.

STEREODON LINDBERGII (Mitt.) Warnst. Swamps, springy roadsides, and wet woods; common.

STEREODON PALLESCENS (Hedw.) Lindb. On logs, stones, and tree bases in woods; common.

STEREODON PRATENSIS (Koch) E. G. Britton. On the ground in swamps; frequent. Reese's Bog; Big Stone Bay.

STEREODON RECURVANS (Schwaegr.) Broth.* On logs and humus in the woods; common.

STEREODON REPTILIS (Michx.) Mitt. On logs, stones, and tree bases; common in moist woods. Douglas Lake; Cecil Bay.

Brachytheciaceae

BRACHYTHECIUM CYRTOPHYLLUM Kindb.* On a steep gravelly lake bank at Polypody Bluff.

BRACHYTHECIUM OXYCLADON (Brid.) Jaeg. & Sauerb. Earth and bases of trees; common in open woods.

BRACHYTHECIUM PLUMOSUM (Sw.) Br. & Sch. On earth; rare in open woods along lake shore at North Fishtail.

BRACHYTHECIUM RIVULARE Br. & Sch.* On wet ground; common in springy woods, especially along streams, often growing in the water.

BRACHYTHECIUM RUTABULUM (L.) Br. & Sch. Earth, stones, trees, and logs; occasional in moist upland woods. Burt Lake Bluffs; Burt Lake Hardwoods.

BRACHYTHECIUM RUTABULUM FLAVESCENS Br. & Sch.* Wet grassy roadside; Mackinac Island.

BRACHYTHECIUM SALEBROSUM (Hoffm.) Br. & Sch. On the ground and on the roots and bases of trees; frequent in upland woods. Grapevine Point; Smith's Bog; Cecil Bay.

BRACHYTHECIUM STARKEI (Brid.) Br. & Sch.* Earth and rotten logs; occasional in wet or moist woods. Reese's Bog; Colonial Point; Mackinac Island.

BRACHYTHECIUM VELUTINUM (L.) Br. & Sch. On earth in open woods; Cecil Bay.

BRYHNIA GRAMINICOLOR (Brid.) Grout.* Local on a steep, gravelly lake bluff at Fairy Island.

BRYHNIA NOVAE-ANGLIAE (Sull. & Lesq.) Grout.* On the ground; occasional in springy woods. Burt Lake Hardwoods.

CAMPTOTHECIUM NITENS (Schreb.) Schimp. On the ground in wooded swamps; frequently abundant. Reese's Bog.

EURYNCHIUM DIVERSIFOLIUM (Schleich.) Br. & Sch.* Locally abundant on shaded gravelly hillsides; Colonial Point.

Eurynchium strigosum (Hoffm.) Br. & Sch. Earth, logs, and bases of trees; common in moist woods.

Oxyrrhynchium rusciforme (Neck.) Warnst.* On rocks in a stream; Scotty Bay Creek (Ehlers).

Dendroidaceae

Climacium americanum Brid. On logs and the ground; common in swampy woods.

Climacium dendroides (L.) Web. f. & Mohr. On logs and the ground; frequent in wet woods. Bryant's; Smith's Bog.

Weberaceae

Webera sessilis (Schmid.) Lindb. On an earth bank in moist upland woods; Colonial Point.

Buxbaumiaceae

Buxbaumia aphylla L. On earth banks rich in humis; local in woods along Carp Creek and at Colonial Point.

Georgiaceae

Georgia pellucida (L.) Rabenh. On rotten logs and stumps; common in moist woods.

Polytrichaceae

Catharinea angustata Brid. On earth; frequent in open upland woods. Mud Lake; Smith's Bog; Burt Lake Hardwoods; Colonial Point; Pellston.

Catharinea undulata (L.) Web. f. & Mohr. On earth; occasional in moist open woods. Grapevine Point; Mud Lake Hardwoods; Burt Lake.

Polytrichum commune L. On the ground in all sorts of situations; common and abundant.

Polytrichum decipiens Limpr.* Locally abundant on moist earth in hardwoods near Carp Lake (Ehlers).

Polytrichum formosum Hedw.* Frequent on moist earth in hardwoods west of Pellston.

Polytrichum juniperinum Willd. On the ground in open situations; very common and abundant.

Polytrichum ohioense Ren. & Card. Occasional on earth banks in Colonial Point Hardwoods.

Polytrichum piliferum Schreb. Dry, open ground; common and abundant.

Polytrichum strictum Banks. On the ground in bogs; probably frequent. Reese's Bog.

By way of summary it may be stated that, so far as published records show (and as tabulated in the present paper), the bryophyte flora of Michigan comprises a total of 321 species, distributed as follows: Marchantiaceae 4, Ricciaceae 2, Metzgeriaceae 9, Jungermanniaceae 56, Anthocerotaceae 1, Sphagnaceae 17, Bryaceae 232.

YALE UNIVERSITY

[From The American Journal of Science, Vol. IV, October, 1922]

A MID-DEVONIAN CALLIXYLON.

By C. J. Hylander.

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ART. XXX.—*A Mid-Devonian Callixylon;* by C. J. HYLANDER.

In the paleobotanical collections of Yale University there have long been some unstudied sections of a Devonian wood from Eighteen Mile Creek, New York. These sections were made by Dr. Wieland about 1900, from material collected by O. C. Marsh in 1860. They bear numbers 240, 241, and 242. Since this wood consists merely in siliceous fragments containing much residual carbon, and is otherwise poorly preserved, the structure is difficult to make out. Only the transverse and radial longitudinal sections are diagnostic. The tangential section failed, cutting a region of especially poor preservation, with oblique compression.

Nevertheless, a new species of Zalessky's genus CALLIXYLON (7)[1] is indicated, and attention to the plants rather than associated vertebrates must bring to light better material of the original stem type, supposedly a foot or more in diameter. If so, further sectioning must disclose the better conserved areas as in various other instances of petrified stems. Accordingly, it has been considered worth while to give the description which follows. The value of these notes rests in the fact also, that the fine type from the Indiana Black Shale, CALLIXYLON OWENI (6), is at hand for close comparison and renders less doubtful features that otherwise would be obscure. The camera lucida figures here reproduced are accurate to scale, and are not restored, but actual drawings of the areas they show.

Generic Position.

The grouping of the radial pits in discontinuous masses undoubtedly puts the wood of these sections into the genus *Callixylon.* Other characters also are those of typical Cordaitean wood, as described by Penhallow (5), or Elkins & Wieland (3). In regard to the specimens and their inclusion in Zalessky's genus, Dr. Wieland has the following to say:

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[1] For Literature references see the end of this paper.

"Seward in his great textbook (vol. III p. 292) says of the reference of the Indiana black shale Cordaite to CALLIXYLON—'Miss Elkins and Dr. Wieland refer some upper Devonian wood from Indiana characterized by a grouping of the circular or elliptical bordered pits in the radial walls of the tracheids similar to those in CALLIXYLON TRIFILIEVI, which they include together with the middle Devonian species of CORDAITES NEWBERRYI in Zalessky's genus. Though these two American species are comparable in the discontinuous arrangement of the tracheal pits with the Russian type, the latter is characterized by primary xylem strands, a feature not recognized in the American stems; it would seem, then, undesirable to adopt the designation CALLIXYLON in preference to DADOXYLON unless there is evidence as to similar characteristics in the primary xylem.'

Is this either a guide to convenient usage or a logical conclusion? It is not well to lay stress on the precise position in the middle or upper Devonian for any of these forms, since their time range is only inferable. The interesting and decisive point is that in middle to later Devonian time there was a cosmopolitan group of Cordaites with the grouped pits, and such forms are known in a typical instance to have the old cryptogamic wood. The probability is that all have it. But if any of the species referred to CALLIXYLON with reservations well within the recognized usages of Paleobotany, were later found to lack cryptogamic wood, then a new genus would be indicated, perhaps a new family. Moreover, mere reference to *Dadoxylon* would settle nothing, where these recurrently variant forms are concerned. With or without the cryptogamic wood, there would still remain the chance that the leaf or floral characters varied strongly from the forms primarily designated as *Dadoxylon*. Like so many of the genera of Paleobotany, *Dadoxylon* is now more a group name than a genus in the purely botanical sense. And similarly *Callixylon,* in the first instance a needed generic distinction, must share the same fate of ultimate and convenient inclusiveness. Only thus may we avoid the use of over-many generic names in our descriptions and groupings of ancient plants. The other alternative must be genera of mainly one sole species.

These more or less silicified bits of lignitic wood must have attracted the attention of Marsh while searching in the limestone which thinly covers the Hamilton, and carries both fish and plant remains. They would thus be from near the close of the mid-Devonian. But the horizon might be in the Hamilton shale, or higher in the black shale of the Portage, also carrying plants. The bits were marked by Marsh as from the Hamilton group.

This Cordaite is not likely to be as old as the PALEOPITYS MILLERI of the Old Red of Scotland;[2] and, incidentally, even the wood-cuts of the latter given by Hugh Miller in the 'Testimony of the Rocks,' fig. 3, permit fair judgment of the main features. It is seen that the pitting is of the Dadoxylon type (2 to 3-seriate), and the rays thin (uniseriate), as Miller discerned.

'The fossil botanist on taking leave of the lower Carboniferous beds, quits the dry land and puts out to sea.' So wrote the stylist of Cromarty over seventy years ago; and while not intended in the very severest literal sense, the epigram was long justified. But new methods of study and new discoveries have broadened the paleobotanic horizon, and helped to give material once thought inadequate, high value as evidence of structure, or distribution, or both. Perhaps no further answer is needed to any question why the fossil tree type here described was not earlier taken up."

Structure.

The tracheids of the sections cited are mostly rectangular in cross-section, and vary much in size. The average is thirty-five to forty-five microns across, in this respect differing sharply from the larger tracheids of CALLIXYLON OWENI (3), which run from forty-five to sixty microns across. The walls appear thick, from three to five microns. In radial longitudinal section, the tracheids show the chief characteristic of the genus—the bordered pits of the radial walls, aligned in discontinuous groups. As in CALLIXYLON OWENI (3), the pits are circular or irregularly elliptical in outline, and occur in a varying number of vertical rows, from one to three (in rare instances, four). These vertical rows of pits are rather closely set, without compression to marked hexagonal form, in the groups as aligned in radial bands that correspond to the bands of pit groups on the neighboring tracheid. Only in a few places in the Eighteen Mile Creek material is the grouping of the pits fully visible over any great area; the best area of preservation is shown in fig. 2. These features can of course only appear to advantage where there is little compression and the section cuts closely to the true radial wood lines.

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[2] McNab, W. R.: On the Structure of a Lignite from the Old Red Sandstone; Trans. Bot. Soc. of Edinburgh, vol. 10, p. 312.

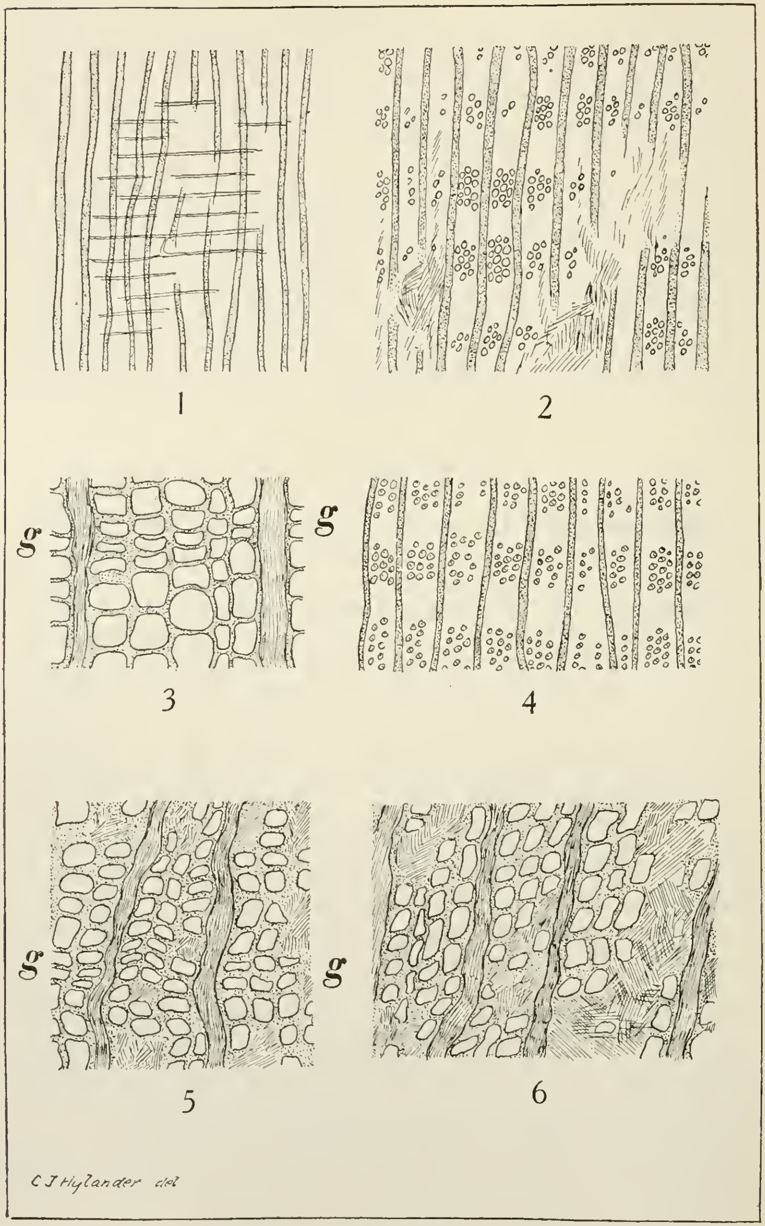

Fig. 1–6. Explanation opposite.

In the transverse section, the wood rays appear unusually wide, compared with the tracheids. They are also of considerable depth, varying from ten to fully twenty cells deep. In only one instance, in the radial longitudinal section, could the end of a ray cell be distinguished, and that is shown in fig. 1. The ray cells appear to be about the same size as those of CALLIXYLON OWENI. The cell-width of the rays is not visible in the imperfect tangential section, but the rays must be in part two-cells wide, as in *C. Oweni*. Wieland (6, p. 123) notes that in Araucarioxylon stems the wood rays are never more than two cells wide, although rays three and four cells wide are not infrequent in the older Cordaites.

The growth ring (fig. 5), as also in *C. Oweni* (fig. 3), is a significant feature of this wood, which may have been widespread in the mid-Devonian. Such growth rings are not present in the Russian *Callixylon;* nevertheless it is likely that the feature is more or less general in *Callixylon,* and it occurs in various other typical American Cordaites. Miss Goldring finds it in a Carboniferous Cordaite as far south as southern Texas (4). These ancient rings are not thought to indicate as sharp a seasonal change as the rings in Dicotyledonous plants. But on the other hand, little attention has been given to the fact that in old and simpler types of wood, growth rings do not become a feature of the wood structure. The simpler type of growth ring occurs in both Mesozoic and recent Cycads, and Chamberlain (1) has now observed it in a Monocotyl. Accentuation of growth ring is mainly correlated with the more marked tracheidal and ray differention of mid to later Mesozoic time.

EXPLANATION OF FIGURES 1-6. (All figures enlarged 100.)

CALLIXYLON MARSHII, sp. nov.

FIG. 1. Radial long. section showing approximate height of wood ray.

FIG. 2. Radial long. section showing the aligned grouping of the radial pits.

FIG. 5. Transverse section showing growth ring and average appearance of tracheids in one of the less compressed areas.

FIG. 6. Transverse section showing typical wood and conservation.

CALLIXYLON OWENI, Elkins & Wieland.

FIG. 3. Transverse section, showing growth ring and larger and well preserved tracheids. [Tracheid ends probably aligned.]

FIG. 4. Radial long. section, showing radial grouping of pits, for comparison with fig. 2.

Specific Characters.

Comparison of the type sections of CALLIXYLON OWENI with those of the present Eighteen Mile Creek wood sections, reveals specific variation. There are the same discontinuous pit groups and obscure growth rings, but the tracheids are of a consistently smaller size not accounted for by compression or accidental variations, and the wood rays are relatively broader. Therefore, there need be no doubt in naming it after its finder of sixty years ago, who later became so famous as an indefatigable collector and paleontologist.

CALLIXYLON MARSHII sp. nov. Tracheids 35-45μ in diameter, walls 3-5μ thick, radial pits of the bordered crossed slit type, arranged in from one to three vertical rows in discontinuous groups of few to 12 or 13 pits to the grouping, groupings radially aligned; wood rays few to 20 cells deep, two cells wide, conspicuously broad in cross section; growth ring of primitive type present but difficult to see. Horizon, upper mid-Devonian of New York. Type locality, Eighteen Mile Creek, New York.

The following comparison is added for convenience: TRANS. SECT.—Diameter of tracheids: C. Marshii, 35-40μ; C. Newberryi, 44-55μ; C. Oweni, 45-60μ. Thickness of walls: C. Marshii, 3-5μ; C. Newberryi, 6μ; C. Oweni, 5μ. Growth rings absent in C. Newberryi, also C. Trifilievi, present in the other two species. RADIAL LONG. SECT. Pit groups: 3-13 in C. Marshii, 6-13 in C. Newberryi, and 3-40 in C. Oweni. Pit diameter: 9.3μ in C. Newberryi, 8-10μ in C. Marshii, and 10-11μ in C. Oweni. TANG. SECT. Height of rays: C. Marshii, 1-20; C. Newberryi, medium height; C. Oweni, 1-40. Thickness of rays: C. Marshii, at least 2-seriate; C. Newberryi, 3-seriate rarely; C. Oweni, 2-seriate.

Thus it is seen that the C. MARSHII is closer to C. NEWBERRYI (2) than to C. OWENI. And this is an interesting point since the C. NEWBERRYI is given from the mid-Devonian of Ohio. Neither of these forms can be confused with the forms called *Dadoxylon Ouangondianum* and *D. Halli* (2), from the mid-Devonian of New York. These are distinct as forms with four and five pit rows, the adpressed pits, and broad wood rays. They are mentioned merely because figured by Dawson along with the

C. Newberryi (2). A form ORMOXYLON (2) is given with three pit rows, as having very narrow wood rays one cell thick, but this is more likely a typical *Dadoxylon*.

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Reprinted from Rhodora, Vol. 24, Nos. 287 & 288, November and December 1922.

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A PRELIMINARY REPORT ON THE DESMIDS OF CONNECTICUT.[1]

C. J. Hylander.

I. Introduction.

Of the New England States, New Hampshire, Massachusetts, Rhode Island and Maine have had their desmid flora investigated by Bennett, Cushman, Johnson and Harvey. The only published list of Connecticut desmids, however, is the one found in H. W. Conn and L. W. Webster's "Preliminary Report on the Algae of the Fresh Waters of Connecticut (**2**)." Conn and Webster enumerate 109 species and varieties of desmids in their report, but their list is unsatisfactory in that it contains no accurate data and that no localities are given. Since they state in their introduction that the majority of their collections were made from the vicinity of Middletown, I have taken the liberty to list any species found by them, as coming from Middletown.

Except for the above-mentioned report, the only references to Connecticut stations are found in general reports on North American species. In 1894, L. N. Johnson, in his articles on "Some new and rare desmids of the United States" (**5**,**6**), includes several Connecticut localities, most of which are from the vicinity of Bridgeport. Four years later, after Johnson's death, W. & G. S. West worked over some of his material and published their results in a report on "Some desmids of the United States (**7**)"; this includes also some Connecticut localities, all from the vicinity of Bridgeport.

The only other references to Connecticut records are the following: one species of *Penium*, reported for Connecticut by Wolle in his

APR 11 1924

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[1] Contribution from the Osborn Botanical Laboratory.

"Desmids of the United States (**8**)"; several species of *Closterium* in Cushman's "New England species of *Closterium* (**4**)"; two species in his "New England Saccodermae (**3**)"; and two species distributed in the Phycotheca Boreali-Americana of Collins, Holden and Setchell (**1**).

II. The Collecting of the Material.

The material which forms the basis of this report was collected in three types of habitat; in bogs, in swamps, and in ponds and lakes. Thirty-one localities were visited in the course of the collecting, and the yield was found to vary greatly according to the type of habitat. In respect to number of species, it was found that the bogs, three of which were visited, resulted in the least yield—ten to twenty species to each collection. The swamps seemed a slightly more favorable habitat, for of the nine swamps visited, each one resulted in a yield of from fifteen to thirty species. But by far the best habitat seemed to be the swampy margin of the small meadow pond, or the marshy coves of the larger lakes. Here, in the quiescent but clear water, the floating and submerged masses of moss, sphagnum or aquatic plants contained an abundant desmid flora. One small pond at Morris, not over fifteen yards wide, yielded fifty-two different species in abundance; and squeezings from floating masses of *Riccia fluitans* and *Drepanocladus* at Lake Congamond and Lake Quassapaug resulted in a yield of over seventy desmids at each locality. Without exception, sphagnum appeared to be a less favorable habitat than floating masses of moss or grass, or submerged masses of *Myriophyllum* and *Chara*.

All of the counties in Connecticut were visited by the writer except Tolland, Windham and New London. The places of collection were distributed as follows:

Litchfield County: Bethlehem (Longmeadow Pond); Litchfield (*a*, Bantam Lake, and *b*, swamp in the "Pines"); Morris (small pasture pond); Plymouth (ice pond near Waterville); Thomaston (sphagnum swamp); Washington (Lake Waramaug); Watertown (small meadow pond fringed with sphagnum).

Hartford County: Southington (small meadow pond); Suffield (Lake Congamond).

Fairfield County: Monroe (*a*, pond near Stepney, and *b*, swamp at East Village); Newtown (Botsford tamarack bog).

New Haven County: Bethany (quaking bog); Branford (Lake Saltonstall); Guilford (swamp in North Guilford); Hamden (*a*, Lake Whitney, and *b*, swamp at summit of Mt. Carmel); Madison (swamp at North Madison); Middlebury (Lake Quassapaug); New Haven (*a*, Beaver Park bog, and *b*, pools at foot of West Rock); North Branford (*a*, roadside swamp at Totoket, and *b*, Linsley Ponds); Orange (roadside pond); West Haven (*a*, Lake Maltby, and *b*, Maltby Park swamp); Woodbridge (Dawson Falls pond).

Middlesex County: Killingworth (*a*, swampy pond, and *b*, sphagnum swamp).

In the following list of species, the stations are arranged alphabetically by townships. The records are all based on material collected and preserved by the writer, except where otherwise stated. References to Connecticut specimens in the literature are definitely indicated. Citations for the names of species and varieties are given only in those cases where the forms in question are not found in the four published volumes of "A Monograph of the British Desmidiaceae," by W. & G. S. West. The sequence followed is that adopted by these authors in their first volume.

In the preparation of this report, I am very much indebted to the helpful criticism and inspiration of Dr. Alexander W. Evans, under whose direction I commenced and brought to a conclusion this report. I am likewise very much indebted to Dr. Nellie Carter, who during the past year was a research fellow at the laboratory. Her critical knowledge of the group was an invaluable aid to me in identifying the material; without her assistance this report would have been an impossibility.

III. List of the Connecticut Species.

[An asterisk (*) indicates that the plant is new to Connecticut; two asterisks (**) that it is new to North America; and a dagger (†) that it is known only from North America.]

GONATOZYGON De Bary

*G. Brebissonii De Bary. Suffield.

G. pilosum Wolle. Fairfield (*Johnson*, **6**, p. 280; see also **3**, p. 344).

SPIROTAENIA Bréb.

S. condensata Bréb. Bethlehem, Fairfield (*Johnson*, see **7**, p. 280, and also **3**, p. 345), Hamden (*Carter & Evans*), Middlebury, Washington, West Haven.

MESOTAENIUM Näg.

*M. Endlicherianum var. grande Nordst. Orange.

M. micrococcum (Kütz.) Roy & Bissett. Middletown (*Conn*, see **2**, p. 57).

CYLINDROCYSTIS Menegh.

*C. Brebissonii Menegh. Bethany, Killingworth (*a*), Madison, Newtown, West Haven.

NETRIUM Näg.

N. digitus (Ehrenb.) Itzigs. & Rothe. Bethany, Bethlehem, Branford, Bridgeport (*Johnson*, see **3**, p. 349), Cheshire, Hamden (*b*), Killingworth, Middlebury, Middletown (*Conn*, see **2**, p. 58), New Haven (*a*), Orange, Suffield, Thomaston, Washington.

**N. digitus var. constrictum West & G. S. West. New Haven (*b*), West Haven (*a*).

N. interruptum (Bréb.) Lütkem. Middletown (*Conn*, see **2**, p. 58).

PENIUM Bréb.

P. margaritaceum (Ehrenb.) Bréb. Madison, Middletown (*Conn*, see **2**, p. 60), Morris, Orange, Washington. See also Wolle, **10**, p. 35.

P. Navicula Bréb. Bethlehem, Middlebury, Middletown (*Conn*, see **2**, p. 60), Suffield.

P. polymorphum Perty. Bethlehem, Middletown (*Conn*, see **2**, p. 60).

*P. spirostriolatum Barker. Hamden (*b*).

ROYA West & G. S. West

R. obtusa (Bréb.) West & G. S. West. Middletown (*Conn*, see **2**, p. 60).

CLOSTERIUM Nitzsch

*C. abruptum West. Hamden (*b*), West Haven (*a*).

C. acerosum (Schrank) Ehrenb. Middletown (*Conn*, see **2**, p. 60).

C. acuminatum Kütz. Phycol. Germ. 130. 1845. Litchfield, Middletown (*Conn*, see **2**, p. 60).

*C. acutum (Lyngbye) Bréb. Litchfield, Middlebury, Morris, Orange, Southington, Washington, Watertown.

†C. angustatum var. clavatum Hastings, Am. Month. Micr. Jour. **13** : 155. *pl. 1, . 7.* 1892. Bridgeport (*Johnson*, **6**, p. 291; see asol **4**, p. 113).

C. Braunii Reinsch, Algenfl. Frank. 196. *pl. 12, f. 5.* 1867. Bridgeport (*Johnson,* **6**, p. 291, as *C. maculatum*; see also **4**, p. 130), Middletown (*Conn,* see **2**, p. 61, as *C. areolatum*).

C. Brebissonii Delp. Mem. R. Accad. Sci. Torino II. **30**: 111. *pl. 18, f. 20, 21.* 1876. Middletown (*Conn,* see **2**, p. 61).

**C. Ceratium Perty. Litchfield (*a*).

*C. cornu Ehrenb. Hamden (*a*), Branford (*a*), Hamden (*Carter & Evans*), Middlebury, Plymouth, West Haven (*a*).

C. costatum Corda. Hamden (*b*), Middletown (*Conn,* see **2**, p. 60), Morris.

C. Cucumis Ehrenb. Phys. Abh. Preuss. Ak. Wiss. Berlin **1843**: *pl. 4, f. 29.* 1843. Middletown (*Conn,* see **2**, p. 60), Orange.

*C. Cynthia DeNot. Hamden (*b*), Killingworth, Middlebury, Monroe (*b*), Orange, Southington, Suffield.

C. decorum Bréb. Bridgeport and Easton (*Johnson,* see **7**, p. 283, and also **4**, p. 132), Middletown (*Conn,* see **2**, p. 61), New Haven (*b*), Suffield, Washington.

†C. Delpontei Klebs, Schrift. Physik.-Oekonom. Gesell. Königsberg **5**: 22. 1879. Bridgeport and Easton (*Johnson,* see **7**, p. 283), Middletown (*Conn,* see **2**, p. 60).

C. Dianae Ehrenb. Bethany, Bethlehem, Branford, Hamden (*b*), Killingworth, Madison, Middlebury, Middletown (*Conn,* see **2**, p. 61), Newtown, New Haven (*b*), North Branford (*b*), Orange, Suffield.

C. didymotocum Corda. Bridgeport (*Johnson,* **5**, p. 286), Hamden (*a*), Newtown.

*†C. dilatatum West, Trans. Linn. Soc. Bot. II. **5**: 237. *pl. 13, f. 20–22.* 1896. Hamden (*b*), Morris, North Branford (*b*).

*C. Ehrenbergii Menegh. Bethlehem, Litchfield (*b*), Middlebury, New Haven (*b*), North Branford (*b*), Orange, Suffield.

†C. Ehrenbergii var. immane Wolle, Desm. U. S. 48. *pl. 8, f. 17.* 1884. Bridgeport (*Setchell & Holden,* see **1**, No. 1017).

*C. incurvum Bréb. Hamden (*b*), Middlebury, West Haven (*a*).

*C. intermedium Ralfs. Hamden (*b*), Madison, Middlebury, Newtown, Orange, Thomaston.

C. Jenneri Ralfs. Guilford, Hamden (*b*), Middlebury, Middletown (*Conn,* see **2**, p. 61), Newtown, Orange.

**C. Jenneri var. robustum G. S. West. Morris.

*†C. Johnsonii West & G. S. West, Jour. Linn. Soc. Bot. **33**: 284. *pl. 16, f. 1, 2.* 1898. Guilford.

*C. juncidum Ralfs. Bethlehem, Madison, North Branford (*b*).

*C. Kuetzingii Bréb. Litchfield, Middlebury, North Branford (*b*), Orange, Plymouth.

C. lanceolatum Kütz. Middletown (*Conn*, see **2**, p. 60), North Haven.

C. Leibleinii Kütz. Bethlehem, Branford, Guilford, Hamden (*b*), Killingworth, Litchfield (*a*), Middlebury, Middletown (*Conn*, see **2**, p. 61), Morris, New Haven (*b*), Newtown, Suffield, Washington, West Haven (*a*).

C. Leibleinii var. curtum West. Middletown (*Conn*, see **2**, p. 61).

*C. Libellula Focke. Middlebury, Middletown (*Conn*, see **2**, p 60, as *Penium clysterioides*), Orange, Plymouth, Thomaston, West Haven (a).

C. lineatum Ehrenb. Middlebury, Middletown (*Conn*, see **2**, p. 61), Morris, New Haven (*b*), North Branford (*a*), Orange.

†C. lineatum var. costatum Wolle, Fresh Water Algae U. S. 25. *pl. 61, f. 3*. 1887. Bridgeport (*Johnson*, **5**, p. 286; see also **4**, p. 129).

*C. littorale Gay. Washington.

C. lunula (Müll.) Nitzsch. Bethlehem, Bethany, Madison, Middletown (*Conn*, see **2**, p. 60), Morris, West Haven (*a*).

**C. lunula var. coloratum Klebs. Plymouth.

*C. macilentum Bréb. Newtown, Suffield.

C. moniliferum (Bory) Ehrenb. Litchfield, Middletown (*Conn*, see **2**, p. 61), Middlebury, Monroe (*b*), North Branford (*a* and *b*), New Haven (*a*), Plymouth, Suffield, West Haven (*a*), Washington, Woodbridge.

C. parvulum Näg. Bethlehem, Litchfield (*a*), Middlebury, Middletown (*Conn*, see **2**, p. 61), West Haven (*a*).

C. praelongum Bréb. Middletown (*Conn*, see **2**, p. 61).

*C. Pritchardianum Arch. Hamden (*b*).

*C. pronum Bréb. Middlebury, New Haven (*a*, *b*), Southington, Thomaston.

*C. pseudodianae Roy. Litchfield (*a*).

C. Ralfsii var. hybridum Rabenh. Bethany, Bridgeport (*Johnson*, see **7**, p. 284, and also **4**, p. 130), Guilford, Middlebury.

*C. regulare Bréb. Watertown.

C. rostratum Ehrenb. Bethlehem, Middletown (*Conn*, see **2**, p. 61), Suffield.

C. rostratum var. brevirostratum West. Middletown (*Conn*, see **2**, p. 61).

*C. SETACEUM Ehrenb. Bethlehem, Middlebury, Orange, Washington.

C. STRIGOSUM Bréb. Middletown (*Conn*, see **2**, p. 60).

*C. STRIOLATUM Ehrenb. Madison, Middlebury, Morris, New Haven (*a*).

C. SUBCOSTATUM Nordst. in Wittr. & Nordst. Alg. Exs. *370*. Middletown (*Conn*, see **2**, p. 61).

*C. TOXON West. Southington.

*C. TUMIDUM Johnson. Hamden (*a*), Monroe (*b*), Southington.

C. TURGIDUM Ehrenb. Middletown (*Conn*, see **2**, p. 60).

*C. ULNA Focke. Orange, Thomaston.

*C. VENUS Kütz. Hamden (*a*, *b*), Killingworth, Litchfield (*a*), Middlebury, Morris, North Branford (*a*), Orange, Thomaston, Suffield, Washington.

DOCIDIUM Bréb.

*D. UNDULATUM Bailey Middlebury.

D. BACULUM (Bréb.) DeBary. Middlebury, Middletown (*Conn*, see **2**, p. 61).

PLEUROTAENIUM Näg.

*P. CORONATUM (Bréb.) Rabenh. Middlebury, Morris.

P. CORONATUM var. FLUCTUATUM West. Bethlehem, Middletown (*Conn*, see **2**, p. 61, as *P. crenulatum*), Orange.

P. NODOSUM (Bailey) Lund. Middlebury, Middletown (*Conn*, see **2**, p. 61).

*P. TRUNCATUM (Bréb.) Näg. Bethlehem, Middlebury.

P. TRABECULA (Ehrenb.) Näg. Bethlehem, Middlebury, Middletown (*Conn*, see **2**, p. 61), New Haven (*a*), Newtown, North Branford (*b*), Killingworth, Suffield, West Haven (*Evans*), Washington.

TRIPLOCERAS Bailey

†T. GRACILE Bailey. Washington.

†T. VERTICILLATUM Bailey. Middletown (*Conn*, see **2**, p. 61, as *Docidium*.)

TETMEMORUS Ralfs

*T. BREBISSONII (Menegh.) Ralfs. Bethany, Hamden (*Carter & Evans*,) Killingworth, Newtown, West Haven (*a*).

*T. LAEVIS (Kütz.) Ralfs. Bethany.

EUASTRUM Ehrenb.

*E. AFFINE Ralfs. Southington.

E. ampullaceum Ralfs. Middlebury, Middletown (*Conn*, **2**, see p. 62).

E. ansatum Ralfs. Middletown (*Conn*, see **2**, p. 63).

*E. bidentatum Näg. Bethlehem, Bethany, Hamden (*a*, *b*), Killingworth, Litchfield (*a*, *b*), Madison, Monroe (*b*), Middlebury, Newtown, Plymouth, Suffield, Thomaston, West Haven (*b*).

*E. binale (Turp.) Ehrenb. Bethlehem, Bethany, Cheshire, Hamden (*b*), Monroe (*a*), Middlebury, Newtown, New Haven (*a*), Southington, Suffield, Thomaston, Watertown.

**E. binale f. Gutwinskii Schmidle. Madison.

*E. didelta (Turp.) Ralfs. Plymouth, West Haven (*a*).

E. elegans (Bréb.) Kütz. Middletown (*Conn*, see **2**, p. 62).

†E. evolutum var. integrius West & G. S. West, Trans. Linn. Soc. Bot. II. **5**: 244. *pl. 14, f. 23–25*. 1896. Bridgeport (*Johnson*, see **7**, p. 293), Middlebury.

E. gemmatum Ralfs. Bridgeport (*Johnson*, **5**, p. 286; see also **7**, p. 289).

E. insulare (Wittr.) Roy. Bridgeport (*Johnson*, **5**, p. 286, as *E. binale* var. *insulare*), Suffield.

†E. integrum Wolle, Fresh Water Algae U. S. 36. *pl. 27, f. 18–22*. 1887. Middletown (*Conn*, see **2**, p. 62), Morris.

†E. Nordstedtianum Wolle, Bull. Torrey Club **11**: 16. 1884. Middletown (*Conn*, see **2**, p. 62).

E. oblongum (Grev.) Ralfs. Bethany, Guilford, Madison Middlebury, Middletown (*Conn*, see **2**, p. 62), Morris, Monroe (*a*), Newtown, West Haven (*a*).

**E. pictum Borg. Killingworth (*a*).

E. pinnatum Ralfs. Bridgeport (*Johnson*, **5**, p. 287).

**E. pulchellum Bréb. Morris.

*E. sibiricum Boldt. Middlebury.

E. verrucosum Ehrenb. Branford, Middlebury, Middletown (*Conn*, see **2**, p. 62), Morris, Suffield, West Haven (*a*, *b*).

MICRASTERIAS Ag.

M. americana (Ehrenb.) Ralfs. Middletown (*Conn*, see **2**, p. 63), Morris, Newtown, Plymouth, Suffield, West Haven (*a*, *b*).

*M. americana var. Lewisiana West. Monroe (*a*).

**M. americana var. Boldtii Gutw. Newtown.

M. apiculata (Ehrenb.) Menegh. West Haven (*a*, *Carter & Evans*), Middletown (*Conn*, see **2**, p. 63).

*M. crenata Bréb. New Haven (*a*), Newtown.

M. crux-melitensis (Ehrenb.) Hass. Litchfield (*b*), Middletown (*Conn*, see **2**, p. 63), Washington.

*M. denticulata Bréb. Bethlehem, New Haven (*a*), Washington.

*M. laticeps Nordst. Vidensk. Medd. Fören. Kjöbenhavn **14**:290. *pl. 2, f. 14.* 1870. Bethlehem, Middlebury, Suffield, Washington, West Haven (*a*).

M. muricata (Bailey) Ralfs. Middlebury, Middletown (*Conn*, see **2**, p. 63).

*M. papillifera Bréb. Bethlehem, Middlebury.

**M. papillifera var. glabra Nordst. Bethlehem, Madison.

M. radiata Hass. Bethlehem, Middlebury, Middletown (*Conn*, see **2**, p. 63, as *M. furcata*), Morris, Washington.

M. rotata (Grev.) Ralfs. Bethany, Litchfield (*b*), Madison, Middletown (*Conn*, see **2**, p. 63), Suffield, West Haven (*a*).

M. sol (Ehrenb.) Kütz. Hamden (*b*), Middlebury, Middletown (*Conn*, see **2**, p. 63), Orange, Plymouth, Suffield, Washington, West Haven (*b*).

*†M. speciosa Wolle, Desm. U. S. 119. *pl. 45, f. 1, 2.* 1884. Bethlehem.

M. truncata (Corda) Bréb. Hamden (*Evans*), Killingworth, Middletown (*Conn*, see **2**, p. 63), New Haven (*a*).

COSMARIUM Corda

*C. amoenum Bréb. Bethany, Middlebury, Newtown.

*C. bioculatum Bréb. Bethlehem, Middlebury, Morris, Orange, Plymouth, Suffield.

*C. biretum Bréb. Guilford, Madison, Monroe (*a*).

C. Boeckii Wittr. Bridgeport (*Johnson*, **5**, p. 287).

C. Botrytis Menegh. Hamden (*b*), Middletown (*Conn*, see **2**, p. 64), North Branford (*a*), Washington, West Haven (*a*).

C. Broomei Thwaites. Middletown (*Conn*, see **2**, p. 64), Suffield, West Haven (*a*).

*C. caelatum Ralfs. West Haven (*a*), Woodbridge.

*C. circulare Reinsch. Middlebury.

*C. conspersum Ralfs. Morris, West Haven (*b*).

C. contractum Kirch. Killingworth, Middletown (*Conn*, see **2**, p. 64).

**C. Corbula Bréb. Suffield.

C. crenatum Ralfs. Middletown (*Conn*, see **2**, p. 64).

*C. Cucumis Corda. Middlebury, Newtown, Suffield, Watertown.

C. Cucurbita Bréb. Bethany, Middletown (*Conn*, see **2**, p. 64).

†C. dentatum Wolle, Desm. U. S. 76. *pl. 13, f. 15.* 1884. Bridgeport (*Johnson*, see **7**, p. 308), Middlebury.

*C. depressum (Näg.) Lund. Bethlehem, Middlebury, Suffield.

**C. exiguum var. subrectangulum West & G. S. West. Thomaston.

C. galeritum Nordst. Middletown (*Conn*, see **2**, p. 64), Washington, West Haven (*a*).

C. granatum Bréb. Branford, Middletown (*Conn*, see **2**, p. 64), Morris.

*C. Hammeri Reinsch. Middlebury, Suffield, Washington.

C. intermedium Delp. Middletown (*Conn*, see **2**, p. 64).

*C. laeve Rabenh. Morris.

**C. latifrons Lund. Madison.

C. Meneghinii Bréb. Bethlehem, Killingworth, Middletown (*Conn*, see **2**, p. 64), Suffield, West Haven (*b*), Woodbridge.

†C. modestum West & G. S. West, Jour. Linn. Soc. Bot. **33**: 304. *pl. 17, f. 12.* 1897. Plymouth.

*C. moniliforme Ralfs. Washington.

*C. moniliforme var. panduriforme Heimerl. Middlebury, Morris, Orange, Suffield, Washington.

C. Naegelianum Bréb. Middletown (*Conn*, see **2**, p. 64).

C. octhodes Nordst. Litchfield (*a*), Madison, Middletown (*Conn*, see **2**, p. 64), North Branford (*b*), New Haven (*b*), Suffield, West Haven (*a*).

C. orbiculatum Ralfs. Middletown (*Conn*, see **2**, p. 64).

C. ornatum Ralfs. Bethlehem, Cheshire, Middlebury, Middletown (*Conn*, see **2**, p. 64), Morris, New Haven (*b*), Thomaston.

*C. orthostichum Lund. Middlebury, New Haven (*b*), Southington.

C. ovale Ralfs. Bethlehem, Middletown (*Conn*, see **2**, p. 64).

*C. pachydermum Lund. Branford, Hamden (*b*), Middlebury, Monroe (*b*), Washington, West Haven (*a*).

C. perforatum Lund. Middletown (*Conn*, see **2**, p. 64).

C. Portianum Arch. Middlebury, Middletown (*Conn*, see **2**, p. 64), Morris, Suffield, Washington, West Haven (*b*).

*C. protractum (Näg.) Arch. Madison.

C. pseudobroomei Wolle. Middletown (*Conn*, see **2**, p. 64).

*C. pseudoconnatum Nordst. Bethlehem, Killingworth, Middlebury, Washington, West Haven (*a*).

*C. PSEUDOPYRAMIDATUM Lund. Bethany, Madison, West Haven (*a*).

*C. PUNCTULATUM Bréb. Bethlehem, Killingworth, Litchfield (*a*), Madison, Middlebury, Morris, New Haven (*b*), Plymouth, Washington.

*C. PYGMAEUM Arch. Bethlehem, Middlebury, Morris, Plymouth, Suffield, Watertown, West Haven (*b*).

C. PYGMAEUM var. SCHLEIPHACKIANUM West & G. S. West. Bridgeport (*Johnson*, see **7**, p. 302).

C. PYRAMIDATUM Bréb. Bethany, Killingworth (*b*), Madison, Middlebury, Middletown (*Conn*, see **2**, p. 64), New Haven (*a*), Thomaston.

*C. QUADRATUM f. WILLEI West & G. S. West. Bethany, Hamden (*b*), Watertown, West Haven (*a*).

*C. QUADRUM Lund. Hamden (*b*), West Haven (*a*).

*C. RENIFORME Ralfs. Middlebury.

**C. REPANDUM f. MINOR West & G. S. West. Hamden (*b*).

*C. SPECIOSUM Lund. Hamden (*b*), Washington.

C. SINOSTEGOS Schaarschm. Bridgeport (*Johnson*, **6**, p. 294).

*C. SPHALEROSTICHUM Nordst. Watertown.

**C. SUBCUCUMIS Schmidle. Bethlehem, Hamden (*Carter & Evans*)

*C. SUBDEPRESSUM (Näg.) Lund. Suffield.

†C. SUBORBICULARE Wood, Smithson. Contr. Knowl. **241**: 129. *pl. 21, f. 9.* 1872. Middlebury, Middletown (*Conn*, see **2**, p. 64).

*C. SUBTUMIDUM Nordst. Killingworth.

C. SULCATUM Nordst. Bridgeport (*Johnson*, **5**, p. 287).

C. TETRAOPHTHALMUM (Kütz.) Bréb. Middletown (*Conn*, see **2**, p. 64).

*C. THWAITESII Ralfs. Bethany.

*C. TRILOBULATUM Reinsch. Middlebury.

†C. TRIPLICATUM Wolle, Bull. Torrey Club **10**: 16. *pl. 27, f. 8.* 1883. Bridgeport (*Johnson*, **5**, p. 288), Middlebury, Morris, Suffield.

C. TUMIDUM Lund. Middletown (*Conn*, see **2**, p. 64).

*C. TURPINII Bréb. Hamden (*Carter & Evans*).

C. UNDULATUM Corda. Middlebury, Middletown (*Conn*, see **2**, p. 64), Monroe (*a*), Morris, New Haven (*b*), Orange, Southington, Suffield, Thomaston, Washington, Watertown, West Haven (*a*, *b*).

**C. UNDULATUM var. MINUTUM Wittr. Washington, West Haven (*a*).

*C. UNDULATUM var. WOLLEI West. West Haven (*a*).

*C. viride (Corda) Josh. Bethany, Hamden (*Carter & Evans*), New Haven (*a*), West Haven (*a*).

XANTHIDIUM Ehrenb.

X. aseptum Nordst. Middletown (*Conn*, see **2**, p. 64).

X. antilopaeum (Bréb.) Kütz. Bethany, Guilford, Middletown (*Conn*, see **2**, p. 64), Morris, Plymouth, Suffield, West Haven (*a*, *b*).

**X. antilopaeum var. hebridarium West & G. S. West. Morris.

*X. antilopaeum var. polymazum Nordst. Bethlehem, Middlebury, Morris, Suffield, Washington.

*†X. antilopaeum var. minneapoliense Wolle, Desm. U. S. 94. *pl. 52, f. 16.* 1884. Bethlehem, Middlebury, Morris, West Haven (*b*).

X. cristatum Bréb. Hamden (*b*), Killingworth, Middlebury, Middletown (*Conn*, see **2**, p. 64).

*X. cristatum var. uncinatum Bréb. Hamden (*b*), West Haven (*b*).

X. fasciculatum Ehrenb. Madison, Middletown (*Conn*, see **2**, p. 64).

†X. Johnsonii West & G. S. West, Jour. Linn. Soc. Bot. **33**: 299. *pl. 17, f. 1.* 1897. Bridgeport (*Johnson*, see **7**, p. 299).

**X. subhastiferum var. Murrayi West & G. S. West. Monroe (*a*).

*†X. Tylerianum West, Jour. Roy. Micr. Soc. **17**: 19. *pl. 2, f. 1-4, pl. 3, f. 14.* 1889. Monroe (*a*), Suffield.

ARTHRODESMUS Ehrenb.

A. convergens Ehrenb. Killingworth, Middlebury, Middletown (*Conn*, see **2**, p. 63), Morris, New Haven (*b*), Suffield, Watertown, West Haven (*b*).

*A. incus var. Ralfsii West & G. S. West. Hamden (*Carter & Evans*), Litchfield (*a*), Middlebury, Orange, Southington, Suffield, Thomaston, West Haven (*b*).

A. octocornis Ehrenb. Middlebury, Middletown (*Conn*, see **2**, p. 63), Plymouth, Suffield, Washington.

*A. triangularis Lagerh. Plymouth, Suffield.

(*To be continued*)

A PRELIMINARY REPORT ON THE DESMIDS OF CONNECTICUT.

C. J. Hylander.

(*Continued from page 224.*)

STAURASTRUM Meyen

**S. aciculiferum (Borge) West. Hamden (*Carter*).

S. Arctiscon (Ehrenb.) Lund. Nova Acta Reg. Soc. Sci. Upsala

III. **8**: 70. *pl. 4, f. 8.* 1871. Bethlehem, Bridgeport (*Johnson*, see **7**, p. 319), Middletown (*Conn*, see **2**, p. 62), Morris.

†S. ASPINOSUM Wolle, Desm. U. S. 143. *pl. 51, f. 22, 23.* 1884. Bridgeport (*Johnson*, **5**, p. 288).

*S. AVICULA Bréb. in Ralfs, Brit. Desm. 140. *pl. 23, f. 11.* 1848. Litchfield (*a*), Morris, Suffield, Washington, West Haven (*b*).

†S. BICORONATUM Johnson, Bull. Torrey Club **21**: 290. *pl. 211, f. 9.* 1894. Bridgeport (*Johnson*, **5**, p. 290).

*S. BIENNIANUM var. ELLIPTICUM Wille, Öfvers. K. Vet.-Akad. Förh. **5**: 50. *pl. 13, f. 49.* 1879. Guilford, Killingworth, West Haven (*a*).

*S. BREBISSONII Arch. in Pritchard, Infus. 739. 1861. Litchfield (*a*), Plymouth, Suffield, Washington, West Haven (*b*).

S. BREVISPINUM Bréb. Middletown (*Conn*, see **2**, p. 62).

†*S. CONCINNUM West & G. S. West, Jour. Linn. Soc. Bot. **33**: 317. *pl. 18, f. 17.* 1897. Middlebury, Southington.

†S. CORONULATUM Wolle, Desm. U. S. 135. *pl. 44, f. 11, 12.* 1884. Middletown (*Conn*, see **2**, p. 62).

S. CRENULATUM Näg. Gatt. einz. Alg. 129. *pl. 8 Ba.* 1849. Guilford, Madison, Middletown (*Conn*, see **2**, p. 62), Monroe (*a*), New Haven (*b*), Suffield, Washington.

S. CUSPIDATUM Bréb. in Meneghini, Linnaea **14**: 226. 1840. Bridgeport (*Johnson*, **5**, p. 288), Litchfield (*a*), Middlebury, Morris, North Branford (*b*), Orange, Plymouth, Suffield, Thomaston, Watertown, Washington, West Haven (*b*).

*S. CYRTOCERUM Bréb. in Ralfs, Brit. Desm. 139. *pl. 22, f. 10.* 1848. Hamden (*b*), West Haven (*b*).

S. DEJECTUM Bréb. in Meneghini, Linnaea **14**: 227. 1840. Middlebury, Middletown (*Conn*, see **2**, p. 62), Orange, Suffield, Washington.

†S. DEJECTUM var. CONVERGENS Wolle, Desm. U. S. 121. *pl. 40, f. 7, 9, 10, 11.* 1884. Middletown (*Conn*, see **2**, p. 62).

*S. DICKIEI Ralfs, Brit. Desm. 123. *pl. 21, f. 3.* 1848. Suffield, Washington.

*S. DILATATUM Ehrenb. Infus. 143. *pl. 10, f. 13.* 1838. Bethlehem, Monroe (*a*), Morris, Orange.

†S. ELEGANTISSIMUM Johnson, Bull. Torrey Club **21**: 290. *pl. 211, f. 16.* 1894. Bridgeport (*Johnson*, **5**, 290).

S. ERASUM Bréb. Mém. Soc. Imp. Sci. Nat. Cherbourg **4**: 143. *pl. 1, f. 28.* 1856. Middletown (*Conn*, see **2**, 62).

S. eustephanum (Ehrenb.) Ralfs, Brit. Desm. 215. 1848. Middletown (*Conn*, see **2**, p. 62), Washington, West Haven (*b*).

S. furcigerum Bréb. in Meneghini, Linnaea **14**: 226. 1840. Middletown (*Conn*, see **2**, p. 62), Morris.

S. gracile Ralfs, Ann. Mag. Nat. Hist. **15**: 155. *pl. 11, f. 3.* 1845. Middlebury, Middletown (*Conn*, see **2**, p. 62), Morris, Monroe (*a*), New Haven (*b*), Suffield, Thomaston, Washington.

S. grande Bulph. Bridgeport (*Johnson*, **6**, p. 294), Bethlehem.

*S. grande var. parvum West & G. S. West. Bethlehem, Plymouth.

*S. granulosum (Ehrenb.) Ralfs. Guilford, Litchfield (*a*).

†S. hexacerum var. aversum West & G. S. West, Jour. Linn. Soc. Bot. **33**: 313. *pl. 18, f. 13.* 1897. Bridgeport (*Johnson*, see **7**, p. 313).

S. hirsutum (Ehrenb.) Bréb. in Ralfs, Brit. Desm. 127. *pl. 22, f. 3.* 1848. Hamden (*b*), Middletown (*Conn*, see **2**, p. 62), Monroe (*a*).

†S. incisum Wolle, Desm. U. S. 132. *pl. 41, f. 12–14.* 1884. Bridgeport (*Johnson*, **5**, p. 288), Morris.

S. inflexum Bréb. Mém. Soc. Imp. Sci. Nat. Cherbourg **4: 140. *pl. 1, f. 25.* 1856. Killingworth (*b*).

†S. iotanum Wolle, Desm. U. S. 137. *pl. 51, f. 5–7.* 1884. Bridgeport (*Johnson*, see **7**, p. 315), Middletown (*Conn*, see **2**, p. 62).

S. irregulare West, Jour. Roy. Micr. Soc. **1894**: 12. *pl. 2, f. 49, 50.* Bridgeport (*Johnson*, **5**, p. 288).

S. leptocladum Nordst. Vidensk. Medd. Fören. Kjöbenhavn **1869**: 228. *pl. 4, f. 57.* 1870. Middlebury, Middletown (*Conn*, see **2**, p. 62), Suffield, Thomaston.

S. leptocladum var. cornutum Wille, Bih. K.-Vet. Akad. Handl. **18**^{3}: 19. *pl. 1, f. 39.* 1884. Bridgeport (*Johnson*, **5**, p. 289).

S. margaritaceum (Ehrenb.) Menegh. Linnaea **14**: 227. 1840. Bethany, Guilford, Hamden (*b*, also *Carter & Evans*), Killingworth, Litchfield (*a*), Madison, Middlebury, Middletown (*Conn*, see **2**, p. 62), New Haven (*b*), Southington, Suffield, Thomaston, Watertown, Washington.

S. megacanthum Lund. Nova Acta Reg. Soc. Sci. Upsala III. **8**: 61. *pl. 4, f. 1.* 1871. Bridgeport (*Johnson*, **5**, p. 288), Middletown (*Conn*, see **2**, p. 62).

*S. Meriani Reinsch, Act. Senckenb. **6**: 125. *pl. 33, DI.* 1867. Hamden (*Carter & Evans*), West Haven (*a*).

*S. MONTICULOSUM Bréb. in Meneghini, Linnaea **14**: 226. 1840. Monroe (*a*), Suffield.

S. MURICATUM Bréb. in Meneghini, Linnaea **14**: 226. 1840. Hamden (*b*), Middletown (*Conn*, see **2**, p. 62).

*S. MUTICUM Bréb. in Meneghini, Linnaea **14**: 226. 1840. Middlebury, Orange, Suffield, West Haven (*a*, *b*).

†S. ODONTATUM Wolle, Bull. Torrey Club **8**: 2. *pl. 6, f. 11*. 1881. Middletown (*Conn*, see **2**, p. 62).

S. OPHIURA Lund. Nova. Acta Reg. Soc. Sci. Upsala III. **8**: 69. *pl. 467*. 1871. Bethlehem, Bridgeport (*Johnson*, **5**, p. 289), Hamden (*a*).

*S. ORBICULARE var. RALFSII West & G. S. West. Middletown, Morris, West Haven (*b*).

*S. PARADOXUM Meyen, Nova Acta Acad. Caes. Leop. Carol. **5**: 14. *pl. 43, f. 37, 38*. 1828. Plymouth.

*S. POLYMORPHUM Bréb. in Ralfs, Brit. Desm. 135. *pl. 22, f. 9, pl. 34, f. 6*. 1848. Orange.

**S. POLYTRICHUM Perty, Kleinst. Lebens. 210. *pl. 16, f. 24*. 1852. Bethany, Hamden (*a*).

**S. PROBOSCIDEUM Arch. in Pritchard, Infus. 742. 1861. Orange.

*S. PUNCTULATUM Bréb. Branford, Hamden (*a*), Killingworth, Newtown, New Haven (*b*), North Haven, Plymouth.

S. PYGMAEUM Bréb. in Ralfs, Brit. Desm. 213. *pl. 35, f. 26*. 1848. Middletown (*Conn*, see **2**, p. 62).

†S. RAVENELII Wood, Smithson. Contr. Knowl. **241**: 153. *pl. 21, f. 22*. 1872. Middletown (*Conn*, see **2**, p. 62).

*S. SEBALDI Reinsch, Act. Senckenb. **6**: 133. *pl. 24, DI, f. 1–3*. 1867. Guilford, West Haven (*b*).

*S. SETIGERUM Cleve, Öfvers. K. Vet.-Akad. Förh. **20**: 490. *pl. 4, f. 4*. 1863. Bethlehem, Middlebury, Suffield.

*S. SPONGIOSUM Bréb. in Ralfs, Brit. Desm. 141. *pl. 23, f. 4*. 1848. Guilford, Monroe (*a*), Suffield.

*S. TETRACERUM (Kütz.) Ralfs, Ann. Mag. Nat. Hist. **15**: 150. *pl. 10, f. 1*. 1845. Bethlehem, Middlebury, Morris, Thomaston, Washington.

*S. TUMIDUM Bréb. Madison.

†S. VESTITUM var. TORTUM West & G. S. West, Jour. Linn. Soc. Bot. **33**: 317. *pl. 18, f. 16*. 1897. Bridgeport (*Johnson*, see **7**: p. 317).

COSMOCLADIUM Bréb.

*C. saxonicum DeBary, Flora **48**: 321. *pl. 1, f. 1–3.* 1865. Branford (*Carter*).

SPHAEROZOSMA Corda

S. pulchrum Bailey in Ralfs, Brit. Desm. 209. *pl. 35, f. 2.* 1848. Middlebury, Middletown (*Conn*, see **2**, p. 65).

S. spinulosum Delp. Mem. R. Accad. Sci. Torino II. **28**: 78. 1876. Middletown (*Conn*, see **2**, p. 65), Suffield.

ONYCHONEMA Wallich

O. filiforme (Ehrenb.) Roy & Bissett. Bridgeport (*Johnson*, **5**, p. 286), Middlebury, Middletown (*Conn*, see **2**, p. 64, as *Sphaerozosma*), Morris, Thomaston.

O. laeve Nordst. Vidensk. Medd. Fören. Kjöbenhavn **1869**: 209. *pl. 3, f. 34.* 1870. Bethlehem, Bridgeport (*Johnson*, **5**, p. 286), Middlebury, Middletown (*Conn*, see **2**, p. 65), Morris, Washington.

SPONDYLOSIUM Bréb.

S. papillosum West & G. S. West, Trans. Linn. Soc. Bot. II. **5**: 41. *pl. 9, f. 19.* 1895. Bethlehem, Middletown (*Conn*, see **2**, p. 65,) Morris, Orange, Plymouth.

*S. planum (Wolle) West & G. S. West, Per. Plank. 430. *pl. 19, f. 5–8.* 1912. Killingworth, Thomaston, Washington, Watertown.

S. pygmaeum (Cooke) West, Jour. Linn. Soc. Bot. **29: 116. 1892. Thomaston.

HYALOTHECA Ehrenb.

H. dissiliens (Smith) Bréb. in Ralfs, Brit. Desm. 51. *pl. 1, f. 1.* 1848. Bethlehem, Hamden (*b*), Guilford, Hamden (*Carter & Evans*), Litchfield (*a*), Madison, Middlebury, Middletown (*Conn*, see **2**, p. 65), New Haven (*b*), North Branford (*a*), Plymouth, Washington.

H. undulata Nordst. Bridgeport (*Johnson*, **5**, p. 286).

DESMIDIUM Ag.

*D. aptogonum Bréb. Mém. Soc. Acad. Falaise **1835**: 268. 1835. Hamden (*b*), Middlebury, Washington.

*†D. Baileyi (Ralfs) Wolle, Desm. U. S. 27. *pl. 2, f. 8–12.* 1884. Bethlehem, Plymouth, Suffield.

D. cylindricum Grev. Scottish Cryptog. Flor. **6**: 38. *pl. 293.* 1827. Bridgeport (*Holden*, see **1**, No. 1262), New Haven (*a*) Newtown, Middletown (*Conn*, see **2**, p. 65).

D. Swartzii Ag. Syst. Alg. 9. 1824. Bethlehem, Madison, Middletown (*Conn*, see **2**, p. 65), Morris, New Haven (*a*), Plymouth.

GYMNOZYGA Ehrenb.

G. moniliformis Ehrenb. Berlin Monatz. 212. 1840. Bethlehem, Killingworth, Middlebury, Middletown (*Conn*, see **2**, p. 65), Monroe (*a*), Newtown.

This list includes 266 species and varieties, of which 125 are new to Connecticut and 22 new to North America.

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Reprinted from SCIENCE, pages 26-28, Vol. LVII, No. 1462, January 5, 1923.

THE MUSCH RAIN-CORRECTING MOUNTING FOR POROUS PORCELAIN ATMOMETERS[1]

Two years ago Livingston and Thone[2] described "A simplified non-absorbing mounting for porous porcelain atmometers" which, by reason of its simplicity of construction and operation as well as its inexpensiveness, has since come into very general use. The essential feature of this mounting is a short column of mercury placed near the upper end of the straight glass feed-tube which connects the atmometer above with the water reservoir below. This column of mercury, held in place by two plugs of glass wool (one above and the other below), acts very effectively as a valve to prevent the passage of water from the atmometer down the tube into the reservoir, at the same time having no effect whatever on the passage of water up the tube to replace that lost by evaporation.

Notwithstanding the obvious advantages of the Livingston-Thone mounting, there are certain objectionable features attendant upon its use which can not be overlooked. To begin with, the mercury valve with its glass wool plugs has to be properly constructed every time it is needed for use: once a season at any rate. Again, in sucking water through the tube, during the setting up of the apparatus, there is danger of drawing slivers of glass wool into the mouth. But perhaps the most serious objection has to do with the accumulation of

APR 11 1924

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[1] Contribution from the Osborn Botanical Laboratory.

[2] SCIENCE, N. S., 52: 85-87, 1920.

air-bubbles in the atmometer or in connection with the glass wool plugs. It is impossible to detect bubbles in the atmometer except by taking the whole apparatus to pieces, while a bubble in the tube may sometimes become so large as to endanger the continuity of the water column.

The device to be described below was designed by Mr. Frederick Musch of New Haven as a result of experience in operating a series of porcelain atmometers for Dr. Norman Taylor—instruments equipped with the Livingston-Thone mounting. Like the latter,[3] the Musch mounting depends on a mercury valve to prevent the absorption of water, but here the resemblance ceases. The Musch device (Fig. 1, *A*) consists primarily of a J-shaped glass feed-tube, the straight end of which (*a*) extends up through the stopper of the reservoir while the curved end (*c*) passes down into the reservoir, reaching to within about half an inch of the bottom when in place. The atmometer is of course attached to the upper end of the tube, and a column of mercury (*Hg*) in the curve at the bottom of the J forms the valve. The short arm of the J is long enough to prevent the mercury splashing or being forced out of the tube into the bottle. A second important feature consists in a short side-arm (*b*), attached to the tube about an inch and a half above the bottom of the J and extending outward and upward. The outside width of the J and the outside distance between arm and tube are gauged to insure their easy insertion through the neck of the reservoir bottle. The side arm is attached at a point just high enough above the curve of the J to permit the latter to clear the bottom of the neck, while

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[3] And like several others that had been described previously: see references in SCIENCE, 52, p. 86 (1920).

inserting, before the arm strikes the top. The side arm is long enough so that the straight part of it more than holds the mercury column, when desired, and at the same time short enough so that when in position it lies about half an inch below the shoulder of the reservoir bottle. The proper dimensions can readily be ascertained by the use of a cardboard model and a bottle of the type it is intended to use as the reservoir. The glass tubing should be of sufficiently large bore to permit the ready passage of large air bubbles.

In setting up the apparatus the feed tube is first shoved through the reservoir stopper from below and the atmometer stopper affixed to its upper end in the usual way. Next, enough mercury is placed in the crook at the bottom of the tube to completely block the passage. The whole thing is then carefully turned upside down, in such a way that the mercury column runs out of the J and into the side-arm. With mercury and tube in this position the atmometer, filled with water, is attached (or it

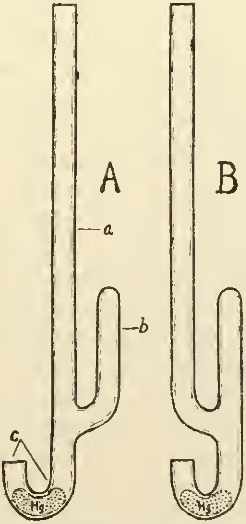

Fig. 1

can be attached empty and then filled either by suction or in the manner described below). The mount with attached atmometer is then turned right side up, the mercury resuming its position in the crook of the J, the feed-tube is lowered into the reservoir, and the stopper is forced home. The filling of atmometer and tube is completed by turning the whole apparatus upside down and then alternately back and forth, in a manner which a little experimentation will readily suggest, due precautions being taken during this operation that the mercury retains its position in the side-arm. This same simple expedient is adopted at any time when it is desired to ascertain whether air bubbles are present in the atmometer and for getting rid of them. Any difficulty in persuading air bubbles to emerge from the atmometer into the feed-tube can be overcome by tapping the base of the instrument or by variously shaking the whole apparatus.

The Musch atmometer mounting has been thoroughly tested under various conditions, both by the writer and by others. It has already been adopted by several investigators for field work during the past season and appears to have given uniformly satisfactory results. The chief objection to which it may be open seems to be this: that during a heavy or protracted rain (or when left under a tap) there may be an initial absorption of water from without amounting to as much as 0.6 cc.[4] This absorption is due to the fact that the mercury valve does not remain stationary before the downward-pressing water column but retreats a short distance up into the short arm of the J. During a period when the weather at relatively brief intervals is alternately wet and dry it is conceivable that an error of sev-

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[4] The amount of absorption may be greater if too short a column of mercury is used.

eral cc. might be introduced by the intermittent fluctuation back and forth of the mercury column; but ordinarily the error would be relatively inconsequential and could be corrected with reasonable accuracy if desired. The most obvious advantages of this style of mounting are (1) that it is possible to detect the presence of air bubbles in the atmometer by simply turning the whole apparatus upside down, and to get rid of them without even taking the cork out of the reservoir bottle; (2) that bubbles can not accumulate in the feed-tube; (3) that any objections which may arise from the use of glass wool are eliminated; and (4) that the mounting is always ready for immediate use. The contrivance can readily be made by any one adept at glass-working or it can be secured from at least one dealer in apparatus and supplies for about fifty cents.

In conclusion, brief attention is called to a modification of the Musch mounting which has been devised by Dr. F. C. Gates (see Fig. 1, *B*). This modified model recommends itself in being somewhat easier to construct and somewhat more compact and also in the fact that the mercury runs more readily back and forth between arm and valve curve than in the original model. This latter feature, however, while of advantage in some respects, may prove a disadvantage when it comes to the rapid filling of atmometer and mount, except where this is done under water (the practise followed by Dr. Gates) or by the suction method: the replacement of long air columns and large bubbles of air is interfered with by the very ease with which the mercury slides back and forth.

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Reprinted from the Bulletin of the Torrey Botanical Club, Vol. 50, No. 1, January, 1923.

Apogamy in Phegopteris polypodioides*

Elizabeth Dorothy Wuist Brown

(with twenty text figures)

Introduction

The wide-spread occurrence of apogamy in various genera of ferns has led to a great deal of investigation of the subject. In most of this study, however, greater emphasis has been laid upon the morphological and cytological than upon the physiological phase.

Leitgeb ('85), who was the first to study apogamy from this latter point of view, carried out a series of experiments to determine the light reactions of apogamous fern prothallia. Among the things he discovered was the fact that when prothallia of *Aspidium falcatum* bearing very young sporophytes were illuminated from the ventral side, the sporophytes were suppressed, new ones being formed on the dorsal side. In rare cases both dorsal and ventral sporophytes would survive and then they seemingly would give rise to a single sporophyte, with its various parts on both sides of the prothallium. Leitgeb considers the alterations of the light relations, during the growth of the prothallia, to be the probable cause of some of the modifications in the apogamous sporophytes described by DeBary ('78).

Bower ('88), although he did not make a physiological study of apogamy, calls attention to the importance of the environmental conditions in the life history of a fern. He cites the fact that the Hymenophyllaceae are exceedingly susceptible to changes of moisture in the air, and concludes that such changes react upon their mode of growth.

Lang ('98) found, in the case of nine different ferns, that by exposing the prothallia to direct sunlight and watering them from below, a condition favorable for vegetative growth but preventing fertilization, sporophytes were produced, although some of them were aborted.

Nathansohn ('00), experimenting with *Marsilia Drummondii*, concluded that exposure to higher temperature for a limited

APR 11 1924

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* Contribution from the Osborn Botanical Laboratory.

time stimulated the development of apogamous embryos in this species.

Woronin ('07) believes dryness to have been the cause of apogamy in the cultures of *Pellaea* and *Notholaena* with which she worked. By growing the prothallia of *Pellaea flavens* in poor light or on poor soil she was able to secure modifications in apogamous outgrowths, which showed transitions between gametophytes and sporophytes as varied as those described by Lang.

Yamanouchi ('08), in his study of *Nephrodium molle*, found that when conditions for fertilization were supplied this species reproduced normally, but that if the cultures were placed in strong light and watered from below fertilization was prevented and apogamous outgrowths were formed instead.

Outgrowths of an apogamous nature were described by Miss Pace ('10) as occurring on some unidentified prothallia which she kept well watered in bright light.

Heilbronn ('10), finding that dryness was not the cause of apogamy in the forms he studied, suggested that summer rather than winter cultures were more likely to become apogamous. But his investigations with different qualities and intensities of light, in moist cultures and at a high temperature, did not verify these conclusions.

Schlumberger ('11) found that by decreasing the moisture for old prothallia of *Woodsia ilvensis*, whose vitality had become lowered by the growth of algae and fungi in the cultures, the production of apogamous outgrowths was induced. He believes the observed enlargement of the apices of these apogamous outgrowths to be analogous to that described for *Anogramma chaerophylla* by Goebel ('97), who considered their development to be an adjustment on the part of the plant to the unfavorable environmental conditions caused by dryness.

Allen ('11) found apogamous sporophytes occurring on prothallia of *Aspidium falcatum* which had been grown in pots of red clay surrounded by sphagnum or moist sand, and kept either in a Wardian case or under bell jars for five, six, and in one case eleven months. These prothallia were not watered from above, the water in the sphagnum or sand keeping the clay uniformly moist.

Nagai ('14), describes cases of apogamy on prothallia of *Asplenium Nidus* grown on agar-agar and on filter paper saturated with nutrient solutions. These cultures were kept somewhat dry, in bright light, and at room temperature. The occurrence of apogamous sporophytes is also described on prothallia which, after growing on nitrogen- and phosphorus-free nutrient solution, had been transferred to sand saturated with nitrogen-free nutrient solution and left in bright light and at higher temperature. He does not attribute the development of these apogamous outgrowths to dryness but to unfavorable or unknown internal physiological conditions.

Stokey ('18) reports a case of apogamy in the genus *Dicksonia* and a few cases in the genus *Cyathea*. These occurred in cultures which had been exposed to rather intense light and grown on a medium of moist peat. While she does not consider dryness to be the determining factor, and while she does not state definitely that the intense light was the stimulus, she is of the opinion that the determining factor in one case of apogamy is not necessarily the determining one in another.

Steil ('18) found apogamy occurring in the genera *Pellaea*, *Pteris*, and *Aspidium*, in cultures on nutrient solution, sphagnum, nutrient agar, peat, clay, and loam, which were kept under bell jars in a Wardian case in the greenhouse. He does not consider the cultural conditions as the factor which induces apogamy in any of these cases.

MATERIAL

While collecting fern spores in and about Ithaca, New York, during the summer of 1915, my attention was called to a sporophyte of *Phegopteris polypodioides* Fée growing on a lawn in the city. It had been transplanted from its native habitat and did not appear normal or healthy, owing, doubtless, to the unfavorable conditions under which it was growing. As there was only one fertile frond, and this a small one, few spores were obtained. Cultures were made from these spores in the early fall upon Prantl's and Knop's full nutrient solutions and on certain modifications of these solutions. After the spores were sown the cultures were placed before an east window where conditions of light and temperature were approximately uniform for all. Once each week the prothallia were transferred to fresh nutrient solutions. About six months later, cases of apogamy were observed in cultures on Prantl's solution from which the NH_4NO_3 had been omitted. In view of the small number of such cases, however, it was thought best to repeat the experiments, and also to make cultures from spores of the same species whose sporophytes had grown under normal environmental conditions. In this way it was hoped that it might be possible, by a comparison of the results obtained, to determine whether apogamy was characteristic of this species, and, if so, under what environmental conditions this condition was induced.

For this purpose, during the following summer (1916), fresh spores were obtained from the same plant at Ithaca and also from wild plants at Brooklin, Maine (the latter through the courtesy of Dr. A. H. Graves). Cultures of these were started early in October on Prantl's and Knop's full nutrient solutions; on modifications of Prantl's solution from which NH_4NO_3, K_2SO_4, $NaCl$, $CaSO_4$, $MgSO_4$, Na_3PO_4, and both $NaCl$ and Na_3PO_4, respectively, were omitted; and on Knop's solution minus the $Ca(NO_3)_2$. In preparing the cultures, about 25 cc. of the nutrient medium was poured into a small glass dish, a drop of a 1 per cent solution of ferric chloride added, and the spores sown upon the surface of the solution. The dishes were covered with loose-fitting glass tops. Two series of cultures were prepared from each of the two lots of spores, one of which was placed in the greenhouse in bright light, the other in the laboratory before an east window. The germinating prothallia, instead of being transferred at intervals to fresh solutions (as had been done the preceding year) were allowed to remain upon the original solution on which the spores were sown, and the increasingly unfavorable conditions of environment which thus resulted were further enhanced by a luxuriant growth of algae which developed in all the dishes.

DEVELOPMENT OF THE PROTHALLIA

Practically no difference was noted in the germination of the spores or in the early development of the prothallia from the two sources. Germination began in about one week after the spores were sown. The early growth and development of the prothallia was rapid in all the cultures, but later it varied according to the particular solution upon which they were growing.

In the case of the cultures which were kept in the greenhouse, the majority of the prothallia growing on the modified Prantl's and Knop's solutions did not develop beyond a filamentous stage and lived only from five to six weeks. This behavior was attributed to temperature rather than light: the temperature in the greenhouse being very high during the greater part of the day, the culture media became overheated, with the result that the prothallia, lacking in vigor on account of an insufficient supply of some essential element in the nutrient solution, were unable to withstand the unfavorable conditions of temperature. A few prothallia in the greenhouse cultures on Prantl's and Knop's unmodified solutions survived, however, and developed into normal heart-shaped thalli.

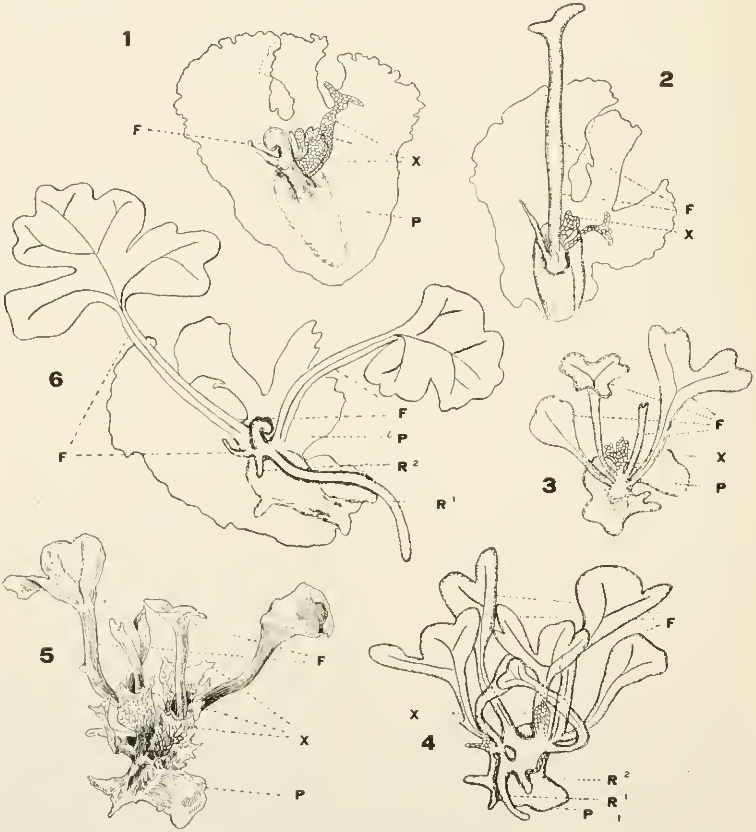
The length attained by the prothallium during its filamentous stage varied greatly, but even in cultures on the full nutrient solutions it was not uncommon to find prothallia with filaments of seven and eight cells in length. These usually occurred in crowded regions of the cultures. In the cultures on the modified solutions the length of the filaments was even greater, some having as many as twelve to fifteen cells. The length of the cells also varied, some being long and others short, but with the long cells predominating. It is customary for the length of the filament of the prothallia of any species of ferns to vary under unfavorable environmental conditions, but the range of variability in length seems fixed for each species. In this respect *Phegopteris polypodioides* showed the greatest range of variability of any prothallia of the Polypodiaceae that have come under the author's observation.

Branching was exceedingly varied and occurred frequently in the cultures on the modified solutions, while on the unmodified solutions it was not uncommon. Many times the first cell of the filament, instead of dividing transversely, divided lengthwise, giving rise to two distinct filaments, which later broadened into prothallia. Sometimes other cells of the filaments divided, giving rise to branches which in turn broadened into prothallia. In other cases a filament of three cells was first formed, and then the first and second cells of the filament divided lengthwise, giving rise to side branches. These side branches continued their growth as filaments for a time, and then branched dichotomously. In still other cases the end cell of a filament of four cells elongated transversely instead of longitudinally and divided crosswise, giving rise to two distinct branches which in turn branched. Some of these branches, after broadening into filaments of two cells in width, reverted to a one-cell stage. Again a short filament was formed, which broadened out, and then, from this broadened region side branches were formed; the cells of the apical margin of the broadened portion also gave rise to branches which in turn formed other branches. Some of these branches, after forming either a long filament or a short one of only three cells, broadened into a prothallium bearing antheridia, after which it reverted to a filamentous condition. This capacity of the prothallia to branch extensively seems to be of advantage to the plant in enabling it to meet unfavorable environmental conditions, by increasing the number of prothallia, thus giving rise to an extended area of rhizoids, as well as insuring the formation of a larger number of sporophytes, either normally or apogamously. Atkinson designates the branched prothallia of *Adiantum cuneatum* described by him as "starved prothallia," and the author ('16) has shown that branching in various prothallia of the Polypodiaceae is intimately associated with conditions of nutrition, poor nutritive conditions accelerating the stimulus for branching and good nutritive conditions weakening it. Another interesting feature in connection with the development of the young prothallia in the modified solutions was the frequency with which they met the unfavorable conditions for nourishment by reversion to a filamentous condition. Prothallia several cells in width and bearing antheridia would revert to a filamentous condition; then, after forming a filament three to eleven cells in length, they would broaden again to form a prothallium which in turn bore antheridia. Goebel considers a reversion to a juvenile form to be the result of unfavorable conditions, which in this case was doubtless an insufficient food supply.

In the cultures which were kept in the laboratory, sexual organs, both male and female, developed on the prothallia in all the solutions, both modified and unmodified. They also developed on the few prothalia which survived on the unmodified solutions in the greenhouse cultures. Antheridia appeared in four to six weeks after the spores were sown. Both monoecious and dioecious prothallia occurred in the laboratory cultures on the unmodified Prantl's and Knop's solutions, while only dioecious prothallia were observed in the greenhouse cultures on the same solutions. In the younger cultures, those not more than six or eight weeks old, the majority of the prothallia were dioecious, the percentage of monoecious individuals being very low even in cultures on the modified solutions. Among older prothallia it was not infrequent to find monoecious specimens, the antheridia developing on or near the margin of the larger heart-shaped prothallia. Antheridia were never observed on the cushion, among the archegonia, as is the case in typical monoecious prothallia. The percentage of male prothallia was much higher than that of female, as is usually the case on the modified solutions. While many of the male prothallia were mere filaments of from one to three cells in width bearing antheridia, there were also a large number of small irregularly-shaped cell-plates one cell in thickness, bearing antheridia over both the upper and lower surfaces. The antherozoids in all the cultures appeared normal. The majority of the larger prothallia on the modifiedsolutions were more or less heart-shaped, without a sinus but with a well-developed meristem upon which archegonia were formed. Evidently these were not functional, as no normal sporophytes developed. In rare cases a few antheridia were formed from the marginal cells of the prothallia which developed the apogamous outgrowths and sporophytes.

DESCRIPTION OF THF APOGAMOUS OUTGROWTHS AND SPOROPHYTES

In the first observed cases of apogamy the prothallia bearing the apogamous sporophytes were irregularly heart-shaped, with a well-developed meristem. Archegonia were formed on some of the prothallia, but not antheridia. The apogamous sporophytes, in all these cases, originated as slight swellings of the archegonial cushion, either on the dorsal or ventral side, at some point near the notch or at the center of the cushion. These swellings gradually increased in size until dome-shaped cellular masses were formed, from which the parts of the apogamous sporophytes appeared in the following order: leaf or leaves, root, and stem. No foot was formed. In some cases proliferations, either filamentous or slightly expanded at the apices, developed from the cellular mass. Also, multicellular hairs or outgrowths frequently formed at the base of the first leaf or leaves of the young sporophytes. Figs. 1–4 show the development of one of these apogamous sporophytes. In this case the prothallium was lobed and the apogamous sporophyte developed at the center of the cushion as a cellular mass (Fig. 1).



Figs. 1–6

From this cellular mass, seven normal leaves were developed before a root was formed. Soon after the first root formed, another began to develop (Fig. 4). Meanwhile the old prothallium became greatly reduced in size. The subsequent growth of the apogamous sporophyte was normal and rapid. Figs. 5 and 6 represent other examples of apogamous sporophytes.

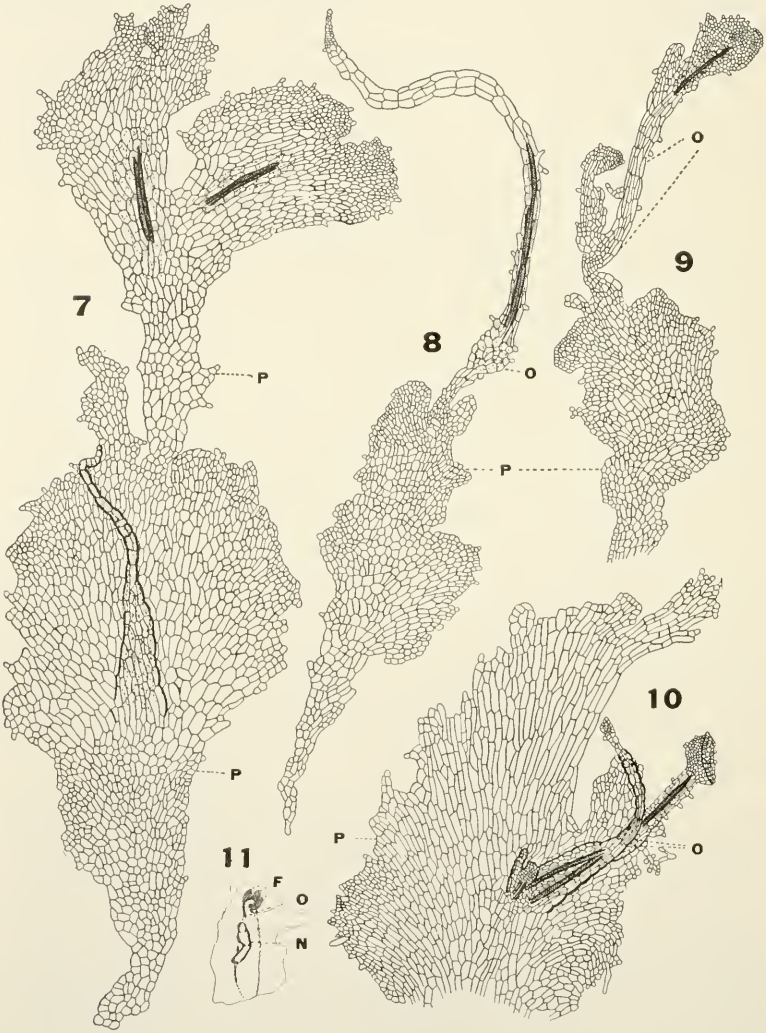
In the experiments of the second year apogamous outgrowths were first observed in the laboratory cultures on Knop's full solution about four to six months after sowing. Subsequently they developed in essentially all the cultures. These outgrowths were very diversified in form, and while some originated as cellular masses, at various places on the archegonial cushion, the majority developed as outgrowths of the prothallia in the region where the sinus usually occurs. It was only in rare cases that sexual organs, either antheridia or archegonia, formed on the prothallia bearing apogamous outgrowths.

FIG. 7 shows an apparently normal and slightly elongated prothallium with a broad lobed apex. No sexual organs developed, although a well-developed archegonial cushion was present. From the region of the sinus a lobe formed. Narrow at first, it gradually widened and then branched to form two prothallia with broad apices, each having a sinus. In the thickened central region of each of these branch-prothallia a cluster of tracheids appeared. In the meantime, from the center of the archegonial cushion of the original prothallium a cellular mass began to form. This continued to grow as a thick conical mass.

The apogamous outgrowth shown in FIG. 8 formed as a lobe from the sinus of a very irregular, elongated prothallium whose apex was lobed. This lobe, which later became an apogamous sporophyte, was at first one cell in thickness and several cells in width. It broadened and thickened into a bulbous cellular mass, then elongated and formed a series of tracheids in the center. Finally it reverted to a filament one cell in thickness.

FIG. 9 shows an apogamous outgrowth which originated as a lobe from the irregular apex, a little to one side of the center of an elongated prothallium. This lobe broadened and thickened, forming two branches. One branch did not develop as rapidly as the other and appeared more thallus-like, being only one cell in thickness. The other branch, after elongating slightly, broadened into a prothallium thickened at the center and with a heart-shaped apex. Tracheids formed in this thickened area and a small branch developed at one side of the prothallium near the apex.

The apogamous sporophyte shown in FIG. 10 developed first as a cellular mass on the meristem near the sinus of a very irregular-shaped old prothallium whose basal portion had died. The apex of this prothallium was strongly indented, the sinus being situated slightly to one side of the middle. From one side of the prothallium a very much branched proliferation developed, while from the cellular mass outgrowths resembling somewhat the normal leaves of young sporophytes were formed.



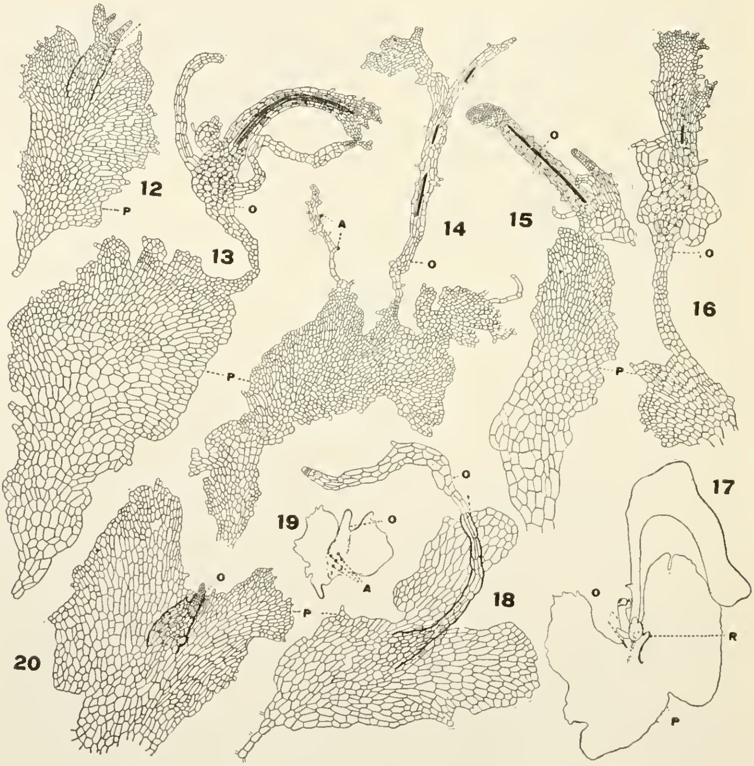
Figs. 7–11

The first outgrowth, after forming an elongated flat structure several cells in thickness and width, broadened into a prothallium with a slight sinus. Tracheids formed in the thickened region at the center. The second outgrowth continued its development as an elongated, thick, club-shaped structure bearing tracheids near the base. The third outgrowth at a very early stage formed a slightly elongated prothallus-like structure, distinctly notched and bearing a series of very short tracheids in the elongated portion.

On the very irregular prothallium shown in FIG. 11 a normal embryo was formed near the base of the archegonial cushion, while near the sinus an apogamous sporophyte developed. This appeared as a cellular mass surrounded by proliferations, from which the first leaf was formed.

Of the apogamous outgrowths represented by FIGS 12–20, those of FIGS. 12, 16–18, and 20 originated as cellular masses on the archegonial cushion of the prothallia; those of FIGS. 13–15 originated as lobes from the margins of the prothallia and that of FIG. 19 as a lobe in the sinus. The cells in most of these marginal lobes were large. The prothallium shown in FIG. 13 was somewhat elongated and bore many lobes on the margin of its apex. One of these lobes, after elongating into a prothallus-like structure, several cells in width and one cell in thickness, formed a cellular mass. From this were given off three branches. The development of the apogamous outgrowth was continued by a reversion to a broad thick prothallium with a lobed apex. A series of tracheids were formed in the thickened region of this outgrowth. All the branches given off by the cellular mass were curled after the manner of a normal leaf, in the early stages of their development, and one resembled a normal leaf in shape. However, this was the extent of the similarity between these branches and normal sporophytic leaves. The branches were only one cell in thickness and no tracheids were present.

The apogamous outgrowth shown by FIG. 14 occurred as a lobe on the margin of a very irregular and distinctly notched prothallium, in the region of the sinus. From only a few cells in width the apogamous outgrowth developed into an elongated prothallus-like structure, thickened in the center and branched at its apex. One of these branches was narrow and several cells in thickness, while the other was wider, only one cell in thickness, and with a broad notched apex. Series of short tracheids were formed in both the thickened region of the elongated portion of the sporophyte and on its branch. Another outgrowth, prothallus-like in form, developed from the margin of one wing of the prothallium and bore on its margin an antheridium.



FIGS. 12–20

FIG. 15 shows an apogamous outgrowth which developed by the narrowing and lengthening of the apex of a prothallium one cell in thickness. It soon branched, one branch being very irregular in form and only one cell in thickness. while the other was elongated and several cells in thickness in the central region where it bore a group of long tracheids. A small side branch was given off from the apogamous outgrowth.

The prothallium, upon which the apogamous outgrowth formed as a lobe in the sinus, was irregularly heart-shaped and bore archegonia on a well-developed meristem (FIG. 19).

With the exception on the one shown in FIG. 16, all the prothallia upon which apogamous outgrowths originated as cellular masses on the archegonial cushion were distinctly notched, and the apogamous outgrowths first appeared as conical cellular masses, the apices of some being more pointed than others. However, the outgrowth shown in FIG. 18 varied somewhat in its development. Beginning as a cellular mass, it formed an elongated, slightly flattened and thickened prothallus-like structure, which in turn reverted to a filamentous condition.

The apogamous sporophyte shown by FIG. 17 began its development as a cellular mass near the sinus on the archegonial cushion of an irregularly shaped prothallium. From this mass there developed first two structures intermediate between leaves and prothallia and then a root. The first of these intermediate structures resembled a very much elongated prothallium one cell in thickness with an expanded and irregularly lobed apex. The second was curled at first in the same way as a normal leaf but resembled the first in being an elongated prothallus like structure one cell in thickness. The root appeared normal.

DISCUSSION

The factors which are considered as the possible controlling or influencing ones in apogamy, as advanced by the previously mentioned workers, are the following: (1) insufficient water for fertilization, (2) weak light, (3) bright light, (4) high temperature, (5) poor soil. In the opinion of five of the writers cited, lack of sufficient water to permit fertilization to take place is regarded as the controlling factor in the particular ferns with which they worked. In the case of *Phegopteris polypodioides*, as well as in the other cases of apogamy previously described by the author ('19, '20), this factor can be entirely eliminated, since the prothallia were grown upon a liquid medium.

Also the factor of light, either bright or weak, can not be considered as the most important one in these cases of apogamy for the following reasons. (1) All cultures were kept under light conditions which not only proved sufficient for the production of normal sporophytes but which failed to retard their development in those cultures of the full solutions which were renewed frequently. (2) In cases where apogamous prothallia from a nutrient solution with one of the essential elements omitted were transferred to a fresh full nutrient solution, thereby permitting the vitality of the prothallia to be renewed, no more apogamous outgrowths or sporophytes were formed, although the cultures were kept under the same light and temperature conditions. In some cases normal sporophytes developed. The formation of these normal sporophytes ceased as soon as the new solution was exhausted and the vitality of the prothallia thereby lowered. (3) Some of the prothallia which had developed upon a full nutrient solution, when removed to a solution from which some essential element was omitted, produced apogamous outgrowths or sporophytes as soon as their vitality was reduced. However, relatively few were formed under these conditions because the prothallia of *Phegopteris polypodioides*, when grown from the spores upon a full nutrient solution which afforded the necessary elements for growth and development, were unable to adjust themselves readily to the physiological action of an incomplete solution. The vitality of the prothallia seemed to be lowered so quickly that it was impossible for them to make an attempt to overcome the unfavorable condition for reproduction by producing apogamous outgrowths and sporophytes. The prothallia of various species of ferns seem to differ in this respect, some being more sensitive, while others are more tolerant. (4) Apogamous prothallia occurred frequently in uncrowded regions of the cultures where light conditions were very good, while on the other hand in the cultures of the full solutions normal sporophytes developed in the most crowded regions where the light condition was the poorest.

The factor of temperature can not be considered as the controlling factor in apogamy in *Phegopteris polypodioides*. The prothallia in all cultures, both those which produced normal sporophytes when the food supply was sufficient and those which produced apogamous ones when the food supply was insufficient, were kept under the same temperature conditions.

Poor soil as a factor in causing apogamy would be operative either through the absence of the elements necessary for development or the presence of those elements in such a form as not to be available for the use of the prothallia. In either case it would be a lack of sufficient nourishment which would be the stimulus to apogamy. The results secured on poor soil would compare with those obtained in *Phegopteris polypodioides* where the apogamous outgrowths and sporophytes were due to insufficient nourishment. The proof for this is the fact that no cases of apogamy were observed in cultures of the full nutrient solution when it was renewed frequently; or, in other words, when a sufficient food supply was available. Also, apogamous outgrowths and sporophytes ceased to develop, and in some cases normal sporophytes were formed, when the nutrient solutions were renewed in the cultures, although other factors remained the same. Still further evidence is the fact that frequently the apogamous outgrowths showed a reversion from a more or less complex structure, several cells in thickness, bearing tracheids to a simple prothallus-like body only one cell in thickness and branched, indicating a still greater lowering of the vitality, which was doubtless due to an insufficient food supply.

Prantl's ('81) work on the nutrition of ferns, Klebs's ('93) valuable studies on the physiology of reproduction, and the work of others have demonstrated that an intimate connection exists between nutrition and growth, and between growth and reproduction. Since both growth and reproduction are dependent upon nutrition, it would seem as if nutrition was the most important if not the controlling factor in causing apogamy. Farmer and Digby ('07), Winkler ('08), Allen ('11), and others are of the opinion that the morphological characters of the gametophyte and sporophyte are not determined by the chromosome numbers as such. It would seem as if the morphological features were determined to a large extent by physiological characteristics, and that the difference between the gametophytic and sporophytic tissue was not a marked one physiologically. Apogamy seems to be due in all cases to a lowering of the vitality of the prothallia to such an extent that normal sporophytes can not be formed. This may be brought about by one or more factors working separately or together. Therefore, apogamy may be regarded, as Bower ('88) has considered it, as a simplification of the life cycle of the fern, or, in other words, as a response to the changed environmental conditions for which a modified life cycle is an advantage to the plant. Doubtless the prothallia of all species of ferns possess this latent quality by virtue of which they can respond to changed environmental conditions by a reversion to this simplified life cycle, which was probably the more primitive.

For this and other reasons the value of the physiological study of the gametophytes of ferns can hardly be overestimated from the standpoint of determining the cause or causes of apogamy and as shedding light upon the physiological problems connected with the interpretation of sexual phenomena and the expression of the individuality of plants in their relation to their environment. The latter point should be emphasized especially, for it is not of so much importance that we determine the exact factor of the environment, which works separately or together with other factors in causing apogamy, as that stress be laid on the individual physiological characteristics of the gametophyte and sporophyte which cause them to respond to the stimulus of the particular situation in the way best adapted to meet their requirements. On account of these individual physiological characterisctics of the gametophyte the same factor or group of factors need not be the cause of apogamy in all species of ferns.

The fact that apogamy occurred frequently in *Phegopteris polypodioides* under cultural conditions unfavorable for nourishment would seem to indicate that apogamy is not a rare occurrence in this species and that it is easily induced.

SUMMARY

1. The filamentous stage of the prothallia of *Phegopteris polypodioides*, grown upon unmodified and modified Prantl's and Knop's solutions, showed a great range of variability in length, the greatest length occurring in the modified solutions.

2. Branching of the prothallia and reversion to a filamentous condition occurred frequently under unfavorable cultural conditions.

3. Sexual organs, both male and female, developed on the prothallia in cultures of the unmodified solutions which were

kept in the laboratory. The percentage of male prothallia was much higher in cultures on the modified solutions, while on the unmodified solutions female prothallia predominated.

4. Both monecious and dioecious prothallia occurred in all the cultures, but the percentage of monoecious prothallia was low, even in young cultures on the modified solutions.

5. Apogamous sporophytes were observed in cultures on Prantl's solution with NH_4NO_3 omitted.

6. Apogamous outgrowths and structures intermediate between mere outgrowths and apogamous sporophytes were observed in cultures on the Knop's full nutrient solution.

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[Reprinted from ECOLOGY, Vol. IV, No. 1, January, 1923.]

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A WORKING BASIS FOR THE ECOLOGICAL CLASSIFICATION OF PLANT COMMUNITIES[1]

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CONTENTS, PART I

I. Introduction

Object and Plan of Paper. During recent years various schemes have been suggested for the ecological classification of plant communities and many divergent views have been brought forward. So much has been written, indeed, that one feels somewhat hesitant about adding anything further to the already voluminous literature on the subject. The present contribution is more or less in the nature of a revision and amplification of an earlier one (Nichols, '17) along this same general line, and it owes its existence primarily to the favorable reception which that paper was accorded. My chief aim here will be to present in as clear and simple a manner as the nature of the material will permit the essential facts and principles which underlie the ecological classification of plant communities, and to suggest a generalized scheme which may be used as a working basis in undertaking an ecological survey of the vegetation in any particular tract of country. Various of the more important recent works dealing with classification are referred to in the text, but it is not my intention either to review these or to enter into any general discussion of controversial points.

The study of plant communities in their relation to environment comprises the field of what might be termed *ecological plant sociology;*[2] more commonly it has been called plant synecology. Various kinds of plant communities may

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[1] Contribution from the Osborn Botanical Laboratory.

[2] *Plant sociology* may be described simply as the study of plant communities. The term ecological plant sociology is used by Pavillard ('18) in a somewhat more restricted sense than that in which it is here employed.

be distinguished, but the one generally recognized as constituting the fundamental unit of vegetation is the *plant association.* The subject-matter of this paper falls more or less naturally into two parts, the first (sections II, III) dealing with the plant association as a vegetation-unit and in its relation to environment, the second (sections IV–VIII) with the ecological classification of plant associations.

Use of Terms. As a preliminary step to the classification of plant communities it is necessary that the various concepts upon which the classification is to be based should be definitely formulated; and for convenience in expressing concepts of any description it is imperative that a rather definite terminology should be adopted. In this connection, however, it should be emphasized that a distinction must always be drawn between a concept and the term by which a concept is designated. In itself a concept may be sound, while the choice of terms may be unfortunate. The two must be judged independently. Given a sound concept, its terminology can be determined only by general usage or definite agreement. It is believed that the concepts advanced in the present paper are logical; time alone will decide whether the choice of terms has been a happy one.[3]

Acknowledgments. Among those to whom I feel indebted for stimulating and suggestive advice in connection with the preparation of this paper are Prof. W. S. Cooper, Prof. A. W. Evans, Dr. H. A. Gleason, Dr. A. F. Hill, Dr. Ellsworth Huntington, Mr. Barrington Moore, Dr. A. G. Tansley, and Mr. Norman Taylor.

II. The Plant Association as the Fundamental Unit of Vegetation

A. THE ESSENTIAL CHARACTERISTICS OF THE ASSOCIATION

The Association as a Concrete Piece of Vegetation. Expressed most simply, a plant association may be described as a group or community of plants which occupy a common habitat. Technically speaking, however, not all plant communities of this description are recognized as associations; it is only those in which the vegetation, taken in its entirety, exhibits certain more or less definite characteristics. To be regarded as an association, a piece of vegetation must be essentially similar throughout its extent in physiognomy, in ecological structure, and in floristic composition. In other words, essential homogeneity in these three particulars is the fundamental criterion of the association. Thus conceived, a plant association may well be epitomized as a "qualitatively and quantitatively homogeneous plant community" (Raunkiaer, '12; Nordhagen, '19).

Criteria of the Association. By the *physiognomy* of a plant community

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[3] For the most part, the terms here used are already more or less familiar. Some of these have had the misfortune to be variously employed by different writers (the term *formation,* for example), but it has seemed better, on the whole, to retain these rather than to introduce new terms.

is meant its general outward appearance—its external morphology, so to speak. When we refer to a piece of vegetation as deciduous forest or evergreen forest or thicket or meadow, for example, we are speaking of it in terms of physiognomy. The physiognomy of a plant community, in turn, is determined by the nature of the more prominent plants which enter into its composition; more precisely, it is determined by the character and abundance of the dominant life-forms. The term *life-form* is here used in its broadest sense to include all features of form and structure by which a plant is adapted to cope with various conditions of environment—peculiarities, for example, in size and habit of growth, in the duration of the plant as a whole and of the stem above ground, in the duration and structure of the leaves, in the position and structure of the resting buds, in the extent and structure of the roots, and in the methods of vegetative reproduction.[4] Briefly stated, life-form is the visible expression of those features in a plant which determine its adaptation to environment.

Under the head of *ecological structure* are included *all* peculiarities in vegetation which are of ecological significance; in fact, physiognomy represents but one phase of ecological structure. The idea of ecological structure is much more comprehensive than that of physiognomy, however, since it takes into consideration various peculiarities of the vegetation which do not express themselves visibly through life-form, as well as those that do—such, for example, as the behavior of the constituent plants in relation to various conditions of light, temperature, and atmospheric humidity, or to various water and other conditions in the soil. Thus, when we speak of plants as being tolerant or intolerant of shade, mesophytic or xerophytic, we are considering features which have an important bearing on the ecological structure of the vegetation, though not necessarily expressed through life-form. Ecological structure also goes further than life-form in taking into consideration the character and abundance of the various subordinate life-forms within the community. Physiognomy, for example, would take no account whatever of the various shrubby and herbaceous elements within a forest association, but these would be included under ecological structure. In short, ecological structure is to the plant community what morphological and physiological structure are to the plant.

As regards the *floristic composition* of a plant community, it is the relatively common or conspicuous species which are of greatest importance—species which are constantly preponderant either numerically or in mass effect: primarily it is the species which typify the dominant life-form of the community (*i.e.*, the *dominant species*); but species belonging to life-forms of subordinate rank (*i.e.*, *subdominant species*) have also to be considered. In a forest, for example, both the dominant species among the trees which form

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[4] For discussion of life-form and related concepts, see Pound & Clements ('98), Raunkiaer ('05, '07), Warming ('09), Drude ('13), Gams ('18), and Clements ('20).

the canopy overhead and the subdominant[5] species among the shrubs and herbaceous plants which go to make up the undergrowth have an important bearing on the nature of the vegetation as a whole. It is the dominant species, of course, which characterize the community in its larger aspects; and it is with reference to these that associations are commonly named. In this connection, a distinction is frequently made between associations in which the position of dominance is shared by two or more species (*e.g.*, oak-hickory association) and those in which a single species is dominant (*e.g.*, pitch pine association), associations of the latter type being designated *consociations.*

Plant Communities of Subordinate Rank within the Association. Within a plant association are commonly included various communities of lower rank, which are designated *societies.* Societies are of two general sorts: layer societies and group societies. A *layer society* is a plant community within an association which results from the tendency of various species of smaller size than the dominant life-form to display their foliage at more or less definite levels. Such societies are particularly characteristic of forest associations (*e.g.*, small tree, tall shrub, low shrub, or herbaceous layer societies in an oak-hickory forest). A layer society tends to be distributed more or less uniformly over the entire area occupied by an association. A *group society* is a plant community within an association which results from the local aggregation to form more or less well-defined clumps or masses of any species other than those which predominate in the association as a whole (*e.g.*, a local clump of sassafras trees or of rhododendron, or a mass of bryophytes on a tree trunk in an oak-hickory forest).

Seasonal Aspects of the Association. An association commonly presents different *aspects* at different seasons of the year—*i.e.*, periodic changes in the appearance of the constituent species, associated with periods of foliation and defoliation or with periods of flowering, etc., which are reflected in the physiognomy of the association as a whole or of its constituent parts.

The Association an Organic Entity. Characterized as above, a plant association may be regarded in its entirety as an organic entity, and as such it occupies a position in the field of ecological plant sociology which is homologous in a general way to that occupied by an individual plant or specimen in such fields of botany as plant morphology or plant taxonomy. As integral parts of the larger community, plant societies bear a relation to the association which is somewhat analogous to that borne by the various organs of an individual plant to the plant as a whole.

B. INTERPRETATION AND APPLICATION OF THE TERM PLANT ASSOCIATION

Divers Interpretations. Notwithstanding the fact that the term plant association is now generally accepted as the designation for what is known as the "fundamental unit of vegetation," there has been considerable diversity

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[5] Subdominance can be interpreted to mean "dominance within dominance."

in the way different ecologists have applied it. By some its use has been restricted to the concrete individual pieces of vegetation which we study in the field—the sense in which I have interpreted it in the preceding section. By others these concrete individual communities have been viewed merely as "examples" of an association—*i.e.,* the term has been applied in a purely abstract sense to a concept which in itself has no material existence. By still others the association has been regarded as a concrete aggregate comprising all the individual pieces of vegetation of a given kind in existence, taken collectively. The situation may be illustrated by a concrete example. We have in central Connecticut any number of pitch pine (*Pinus rigida*) communities, all of them essentially alike in their vegetation, but all (broadly speaking) topographically separated from one another and therefore organically disconnected. Now, to some ecologists each one of these pitch pine communities, by itself, is an association. To others the term "pitch pine association" implies a sort of pigeonhole to which all the individual pitch pine communities can be referred; the individual community is merely a concrete example of the abstract association. Still others would say that all the individual pitch pine communities in existence, considered as a single aggregate and concrete whole, constitute the "pitch pine association," and that the individual pieces of vegetation themselves are but parts or fragments of this association.

Uniform Usage Desirable. Now, to some these differences in interpretation may appear to be of academic interest, but of little practical importance. As a matter of fact, if ecologists were content to confine themselves to the study of plant associations alone, it might perhaps make no particular difference how they used the term, provided each one made clear just what he meant by it. But just as soon as we carry our studies beyond the association, as soon as we begin to arrange associations into units of a higher order than the association, and as soon as we start to call these new units by special names, then, if not before, our troubles begin.

A Definite Proposal Generally Accepted. As a remedy for this somewhat confusing state of affairs, in October, 1921, the following recommendation was submitted by circular letter to about 85 ecologists in the United States and Canada, mostly botanists or foresters and mostly members of the Ecological Society of America: "That the term Plant Association be recognized as applicable both to the abstract vegetation concept and to the concrete individual pieces of vegetation on which this concept is based."[6] Of 76 who replied, 67 were in favor of adopting the recommendation and only 6 were opposed.[7]

[6] This idea was suggested to the writer in replies to an earlier questionnaire on this same topic (September, 1921), by four different ecologists: viz., Prof. W. S. Cooper, Dr. W. A. Dayton, Dr. R. M. Harper, and Prof. C. A. Shull.

[7] This recommendation was also submitted to various European ecologists and was considered favorably by about half of them.

The Abstract-concrete Application of the Term Explained. Just what the proposed interpretation of the term plant association implies can best be made clear, perhaps, by describing a parallel application which we make of the species concept, since the species is quite generally regarded as the taxonomic counterpart of the association. For the sake of illustration let us take the case of the white oak. From the comparative study of a number of individuals of this tree we formulate an abstract concept of "white oak." Then we proceed to generalize: we take this abstract concept of white oak, this creation of our minds, and we call any tree that conforms to it a white oak. Going further, we speak of white oak in technical terms as a species, and we give it a scientific name, *Quercus alba.* But, of course, while the species concept is a modern one, the ideas on which this concept is based date back to the dawn of human intelligence.[8]

With regard to the application of the species concept, then, the conclusion seems inevitable that to all practical intents and purposes it should be taken to include both the generalized concept and the concrete specimens or examples upon which this concept is based. When I point to a particular tree and say, "This is *a* white oak," or "This is *Quercus alba,*" I am applying the species concept in the concrete sense. When I say, "*The* white oak can be recognized by the following characteristics," or "*Quercus alba* is distributed throughout the eastern United States," I am applying the species concept in the abstract sense. And there is no confusion of ideas in this double use.

To return to the plant association. Interpreting the term in both the abstract and the concrete senses, I can point to a particular pitch pine grove and say, "This is *a* pitch pine association," and then in the same breath, if that is physically possible, I can say, "*The* pitch pine association is characteristic of sand plains throughout Connecticut." In the first statement I have applied the term association in the concrete sense; in the second I have given it an abstract interpretation; and here, again, there is no confusion of ideas.

The Aggregate Concept of the Association. With regard to the application of the term association to a specific aggregate of plant communities, *e.g.*, to all the pitch pine communities in existence considered as one concrete whole, there is nothing in the generally accepted recommendation, as stated above, which precludes this use. The abstract concept of pitch pine association includes by implication not only all the pitch pine communities in existence, but all similar communities of the past and of the future as well; and

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[8] In logic, "The active mental process by which concepts are formed is commonly said to fall into three stages: comparison, abstraction, and generalization" (Berkeley). The mental process "whereby ideas taken from particular beings become general representatives of all of the same kind" is termed abstraction (Locke). Wherever we encounter two or more concrete objects of the same kind, by comparative study and abstraction we formulate generalized or abstract concepts. Abstraction and generalization form the basis of all classification.

it is going but one step further to definitely consider all the pitch pine communities in existence as collectively comprising one great association. This, of course, is one sense in which the association has actually been interpreted by some ecologists, including Tansley;[9] it is a sense in which some will doubtless continue to apply the term.

Plant Association Defined. Comparing the idea of the plant association as a concrete piece of vegetation with that of the association as an abstract vegetation-unit, the point to be emphasized in the first case is the homogeneity or uniformity in the structure of the vegetation; in the second it is the constancy or definiteness of this structure. Viewed *in the concrete,* a plant association[10] may be defined as a plant community characterized by its essentially *homogeneous* physiognomy and ecological structure and by its essentially homogeneous floristic composition, at least with regard to dominant species. Viewed *in the abstract,* the association may be defined as a vegetation-unit characterized by an essentially *constant* physiognomy and ecological structure and by an essentially constant floristic composition, at least with regard to dominant species.[11]

C. The Naming of Plant Associations

In a general way, associations can be designated in terms of their dominant species: for example, pitch pine association; oak-hickory association; *Scirpus-Typha* association. More accurately they should be named in terms of both dominant and subdominant species: for example, pitch pine-scrub oak association; oak-hickory-laurel association.

III. The Plant Association in Its Relation to the Habitat

A. The General Situation

Habitat Defined. The term *habitat* may be taken to include "everything relating to the factors operative in a geographically definite locality, so far as these factors influence plants" (Flahault & Schröter, '10). "It is the exact equivalent of the term environment, though the latter is commonly used in a more general sense" (Clements, '05, p. 18). Habitat, to be sure, somehow suggests more the idea of ground relations—the "kind of situation" a plant

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[9] Tansley has expressed himself as completely in agreement with the proposals set forth in my circular letter, but he also strongly advocates this aggregate interpretation. "It is this larger concrete entity," he writes (25 Oct., 1921), "which I should regard as the 'quasi-organism.'" To me the aggregate view of the association seems altogether too intangible to be of practical value; at any rate I am extremely reluctant to regard the association in this sense as being in the nature of an organism. The organism or quasi-organism concept is one that I shall not discuss further in the present paper.

[10] The "Assoziationsindividuum" of Braun-Blanquet ('21).

[11] These definitions, with minor differences in wording, were recommended in my circular letter of October, 1921, and met with the approval of a large majority of the ecologists to whom they were submitted.

grows in—and in this respect it may be that a subtle distinction can be drawn between habitat and environment; but, if so, it is practically a distinction without a difference. The use of the term habitat is sometimes restricted to areas in which *all* the environmental conditions are essentially homogeneous throughout,[12] but the habitat *idea* is capable of much broader application. In a general way, it can be applied to areas of any description, such as north-facing slopes, ravines, flood plains, or salt marshes, which are characterized by uniformity with regard to certain particular environmental conditions.[13]

General Habitat Relations of the Association. The plant population of any particular piece of ground has originated through immigration from surrounding areas. "Of all the immigrants into an area, only those may establish themselves which find in it environmental conditions within the limit of their own environmental demands. The actual mature immigrant population of an area is therefore controlled by two sets of factors: the nature of the surrounding population, . . . and the environment" (Gleason, '17).

In so far as the ecological characteristics of the vegetation are concerned, a plant association is to be looked upon as an effect of which the habitat factors are the cause. And since the vegetation is essentially homogeneous in these particulars, it follows that the habitat must also be homogeneous throughout the area which an association occupies. This may be accepted as a logical corollary to the definition of plant association; in fact, this correlation carries so much weight in the minds of many ecologists that habitat uniformity is specifically included in their definitions of the term association.[14]

Habitat Variations within the Association. A distinction must be made between the *general habitat relations* of the association as a whole and the *specific habitat relations* of its constituent elements. To begin with, each particular life-form which enters into the composition of an association may have its own particular habitat relations. Thus, in a forest the small trees differ in their habitat relations from the dominant trees in whose shade they grow, on the one hand, and from the low shrubs or herbs which carpet the ground, on the other. At the same time, for each of these life-forms the

[12] Such as the area occupied by a specific association: see observations in later paragraphs. This is the sense in which I have interpreted the term in an earlier paper ('17).

[13] Interpreting the term in its more restricted sense, areas of this description would have to be regarded as habitat-complexes (see Nichols, '17).

[14] Rübel ('12, p. 93), for example, defines the association as "a plant community of definite floristic composition, uniform habitat conditions and uniform physiognomy," and I myself ('17) have stated that "uniformity of habitat affords the criterion of the association." The elimination of the habitat idea from the definition of the association has been urged more especially by Du Rietz, Fries, and Tengwall ('18), and, it seems to me, on good grounds. The association is a vegetation-unit which is naturally defined by certain inherent characteristics of form and structure. As soon as we attempt to introduce the habitat as a criterion in defining it we are departing from the facts presented by the vegetation: we are considering the causes of the facts.

habitat relations are essentially the same throughout the area occupied by the association. It therefore follows, with regard to the various layer societies within the association, that for each of these the habitat relations are essentially homogeneous throughout, but that for different layer societies the habitat relations may be quite dissimilar. Group societies may or may not be associated with local peculiarities of habitat.

In this connection, it may be pointed out also that, in the case of the dominant species of an association, the habitat relations differ at different stages of development. In this respect immature individuals of these species rank with the subordinate life-forms which they most nearly approximate. Thus, immature trees in a forest association, at various stages of their development, are subject successively to the same environmental influences (above the surface of the ground, at any rate) as low shrubs, as tall shrubs, and as small trees. This observation is an important one in its bearing on the successional relations of plant associations, to be considered later.[15]

B. The Habitat Factors

The character of the environment in an area occupied by a plant association is determined by the combined influence of all the locally effective habitat factors; in the words of Gleason ('17), it "consists of the resultant of all the external factors."[16] The nature of these factors, which are responsible not only for the ecological characteristics of the vegetation as it exists today, but for the successional changes in vegetation which ensue in the course of time, will now be briefly outlined. For convenience, they are divided into five categories, namely, climatic, physiographic, biotic, anthropeic, and pyric.[17]

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[15] Attention should be called here to a recent contribution by Yapp ('22) on "The concept of habitat," which was received after the present paper had gone to press. Yapp describes the habitat as "the place of abode of a plant, a plant community, or in some cases even a group or a succession of related plant communities, together with all factors operative within the abode, but external to the plants themselves." He distinguishes four main classes of habitat, viz., the *successional habitat* ("the changing habitat occupied by an allied group of plant associations which, as a rule, comprise the stages of a normal succession or sere"); the *communal habitat* ("the general habitat of any recognizable plant community, such as an association or a society"); the *individual habitat* ("the habitat of an individual plant, whether solitary or forming part of a plant community"); and the *partial habitat* ("the habitat of an individual plant during any given period or stage of existence"). My own views, it need hardly be stated, are essentially in agreement with those expressed by Yapp.

[16] Under the term *habitat factor* is included any condition which influences the nature of the habitat. In the present paper the term factor is interpreted in a very general sense and no effort is made to restrict its use with the exact precision which might perhaps be deemed theoretically advisable.

[17] Anthropeic from the Greek ἀνθρώπειος, meaning human; of or belonging to man; of which man is capable. Pyric from Greek πύρ, meaning fire.

1. Climatic Habitat Factors

These include essentially all factors which are associated with atmospheric conditions—conditions chiefly of moisture, temperature, and light.[18] With reference to the extent of their influence, climatic factors may be either regional or local; with reference to the continuity of their effect, they may be either stable or unstable; changes in climate, generally speaking, may be either rhythmical or progressive.

Regional Climatic Factors. These are atmospheric conditions of widespread general uniformity. They are the factors associated with climate as ordinarily conceived—the ones with reference to which the climatic regions of the earth are delimited.

Local Climatic Factors. Here are included modifications of the regional climate due primarily to variations in topography or to the position in relation to one another of land and water bodies. Familiar examples are seen in the different atmospheric conditions of north- as compared with south-facing slopes, of exposed headlands as compared with near-by protected situations, of ravines as compared with level or rounded uplands.[19] Their influence is most pronounced in regions where the topography is varied and where, at the same time, the climate as a whole is relatively unfavorable to vegetation; but, strictly speaking, no two spots on the face of the earth have exactly the same climate.

Rhythmical Changes in Climate. Absolute climatic stability, of course, does not exist. Every climate is characterized by those regularly recurrent alterations which mark the change from day to night and from one season to another. A climate in which these rhythmical cycles of daily and seasonal change continue essentially unchanged from year to year may be regarded as relatively stable.

Progressive Changes in Climate. Progressive changes in climate result from the gradual and progressive alteration in the character of any particular climatic factor or group of factors over a period of years—changes such as are caused by increasing aridity or cold. These changes may be brought about within a relatively brief period of time, for example, within a century;[20] or they may extend over long periods of time, typically geological periods, as, for example, the changes (considered in the large) which have taken place since the last glacial era. Relatively rapid progressive changes may exercise

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[18] It might perhaps be more correct to speak of these as meteorological habitat factors, for two reasons. (1) Strictly speaking, climate is an effect of which certain meterorological factors are the cause. (2) Light is a meteorological factor which is not always regarded as a climatic factor. Or they might be termed atmospheric habitat factors. For various reasons, however, the term climatic habitat factor seems preferable.

[19] In a sense, the influence of shade (see under biotic factors) represents a local modification of the regional climate.

[20] See in this connection the article by C. E. Brooks: Secular variation in climate, Geog. Rev., 11: 120–135, f. 1 + 3 maps 1921.

a relatively immediate effect on the habitat; the immediate effect of relatively slow changes is inconsequential. In the absence of evidence to the contrary, and with reference to its proximate effect on the habitat, the climate of any particular area can be regarded as essentially stable.

Other atmospheric influences are seen in the direct mechanical effect on vegetation of heavy winds, of hail and sleet, of ice storms, of drifting snow and the like, in the effect of irregular extremes of temperature and moisture, etc.

2. Physiographic Habitat Factors[21]

These include influences which are associated with peculiarities in the form, structure, and behavior of the earth's surface. They may be subdivided as follows:

Topographic Factors. The effect of topographic conditions on the nature of the habitat is directly expressed through slope;[22] indirectly it is expressed in many ways. The more favorable soil water relations along the base of a hill as compared with its upper slopes, for example, and the relation of ground water supplies to surface moisture conditions in general are determined very largely by topography.

Edaphic Factors. Here are included conditions due to the physical structure or chemical composition of the soil, or water, or whatever medium plants grow in or on, other than the atmosphere. Examples are seen in the physical influence of rock as compared with sand or clay, or of loose as compared with compact soils, or of land as compared with water; in the chemical influence of acid as compared with basic soils, etc.

Rhythmical Changes in Physiography. Here are included primarily the changes which characterize the littoral zone along the seacoast, associated with the alternate rise and fall of the tides. The annual freezing and melting of the water in lakes and streams and in the surface layers of the ground, the alternate rise and fall of the water level in ponds and swamps at different seasons, and similar periodically recurrent physiographic phenomena might also be classed as rhythmical.

Progressive Changes in Physiography. Erosion and deposition, soil leaching, emergence and subsidence, etc., are factors which in the course of time may bring about progressive changes in the topographic form of the land and in the physical structure and chemical composition of the substratum. Such changes may be effected within a relatively brief period—a period measured by years; or they may take place so slowly that they can be esti-

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[21] The term *physiographic* has been variously interpreted. For present purposes and for want of a better word it is restricted to the application here suggested: specifically, it does not include atmospheric conditions. To include both climatic and physiographic factors, the term *geographic* is used.

[22] That is, the degree in which the surface of the land approaches or departs from the level.

mated only in terms of geological time. Examples of relatively rapid progressive physiographic change are seen in the erosion of ravines and coastal bluffs in sand and clay, and in the building up of flood plains and coastal swamps. Relatively slow changes are exemplified in the emergence, subsidence, and base-leveling of land areas and in the erosion of solid rock along streams and seacoasts. Relatively rapid changes in physiography may exercise a relatively immediate effect on the habitat; the immediate effect of relatively slow changes is inconsequential. In the absence of evidence to the contrary, and with reference to its proximate effect on the habitat, the physiography of any area can be regarded as essentially stable.

Other physiographic influences are seen in the direct mechanical effect on vegetation of water currents, of wave and spray action, of ice, of landslides, etc.

3. Biotic Habitat Factors

These include influences which are associated with the activity or effect of plant or animal agencies (exclusive of man). The more important biotic habitat factors may be summarized as follows:[23]

Shade. Shade may be produced by other than biotic agencies (*e.g.,* the shade cast by the walls of a ravine), but its effect is most generally associated with the influence of vegetation. The influence of shade may be expressed in various ways: it hinders or prevents the growth of various light-requiring plants; it results in increased atmospheric humidity, which in turn means decreased transpiration by plants and decreased evaporation from the ground; it modifies the temperature relations of both the air and the soil.

Root Competition. Competition for water below ground may be quite as influential in its effect on vegetation as competition for light above ground. This is especially true in areas of insufficient soil water.

Humus. Humus arises through the decay of dead organic matter. The accumulation of humus may variously affect the water relations, the aëration, the food supply, the temperature, the acidity, and the toxicity of the soil; it may afford conditions favorable or otherwise to the existence of various soil organisms.

Micro-organisms in the Soil. The precise significance of the complex population of bacteria, fungi, protozoans, and other organisms which inhabit the soil is not yet completely understood, but enough is known to indicate that these organisms may be of the highest importance in their relation to plant communities in general.[24]

Plant or Animal Invasion. The influence of these is exemplified in the widespread destruction wrought on the chestnut in recent years by the chest-

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[23] In this connection, see Cowles '11, pp. 171–179.

[24] For comprehensive discussion of the micro-organic population of the soil and its relation to the growth of plants, see E. J. Russell: Soil conditions and plant growth (fourth edition). London. 1921.

nut blight fungus (*Endothia parasitica*) and on white spruce, balsam fir, and tamarack by the spruce bud moth (*Tortrix fumiferana*) and other insect pests.

Other biotic influences might be mentioned, such as the prevention of forest reproduction in the Rocky Mountain region by rodents which destroy the seed; but these influences are so numerous and varied that they can be merely suggested.

4. Anthropeic Habitat Factors

These are separated from biotic factors chiefly by reason of the fact that they are subject to rational control. The modifying influence of man on the nature of the habitat is expressed in various ways: through lumbering and clearing the land for agriculture, through cultivation and the introduction of grazing animals, through irrigation and forest management, etc.

5. Pyric Habitat Factors

Fires may be caused by lightning, in which respect pyric factors might be classed as climatic, or they may be set by man. For reasons which are obvious, however, it seems best to recognize the influence of fire as belonging in a distinct category by itself. The outstanding effect of fire on vegetation is seen in the actual annihilation of existing plant communities, but scarcely less important may be the modification of the habitat brought about by the destruction of the humus, whereby all of the factors associated with the presence of humus are done away with, and, to a less extent, by the removal of shade.[25]

[*To be concluded*]

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[25] The brief outline of factors here presented is far from complete; it is intended to be suggestive rather than exhaustive. Furthermore, in attempting to group the various factors into particular categories it is unavoidable, if for no other reason than the difficulty of distinguishing between direct and indirect effects, that certain lines should be somewhat arbitrarily drawn. Thus, peculiarities in topography are largely responsible for the existence of localized conditions of climate, and in so far as this is true these conditions may well be looked upon as being in the nature of indirect topographic influences. Again, the humus factors, notwithstanding the organic nature of humus, might well be considered in connection with edaphic rather than biotic influences—as indeed they frequently are. Shade is not invariably due to biotic influences; and so on. In practise, here as elsewhere, individual judgment must be exercised in seeking the logical correlation between cause and effect, and the exact treatment of material will necessarily vary with different points of view.

A WORKING BASIS FOR THE ECOLOGICAL CLASSIFICATION OF PLANT COMMUNITIES

[Reprinted from ECOLOGY, Vol. IV, No. 2, April, 1923.]

A WORKING BASIS FOR THE ECOLOGICAL CLASSIFICATION OF PLANT COMMUNITIES

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CONTENTS, PART II

IV. The Ecological Classification of Plant Associations

Classification, generally speaking, may be described as the arrangement into groups of objects or phenomena which are related to one another by the possession of certain characters in common. The principle of classification, in the words of Hugh Miller,[26] is one which is "inherent in the human mind"; it is a principle "which we find pervading all science, which gives to each of the many cells of recollection its appropriate facts, and without which all knowledge would exist as a disorderly and shapeless mass, too huge for the memory to grasp and too heterogeneous for the understanding to employ." The phase of ecological plant sociology which deals with the classification of plant associations might be called *systematic plant sociology*.[27]

Any attempt to classify natural phenomena presents obvious difficulties. Especially is this true in a field such as ecology, where authorities disagree so strongly on many points, not only in the interpretation of facts, but concerning the nature of principles. To fulfill scientific requirements a scheme of classification must be logical in its concepts, clear-cut in its definitions, and

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[26] The old red sandstone, p. 106. Edinburgh, 1882.

[27] I would employ this term in a somewhat more comprehensive sense than that in which it is used by various European authorities.

consistent in its methods; furthermore, it should be "natural" to the extent that it is based on principles and relationships which exist in nature. To be of practical value such a scheme must possess sufficient elasticity to render it adaptable to a wide range of conditions and to varying points of view.

No scheme for the classification of natural phenomena, especially where these are considered in their relation to cause and effect, can be absolutely automatic and mathematically precise in its practical applications. It is difficult and commonly impossible to draw sharp lines in nature, and it must therefore be recognized, in attempting to classify the facts of nature, that, since we are dealing with "merging phenomena, the only possible procedure is to select the extreme marked types of the groups, and, giving them careful study and description, to describe the intermediate kinds according to their positions between the types" (Ganong, '03). It must further be recognized that our application of abstract ideas of any description to concrete cases can be successful only in so far as we possess not only a thorough understanding of the underlying principles involved, but also a complete knowledge of the facts themselves, coupled with which must be the ability to properly coordinate these facts in their relation to the principles. With the best of classifications, when it comes to the interpretation of particular cases, especially when our knowledge concerning certain of the facts is incomplete, differences of opinion are inevitable. After all, the best that any scheme of classification can hope to do is to furnish a sound framework, based on generalized facts and fundamental principles.

In an earlier paragraph (p. 14) it has been emphasized that the plant association, considered as a concrete piece of vegetation, occupies a position in the field of plant sociology corresponding to that occupied by the individual plant in such fields of botany as plant morphology and plant taxonomy. These concrete associations therefore represent the basic materials with which any classification of plant communities has to work. From the standpoint of ecological plant sociology, the fundamental principle by which the associations are classified is their relationship to environment. Briefly stated, the ecological classification of plant associations consists of the arrangement into common groups of different associations which are related to one another by environment. The groups thus defined represent ecological vegetation units of a higher order than the association, in much the same way that a genus represents a taxonomic unit of a higher order than the species.

Broadly speaking, there are three different ways in which the influence of environment on vegetation may be expressed, and any one of these three ways may be used as a basis of classification. The influence of environment is seen, first of all, in the nature of the vegetation itself. The association, in its ecological characteristics, can be looked upon as an effect of which the environment is the cause: it represents the vegetative product of all the various environmental influences which have led to its development. From this point of view, associations may be classified with reference to their physiognomy and ecological structure (section V). In the second place, the influence of environment is seen in the manner in which plant associations are distributed over the face of the earth in relation to various features of climate and physiography. From this point of view, associations may be classified with reference to their geographic relations (section VI). Finally, the influence of environment is seen in the changes in vegetation which ensue in the course of time. From this point of view, associations may be classified with reference to their successional relations (section VII). The field covered by the first point of view might be termed *physiognomic plant sociology*, that covered by the second *geographic plant sociology*, and that covered by the third *dynamic plant sociology*.

V. Classification Based on Physiognomy and Ecological Structure

The Association-type.—It is a matter of common observation that plant associations which differ from one another more or less markedly in their floristic composition may be essentially identical in their physiognomy and ecological structure. To illustrate: Throughout most of the eastern United States the prevailing type of natural vegetation on the better soils of ordinary well-drained uplands[28] is some sort of a mesophytic deciduous broad-leaf forest. This forest may vary greatly from place to place with regard to its floristic composition—*i.e.*, it may include various floristically different associations—but it is essentially uniform throughout with regard to its physiognomy and ecological structure. Again, the *Chamaecyparis* association of swamps along the Atlantic coastal plain and the *Thuja* association of swamps farther north seem essentially identical as regards their physiognomy and ecological structure. The same is true of the pitch pine association in Connecticut and the jack pine association in Michigan, of various associations of marshy or reedy swamps, and so on almost ad infinitum. This brings us to the idea of the association-type. Briefly stated, all associations which resemble one another in physiognomy and ecological structure, regardless of their floristic composition, may be referred to a common *ecological association-type*.[29]

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[28] The term "upland" is one which I have been accustomed to use, for convenience, to include all types of topography other than depressions occupied by lakes, swamps, etc. Under "ordinary uplands" I have included all areas of this description that are not so situated as to be influenced by the proximity of rivers, streams, or seas.

[29] The term *formation* is employed by various continental European ecologists in the same sense that I have here used the term ecological association-type, and in this procedure they are followed by certain American writers. Following Schimper ('03), Clements ('07, '16), Moss ('10), and Tansley ('11, '20), I have applied the term formation to certain geographically defined groups of associations (see section VI), and the term obviously can not be applied in both senses without confusion.

The term *forest-type* is in general use among American foresters, but by them it is

Characterized, as they tend to be, by more or less obvious peculiarities of external appearance, it is chiefly the different association-types, rather than the associations, which picture themselves before the eyes of most of us, as we view the landscape from speeding train or auto—such types as evergreen and deciduous forests, groves and thickets, meadows and marshes. It is the association-types, rather than the associations, which first impress us when we visit a floristically unfamiliar region. The associations reveal themselves only when the vegetation is considered with reference to its floristic composition, whereas it is quite possible to describe the vegetative features of any region in terms of physiognomy and ecological structure without knowing the name of a single plant. In short, from the point of view of ecological plant sociology the association-type is of much greater fundamental importance than the association, in so far as the latter is regarded as an abstract vegetation unit. It is from this point of view that Cooper ('22) describes the association-type (he uses the term formation), rather than the association, as the fundamental unit of vegetation.[30]

In naming association-types, they are appropriately designated in terms of physiognomy and ecological structure. Thus, in a general way, the various associations of lakes and swamps can be grouped under such heads as: submerged leaf association-type, floating leaf type, reed swamp type, and deciduous swamp-forest type.

Association-type Compared with Association Abstract.—The concept of the association-type is essentially an abstract one, corresponding in this respect to the abstract concept of the association. Both of these abstract concepts are represented in the concrete by the individual association. That is to say, the association concrete is an example both of the association abstract and of the association-type. As an example of the first it is considered more especially with reference to its floristic composition. As an example of the second it is considered with reference to its physiognomy and ecological structure alone. Thus an individual pitch pine forest (association concrete) is an example of pitch pine forest (association abstract); it is also an example of what might be termed xerophytic conifer forest (association-type).[31]

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given the most diverse meanings. There are cover types and site types and management types, none of which are comparable to the ecological association-type. The *ecological forest-type,* however, is identical with the ecological association-type. Unfortunately the term association is little used by the foresters. It seems hardly necessary to more than suggest the desirability that, so far as their work is ecological in character, the foresters should at least adopt the association as the basis of classification.

[30] To quote Pavillard ('20) in this connection: "L'association [= abstract association] est l'unité fondamentale de la Sociologie végétale. . . . La formation [= association-type] est la notion fondamentale de la synécologie."

[31] It is from somewhat this point of view that Pavillard in 1912 (see '22, p. 20) wrote "La formation [= association-type] est à l'association ce que la forme biologique est à l'espèce. On pourrait dire encore: la formation est la 'forme biologique' de l'association." Negri ('14) has expressed the same idea as follows: "Alla *formazione*

Where to draw the line between the association, considered in the abstract, and the association-type is a question which can no more be answered dogmatically than the question of where to draw the corresponding line between genus and species. Thus, in the case of the genus *Pyrus,* Gray's "Manual" places under one genus the species which Britton's "Flora" separates into four. In so far as an association-type is limited to a geographically continuous region, the various concrete associations by which it is represented are commonly coordinated floristically, in greater or less degree, by the general occurrence of certain "binding species."[32] Thus the mesophytic deciduous broad-leaf forests of the eastern United States are characterized throughout their range by the presence of the beech and the sugar maple. It is quite possible in such a case, by interpreting the floristic criteria very broadly and laying stress only on these binding species, to refer all the individual associations of such a type to a single abstract association; in other words, to apply the term association in the abstract to exactly the same unit, for this region, as the term association-type.[33]

But, on the other hand, leaving out of consideration the binding species, these same individual associations exhibit very considerable floristic diversity in different localities and the general tendency, among those who have given most study to the floristic phase of plant sociology,[34] seems to be to delimit associations in the abstract rather narrowly on a purely floristic basis. As concepts, the relation between the association abstract and the association-type seems pretty clearly defined, and when it comes to the application of these concepts the ecologist has to use individual judgment and common sense, taking into consideration both the facts and the point of view from which he is working, just as the taxonomist has to do in applying taxonomic concepts. Strictly speaking, it may be stated that an association-type commonly embraces several to many floristically defined abstract associations; but in plant sociology, as in taxonomy, when it comes to the treatment of particular cases, it

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[= association-type]—*termine biologico*—corrisponde essatamente *l'associazione—termine floristico*." In a recent letter (4 Jan., 1922) Negri expresses the view that "The plant association can be defined only by its floristic composition; to physiognomy and ecological structure corresponds the concept of plant formation. The two terms express two different appreciations of the same plant population of a definite piece of ground subject to a definite local climate.

[32] This term is taken from an unpublished manuscript by Prof. W. S. Cooper.

[33] In my own work I am inclined to thus emphasize the association-type at the expense of the association abstract. I tend to refer the individual concrete associations to particular types, distinguishing the abstract associations only where these are clearly and unmistakably differentiated.

[34] Recent work on the part of European plant sociologists has contributed much toward the detailed understanding of the association, more especially with reference to its delimitation from the floristic point of view. See in this connection recent papers by Pavillard ('19), Du Reitz et al. ('20), Du Rietz ('21), and Braun-Blanquet ('21).

is inevitable that there should always be "splitters" and "lumpers," and this regardless of how we define our terms.

General Application of the Association-type Idea.—Unlike the concept of the association, the association-type idea is not limited in its application to the vegetation of regions which are floristically continuous. In fact, its usefulness becomes most apparent when the vegetation of regions which are totally unlike floristically is compared. The southern California and the Mediterranean coast regions, for example, have nothing in common floristically, but because of the similarity in climatic conditions the associations in the one region tend to be paralleled in the other by associations which are similar in their physiognomy and ecological structure—*i.e.,* by associations which can be referred to a common association-type. And even regions which are both floristically and climatically unlike tend to possess certain association-types in common—types such as occur in lakes or on rock cliffs, or in other situations where physiographic factors exercise a controlling influence in determining the ecological character of the vegetation.

The Association-type as a Basis for Ecological Classification.—In adopting the association-type as a basis for the ecological classification of plant communities, the vegetation itself, as the product of environment, is taken as the criterion. This indirect method of estimating the relation between vegetation and environment is by no means illogical, any more than it is illogical to deduce the facts of evolution from the study of existent organisms. At the same time it should be emphasized that the individual plants which go to make up any particular piece of vegetation are capable, for the most part, of adapting themselves to a rather wide range of habitat conditions. It follows, on the one hand, that the vegetation can give but an approximate measure of the habitat, and, on the other, that an exact parallelism between associations growing under essentially similar conditions of environment is not to be expected. The agreement, both of vegetation and of habitat, is only approximate.[35]

Physiognomy and ecological structure have been made the primary basis for an ecological classification of plant associations by various European writers, notably Warming ('09, '18), Brockmann & Rubel ('12), and Raun-

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[35] From what has been said, it is to be expected that different associations belonging to the same association-type will be approximately parallel in their habitat relations; *i.e.,* the nature of the habitat will be approximately identical wherever these associations occur. Identity in regard to the habitat as a whole, however, does not necessarily mean identity in regard to each individual habitat factor. The nature of the habitat as a whole, as already stated, is determined by the combined influence of all the locally effective habitat factors; but different individual factors are able to offset one another's influence to such a degree that it is possible for different sets of factors, in combination, to produce essentially the same result. Thus it is that the same association, growing in two regions which are somewhat dissimilar climatically, may appear to occupy entirely different habitats, the apparent difference in habitat being explained by the difference in climate.

kiaer ('16), and it does not seem necessary to go further into this phase of classification here.

VI. Classification Based on Geographical Relations

A. INTRODUCTORY

General Correlation between Geography and Vegetation.—The importance of geographic factors in their effect on vegetation is most strikingly seen when areas are compared which differ from one another to a marked degree in either climate or physiography. Thus the dissimilarities in vegetation between arctic and tropical regions and between desert and humid regions are manifestly associated with differences in climate, while the corresponding dissimilarities between lakes and uplands, between ravines and flood plains, and between saline and fresh swamps are quite as manifestly associated with differences in physiography. Fully as significant as these differences, however, are the similarities exhibited by the vegetation of areas which are geographically alike. Thus the similarities in vegetation between arctic and antarctic regions, between the desert regions of America and those of Africa, and between tropical regions the world over are manifestly correlated with resemblances in climate, while the similarities between the vegetation of different individual ravines, flood plains, lakes, and salt marshes are quite as manifestly correlated with resemblances in physiography. Examples which illustrate the influence of climate and physiography on the character of the vegetation might be multiplied indefinitely.

With regard to this relationship in general, it may be stated: (1) that uniformity or similarity in geographic conditions is conducive to uniformity or similarity of vegetation; and (2) *vice versa,* that diversity or dissimilarity of geographic conditions is conducive to diversity or dissimilarity of vegetation. It follows, to be more specific, that an area in which the combined influence of all the locally effective climatic and physiographic factors is essentially homogeneous or uniform throughout—such an area as a sand plain, or a clay bank, or a rock face—will tend to be occupied by a single plant association; and, on the other hand, that an area in which the combined influence of these geographic factors varies from place to place—such an area as a ravine, or a lake, or a salt marsh, or a continent—will tend to be occupied by more than one association.[36] That these tendencies are not universally realized in nature can be attributed primarily to the influence on the habitat of various biotic agencies which are able to compensate in greater or less degree the influence of geographic agencies,[37] secondarily to the disturbing influence of various human agencies and fire.

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[36] Provided of course that these variations are of sufficient magnitude to have a differentiating effect on the character of the vegetation.

[37] See further remarks regarding compensating factors on pp. 166, 173.

The importance of geographic factors in their effect on vegetation is admirably summed up by Livingston and Shreve ('21, p. 25) in the following words: "We can, in brief, put it down as a law of plant geography that the existence, limits, and movements of plant communities are controlled by physical conditions. The conditions that control the movements of the community are those of the soil; the conditions that control the broader geographical limits are almost solely those of the climate. The existence of the community and the extent of the area occupied are, of course, controlled by conditions of both soil and climate." Surely there can be no question as to the fundamental importance, from an ecological standpoint, of a classification of plant communities based wholly or in part on their geographical relations.

The Association-complex.—Areas of essential geographic homogeneity may be of considerable extent, as in the case of a sand plain or a salt meadow, or they may be of comparatively limited extent, as in the case of a clay bank or a rock face. In either case it is seldom that a tract of country of any size is studied which does not exhibit sufficient geographic diversity to produce a more or less pronounced diversity of habitats, with a consequent tendency to diversity of plant associations. In other words, largely as a result of geographic differences of one sort or another the vegetation of any sizeable tract of country comprises what for convenience may be characterized as an association-complex, this term being given to any group of associations which occupies a definitely circumscribed area.[38]

Geographically Defined Association-complexes.—When it comes to the consideration of the geographic distribution of plant associations, and particularly to the way in which associations are grouped into geographically defined complexes, it becomes necessary to distinguish between the influence of climatic and that of physiographic factors. Generally speaking, the subdivisions of the earth's surface determined by climate are of relatively wide extent—so wide that they are spoken of as climatic regions. In comparison with these, the subdivisions determined by physiography are infinitely smaller.[39] A region characterized by uniformity in climate may be anything but uniform in the character of its physiography; and while the uniformity of climate in such a region tends to favor uniformity in the ecological character of the

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[38] Thus we can speak collectively of the associations of a naturally defined area, such as a ravine or a lake or a climatic region, as an association-complex; or we can refer by the same term to the associations of an arbitrarily defined area, such as the State of Connecticut. Interpreted in this sense the term association-complex corresponds in its unrestricted usage to the term community, which by general agreement may be used indiscriminately with reference to any specific assemblage of organisms, regardless of its ecological rank. The term has been given a more restricted application, however, by Du Rietz ('17).

[39] Exceptions to both these statements will of course be obvious. Thus marked differences in climate are found within comparatively limited areas in mountainous regions, while certain physiographic features, such as sand plains and salt marshes, may be essentially widespread in their continuity.

vegetation, the diversity in physiography may hinder or prevent the actual attainment of any such vegetative uniformity. In short, when it comes to the classification of plant communities in their relation to natural geographic features, it becomes necessary to distinguish between geographically defined areas which are determined by climate and those which are determined by physiography, and between the corresponding climatically and physiographically determined association-complexes.

B. CLIMATIC UNIT-AREAS AND CLIMATIC PLANT FORMATIONS

Climatic Unit-areas.—Differences of position in relation to latitude, oceans, mountain barriers, prevailing winds, elevation, and the like, are responsible for widespread differences in climate on different parts of the globe. Any portion of the earth's surface which is characterized by having essentially the same kind of climate throughout and whose boundaries are determined by climate may be designated a climatic unit-area or climatic region: it represents a unit in its relation to the climatic features of the earth as a whole. Familiar examples on this continent are the "damp warm temperate" climatic region of the eastern United States, the "dry steppe" climatic region of the Great Plains, and the "dry desert" climatic region of the Southwest; to which may be added the various climatic belts or zones characteristic of our higher mountains.[40]

Climatic Formations.—Taken in its entirety, the vegetation of any specific climatic unit-area may be designated a climatic formation: it comprises a complex of associations which are geographically linked with one another by climate. The three climatic regions first mentioned above, for example, are characterized in order by what may be termed a mesophytic deciduous forest formation, a xerophytic grassland formation, and a desert formation.

Thus defined, the climatic formation is taken as a concrete vegetation-unit; but, just as in the case of the association, this concept is capable of abstract as well as concrete interpretation. Widely separated regions having similar climate tend also to have similar vegetation. For example, xerophytic grasslands essentially identical in their ecological aspects to the grassland formation of the Great Plains are developed in parts of Russia and China, where essentially identical climatic conditions prevail, and the vegetation of all three areas can be referred in the abstract to the same climatic formation. Again, the mesophytic deciduous forest formation is developed in moist temperate regions in various parts of the world. And so on.

Distinguishing Characteristics of the Climatic Formation.—When account is taken of all the many associations and association-types which go to make up the vegetation in any particular climatic unit-area, it becomes apparent

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[40] For a comprehensive synopsis of the climatic regions of the earth, see W. Köppen: "Klassifikation der Klimate nach Temperatur, Niederschlag und Jahreslauf" (Petermanns Geog. Mitteil. 1918: 193–203, 243–248. *pl. 10, 11*).

immediately that the climatic formation represents an extremely complex vegetation-unit. But this great heterogeneity which impresses one at first thought is counterbalanced by the fact that throughout any area of uniform climate there is an unmistakable tendency, through the phenomenon of succession, for vegetation everywhere to progress toward a condition of ecological uniformity—toward what may be termed the climatic climax association-type.[41] From the standpoint of the vegetation it is this climax by which the climatic formation is primarily characterized and from which it is usually named. Thus the climatic climax in the eastern United States is mesophytic deciduous forest; in the Great Plains region it is xerophytic grassland, etc.[42]

C. Physiographic Unit-areas and Physiographic Plant Formations

Physiographic Unit-areas.—In regions having a uniform climate, differences in vegetation are associated primarily with differences in topography and soil. These latter are not distributed in a wholly haphazard manner. They have arisen in a more or less orderly fashion during the course of physiographic development, and in consequence the various topographically and edaphically determined habitats are arranged more or less definitely in relation to various of the larger physiographic features of the region. It is these larger and more outstanding features to which the term physiographic unit is here applied; generally speaking, such features as ravines, valleys and flood plains, rocky uplands and sand plains, lakes, bogs, coastal swamps, and the like.

Like its climatic counterpart, a physiographic unit-area tends to exhibit more or less pronounced environmental uniformity of a sort; there are certain habitat conditions which prevail throughout the entire area. Thus a ravine is characterized by its relatively high atmospheric humidity and by its protection from sun and wind; a lake by the presence of water; a salt marsh by the presence of salt water; a rocky upland or a sand plain by certain peculiarities of soil or topography, etc. But, on the other hand, the recognition of an area as a physiographic unit does not imply that it possesses absolute uniformity of topography and soil.[43] On the contrary, when examined in detail, there may be very considerable local diversity of habitat; such, for example, as that

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[41] For further discussion of succession and climatic climax, see section VII.

[42] In describing a climatic formation in the abstract, the point to be emphasized is the definite or constant character, in physiognomy and ecological structure, of the climatic climax association-type. In the case of the concrete example of the formation, as already mentioned, it is the homogeneity or uniformity in this respect which is most important. The formation concrete, it may be added, is further characterized by a more or less distinct floristic individuality, but in this respect there may be and commonly is little or no resemblance between the different concrete representatives of the same abstract formation.

[43] Any more than a climatic region is characterized throughout by absolute uniformity of climate.

afforded by the dry cliffs, the moist slopes, the wet ledges, the inundated rocks, etc., in a rock ravine. From this point of view a physiographic unit-area might be described as a physiographically determined habitat-complex: it represents a complex of habitats linked together by physiographic development, and therefore to be regarded as a unit in its relation to the physiographic features of the region in which it occurs.

Demarcation of Physiographic Unit-areas in the Field.—Generally speaking, when it comes to practical field studies it is quite possible to demarcate physiographic unit-areas with reference to conditions of either topography or soil. On the whole, and especially in regions of rugged relief, the topographic conditions, through their influence on ground water relations and exposure, seem to be of the greatest ecological importance; but soil structure and composition may be nearly as influential in determining the nature of the habitat—even more so in regions of gentle relief. In a physiographic classification of plant associations, then, both topographic and edaphic conditions must be taken into consideration, although necessarily either one or the other must be selected as the primary basis.

With regard to the treatment of specific cases, it is not possible to lay down rigid rules. Thus from a purely geographical standpoint it may often be possible to distinguish a larger number of physiographic divisions than is necessary from an ecological point of view. Take, for example, two areas of rocky upland which are alike in their topographic relations, but unlike in the character of the rock concerned. Physiographically these may be different, but it is only as such differences affect the character of the vegetation that they become of ecological consequence. For this reason, in the case of uplands in particular, it is often most practicable to group several areas, which, strictly speaking, may be physiographically distinct, under one head. Thus for ecological purposes it might be quite sufficient to distinguish the two upland areas just mentioned as ordinary rocky uplands (in contrast to sandy uplands, or to rocky uplands along the seacoast or along streams), taking no account of the more detailed physiographic subdivisions based on geological dissimilarities. The difficulty of making any definite rules by which to recognize individual physiographic unit-areas in the field is increased by the fact that for various reasons (suggested on page 166) it may be advisable to interpret physiographic unit-areas more broadly in some cases than in others. After all, it is the vegetation in which we are primarily interested, and the sharpness with which we attempt to draw physiographic boundaries is best governed accordingly.

Physiographic Formations.—Taken in its entirety, the vegetation of any specific physiographic unit-area may be designated a physiographic formation:[44] it comprises a complex of associations which are geographically linked with one another by physiography, and it may therefore be referred to in

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[44] The same as edaphic formation, in part, of Nichols ('17).

terms of physiography. Thus we may speak of a particular rock ravine formation, or a particular flood plain formation, or a particular salt marsh formation.

Like a climatic formation, a physiographic formation may be a very heterogeneous vegetation-unit. Here as there, however, there is a tendency, through the phenomenon of succession, for the vegetation to progress toward a common climax. The nature of this climax, in so far as it differs from the climatic climax, is determined primarily by the habitat conditions already referred to which characterize the area as a whole.[45]

As with the association and the climatic formation, the present concept also is capable of both concrete and abstract interpretation. Thus we can refer in the concrete to the vegetation of a particular flood plain or a particular salt marsh as a flood plain formation or a salt marsh formation, but we can also speak in the abstract of the flood plain formation along the Connecticut River or of the salt marsh formation in New England.[46]

D. Interrelations of the Various Geographical Vegetation-units

The General Situation.—To sum up briefly, a climatic formation comprises a complex of associations linked together by climate; a physiographic formation comprises a complex of associations linked together by physiography. These geographically defined subdivisions of vegetation represent ecological vegetation-units of a higher order than the association. Fundamentally the two are logically and clearly differentiated both from one another and from the association. The climatic formation, in general, is the more comprehensive unit, and a particular climatic formation ordinarily includes numerous physiographic formations.

Apparent Exceptions to Rule.—When it comes to the interpretation of concrete cases in the light of these abstract concepts, there are certain apparent discrepancies between fact and theory which deserve a few words of comment.

To begin with, the line of demarcation between climatic formation, physiographic formation, and association is not always sharply defined. A physiographic unit-area such as a sand plain, for example, may exhibit very little diversity in either topography or soil, with the result that the vegetation is essentially uniform throughout. In such a case it seems obvious that no dis-

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[45] See further discussion of physiographic climax on p. 172.

[46] The abstract use of this term may well be extended to include ecologically similar physiographic formations the world over. Generally speaking, if the term is so used, the same physiographic formation might be expected to occur in regions which are similar to one another in climate and physiography, but it would not be looked for in regions which are climatically different. Formations which occupy corresponding physiographic unit-areas in climatically different regions, however, might be referred to a common physiographic formation-type. Thus a rock ravine formation in the Arizona mountains and one in Connecticut might both be referred to the rock ravine formation-type. The use of the term *type* in this connection would serve to emphasize the physiographic parallelism of the formations concerned.

tinction whatever can be drawn between the physiographic formation and the association: they are one and the same thing. In other words, the vegetation in its entirety can here be referred to either as an association or as a physiographic formation.

Again, it is often difficult to draw sharp lines between different individual physiographic formations. A rugged rocky upland, for example, is occupied very largely by a characteristic formation. Here and there, however, associated with minor variations in topography, are scattered representatives of swamp and ravine formations. In regard to cases of this sort it need only be said that, like other cases of overlapping or intergrading conditions, they are best treated in the light of conditions which prevail in situations where these complications do not exist.[47]

Quite different is the situation in cases where essential similarity in vegetation prevails over areas which are physiographically different from one another. In attempting to explain such conditions it should be recalled, first of all, that the ecological characteristics of any piece of vegetation are the result of the combined influence of all the locally effective factors of the environment. Leaving out of consideration the adaptiveness of the various plants which go to build up the vegetation to a more or less wide range of habitats, it might seem at first thought that if two geographic unit-areas differ from one another in any appreciable degree, there ought to be a corresponding difference in the vegetation. That this is not actually the case is due primarily to the fact, already suggested,[48] that the influence of one habitat factor (or set of factors) may be offset or compensated by the influence of another habitat factor (or set of factors). Thus the favorable influence of humus accumulation and shade may offset to such a degree the influence of physiographic factors that two areas which are physiographically unlike may support essentially the same type of vegetation. Again, to take an extreme example, in the humid tropics the influence of congenial climatic factors may so completely offset that of physiographic factors that vegetation practically everywhere, regardless of the nature of the topography and soil, tends to merge into one great association or association-type.

But one other complication need be mentioned. Generally speaking, the ecological characteristics of a physiographic formation are determined by the combined influence of both climate and physiography. In so far as climatic factors influence the nature of the vegetation, then, the same physiographic formation would hardly be expected to occur in regions of different climate. Yet in some cases the influence of climatic factors is so overshadowed by that of physiographic factors that the same physiographic formation develops under varying climatic conditions. This condition is especially well illustrated by the salt marsh formation, which exhibits essentially the same physi-

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[47] See in this connection the quotation from Ganong on p. 155.

[48] P. 160; but see especially in this connection Nichols '17, pp. 315, 316.

ognomy and ecological structure all along the Atlantic coast from northern Nova Scotia to Florida, and along the Pacific coast as well. It is further illustrated by the bog formation in its southward extension in the East from the cool humid regions where it is best developed, and by the formations of lakes, which may be strikingly similar in regions which are quite different in climate.[49]

VII. Classification Based on Successional Relations

A. Introductory

Environmental Influences Cumulative.—No system for the classification of plant associations in their relation to environment can be ecologically complete which fails to take into consideration the fact, which Cowles ('01) has emphasized, that "environmental influences are normally cumulative." In the case, for example, of the associations now growing on a humus-covered rock surface, or in a swamp which has originated through the filling in of a lake by organic debris, or on a flood plain, the present habitat conditions to a very high degree are a heritage of the past: they represent the cumulative effect of processes and phenomena which not only have originated in the past, but some of which have long since ceased to operate. A classification which takes into account these facts, as Cowles has stated, is "both genetic and dynamic": in the minds of many it affords the only method by which plant associations may be naturally grouped in their relation to environment.

Succession.—The underlying basis for a dynamic and genetic scheme of classification is furnished by the phenomenon of succession. Succession may be broadly described simply as the replacement of one plant association by another. It is a constantly recurring phenomenon in nature and through its continued influence there may follow one another, on any given area of the earth's surface and in the course of time, a series of associations which, taken collectively, may be designated a *successional series* or *sere*.[50] On abandoned farm lands in southern New England, for example, a plowed field may become

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[49] See Tansley's comments on this point ('20, pp. 142–144). Tansley, it may be said, recognizes the climatic formation as being distinct from the physiographic formation, but he specifies that "We can only include in the climatic formation the characteristic climatic climax associations and those associations (or associes) which clearly belong with them developmentally." He objects (p. 143) to treating as a climatic formation the whole of the vegetation within a climatic region (as I have done) on the ground that "nothing like a sharp line can be drawn between one climatic region and another, so that it becomes impossible to delimit climatic formations in Nichols's sense." This objection might well be refuted by an argument which Tansley himself uses in support of a different idea and which happens to appear on the same page, *viz.*, that "gradual transition from one thing to another is never a reason for refusing to regard two things as distinct which are distinct."

[50] The term *succession* is frequently employed in the sense of a *successional series*. In a general way there may be no particular objection to this use, but strictly speaking this term is better restricted to the phenomenon or process of change.

occupied successively by associations of annual weeds, of perennial grasses, of light-requiring shrubs and small trees, and of shrubs and large trees which are relatively tolerant of shade. The various associations in such a series do not arise promiscuously; they appear in more or less orderly sequence as a result of the progressive reaction between the vegetation and its environment. Generally speaking, vegetation everywhere tends to progress from a relatively primitive toward a relatively advanced condition. The process is essentially one of development. As time goes on, associations which are ecologically immature tend to become replaced by others which are ecologically more mature, until eventually, under favorable conditions, a climax stage may be attained beyond which there is no further change.

From the dynamic point of view every plant association may be looked upon as a stage of succession; genetically, it is the contemporaneous representative of a series of associations which are related to one another through development. Of the various associations in a developmental series, only the climax can be regarded as *permanent* in character. All the others are *temporary:* they are destined in the course of succession to be superseded by the climax or else by an association more nearly approximating the climax type.[51]

Succession versus Development.—Not all succession is developmental in character, and, as Tansley ('20) has pointed out, a distinction should be drawn between succession *per se* and development, which is a particular kind of succession. There is nothing developmental, for example, in the succession which is brought about through the activity of fire or erosion. The phenomenon of development is best seen in the succession (of the sort described in the second paragraph above) which results from the colonization by successive plant populations of a particular habitat, "the physical factors of which, apart from reaction by the vegetation, are substantially constant" (Tansley, '20). Tansley, indeed, goes so far as to state that it is *only* in this kind of succession, "in which the reaction of the plant population is the controlling factor," that we can recognize development. Personally I am inclined to interpret the idea of development somewhat more liberally. I would regard the successional changes which characterize the building up of a salt marsh or a flood plain, for example, as developmental in character, notwithstanding the fact that they are not wholly "under organic control."

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[51] In the strict sense, of course, there is no such thing as absolute permanence in vegetation—at least not when account is taken of potential changes in climate and physiography. Relative permanence is understood. The use of the term *association* is restricted by Clements ('16) to climax communities, the corresponding temporary communities being referred to as *associes.* In this procedure he is followed by Tansley. I prefer to give the term association to any community of associational rank, regardless of its developmental relations, since otherwise it is impossible to refer definitely to any such community until its developmental rank is determined. The relative permanence of different associations can be emphasized, when desired, by the use of the qualifying adjectives suggested above. Cooper ('22), among others has adopted this interpretation of the term.

I would describe as *developmental* any succession which is marked by definite progression toward a climax.

Criteria of Classification.—Recognizing, first of all, that every individual association is a member of a particular developmental series, the classification of plant associations from the dynamic point of view has to do fundamentally (1) with the relation of the individual association to the climax of its particular series, and (2) with the recognition and coordination of different types of succession in their relation to cause and trend, origin and climax.

B. Types of Succession in Relation to Cause

Different successional series may be grouped, first of all, with reference to the various agencies by which the succession is brought about—*i.e.,* with reference to the underlying causes of succession. From the causational point of view three types of succession are commonly distinguished, *viz.,* biotic, physiographic (or topographic[52]), and climatic. *Biotic* succession is brought about wholly through the influence of plant and animal agencies. *Physiographic* succession is instituted primarily by changes in physiography—by changes either in topography or in the physical or chemical nature of the substratum. *Climatic* succession is caused by changes in climate.[53] To these three types may be added two others, viz., anthropeic and pyric. *Anthropeic* succession is brought about through the influence of human agencies, *pyric* succession through the influence of fire.

In the series of far-reaching ecological transformations which the vegetation of the earth has undergone during the long course of geologic time climatic change unquestionably has played a leading part, and second only has been the part played by physiographic change. But while the influence of climatic change in instituting marked transformations in vegetation may sometimes be expressed within ecologically brief periods of time—periods which are measured in centuries or even in years—on the whole, in its relation to the more familiar successional phenomena of the present day, it seems to be of relatively subordinate importance. The same may be said of the influence of physiographic change, except for those comparatively localized situations, as along streams and seacoasts, where active erosion or deposition is taking place. The vast majority, at any rate, of the successional changes with which we are immediately concerned are instituted primarily by biotic agencies, secondarily by anthropeic and pyric agencies. In attempting, therefore, to solve the relatively contemporaneous problems of dynamic plant soci-

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[52] The concept of "topographic" succession, originally proposed by Cowles ('01), I have here modified to the extent of including (under the head of *physiographic* succession) successional phenomena which are due to changes in soil as well as those due to changes in topography.

[53] For discussion of these three types of succession see especially Cowles ('01 and '11). The various habitat factors concerned are outlined more fully in section III of the present paper.

ology, changes in climate and physiography need be considered only in cases where these influences exhibit manifest instability.

C. Types of Succession in Relation to Trend

With regard to the direction of its course, succession may be either *progressive* or *retrogressive*. Cowles ('01), who was the first to emphasize this distinction, describes as progressive all succession "away from the hydrophytic or xerophytic and toward the mesophytic"; succession "away from the mesophytic and toward the hydrophytic or xerophytic" is retrogressive. It would seem more strictly accurate to describe progressive succession as succession toward a climax and retrogressive succession as succession away from a climax; for while there is a general tendency for vegetation to become increasingly mesophytic as a result of progressive successional changes, this is by no means an invariable rule. In northern Cape Breton, for example, as a result of progressive succession, forests of balsam fir are superseded on the better soils by deciduous forests, which represent the climax type of the region. So far as relative mesophytism is concerned, there is little to choose between the two, although there is a distinct progression in certain other respects.[54] Again, it is doubtful if the climax stage in a lake-bog series should be considered as being any more mesophytic than certain of the preceding stages, although it certainly is more advanced. Developmental succession is always progressive.

The changes in vegetation which we refer to as succession are typically brought about by gradual degrees. This is especially true of succession which is at the same time developmental and progressive in character. In the case of retrogressive succession the changes may likewise be gradual; in fact, it is only in these gradual changes of vegetation that Tansley ('20) is willing to recognize succession. "If a factor of the environment is gradually and progressively altered," he writes, "so as to effect the gradual replacement of a mature plant population by one of lower type, and the replacing population is actually a phase in the progressive development of the mature type, it is strictly accurate to call the process retrogressive succession." Thus, "the general case of the lowering of ground water level as the result of increasing drainage . . ., or again of the progressive depletion of mineral salts [in the soil] by leaching, would appear to give the conditions for true retrogressive succession."[55] Clements ('16) maintains that there is no such thing as retrogressive succession, and neither Clements nor Tansley is inclined to regard as succession those abrupt regressions in vegetation which are consequent on the modification of the habitat or the destruction of the vegetation by such agencies as erosion, fire, and man. Retrogressive succession of this description might well be differentiated as *cataclysmic*, but in so far as it concerns the

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[54] For discussion of this particular illustration, see Nichols '18, pp. 287–291.

[55] See also Cowles in Bot. Gaz. **68**: 478. 1919.

replacement of one plant association by another, I can see no adequate reason for not recognizing it as one kind of succession.

Considering the various types of succession which have been distinguished in relation to cause, biotic succession is typically progressive.[56] Physiographic succession may be either progressive (as in the building up of flood plains and coastal swamps), retrogressive (in the sense illustrated in the preceding paragraph), or cataclysmic (as in the destruction of forests by erosion or by moving dunes and their consequent replacement by more primitive communities). Climatic succession may be either progressive or retrogressive; it may even be cataclysmic, as in the changes brought about by protracted drought, to say nothing of effects due to hurricanes and tornadoes, severe ice storms, and the like. Pyric succession is invariably retrogressive; most commonly it is cataclysmic. Anthropeic succession likewise is primarily retrogressive and commonly cataclysmic; but man himself may purposely inaugurate secondary successions[57] which are progressive in character. Certain of the changes which are induced by the forester, for example, through his application of ecological principles in silvicultural practice, may be looked upon as being in the nature of progressive anthropeic succession; so also the replacement of prairie grassland by woodland as a result of planting, the changes in vegetation which are effected by irrigation, and, in a very general way at any rate, various of the progressive changes which are instituted in agricultural practice.

D. Types of Succession in Relation to Origin

The character of every successional series of plant associations is determined in very large degree by the nature of the area in which the succession takes place. With reference to their origin, Cooper ('13) has distinguished series of two types, *viz.*, xerarch and hydrarch. A third type is here suggested, *viz.*, mesarch.

Xerarch series are those which, "having their origin in xerophytic habitats, such as rock shores, beaches, and cliffs, become more and more mesophytic [or developmentally advanced] in their successive stages." *Hydrarch* series are "those which, originating in hydrophytic habitats such as lakes and ponds, also progress toward mesophytism," or toward a developmentally more advanced condition. *Mesarch* series are those which originate in mesophytic habitats, such as are afforded by moist, rich soils, and in which the vegetation likewise becomes progressively more and more advanced as a result of development. The advance here may take the form, more especially, of increasing complexity.

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[56] Exceptions to the rule are illustrated by the effect of chestnut blight and similar destructive organic agencies, which may be distinctly retrogressive and even cataclysmic.

[57] The term *secondary* is here applied to successions which are subsequent on the destruction of original vegetation by either man or fire.

E. Types of Succession in Relation to Climax

The nature of the climax which is capable of attainment in any area is controlled in large measure by geographic conditions—by climate, on the one hand; by physiography, on the other. This is true, regardless of the factors by which the succession is instituted. Generally speaking, geographic conditions tend to act as limiting factors to prevent development from progressing beyond a certain stage (or *vice versa*). In a desert region, for example, the attainment of a mesophytic forest climax is prevented by unfavorable climatic conditions; in saline situations along the seacoast it is prevented by unfavorable physiographic conditions. In relation to the geographic conditions of any particular region two types of climax may be distinguished, namely, climatic and physiographic.

A *climatic* (or *regional*) *climax* is one determined by climate. It is an association of the most advanced type that is capable of development under the climatic conditions which characterize a climatic region. Practically speaking, it is a climax of the type which tends to develop on the better soils throughout the region, on well-drained and approximately level or rolling areas, in places where the vegetation is not exposed to the influence of localized climatic or physiographic agencies—*i.e.*, on "ordinary uplands." Throughout most of the eastern United States, for example, mesophytic deciduous forest represents the climatic climax type.

A *physiographic climax*[58] is one determined by physiography. It is an association of the most advanced type that is capable of development in any physiographically uniform area. In a rock ravine, for example, the moist banks, the dry cliffs, and the wet ledges would each be characterized by a different climax because of their physiographic dissimilarity.

The distinction here made between climatic and physiographic climaces is admittedly somewhat arbitrary, but the underlying idea is one of great practical as well as theoretical importance. It is of course obvious that, strictly speaking (and neglecting for the moment the influence of biotic agencies), the nature of the climax in every habitat is determined by the combined influence of both climatic and physiographic conditions. In any region of essential climatic uniformity, however, the effect of climate as a cause for local variations in the nature of the climax can be practically disregarded, for the reason that climate exercises essentially the same influence everywhere. Practically speaking, then, within such a region it is the physiographic conditions which determine differences in climax, and in this sense the terminal member of every developmental series may be regarded as a physiographic climax. When, on the other hand, it comes to the comparison of climaces in regions which are climatically different, it would seem that both climatic and physiographic factors must be taken into consideration; and so they must. The

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[58] In my 1917 paper I have used the term *edaphic climax* in essentially this same sense.

important point here is simply this: that in comparing the climax vegetation of different climatic regions, the thing that concerns us chiefly is the type of climax which most fully expresses the influence of climate as a differentiating factor of the environment. For any particular climatic region this condition is best fulfilled in habitats where localized climatic conditions are absent and where vegetative development is in no way interfered with by unfavorable conditions of soil or topography. Generally speaking, therefore, it seems logical that, for any particular climatic region, the most mesophytic or advanced type of climax which is capable of development on "ordinary uplands," under favorable conditions of soil and topography, should be taken as the climatic criterion. In other words, physiographic climaces of this description represent the climatic climax.[59]

The important part played by biotic factors, especially humus and shade, in compensating the effect of unfavorable physiographic factors, has been emphasized, in particular, by Cowles ('01, '11). In consequence of this influence, during the course of a developmental succession the effect of physiographic factors on the vegetation tends to become less and less pronounced, with the result that while the more primitive associations in a series may be closely restricted by physiographic conditions, those which are more advanced tend to overstep and even to ignore physiographic boundaries. Hence, in general, associations which are developmentally mature tend to resemble one another much more closely than associations which are immature; and *vice versa.* "The general trend of vegetation is from diversity toward uniformity" (Cowles, '11). Notwithstanding this influence of biotic factors, however, it is only in regions of comparatively uniform physiography, or where the influence of physiography is more or less completely offset by that of climate,[60] that it is impossible to distinguish physiographic climaces.[61]

[59] In this connection it should be mentioned that the climatic climax does not necessarily represent either the most mesophytic or the most advanced type of vegetation that is capable of development in a climatic region. In places such as ravines where the regional climate is ameliorated as a result of topographic conditions, or in localized situations where unusual soil conditions compensate the influence of unfavorable climate (as along streams in desert regions), a degree of mesophytism (or advance) may be attained which surpasses that exhibited by the regional climax (the "post-climax" of Clements '16). Neither is the climatic climax necessarily represented by the most widespread type of natural vegetation in a region, although this is commonly the case. On the Atlantic Coastal Plain, for example, the yellow pine forests, which constitute the prevailing type of vegetation over large tracts of country from North Carolina southward, do not represent the type of climax favored by climate on the better soils, but rather a climax . . . due primarily to unfavorable soil conditions.

[60] Extreme humidity in tropical regions may more or less completely offset the influence of physiographic factors; while extreme aridity in some desert regions may accomplish a somewhat similar result.

[61] For further discussion of the influence of physiographic factors on vegetation, see pp. 163–167 of this paper, and also Nichols '17, pp. 313–317.

VIII. Summary and Conclusions

The essential points which it is aimed to emphasize in the present paper are as follows:

It is proposed that the term *plant association* be recognized as applicable both to the abstract vegetation concept and to the concrete individual pieces of vegetation upon which this concept is based. This two-fold usage tends to harmonize the diverse senses in which the term has been applied by different ecologists, and the idea has been indorsed by a large majority of American and Canadian ecologists.

Viewed in the abstract, an association may be described as a vegetation-unit characterized by its essentially constant physiognomy and ecological structure and by its essentially constant floristic composition, at least with regard to dominant species. Viewed in the concrete, it may be described as a piece of vegetation characterized by its essentially homogeneous physiognomy and ecological structure and by its essentially homogeneous floristic composition, at least with regard to dominant species.

The idea of the association as an organic entity is best fulfilled by the association concrete.

The proposed interpretation of the term does not preclude its further application to a series of similar plant communities of associational rank, considered as a concrete aggregate rather than an abstract vegetation unit.

As subordinate communities within the association, societies of two sorts are distinguished: layer societies and group societies.

Taken in its entirety, an association is characterized throughout by essential homogeneity or constancy of habitat, but subordinate variations of habitat within the association make it necessary to distinguish between the general habitat relations of the association as a whole and the specific habitat relations of its constituent elements.

In defining the association, habitat uniformity is not specified as a criterion for the reason that the association, as a vegetation-unit, is naturally delimited by its inherent characteristics of vegetative form and structure.

The nature of any habitat is determined by the combined influence of all the locally effective habitat factors. These latter fall into five categories, *viz.*, climatic (regional climatic factors, local climatic factors, rhythmical changes in climate, progressive changes in climate, etc.), physiographic (topographic factors, edaphic factors, rhythmical changes in physiography, progressive changes in physiography, etc.), biotic (shade, root competition, humus, soil micro-organisms, plant or animal invasion, etc.), anthropeic (factors associated with the influence of human agencies), and pyric (factors associated with the influence of fire).

The ecological classification of plant associations consists in the arrangement into common groups of different associations which are related to one another by environment. These groups represent ecological vegetation-units of a higher order than the association.

There are three distinct points of view from which such a classification may be made. The associations may be grouped (1) with reference to their physiognomy and ecological structure; (2) with reference to their geographical relations; (3) with reference to their successional relations.

From the first point of view all associations which resemble one another in physiognomy and ecological structure, regardless of their floristic composition, may be referred to a common abstract type, which is designated an ecological association-type. Every concrete association may be looked upon as a representative of some specific association-type.

From the second, geographic unit-areas of two sorts are recognized, *viz.*, climatic and physiographic, and correlated with these may be distinguished association-complexes of two sorts, which are designated, respectively, climatic formations and physiographic formations. Every concrete association may be looked upon as a component of some specific climatic formation and also of some specific physiographic formation.

From the third, various successional series of associations are distinguished in relation to origin and cause, trend and climax. Every concrete plant association may be looked upon as a member of some specific successional series.

From the first point of view we recognize the vegetation itself as the ecological product of environment—as an effect by which, if desired, the habitat itself can be indirectly judged. From the second we recognize the influence of climate and physiography in determining the character and distribution of plant associations. From the third we recognize the dynamic and developmental relations of plant associations.

In studying vegetation from either of the first two points of view we see it as a physically existent and concrete reality. Roughly speaking, we take into account only features which might be plotted on a vegetation map. From the third point of view, however, we regard the associations of the present day as being but stages of development: they are the products of past development; they are the starting points for future development.

Each one of these three points of view is logically distinct from the other two; any one of them, in itself, constitutes a rational basis of ecological classification; all of them have actually been used for this purpose by different ecologists. No scheme for the classification of plant communities can be regarded as ecologically complete, however, which fails to take into consideration all three.

IX. The Method in Practice

The General Idea.—The order in which one might logically proceed in applying this three-fold scheme of classification to any practical problem is indicated in the preceding section. It does not follow, however, either that this order should be strictly adhered to or that the three criteria of classification should receive equal emphasis. For one thing, in actual field work we are seldom able to study our material in that orderly sequence which is possible in a laboratory: the exigencies of time and space prevent. The point to be emphasized here is simply this, that in the field these three points of view should be kept clearly in mind; let the order of their application take what form it will. For another thing, the relative emphasis which shall be placed on these different points of view will be determined in part by the bias of the observer, in part by the nature of the facts. This is particularly true when it comes to the process of organizing the data obtained from field work and the actual construction of a comprehensive classification: one or another point of view must be adopted as the primary basis of subdivision. Generally speaking, in attempting to bring out the larger subdivisions of the vegetation of any region in their relation to environment, I am inclined to give precedence to the geographically determined vegetation-units (*i.e.,* the climatic and physiographic formations); but where these are not clearly defined it would seem better to subordinate them to those determined by successional relations (*i.e.,* the successional series), or by physiognomy and ecological structure (*i.e.,* the association-types).

Where an area to be surveyed comprises more than one climatic region, the first step in classification should naturally be to clearly differentiate the climatic formations, since different climatic formations are best considered separately. As the outstanding criterion of the climatic formation, it is the climatic climax association-type, primarily, with reference to which such differentiation is made. When it comes to the study of the vegetation within a particular climatic region, with a view to the detailed classification of the various plant communities which collectively go to make up the climatic formation, a general familiarity with the character of the climate climax and also with the larger features of the vegetation as a whole is a logical prerequisite. Without such familiarity it seems self-evident that lack of perspective may obscure the essential relationships which it is the chief object of classification to make clear.

In practical field studies two general methods of attack are open, which might be characterized, respectively, as (1) working from the top downward and (2) working from the bottom upward. By the first method we start with the larger features of the vegetation and by a process of analysis work out the lesser in their relation to the larger. By the second we start with the lesser features and by a process of synthesis aim to achieve the same result. Of the two, the first is perhaps the better adapted to give one a broad perspective and a proper sense of proportion; it is the method which one would be inclined to follow in making a preliminary survey of any region or a survey designed to bring out only the major features of the vegetation. The second method is one which is naturally employed, in conjunction with the first, in working out the detailed structure and ecological relations of the various plant associations. In either case the ultimate unit with which we work in the field is the association-concrete—the piece of vegetation which we can literally place our hands on.

A Concrete Example.—The manner in which this three-fold scheme of classification may be applied to the vegetation of any particular climatic region can be best illustrated, perhaps, by a concrete example. The outline presented below, in slightly different form, has been successfully used in the classification of the plant associations of northern Cape Breton Island (Nichols, '18).

I. The climatic climax association-type: the climax forest.
II. The physiographic formation-complex of the region.
  A. The primary formations of xerarch and mesarch successional series.
    1. The formations of ordinary well-drained uplands.
      a. The association-types of rock outcrops.[62]
      b. The association-types of talus.
      c. The association-types of glacial till.
      d. The association-types of sand plains.
    2. The formations of well-drained uplands along streams.
      a. The association-types of rock ravines.
      b. The association-types of clay ravines.
      c. The association-types of open valleys.
      d. The association-types of boulder plains.
      e. The association-types of flood plains.
    3. The formations of well-drained uplands along the seacoast.
      a. The association-types of bluffs and headlands.
      b. The association-types of beaches and dunes.
  B. The secondary formations of xerarch and mesarch successional series.
    1. Formations due to the influence of lumbering.
    2. Formations due to the influence of fire.
    3. Formations due to the influence of cultivation.
  C. The primary formations of hydrarch successional series.
    1. The formations of inland lakes and ponds.
      a. The association-types of well-drained lakes.
      b. The association-types of undrained lakes.
    2. The formations of inland lake- and seepage swamps.
      a. The association-types of well-drained swamps.
      b. The association-types of poorly drained swamps.
    3. The formations in and along rivers and streams.
      a. The association-types of ravines.
      b. The association-types of flood-plains.
    4. The formations along the seacoast.
      a. The association-types of salt marshes.
      b. The association-types of brackish marshes.
  D. The secondary formations of the hydrarch successional series.

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[62] Under subdivisions *a, b, c,* etc., the associations are considered, both specifically and in their successional relations.

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OBSERVATIONS ON THE CAUSES OF GREGARIOUS FLOWERING IN PLANTS

WILLIAM SEIFRIZ

[Reprinted from the AMERICAN JOURNAL OF BOTANY, 10: 2, February, 1923]

[Reprinted from the AMERICAN JOURNAL OF BOTANY, X: 93–112, February 1923.]

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OBSERVATIONS ON THE CAUSES OF GREGARIOUS FLOWERING IN PLANTS[1]

WILLIAM SEIFRIZ

(Received for publication May 11, 1922)

One of the most interesting and fundamental of biological problems is that of the extent to which the life processes of an organism are influenced by the external environment. In the past, biologists have been quite content to rest secure in the belief that the most deep-seated characters in organisms are developed in the individual and transmitted from one generation to another little influenced, and certainly not determined, by the external environment of the organism. That so fundamental a character as paired eyes in vertebrates could in any great degree be influenced by a change in external environment was hardly conceivable until Stockard showed that if the eggs of the fish Fundulus are placed in sea water to which a little magnesium chloride has been added they develop into embryos with one medium cyclopean eye.

Equally interesting to the botanist have been the experiments of Garner and Allard (6), who were able by controlling the time of exposure of a plant to light greatly to lower or increase the age at which the plant reaches sexual maturity. Thus, the field aster, which commonly requires four months (May to September) to reach sexual maturity, was made, by decreasing the time of exposure to daylight, to bear flowers within a month after germination (by June 18). Still more remarkable is the fact that these same plants, instead of completing their life cycle by dying after flowering, as they would have done in the field, developed new axillary branches (on being restored to normal light exposure) and flowered a second time in September.

It is thus evident that certain characters of a deep-seated and fundamental nature which heretofore have been regarded as immutable, are relatively unstable and respond readily to changes in the external environment. It is, consequently, not surprising that some biologists hold that all "characters are of the nature of responses to environment" (7, p. 530), and that "every life process must to some degree be dependent upon the external world" (15, p. 285).

While it is difficult to deny the truth of these statements in the face of the remarkable experiments which have been performed, yet one wonders how far such a theory will carry us. We hesitate to admit that the external environment is in any way responsible for the fact that a pine seed develops

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[1] Contribution from the Osborn Botanical Laboratory.

into a pine. We may even go further than this and maintain that the spreading form of the common poplar (*Populus nigra*) and the tall slender form of the Lombardy poplar (*P. nigra* var. *italica*) must, since the latter arose as a mutation of the former and since both forms breed true in the same environment, be due to the special nature of the protoplasm of the two trees and not to environmental factors. Those who hold the extreme view that "all characters are innate, acquired, germinal, somatic, and inheritable in exactly the same sense and degree" (7, p. 596) will find some difficulty in explaining the origin of fluctuations and mutations in certain individuals of a species when other individuals of the same species in the same environment remain true to type.

That external environment plays an important if not an inseparable part in inheritance and development is a fact of far-reaching significance. The problem of the biologist is to determine *to what extent* the heritable disposition of plants is susceptible to influence by the external environment.

In a study of this sort one must guard against concluding that an environmental factor is the *cause* of a vital phenomenon because it has been found to influence the phenomenon. Thus, from Garner and Allard's work we may conclude that length of exposure to light determines the *time* of flowering in certain plants, but we are not justified in regarding this environmental factor as the *cause* of flowering. The act of attaining sexual maturity is innate in all organisms, just as is senility. The *exact point* in the life cycle at which the individual shall become sexually mature is in some plants evidently sensible to external influence; *i.e.*, it is capable of being shoved this way or that by the environment.

The problem of determining the environmental factors which influence the flowering of plants assumes a special interest when considered in reference to those plants which flower only after a period of many years of purely vegetative growth. Particularly interesting does the problem become when applied to those plants in which all the individuals of a species throughout a given region attain sexual maturity simultaneously. The bamboos (many of them) belong to this category.

Drought as a Cause of Gregarious Flowering in Bamboos and Palms

One of the oldest theories of the cause of gregarious flowering in bamboos is that this simultaneous anthesis is occasioned by drought (18, p. 251). This theory is still held by many biologists. Some (8, 16) have advanced another hypothesis, namely, that periodic flowering in bamboos is the result of a depletion of nourishment. Both theories are opposed to that which would attribute this sex phenomenon to a heritable factor in the plant.

The chief criticism to be directed against such theories is that their supporters have failed to look further than the particular group of plants and the special set of environmental factors under observation.

That bamboos have flowered gregariously in India immediately after a drought is not to be doubted. Droughts are of such frequent occurrence in India that it would be surprising if they did not occasionally coincide with the flowering of bamboo forests. It is also possible that severe dry weather may have some *slight* influence on the *exact time* of flowering. When many individuals of a species flower simultaneously immediately after a drought, scientist as well as layman is likely to associate the two phenomena. The occurrence of each phenomenon separately passes unnoticed. But even if our data should warrant the conclusion that the gregarious flowering of a particular species is occasioned by drought in a certain locality, what are we to do with the fact that the same species flowers in another locality where there is no drought? *Bambusa arundinacea*, for example, flowers not only in India, where it is subjected annually to a severe dry season and occasionally to a drought, but also in Buitenzorg, Java, where dry seasons are practically unknown. Then, too, we have the interesting fact that other species of bamboo flower gregariously following an unusually *wet* period, as did, for example, the climbing bamboo, *Chusquea abietifolia*, in Jamaica in 1918 (20). Still other bamboos show no periodicity at all and flower sporadically without any apparent relation to climate. This is true of the Philippine bamboos in general, among which no case of simultaneous flowering of many individuals is known, although these bamboos have been under scientific observation for nineteen years.[2]

So far as I have knowledge, no one has actually investigated the rainfall data of the country where bamboos flower gregariously in order to ascertain, first, whether or not the dry season of the particular year in question was one of sufficient severity to warrant its being regarded as the direct cause of the gregarious flowering of the bamboos; and, second, whether or not, in case a drought did precede the particular flowering period under investigation, other flowering periods of the same species of bamboos in that country (and in other countries) were also preceded by droughts.

The meteorological conditions prevailing in India are so extreme that one must be thoroughly aware of them in order to investigate intelligently a question such as that under consideration. The greater part of India is almost rainless for about seven months of the year. It is not an uncommon occurrence for no rain whatever to fall at certain stations during eight months of the year. The absence of rain during such a normal dry season cannot, of course, in any sense be regarded as a drought. What rain does fall during the dry season (averaging 0.2 to 0.3 of an inch a month) is of little consequence to plant life. Vegetation depends solely on the monsoons, which occur from June to September in Hyderabad and the Central Provinces, for example, and from October to December in Southeast

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[2] Dr. E. D. Merrill, Director of the Philippine Bureau of Science, has kindly given me this and other valued information.

Madras. If the monsoon rains fail, severe consequences follow. This is what happened in 1899 and 1900. There was a phenomenal failure of the rains over a large part of India during the 1899 monsoon (June to September). As a consequence, a disastrous drought prevailed in the early months of 1900. *Both* immediately *before* and some time after this severe drought large bamboo forests flowered in northern India.

In the Indian Forester for 1899 there appears the following note (10, p. 178):

> The flowering of *Bambusa arundinacea* is reported . . . to be general this year in the Angul Division[3] of the Bengal Presidence.

The drought of 1899–1900 above referred to could have had no effect on the life of these bamboo forests, since the bamboos were in flower (in April) before the failure of the monsoon rains (June to September), the disastrous consequences of which could not have been felt by plants until early 1900. In 1898, the year preceding the flowering of the bamboos in the Angul District, the monsoon was normal—at Angul (41.29 inches) slightly below the average (49.34 inches), and at Bissipara (58.49 inches) somewhat above the average (55.07 inches). For the four preceding years (1894–1897) the total annual rainfall in the Angul District was either just at the average or considerably above average—never below. We cannot, therefore, accredit the general flowering of *Bambusa arundinacea* in the Angul District of India in 1899 to a drought.

In the Indian Forester for 1901 (11, p. 126) is reported

> The flowering on a large scale of the ordinary bamboo (*Dendrocalamus strictus*). The area over which the flowering extends is estimated at 1200 square miles, and in this area, although a few clumps here and there have escaped, the phenomenon is universal.

The flowering occurred in the Chanda District of the Central Provinces of India. The rainfall data for 1900 from sixty-seven observation points in the Central Provinces indicate that the monsoon of that year was all that could be desired. For example, the total annual rainfall for forty-five of the sixty-seven stations was, in 1900, above the annual normal (in several instances nearly double the average annual precipitation).

It would hardly seem necessary to go further back than the favorable monsoon of 1900 in our investigation of meteorological conditions and of their bearing on the flowering of the bamboo forests in the Central Provinces of India in 1901. This statement is based on the assumption that the visible effect of a climatic influence which is potent enough to affect the physiological state of plants is likely to become evident within a year after the climatic factor came into existence. To what extent such an assumption is justifiable is an open question. Brandis (1, p. 14) believes "that such stimulating conditions must act upon the plant at least a year before the flowering actually takes place." Yet in the same article he refers to

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[3] The official meteorological designation of the "Division" in which the Angul "District" occurs is the "Chota Nagpur Division" of the Bengal Presidency.

the observations of Kurz in Burma where an unexpectedly large number of bamboos were collected in flower "*during* [italics mine, W. S.] the two dry seasons of 1868 and 1869." Brandis further quotes Kurz as stating "that in the Calcutta Botanic Garden there never had been so many species in flower as in 1874, which was a year of great drought" (10, p. 14). It will be noticed that the abundant flowering of the bamboos in the Calcutta Garden occurred *in* 1874, *i.e.*, during the year of great drought, and that the supposed stimulating conditions did not act upon the plant "at least a year before the flowering" actually took place, as Brandis elsewhere maintains must be true.

To go further back than the favorable monsoon of 1900, *i.e.*, to go back more than a year previous to the flowering of the bamboos in 1901, involves the question whether or not meteorological conditions, occurring more than a year before the appearance of the vital process which they are supposed to initiate, can be taken into consideration. It seems hardly likely that bamboo plants which flowered in early 1901 and whose flowering was preceded by a favorable rainy season in the mid-year of 1900 should have flowered as a result of a drought in early 1900. Not only Kurz, whom Brandis quotes, but others who have ascribed the gregarious flowering of bamboos to drought, have spoken of the flowering as occurring in *times* of drought.

Owing to the severity of the drought of 1899–1900, we cannot altogether ignore the possibility of the unfavorable climatic condition having initiated in the bamboos of northern India a physiological process which did not become externally evident until a year and a half later (in the simultaneous flowering of the bamboo forests in 1901). Once the marked change in the physiological state of the plants was initiated, a subsequent favorable climatic condition (the monsoon of 1900) would be of no effect.

The question cannot be conclusively answered. It is possible that the extreme drought of 1899–1900 of the Central Provinces of India had a telling effect on the bamboos of that region. But that the drought was the *cause* of the simultaneous flowering of the bamboos is not, in the face of other data, a possible deduction. The most that can be said is that when bamboos are near their time of reproduction an unusually dry season may have the effect of accelerating the formation of flower buds.

Whatever our decision regarding the possible effect of the drought of 1899–1900 on the general flowering of *Dendrocalamus strictus* in the Central Provinces of India in 1901, we have the definite fact that *Bambusa arundinacea* flowered gregariously in India in 1899 in the absence of a drought for at least five years previous to the flowering.

Another interesting bit of evidence against the theory that drought is the cause of gregarious flowering in bamboos of long life cycle is to be found in the behavior of an immense bamboo forest region in Burma. The bamboo in this case is of another species (*Bambusa polymorpha*) than the two (*Dendrocalamus arundinacea* and *D. strictus*) we have just been considering.

The sexual cycles of *D. arundinacea* and *D. strictus* are about thirty-two years in length. *Bambusa polymorpha* is known to have a very long life period. I know of no authentic record of two successive flowering dates.

In the Indian Forester for 1903 appears the statement that "the last recorded flowering of the Kyathaung was . . . in 1853" (13, p. 244). The flowering of this bamboo, *Bambusa polymorpha*, was expected to recur shortly after 1883 on the general belief that the life of bamboos is about thirty years. The flowering of *B. polymorpha* in the forests of Burma has not yet occurred. Certain "signs" of an expected flowering have from time to time been seen. These signs refer to the well-known habit which bamboos have of producing no new shoots in the year of flowering.

The bamboo forests of *B. polymorpha* in Burma may be reckoned by hundreds if not by thousands of square miles. In this extensive region of bamboos there have been, since 1883, one or two false alarms of gregarious flowering when a clump or two has blossomed. In 1918 and 1919 an area of several hundred acres in two or three distinct but neighboring blocks in the Tharrawaddy Division flowered gregariously.[4] (The plants of *B. polymorpha* were at this time sixty-five years of age.) This was thought to be the forerunner of a general flowering, since the flowering of odd clumps is considered to be an indication that the flowering of the whole area is imminent. But so far no general flowering has taken place.

During their sixty-eight years of existence the bamboos of these forests have endured many droughts which apparently have had no effect whatsoever on the sexual maturity of the plants. For at least the latter half of their life the bamboos must certainly have been mature enough to respond to an external stimulus, if this stimulus is of such a nature as to exercise any prominent influence on the sexual life of the plants.

We have so far seen, first, that bamboos of long and rhythmic life cycles reach sexual maturity when experiencing only the normal annual dry season of the tropics; and second, that other bamboos of long periodicity have for sixty-eight years failed to attain sexual maturity even though they have experienced many seasons of both normal dry weather and drought. There now remain to be considered those instances in which flowering takes place in the entire absence not only of drought but even of a typical tropical annual dry season.

The most striking instance of this is the behavior of the bamboos at Buitenzorg, Java, where droughts are unknown and dry seasons are few and far between. Before passing on to the Buitenzorg data it will be interesting to consider in more detail the similar case of the climbing bamboo, *Chusquea abietifolia*, already referred to. This bamboo, a slender scandent form, occurs in great abundance throughout the mountains of Jamaica. The high altitude regions of Jamaica receive abundant moisture

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[4] I am indebted to H. R. Blanford, Esq., O. B. E., Government silviculturist at Maymyo, Burma, for this information.

at all times of the year. Some few arid localities occur, but they are small and infrequent above 4000 feet. Relatively dry weather may come ccca-sionally at high altitudes, but never a drought above 5000 feet, the elevation at which Chusquea grows. *Chusquea abietifolia* flowered gregariously in the mountains of Jamaica in 1918 (20). Over an area ten miles in length (investigated by the writer) the trails were, in 1919, lined with dead tangled masses of this climbing bamboo. The two years immediately preceding the flowering of Chusquea were (at Cinchona) unusually moist ones. It is interesting to note that specimens of *Chusquea abietifolia* sent to Kew, England, in 1884, a year prior to the last previous flowering of the plants (in 1885, the life cycle of Chusquea being thirty-three years), flowered simultaneously with the plants in Jamaica.

The behavior of Chusquea in Jamaica stands in further opposition to the belief that lack of moisture may cause flowering in bamboos in that it does not support the statement of Brandis that "there are indications, that in dry stony places . . . bamboos flower earlier and more abundantly" (1, p. 662). It was in just such places that the only green living specimens of *Chusquea abietifolia* were found in the mountains of Jamaica. On an exposed hot and dry spur, sparsely covered by a typically xerophytic vegetation, were growing a quantity of old, green, and thriving specimens of the climbing bamboo. Immediately below this dry spur on which living old plants of Chusquea were growing, there is a moist, cool ravine. Here no adult living specimens were found, but there existed instead the condition prevailing generally throughout the mountains: old plants were dead and growing seedlings were abundant. The old living specimens on the arid spur above were not in fruit. Flowering had not taken place earlier, as Brandis suggests, but, on the contrary, had been delayed. Possibly the climbing bamboo had in this more arid region assumed an altered life cycle.

In comparing the behavior of the bamboos at Buitenzorg, Java, where droughts are unknown and dry seasons are infrequent, with the behavior of the bamboos in India and Ceylon, where dry seasons of several months come annually and droughts occur frequently, it will be well to consider with the bamboos the equally instructive case of the talipot palm, *Corypha umbraculifera*, which, like some bamboos, has a long vegetative period at the expiration of which the palm flowers and dies. Ordinarily *Corypha umbraculifera* does not flower gregariously nor at a fixed age, as do certain bamboos. Consequently, when many specimens of the talipot palm do flower simultaneously, one is likely to suspect the presence of some external factor which has aroused the palms to sexual activity.

The most remarkable case of simultaneous flowering of plants of which I know is that which recently occurred at Peradeniya, Ceylon. In the annual report for 1918 of the Director of the Royal Botanic Gardens at Peradeniya (4) there appear the following three notes:

> Seven out of the sixteen talipot palms (*Corypha umbraculifera*) forming the avenue,

> started by seed sown *in situ* in 1881, commenced to flower in June, and continued in blossom until the end of the year, being at their best in October–November [Pl. XII, fig. 1].
>
> *Bauhinia anguina*, a very large woody climber with peculiar alternately compressed chain-like stems, has this year fruited for the first time on record at Peradeniya. Trimen, in his Flora, states: "Very rare, flowers and fruit not seen."
>
> The flowering of the giant bamboo (*Dendrocalamus giganteus*) is not now the rare event in Ceylon it used to be. Nine clumps produced flowering stems during the early dry months of the year. . . . None of these clumps have died. Eleven clumps of the "male bamboo" (*Dendrocalamus strictus*) also flowered profusely early in the year. Of these, five clumps have died in consequence.

To this is to be added the interesting fact that at the same time that the talipot palms were blossoming in the Gardens there were counted from one observation point elsewhere in Ceylon two hundred talipots in flower. So extraordinary a concurrence of the profuse flowering of four species of plants, all of whose life cycles are very long—in the case of the two bamboos about thirty-two years, of the talipot palm nearly forty years, and of the liane Bauhinia so long that there is no record of it—is indeed an event that forces one to search for some possible environmental factor which might be responsible.

The annual dry season of 1918 was in Ceylon longer than usual, sufficiently long to be locally termed a drought. The remarkable flowering of so many talipot palms throughout Ceylon and the simultaneous flowering of three other species of plants of long sexual periodicity was attributed to this drought.

Three objections can be raised against such a deduction. First, the drought of 1918 was a relatively mild one. The total precipitation for the four months (January to April) of the dry season was, to be sure, below the average for this time of year (12.9 inches in 1918 as compared with a normal of 17.05 inches for these four months, all averages being based on twenty years' records from 1901 to 1920); yet the difference is not very great. Furthermore, if we review the records of the years immediately preceding, we see that the dry season of the second year before the flowering of the talipots and bamboos in the Gardens was also below the average; not quite so low for the four months of the dry season as in 1918, but much lower for January, when but 1.0 inch of rain fell (in 1916) as compared with 5.23 inches in 1918. And in February, 1916, there was but 0.03 inch of precipitation. One would expect these two very dry months of 1916 to have a more telling effect on plant life than the dry season of 1918. If we go further back we find that there was a drought in 1903, and again in 1905, of much greater severity than that of 1918, especially the latter one (1905) when the total rainfall for the four months January to April was the lowest on record for twenty years (1901 to 1920), namely, 4.9 inches or nearly one third that of 1918. In 1911 there occurred at Peradeniya a drought which, because of its duration, was more severe than any so far mentioned. In this year there fell during the *five* months of January to May but 12.78

inches of rain as compared with a normal average of 21.95 inches for this period. Especially trying must this drought have been on plant growth in view of the fact that the precipitation in April, which usually ends the normal dry season, was less than half the average, while in May there fell but 0.75 inch of rain as compared with a normal precipitation for this month of nearly five inches (4.90). In 1911 the talipot palms were but seven years younger than in 1918, *i.e.*, they were thirty years old, not too young to respond sexually to an external stimulus of some force.

Through all these droughts the six talipots, with others in the Peradeniya Gardens and hundreds throughout Ceylon, the twenty clumps of bamboo, and the liane Bauhinia, grew on without flowering. It is therefore hardly likely that the relatively mild drought of 1918 had any influence on the flowering of these plants.

The second objection to be raised against the conclusion that drought caused the flowering of the plants in the Peradeniya Gardens is that nine out of the sixteen talipot palms did *not* flower, and these nine were of the same age and had been growing under the same conditions as the seven which did flower. Obviously, if flowering was the direct result of drought or of any other climatic factor, the seven palms which were affected must have been in such a physiological state as to be susceptible to the influence while the other nine palms were not in such a state. That is, if drought is a factor it is a secondary one, the physiological condition of the plant being the primary determining factor.

If we conclude that the ultimate cause of the time of attaining sexual maturity lies in the hereditary disposition of the plant, the interesting question arises, Why did seven of the talipots flower and nine not, since all in the avenue were of the same age? We can only attribute this difference in behavior to individual differences in the germ plasm, concerning the causes of which we know nothing. The age at which *Corypha umbraculifera* reaches sexual maturity is not the same in all individuals.

The final and most convincing evidence against the hypothesis that drought is the *direct* cause of flowering, or even a factor of any great significance in the flowering of certain palms and bamboos, is the behavior of another talipot at Peradeniya and of a talipot and the bamboos at Buitenzorg. The talipot in question at Peradeniya is one which flowered some years ago, in 1903 (fig. 2). For four years (1899–1902) previous to the flowering of this palm at Peradeniya the average annual rainfall was, in each of these four years, above the normal average. In 1902, the year immediately preceding the flowering, the total annual rainfall was approximately one third above the normal average. It is quite evident that the flowering of this talipot can in no way be attributed to drought.

When the many talipots in Ceylon were blossoming in 1918, the only old specimen of this palm in the gardens at Buitenzorg was also in flower (fig. 3). At Buitenzorg there is no such thing as drought. The writer was there during the so-called dry season and rain fell in torrents nearly every afternoon. While the dry season characteristic of Java as a whole is sometimes more or less evident at Buitenzorg, it never assumes the proportions of a drought. The avenue of talipot palms at Peradeniya and others on the island of Ceylon which flowered in 1918 had been subjected to a prolonged dry season immediately preceding the time of flowering and to several severe droughts during their thirty-eight years of existence. The Corypha at Buitenzorg, on the other hand, had been drenched in rain nearly every day of its life; yet on both islands the palms flowered in the same year.

It would be interesting to know if the flowering of the Buitenzorg talipot commenced in the same month, June, 1918, as did that of the Ceylon palms. One would be inclined in such a case to suspect the presence of some meteorological influence of wide distribution, if one is willing to place any faith in an external stimulus as an influencing factor of even secondary importance. That the palms in Ceylon and at Buitenzorg did flower at very nearly the same time of year is evident from the Peradeniya data and from my observations in Java. (Unfortunately no records are kept of the date of flowering of plants in the Buitenzorg Gardens.) The palms at Peradeniya flowered in June, 1918, fruited during the latter part of 1919 and early in 1920, and died in 1921. The Corypha at Buitenzorg had just dropped its fruit when I first saw it in August, 1920 (fig. 3).

What is true of the talipot palms at Peradeniya and at Buitenzorg is also true of the bamboos at the two gardens. At the time of my stay in Buitenzorg, seven species, out of a total of twenty-four in the Gardens, were in flower. One of these species was *Dendrocalamus giganteus*, which was in heavy flower. The species is the same as that of one of the bamboos which flowered at Peradeniya in 1918. This *D. giganteus* and the six other flowering species of bamboo at Buitenzorg had not been subjected to a drought nor even to a characteristic tropical dry season.

We are, it seems to me, forced to conclude that the ultimate cause of gregarious flowering in bamboos of long life cycle, in particular *Chusquea abietifolia*, *Bambusa arundinacea*, *B. polymorpha*, *Dendrocalamus giganteus*, and *D. strictus*, and in the talipot palm, *Corypha umbraculifera*, is not drought. If drought is at all an influencing factor, then its effect must be relatively slight. While the simultaneous attaining of sexual maturity of three widely differing genera of plants, all of whose life periods are of great length, is an event of such unusual occurrence that one is inclined to wonder if there might not be an external stimulus which is responsible, yet if some such environmental cause does exist we are totally ignorant of what it may be.

The Rhythm in the Sexual Cycle of Bamboos

Evidence of a different kind, which stands in opposition to the assumption that the attaining of sexual maturity of bamboos of long life cycle is greatly influenced by environmental factors, are the observations made in India which have twice established the cycle of *Bambusa arundinacea* to be exactly thirty-two years. This bamboo flowered in Cisgangetic India (the west coast) in 1804, 1836, and 1868 (18, p. 251). It is of interest to note here that the life cycle of *Chusquea abietifolia*, quite a different type of bamboo, is also about thirty-two years (recorded as thirty-three years) (20).

Less definite, and tending more strongly to support the supposition that the *exact time* of flowering may possibly be somewhat advanced or delayed by external factors, are the interesting data of Kawamura who states that the flowering of *Phyllostachys puberula* has been recorded in old manuscripts of China and Japan as occurring in the following years: 292, 813, 931, 1114, 1247, 1666, 1786, 1848, and 1908 (14). It will be noted that most of the intervals between these dates are either about sixty or multiples of sixty years.

One can, of course, fall back upon the assumption that climatic cycles of rhythmic periodicity also occur and that these determine the regularity of the sexual functioning of bamboos. While certain meteorological phenomena take place rhythmically, *e.g.*, the annual seasonal cycle, it is as yet by no means well established that climatic changes of many years' duration are periodic, and there is little evidence that droughts occur rhythmically.

The evidence so far presented is overwhelmingly against the belief that drought is either the cause of gregarious flowering or that it has any marked influence on reproduction in bamboos. That climate may possibly exert some slight effect on flowering is not, however, to be emphatically denied. While there is little and only indirect evidence in support of this possibility, it is quite conceivable that as a plant of long sexual cycle nears its time of reproduction, unfavorable conditions may hasten the sexual process somewhat. Such a supposition would assist in explaining so remarkable a concurrence of simultaneous flowering as occurred in the Peradeniya Gardens in 1918, though here we must presuppose some climatic factor other than drought.

Depletion of nourishment and injury are two other factors external to the plant which have been advanced as causes of flowering in bamboos. One of these, injury, cannot be regarded as a natural cause of flowering. It has, therefore, no direct bearing on our problem, but it is of interest, and we shall consider it.

Depletion of Nourishment as a Cause of Flowering in Bamboos

The Japanese worker Hori (8) is of the opinion that flowering in bamboos is a "physiological disease." This opinion is in contradiction to that of his fellow countryman Kawamura, who attributes the cause of flowering to the hereditary disposition of bamboos.[5] (The observations of Kawamura

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[5] I am indebted to Professor Manabu Miyoshi for calling my attention to work done in Japan on the flowering of bamboos.

will be considered later.) Hori regards flowering in bamboos as a result of an increase in sugar content of the sap due to the inability of the plant to attain the necessary salts for nourishment owing to the dryness of the soil. While Dr. Hori's interesting observations (of which he has kindly given me a *résumé*) tend to support his theory, they cannot be regarded as generally applicable, since, as we have seen, bamboos flower even though profusely watered, and also fail to flower though subjected to repeated seasons of drought.

Macmillan (16) is also of the opinion that a depletion of nourishment is the cause of flowering in some bamboos. He states (p. 125):

> It would thus seem as if the exhaustion of nutriment rather than an infectious influence were responsible for the more or less simultaneous flowering of the Giant Bamboo. The vigorous growth of the plant is such that it cannot go on growing and extending indefinitely. The enormous demands it makes on the soil can be realized by any one who has seen the "ruins" of an old clump, the huge crevices and upheavals formed by the elevated stumps as if the result of an earthquake.

Macmillan's description of the elevated base of an old bamboo clump is very graphic. But on such a mound of stumps measuring fully eight feet in diameter and three feet in height I have seen healthy culms growing as luxuriantly as those of any bamboo clump in the Buitenzorg Gardens.

Macmillan reports the continuation of the vegetative growth of two clumps of *Dendrocalamus giganteus* as a result of increased nourishment. It seems that two of the flowering clumps at Peradeniya, having regained a more vigorous condition, "gave up blossoming entirely, presumably because their circumference had struck richer soil" (16, p. 125).

This instance at Peradeniya is especially interesting because the bamboo in question happens to be of the same species as a young plant recently growing in the Buitenzorg Gardens, which was transplanted from an old clump and thus given an opportunity to regain a more vigorous condition by striking new soil. But it refused the opportunity and soon followed in the path of the parent plant.

There had been growing for many years in the Buitenzorg Gardens a magnificent clump of *Dendrocalamus giganteus* remembered for its size and beauty by all the older workers of the's Lands Plantentuin. In 1918 this entire clump of bamboos flowered and died. Not wishing to lose the last specimen of so fine a bamboo (seeds are not produced), the director of the gardens had a few culms, which were still in healthy condition, removed from the parent clump as soon as the latter commenced to flower. It was hoped that these transplanted culms would continue their vegetative growth without flowering. Such was not the case, however. One of the transplanted clumps soon flowered and died. The second clump lived scarcely more than a year after transplanting, when it too flowered and died. I saw this small plant when the long pendent blooms were still hanging to the then nearly dead culms (fig. 4). New and richer soil did not cause this

Dendrocalamus giganteus to give up flowering and continue its purely vegetative growth. Similar observations must have been made by Brandis, since he writes that "offsets taken from a clump some time before it flowers come into flower at the same time as the parent clump" (1, p. 662).

The hypothesis of depletion of nourishment as the cause of flowering in bamboos could never be applied to those bamboos which flower gregariously. It is quite untenable that each individual of the multitude of plants in a forest of *Dendrocalamus strictus*, one thousand square miles in area in India, or of *Chusquea abietifolia* extending over a region ten miles in length in the mountains of Jamaica, should simultaneously exhaust the supply of food in the soil where they are growing.

Injury as a Cause of the Flowering of Bamboos

Several interesting cases have been reported which support the theory that injury may cause anthesis in bamboos. While injury has no bearing on our problem of the natural cause of gregarious flowering in plants, yet it is worthy of consideration, since it is a probable stimulus which apparently arouses some bamboos to sexual activity.

Gamble states that single clumps of *Bambusa Tulda*, "if badly treated by over cutting or partly uprooted, will afterwards produce flowers without any general flowering" (5, p. 31).

Another instance of the flowering of bamboos being caused by injury is reported by Merrill from the Philippines. In an extensive bamboo forest of Schizostychium one single culm was seen in flower. This culm had been cut by a bolo (machete). The culm was about two thirds severed and in full flower.

Knowledge of these two instances reported from India and the Philippines caused me immediately to suspect that two injured clumps of *Bambusa arundinacea* which I noticed in flower in the Buitenzorg Gardens had also flowered because of the injury received. In each clump several culms were in profuse flower, and these culms were broken off about midway of their length, while all those culms which were not in flower were healthy, uninjured shoots. It seemed possible, therefore, that the broken culms had flowered as a consequence of injury. On second thought it was evident that there was no way of determining without previous data whether the culms had flowered as a result of injury or whether they had broken as a result of flowering. The culms of *Bambusa arundinacea* die after flowering. A dead culm is much less resistant than is a live one to strain from wind, which may be very great on a culm forty to sixty feet in height. In order to ascertain which event, the flowering or the breaking, had preceded the other, I had several culms cut in a large and healthy clump of *Bambusa arundinacea*. These culms when observed one year after cutting had not flowered. The injured culms above mentioned had in all probability broken as a result of flowering and dying and consequent weakening of the culms.

My experiment in cutting these culms was merely to test the effect of injury on this particular species. I subsequently obtained data from India far more convincing. The Chief Conservator of Forests of the Madras Presidency, India, has kindly informed me that in the bamboo-forest areas, many of which are twenty square miles and more in extent, with *Dendrocalamus strictus* and *Bambusa arundinacea* as the predominating growth, the bamboo culms are worked on a rotation of three to four years.

> The periodical cutting over and clearing of the individual clumps has had no known effect on the periodicity of flowering.

As for other species of bamboo, there is evidence galore showing how little injury affects the continued vegetational growth of the plants. The most common method of raising bamboos is by cuttings, and so far as I am aware all species lend themselves satisfactorily to this method. The little slender bamboo *Bambusa nana* is commonly used as a hedge plant and is therefore subjected to frequent cutting without any apparent effect on flowering.

Another form of injury which is said to produce anthesis in bamboos is burning. From the Philippines comes the report that, in a clump of Dendrocalamus (species not given) which had been severely injured by fire, the few uninjured or but slightly injured culms had produced flowers. The case was of especial interest because of an observation made by the writer in Jamaica. Fully ninety-eight percent of the plants of *Chusquea abietifolia* seen in the mountains of Jamaica had flowered and died in 1919. Two small patches, however, were found which contained green, healthy plants, and one of these patches had recently been burnt over. The charred stubble was still evident. The parent plants had been burnt to the ground before their life cycle was complete, and the living rootstocks had sent up new shoots which were continuing the growth of the plants and thus carrying on the vegetative portion of the life cycle beyond the normal limit. Burning here not only did not cause flowering, but had, on the contrary, apparently prevented it.

The most convincing example of bamboos flowering as a result of injury that I know of is the report of Branthwaite. He tells of the flowering of three clumps of *Dendrocalamus strictus*. The flowers were borne on short stems which had their origin just below the surface of the ground from the base of culms which had been cut for a clearing on which a hut was built (2, p. 233).

While the sum total of evidence is decidedly against the fact that flowering of bamboos can be induced by injury, the reports of Branthwaite, Merrill, and Gamble suggest that injury may at least sometimes in certain species of bamboos produce anthesis.

THE GREGARIOUS FLOWERING OF THE ORCHID *Dendrobium crumenatum*

Gregarious flowering is characteristic not only of bamboos (and to a limited extent of the talipot palm), but also of the orchid *Dendrobium crumenatum.*

Wherever a number of individuals of the orchid *Dendrobium crumenatum* occur within the same general locality, the plants flower simultaneously. The blossoms of every plant burst forth on the morning and wither in the evening of the same day.

Among the specimens of *Dendrobium crumenatum* in the Buitenzorg Gardens in Java there are plants collected from nearly all parts of the Dutch East Indies, from Riouw (near Singapore), from Sumatra, Java, Borneo, Celebes, and Ambon (a small island at the eastern end of the archipelago). These plants, after being brought to Buitenzorg, *all* flowered on the same day, if they flowered at all. Yet in their native habitat the flowering periods of the plants do not at all coincide. Thus, orchids growing in the virgin mountain forests flower on different days from those in the lowlands. Plants growing at two stations but three kilometers apart may differ in their times of flowering by one or two days. But wherever their original home and whatever the date of flowering there, the plants, when assembled in one locality, flower simultaneously with each other and with the plants which have grown in that locality from youth. There is no other explanation here but that some external factor determines the *exact* time of flowering. The interesting question arises, What is the controlling external factor?

Burkhill, from data obtained in the Straits Settlements, comes to the conclusion that "climatic conditions some eight days in advance of the flowering are a controlling factor" in the gregarious flowering of *Dendrobium crumenatum* (3, p. 405).

The writer has recently (21) published data from Buitenzorg which support the conclusion of Burkhill. If the flowering dates of the orchid are compared, in a table, with the daily precipitation data preceding all the flowering dates, it will be seen that in the majority of instances the rainfall on the eighth day preceding each day of gregarious flowering is unusually heavy. Especially evident does this become when the totals of the precipitation figures for the respective series of days are compared. The total rainfall occurring on the eighth day previous to all the flowering dates is five ninths greater than that of the next highest. The data strongly support the possibility that heavy rainfall eight days in advance of flowering is the cause of simultaneous flowering of the plants. But several striking exceptions occur which force one to conclude that the stimulating factor which arouses the resting flower buds to further activity is not rainfall but some other as yet unknown factor (possibly temperature) commonly associated with heavy rainfall.

At first thought, the gregarious flowering of *Dendrobium crumenatum* is conclusive evidence that simultaneity of flowering is at least in some plants determined by an external environmental factor. Two striking differences between the gregarious flowering of *Dendrobium crumenatum* and that of bamboos tend further to support this belief. In the bamboos flowering is rhythmic. In the orchid the periods between flowering dates vary from a few days to several months. There is no rhythmic periodicity here.

The second striking difference between the gregarious flowering of orchids and that of bamboos is that in the latter case all the individuals of a bamboo forest are of the same age, while among an assemblage of orchids the individuals may be of quite different ages. Without further consideration one would be inclined to regard some external stimulus as the cause of the irregular gregarious flowering in the pigeon orchid.

The writer has shown, in the article referred to (21), that *simultaneity* of flowering in *Dendrobium crumenatum* rests not upon a climatic but upon a heritable factor, namely, the innate disposition of the plants to develop all their flower buds to the same degree of advancement, at which point growth ceases.[6] The climatic factor arouses the buds—which are all of the same age and which, therefore, all require the same length of time (eight days) to complete development—to further activity, and thus determines merely the *exact time* of flowering and not the simultaneity of it.

Conclusion

As biological science progresses, many vital phenomena, which in the past have been regarded as resident wholly within the organism and in no way determined by the external environment, are one by one shown to be in many instances materially influenced, and in some instances directly determined, by environmental factors. While it must be admitted that one cannot altogether dissociate an organism from its environment, yet this hardly precludes one from regarding some vital phenomena as strictly innate. The origin of variations and mutations forces one, it seems to me, to admit the existence of at least a certain amount of independence of function of the germ plasm from its environment.

The opposition of some biologists to the belief in a hereditary disposition of plants which is responsible for periodicity (in growth, reproduction, etc.) is apparently based on a fear of giving support to any hypothesis which would attribute to a plant self-regulation and would tend to dissociate the plant from its environment. But there is nothing mysterious in periodicity any more than in the radio-activity of certain metals or in the chemical reaction which takes place in a test tube regardless of the surrounding conditions. The causes are merely internal instead of external.

Of the many vital phenomena which are rhythmic in plants—leaf production, leaf fall, cambium activity, reproduction, the synthesis and

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[6] For a complete discussion of the possible mechanism involved see the article referred to (21).

solution of starch, etc.—some are undoubtedly susceptible to environmental factors. Furthermore, the same phenomenon varies in different plants in the readiness with which it can be influenced by surrounding conditions. Thus, the winter's rest in some plants is easily altered, in others it can not by any known artificial means be broken. Klebs first clearly showed experimentally that periodicity in plants can be disturbed. In this lies his contribution to biology. But when Klebs would have us believe that *all* the activities of plants are to some extent determined by the outer world, we question his right to do this in the face of his own experiments since he found certain plants which could not be aroused from their winter's rest (15).

But even in those cases in which the normal periodicity can be disturbed, the question arises whether or not the mere ability to alter the normal rhythm of growth by changing the external environment is an indication that this periodicity is actually the direct result of an environmental rather than of a germinal factor. There are some striking instances in which the normal alternation of growth and rest is upset but the plant suffers in consequence. Disturbing the usual growth rhythm results in weakening the plant's vitality. An excellent illustration of this exists at Tjibodas, Java, where there is a small apple tree growing in the acclimatization garden in the mountains. This temperate-zone tree has been growing in the tropics for some twelve years or more, in a climate which has no pronounced seasonal change. Its normal periodicity of growth and rest has been disturbed but *not done away with.* The tree is undersized (four feet high) and has never borne fruit. It stands there an unhappy specimen, with, when I saw it, one branch in full foliage, another without any leaves at all, and still another with well-developed buds. It seems to be having a sad time trying to exist in a seasonless climate with an inherent periodicity of growth and rest manifesting itself at different times of the year on different branches. The periodicity is there. The seasonal cycle of temperate regions would have determined *when* the rest and growth periods should occur. In a tropical climate this seasonal guidance is lacking and the normal rhythm of growth and rest is disarranged, but the inherent periodicity is still evident.

The fact that the winter's rest in plants can in many cases be disturbed has led other workers than Klebs to come to rather far-reaching conclusions. Thus Howard, as a result of some very extensive work on the treatment of dormant woody plants for forcing them into growth, concludes that "all of these forms of rest are caused by unfavorable external conditions" (9, p. 5).

Just what the unfavorable conditions are which cause all kapok trees (*Ceiba pentendra*) *simultaneously* to become completely defoliated each year at Buitenzorg, where there is no pronounced seasonal change, it is difficult to see. Even more striking is the case of Ceiba (*C. occidentalis* ?, the silk-cotton tree) in Jamaica which annually loses all its leaves, but not simultaneously with other silk-cotton trees. Why do the "unfavorable external conditions" which cause one silk-cotton tree in Jamaica to rest from leaf production not likewise cause another silk-cotton tree standing near by to rest also?

Howard's further deduction, that "a plant readily adapts itself to the new demands and the rest becomes a habit," is perhaps applicable to some plants, but not to all. The tropical palm has not yet adapted itself to a temperate climate and acquired the habit of resting in the winter; nor has the temperate-zone apple tree at Tjibodas very successfully adapted itself to a tropical climate after twelve years or more of existence there, even though the climate at Tjibodas is not unlike a temperate summer as regards moisture, temperature, and light.

One fundamental objection to the belief in a heritable periodicity in bamboos has been raised by several writers. It is pointed out as a remarkable fact that "not only mature clumps but quite slender seedlings" (11, p. 126), "even the buds which have just appeared out of the ground" all blossom at the same time (19, p. 6). This brings us to the consideration of a rather theoretical question, What constitutes age?

That the parent culms in a large bamboo forest of Dendrocalamus or Chusquea are all of the same age is self-evident. They all sprang from seed sown at the same time, *i.e.*, at the time of the simultaneous death of the individuals of the previous forest. As for the "young" shoots, their age is, from one viewpoint, the same as that of their parents since they arose from the same rootstock. Meristematic cells, in the cambium ring, for example, remain perpetually young, though in years they are older than most of the cells which make up the tree. Old cells become young when lateral shoots are formed from old wood in trees, or when in lower animals limbs are regenerated. If we grant that the morphology and function of cells is dependent on their location in the plant, that is, that there is no such thing as specificity of cells, then all the cells of a bamboo clump, in "young" shoots as well as in "old" culms, are potentially the same; therefore, all are alike affected by age. Consequently, the determiner present in the germ plasm of the "old" culms which causes them to reach sexual maturity at a definite time is likewise present in the "young" culms which arise from a common rootstock.

How this innate sexual periodicity of some bamboos came into existence it is impossible to say. Either it must have been established in the past as an acquired habit, or it must be purely the expression of the original physical and chemical make-up of the germ plasm. The nicety with which the life cycle of annuals and the growth rhythm of perennials fit in with the seasonal changes of temperate regions leads one to believe that these periodic vital phenomena have been induced through the ages by climatic conditions, with the result that the periodicity has become innate, the habit being more firmly established in some plants than in others. The same may be true of bamboos of long life cycle, although in this case the climatic factor is apparently no longer active.

The belief in a germinal factor as the cause of gregarious flowering in bamboos does not imply that this heritable determiner is past being influenced by the external environment. The finding of green specimens of *Chusquea abietifolia* in the mountains of Jamaica when fully ninety-eight percent of the total number of plants were dead suggests that the usual periodicity of this bamboo has in some individuals become altered. As was pointed out in the introduction of this article, it is the task of the biologist to ascertain to what extent this or that character is susceptible to external influence, *i.e.*, to ascertain the degree of fixity of the innate factor. If it is found that a vital process cannot be altered, then we must admit either that it is too firmly established in the germ plasm to be disturbed, or else that we have not found the requisite environmental factor. This latter assumption is made by Klebs.

It is impossible to deny the assumption of Klebs that where we are unable to find the controlling environmental factors we have simply failed to search far enough; yet, until the exact combination of external stimuli is found, the theory that gregarious flowering is determined by a germinal factor stands without disproof.[7]

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[7] After this article was written there appeared an account by Wieland (Amer. Jour. Bot. 8: 218-230. 1921) of monocarpy in the cycadeoids. There is evidence that at least two species of fossil cycads flowered but once in a lifetime. Four other species show a tendency toward monocarpy. The most convincing record is that of a specimen of *Cycadeoidea Dartoni*, the armor of which is packed with hundreds of mature cones. Ample sections of this specimen show no trace of a succeeding foliar crown; although in the very different species, *C. ingens*, a fine crown of young fronds surmounts a scattered growth of flower buds. It is, therefore, reasonably evident that *Cycadeoidea Dartoni* was monocarpic.

It is most interesting to have so authentic a record of monocarpy among the gymnosperms of past geologic ages.

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EXPLANATION OF PLATE XII

FIG. 1. The avenue of talipot palms, *Corypha umbraculifera*, in the Peradeniya Gardens, Ceylon, in December, 1920. Seven of the sixteen palms forming the avenue flowered in June, 1918. One of the palms which had flowered stands in the front on the right side of the picture. The fruit has fallen, leaving only the bare stalks of the inflorescence.

FIG. 2. Another Corypha in the Peradeniya Gardens which flowered some years before those shown in figure 1, and which, unlike those palms, received for at least four years previous to the time of flowering an annual rainfall above the average normal. This picture gives some idea of the luxuriance of the inflorescence. (The photograph is published through the courtesy of Plâté, Ltd., Ceylon.)

FIG. 3. A telephotograph of the crown of a *Corypha umbraculifera*, after fruiting, in the Buitenzorg Gardens. This talipot palm had never experienced a drought; indeed, it was drenched in rain nearly every afternoon of its life, while those palms shown in figures 1 and 2 were annually subjected to a dry season which frequently assumed the proportions of a drought. Some few of the leaves of the former crown of foliage are still to be seen clinging to the trunk. The palm is dead, or nearly so.

FIG. 4. A small clump of *Dendrocalamus giganteus* in full flower in the Buitenzorg Gardens. Long pendent inflorescences are abundant, while but few leaves remain on the now nearly dead culms. These bamboo shoots were taken from an old clump of *D. giganteus* which was beginning to flower. The "young" transplanted culms flowered soon after the parent plant.

SEIFRIZ: CAUSES OF GREGARIOUS FLOWERING

58—7

Proceedings of the American Academy of Arts and Sciences.

Vol. 58. No. 7.—March, 1923.

CONTRIBUTION FROM THE OSBORN BOTANICAL LABORATORY.

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By Alexander W. Evans.

(Continued from page 3 of cover.)

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THE CHILEAN SPECIES OF METZGERIA.

Alexander W. Evans.

Received November 10, 1922. Presented March 14, 1923.

Species of *Metzgeria* form a conspicuous part of the hepatic flora of Chile and the neighboring antarctic regions of South America. The first member of the genus to be reported definitely from this general area was the northern *M. furcata* (L.) Dumort., which was listed by Hooker and Taylor in 1844 (**8**, p. 480) under the name *Jungermannia furcata* L. Their report was based on specimens collected by Hooker during the voyage of the "Erebus" and "Terror," the locality being given as St. Martin's Cove, "Cape Horn." Three years later (**27**, p. 445) they gave somewhat fuller details, citing the species from Hermite Island, Cape Horn, and adding that it occurred there not only in the typical form but also as a var. *pubescens*, which they considered the same as the northern *Jungermannia pubescens* Schrank, usually known even at that early date as *M. pubescens* (Schrank) Raddi. In fact Montagne (**13**, p. 214) had already reported *M. pubescens* from the Straits of Magellan, on the basis of specimens collected by Jacquinot. The Synopsis Hepaticarum (**6**, pp. 504, 505), in 1846, accredited *M. furcata* to Cape Horn on the authority of Hooker and Taylor and *M. pubescens* to the Straits of Magellan on the authority of Montagne, but added nothing to the statements of these earlier writers. Four years later Montagne (**14**, p. 297) designated *M. furcata* as a widely distributed species in Chile, without giving definite localities, basing his statement on collections made by Gay.

In 1877 Lindberg published his Monographia Metzgeriae (**10**), in which he made a systematic use of anatomical features in characterizing the species and thus placed the study of the genus on a more scientific basis. Although the authors of the Synopsis recognized nine species in their treatment of *Metzgeria*, five of these really belong to the genus *Riccardia*, thus leaving a residue of only four species. Lindberg increased the number to eleven. Of the forms occurring in the Chilean region he was able to study some of the material collected by Hooker and by Jacquinot. He showed that Hooker's specimens of "*J. furcata* var. *pubescens*" and Jacquinot's specimens of "*Metzgeria pubescens*"

APR 11 1924

were very distinct from the true *M. pubescens* of the Northern Hemisphere and that they represented an undescribed species. To this he gave the name *M. frontipilis.* He showed further that some of Hooker's specimens of "*J. furcata*" were distinct from the northern *M. furcata* and referred them to his new *M. hamata,* a species having a wide distribution in tropical and temperate regions. He made no definite allusion to Hooker's other specimens of "*J. furcata*" or to Gay's specimens of "*M. furcata*" but stated explicitly that he had seen no material of the true *M. furcata* from the American continent.

In 1885 Massalongo (**11**) issued his report on the Hepaticae collected by Spegazzini in the Fuegian region and recorded new localities for both *M. frontipilis* and *M. hamata.* He likewise restored *M. furcata* to a place in the flora, on the basis of sterile material from Basket Island, and described a new variety of this species from Staten Island under the name *β. decipiens.* This variety was said to be intermediate between the true *M. furcata* and *M. hamata,* and it was suggested that it might represent an undescribed species. In 1889 Bescherelle and Massalongo (**2**, pp. 246, 247) listed *M. frontipilis, M. furcata* var. *decipiens,* and *M. hamata* from numerous additional localities in Tierra del Fuego, the Straits of Magellan and southern Patagonia, basing their records on material collected by Savatier, Hariot, and other members of the French Scientific Expedition to Cape Horn. In the following year Schiffner (**16**), in his account of the Hepaticae collected by Naumann of the "Gazelle" Expedition, raised the var. *decipiens* to specific rank, under the name *M. decipiens* (Massal.) Schiffn. & Gottsche, and proposed *M. magellanica* Schiffn. & Gottsche as a new species. Both of these were found at Tuesday Bay in the Straits of Magellan. In addition he reported *M. frontipilis* and "*M. linearis* (Sw.) Lindb." from the same locality and also from Punta Arenas. The "*M. linearis,*" however, is not the same as the West Indian *M. linearis* (Sw.) Aust. but is merely a synonym of *M. hamata,* as Lindberg had already shown in his Monographia.

No additional species were reported from the region until 1899, when Stephani published a monograph of *Metzgeria* in the first volume of his Species Hepaticarum (**19**). In this important contribution he recognized *M. frontipilis, M. furcata,* and *M. hamata* as members of the flora but reduced *M. magellanica* to synonymy under *M. nitida* Mitt. (**12**, p. 243), a species based on Australian and New Zealand material, and expressed the opinion that *M. decipiens* probably represented another synonym of the same species. A third species that he included among the synonyms of *M. nitida* was his own *M. australis*

(**18**, p. 266), which had been described from specimens collected on Lord Howe's Island and in Australia. Two other well-known species that he accredited to the Chilean flora were the northern *M. conjugata* and *M. Liebmanniana* Lindenb. & Gottsche, a species originally known from Mexico. His record for *M. Liebmanniana* was based on a specimen collected at Valdivia by Hahn, and his record for *M. nitida* on Naumann's material from the Straits of Magellan. Most of his other data are more general, *M. conjugata* and *M. furcata* being cited merely from "Chile," *M. hamata* from "Patagonia" and *M. frontipilis* from the Straits of Magellan and "Chile." Under *M. furcata* and *M. hamata* he made no mention of Hooker as a collector and failed to cite either Hooker or Jacquinot in connection with *M. frontipilis*. He therefore gave no information regarding the earliest specimens of *Metzgeria* found in the region, including those upon which Lindberg's records were based.

In addition to the species already mentioned Stephani proposed as new no fewer than ten Chilean species, although he assigned to three of these a range extending far beyond the boundaries of the region. These species are the following, only the Chilean stations being indicated: *M. angusta*, "Chile" and Patagonia (*Dusén*); *M. chilensis*, "Chile" (*Dusén*); *M. corralensis*, Corral (*Krause*); *M. decrescens*, "Straits of Magellan" (*Dusén*); *M. Dusenii*, Desolation Island (*Dusén*); *M. glaberrima*, Straits of Magellan (*Spegazzini, Dusén*, "Gazelle" Expedition) and "Chile" (*Gay, Krause*); *M. Lechleri*, Arique (*Lechler*); *M. longiseta*, Straits of Magellan (Warnstorf Herbarium); *M. patagonica*, Newton Island (*Dusén*); and *M. terricola*, Straits of Magellan (*Savatier, Dusén*). It will be noted that Spegazzini and the "Gazelle" Expedition are mentioned in connection with *M. glaberrima* and that Savatier is named as one of the collectors of *M. terricola*. Since the collections of Spegazzini, Naumann and Savatier had already been reported upon (see **11**, **16**, and **2**), it is evident that the authors of these reports must have listed *M. glaberrima* and *M. terricola* under other names or else have made no allusion to the specimens here cited. Unfortunately Stephani throws no light upon these doubtful points. It will be noted further that more than half of the new species were based wholly or in part on material collected by Dusén. In regard to some of this material Stephani has given fuller details about localities in two subsequent papers (**21** and **22**), published respectively in 1900 and 1901.

In the first of these papers he listed *M. australis* as a valid species, apparently no longer regarding it as a synonym of *M. nitida*, and accredited it to Corral. He likewise cited *M. Dusenii* from the same locality and described *M. brevialata* from San Pedro Island as a new species. In the second paper he listed *M. pubescens* from Tierra del Fuego, although in his monograph he had restricted it to the Northern Hemisphere. Other data regarding stations will be noted later in connection with individual species. Strange to say Stephani made no mention in either paper of *M. chilensis, M. decrescens,* or *M. terricola,* in spite of the fact that he had used Dusén's specimens in drawing up the original descriptions of these species. It might at first appear that he had repudiated them, but this is clearly not the case, so far as *M. chilensis* and *M. terricola* are concerned, because he has referred to both of them in his later writings. In 1901, for example, he reported *M. chilensis* from Clarence Island in the Straits of Magellan (**22**, p. 4); in 1911 he reported the same species from Chiloé and Juan Fernandez (**23**, p. 10); and in 1916 he reported *M. terricola* from Bolivia (**25**, p. 180). These reports were based on specimens collected by Racovitza, Skottsberg and Herzog, respectively. In his report on Skottsberg's ample Chilean collections Stephani cited new stations for several other species of *Metzgeria* and also listed, as an addition to the flora, *M. albinea* Spruce, previously known from a single locality in Brazil. His record was based on a specimen from Huafo Island. In 1917 (**26**, p. 47) he made his last contribution to our knowledge of the Chilean *Metzgeriae* by proposing as a new species *M. antarctica* from Punta Arenas, basing his description on a specimen collected by Von Schrenk. According to his published writings Stephani recognizes twenty species of *Metzgeria* as members of the flora.

As in other large and natural genera of plants the species of *Metzgeria* are often difficult to distinguish. This is partly because most of the differential characters are drawn from variable structures and partly because the plants sometimes remain for a long time in an embryonic or juvenile stage of development, during which certain of the specific features fail to reveal themselves. Var. *ulvula* Nees of *M. furcata,* as shown by Goebel (**5**), is an excellent example of this condition, and equally good examples occur among the Chilean species. One unfortunate result of the difficulties involved in the determination of specimens has been an accumulation of incorrect records, not only in herbaria but also in the literature. This has been strikingly shown by Schiffner (**17**) in the case of *M. dichotoma* (Sw.) Nees, a species first described in 1788 and therefore one of the earliest to be recognized. In the Lindenberg Herbarium at Vienna he found eleven specimens bearing this name. Three of these were from Jamaica and represented original material of *Jungermannia dichotoma* from the Swartz collections; the others came from Guadeloupe, St. Vincent, Mexico, Brazil and Peru. The Jamaican specimens were the only ones that included plants of the true *M. dichotoma,* as this species is now understood, and two of these contained an admixture of *M. hamata;* the eight remaining specimens represented seven distinct species, three of which were at that time undescribed. In the Stephani Herbarium, now at Geneva, Schiffner found eight specimens bearing the name *M. dichotoma,* all of which had been collected in Brazil. Not one of these represented the true *M. dichotoma.* They represented instead three distinct species, not duplicated in the Lindenberg Herbarium. These two authoritative herbaria, therefore, which have served as the basis for many printed records, contained ten different species that had been incorrectly determined as *M. dichotoma.*

In view of these facts the writer has made an attempt to obtain for examination a full series of Chilean *Metzgeriae* and especially of specimens upon which printed reports have been based. This has been made possible through the kindness of correspondents and the curators of herbaria, and the writer would express his sincere thanks to all who have assisted him in his work. As a result of this study seven of the species based on Chilean material are reduced to synonymy, two species are proposed as new, and several incorrect determinations are rectified. These various changes reduce the number of known species to eleven, although certain fragmentary and undeterminable specimens indicate that this number is too low. In the citation of specimens the following abbreviations are used: B, Stephani collection in the Boissier Herbarium, University of Geneva; H, Cryptogamic Herbarium of Harvard University; M., Mitten Herbarium, at the New York Botanical Garden; Massal., collection of Professor Massalongo at Verona; Möll., collection of Dr. Möller at Stockholm; N. Y., herbarium of the New York Botanical Garden; S., collection of Professor Schiffner at Vienna; St., herbarium of the Swedish National Museum at Stockholm; U., herbarium of the University of Upsala; Y, herbarium of Yale University (including the private collection of the writer).

Key to the Species.

a. Upper surface of thallus densely covered with hairs
1. *M. frontipilis* (p. 276).
a. Upper surface of thallus naked .... *b.*
b. Costa bounded dorsally, on robust thalli, by more than two rows of cortical cells .... *c.*
b. Costa bounded dorsally by only two rows of cortical cells .... *d.*

c. Ventral surface of wings naked, the ventral hairs (when present) being restricted to the costa; gemmae lacking 2. *M. decrescens* (p. 279).
c. Ventral surface of thallus, including the wings, more or less densely covered with hairs; gemmae dorsal . .3. *M. corralensis* (p. 285).
d. Costa bounded ventrally by four rows of cortical cells; gemmae marginal..*e.*
d. Costa bounded ventrally by only two rows of cortical cells............*f.*
e. Marginal hairs often in divaricate pairs; ventral surface of wings usually with scattered hairs........4. *M. divaricata* (p. 288).
e. Marginal hairs borne singly; ventral surface of wings naked. 5. *M. patagonica* (p. 291).
f. Gemmae lacking..*g.*
f. Gemmae present, borne on more or less specialized branches becoming narrower toward the tips..............................*i.*
g. Thallus plane or nearly so; marginal hairs usually borne singly and sometimes scantily developed or lacking...............*h.*
g. Thallus convex, the wings more or less revolute......................*j.*
h. Autoicous...............................6. *M. chilensis* (p. 294).
h. Dioicous................................7. *M. decipiens* (p. 296).
i. Plants not turning bluish when dried; thallus and gemmae plane or nearly so.......................8. *M. epiphylla* (p. 303).
i. Plants turning bluish when dried; thallus and gemmae more or less convex.....................9. *M. violacea* (p. 306).
j. Marginal hairs borne singly and often scantily developed. 10. *M. magellanica* (p. 313).
j. Marginal hairs usually in pairs...............11. *M. hamata* (p. 315).

1. Metzgeria frontipilis Lindb.

Metzgeria frontipilis Lindb. Acta Soc. F. et Fl. Fenn. **1**^{2}: 14. *pl. 1, f. 2.* 1877.
Metzgeria brevialata Steph. Bihang K. Svenska Vet.-Akad. Handl. **26**^{3} (No. 6): 20. 1900.

Specimens examined: Newton Island, May, 1896, *Dusén,* mixed with *113* (B., St., U., see **20**, p. 19); San Pedro Island, *Dusén 533* (Möll., type of *M. brevialata*); shores of Trinidad Canal, *Coppinger* (M.); York Bay, September, 1853, *Lechler 1354* (M., as *M. pubescens*); same locality, *Lechler* (N. Y., as *M. pubescens* var. *subglabra*); southern part of Smith Sound, near the entrance to the Straits of Magellan, 1883, *Görtner,* mixed with *Riccardia fuegiensis* and other bryophytes (Y., specimen received from the Warnstorf Herbarium); Puerto Angosto, Desolation Island, March, 1896, *Dusén,* mixed with *159* (B., M., St., U., see **21**, p. 10); Straits of Magellan, 1868, *Dow* (Y.); Rio Azopardo, Tierra del Fuego, March, 1896, *Dusén 72* (U., as *M. pubescens,* and listed under this name by Stephani, **21**, p. 10); without definite locality, Tierra del Fuego, 1896–97, *Hatcher* (Y., **3**, p. 426); Cape Horn, *Hooker* (M., **10**, p. 15; listed as *Jungermannia furcata β.*

pubescens by Taylor and Hooker, **27**, p. 445); Staten Island, 1882, *Spegazzini 65* in part (Massal., Y., **11**, p. 257).

The following additional stations may be cited from the literature: Hanover and Atalaya Islands, *Skottsberg* (**24**, p. 10); Clarence and Hoste Islands, *Hariot* (**2**, p. 247); Tuesday Bay and Punta Arenas, Straits of Magellan, *Naumann* (**16**, p. 43); Brecknock Pass, *Spegazzini* (**11**, p. 257); Tekenika Bay, Almirantazgo, and Lake Fagnano, Tierra del Fuego, *Skottsberg* (**23**, p. 9, and **24**, p. 10); Mount Sarmiento, Tierra del Fuego, *Spegazzini* (**11**, p. 257).

The presence of hairs on the dorsal surface of the thallus is the most remarkable feature of *M. frontipilis* and will at once distinguish it from all the other known species of the genus except *M. pubescens*. In the northern species, however, the thallus is scarcely convex and the hairs are equally abundant on the ventral surface, being situated on both costa and wings; whereas in *M. frontipilis* the thallus is usually distinctly convex and the ventral hairs are largely restricted to the costa, the wings being almost or entirely free from them. To a certain extent the female branches offer an exception to this description, so far as the arrangement of the hairs is concerned, since in these both surfaces are equally hairy throughout. The male branches are still unknown.

Other noteworthy characters are derived from the costa and especially from its cortical cells, which show marked variations in number. According to Lindberg's original account these cortical cells are in eight to twelve rows both dorsally and ventrally. Stephani (**19**, p. 932), with a larger series of specimens at his disposal, places the extremes at six and eighteen and associates the lower numbers with the branches and the higher with the main axis. As a matter of fact only four rows are present in some of the slender branches studied by the writer. Stephani brings out in addition the interesting fact that the wings are sometimes two or three cells thick at their junction with the costa, a feature overlooked by Lindberg.

Although the published descriptions of *M. frontipilis* state emphatically that the ventral surface of the wings is wholly naked, this condition is by no means always realized. The hairs show a tendency to encroach, as it were, upon the ventral surface, not only from the margins but also (less frequently) from the costa. This tendency sometimes expresses itself by a very slight displacement of the marginal hairs, so that they are not truly marginal (Fig. 1, A); but the displacement may be much more marked than this, so that the hairs appear on the ventral surface one, two, three or even four cells away from the margin. Occasional hairs of this type are to be expected on almost any thallus, but it is usually difficult to detect them, except in section, on account of the revolute wings. When such hairs are more abundant forms are produced like Dusén's specimens from the Rio Azopardo, which Stephani referred to *M. pubescens.* A comparison of these specimens with European material of *M. pubescens* shows at once that the two plants are not the same. In the Rio Azopardo specimens, the greater part of the ventral surface of the wings is still free from hairs, and the thallus shows the marked convexity characteristic of *M. frontipilis.*

The plants from San Pedro Island, upon which Stephani based his *M. brevialata,* represent a more aberrant type. According to his description the most important features of this species are the following: a large costa, bounded both dorsally and ventrally by ten rows of cortical cells on the main axes and by four rows on the ultimate branches; narrow wings, unistratose throughout and only slightly decurved, ten cells wide on the ultimate branches but only five cells wide on the main axes; and an abundance of hairs on both surfaces of costa and wings. The plants show that the description is essentially correct in most respects except that the numbers of cortical and alar cells are less definite than is implied. The thalli exhibit, however, two marked discrepancies, when compared with his description. In the first place the wings are not always unistratose throughout but may be bistratose at their junction with the costa; and in the second place the wings, except when very narrow, are distinctly decurved and show a broad band next to the costa entirely free from ventral hairs. The latter, to be sure, are abundant and show the

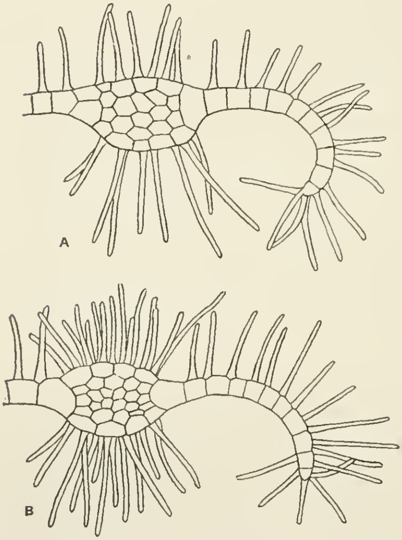

FIG. 1. METZGERIA FRONTIPILIS Lindb.

A, B. Transverse sections of rather slender thalli, × 100. A was drawn from a specimen collected on Desolation Island by Dusén, No. 159 in part; B, from the type material of *M. brevialata.*

extreme displacement noted above (Fig. 1, B), some of the hairs being three or four cells distant from the margin; but it is only on the narrowest wings that they are scattered over the entire ventral surface. The writer feels, therefore, that these specimens, although at first sight so striking, can not be separated specifically from *M. frontipilis*. They apparently represent a xerophytic modification of the species, both the narrow wings and the abundant hairs being in accordance with this view. It may be noted also in this connection that *M. pubescens* sometimes produces thalli with exceedingly narrow wings. Specimens showing this feature in a marked degree were discovered by Kaalaas near Christiania, Norway, and distributed by Schiffner in his Hepaticae Europaeae, No. 21, as forma *attenuata*. On some of the ultimate branches the wings are so strongly narrowed that they almost disappear, and the thalli thus acquire an appearance very different from that of typical *M. pubescens* with its broad wings.

2. Metzgeria decrescens Steph.

Metzgeria decrescens Steph. Bull. Herb. Boissier **7**: 932. 1899.
Metzgeria terricola Steph. op. cit. 933. 1899.
Metzgeria longiseta Steph. op. cit. 934. 1899.
Metzgeria Dusenii Steph. op. cit. 942. 1899.

Specimens examined: valley of the Aysen River, January, 1897, *Dusén 416* (M., Type; Möll., St., Y., as *M. glaberrima*, and listed under this name by Stephani, **20**, p. 20); Newton Island, May, 1896, *Dusén 113* in part (B., as *M. terricola*, and listed under this name by Stephani, **19**, p. 934; St., U., as *M. Dusenii*); southern part of Smith Sound, near the western entrance to the Straits of Magellan, 1883, *Görtner*, mixed with *Riccardia fuegiensis* and other bryophytes (Y., specimen received from the Warnstorf Herbarium); Alert Bay, western coast of Patagonia, 1882, *Coppinger* (N. Y.); Churucca, Desolation Island, *Savatier* (B., presumably the type of *M. terricola*, but listed as *M. furcata* var. *decipiens* by Bescherelle & Massalongo, **2**, p. 246); Puerto Angosto, Desolation Island, March, 1896, *Dusén 159* in part (M., St., U., type of *M. Dusenii*); Straits of Magellan, July, 1885, collector unnamed (B., type of *M. longiseta*, specimen received from the Warnstorf Herbarium); Cape Horn, *Hooker*, mixed with *M. decipiens* (M.).

The following additional station may be cited from the literature: Corral, *Dusén* (**20**, p. 19, as *M. Dusenii*).

In his monograph of the genus *Metzgeria* (**19**) Stephani divides the species into the two groups *Pinnatae* and *Furcatae*. Unfortunately, as Schiffner has since emphasized (**17**, p. 184), the distinction between these groups is based on variable features, since a thallus may be more or less pinnate in one part and distinctly furcate in another. Even in the more typically pinnate species, such as *M. filicina* Mitt. of the Andes, *M. pubescens* and *M. frontipilis,* the differentiation between an axis and its branches is relatively slight and expresses itself quantitatively rather than qualitatively. In certain species which Stephani includes among the *Pinnatae,* such as *M. decrescens,* he utilizes these quantitative differences in determining the relative rank of the branches in a branch-system. In the main axis of *M. decrescens,* according to his description, the costa is bounded dorsally by five rows of cortical cells and below by seven; in the pinnae (or branches of the first rank) the numbers are four and five, respectively; while in the pinnules (or branches of the second rank) the costa is bounded both dorsally and ventrally by two rows of cortical cells. He describes further a decrease in the width of the wings, corresponding with this decrease in the number of cortical cells. Apparently on the basis of these differences he states that the thallus is irregularly pinnately branched and adds that long pinnae and pinnules are mixed with much shorter ones.

A careful study of the type specimen of *M. decrescens* in the Mitten Herbarium shows that a pinnate habit is not apparent and that the branches arise in the usual dichotomous manner. These branches, to be sure, show the differences described by Stephani, and there are also intermediate conditions connecting his three types; but these differences do not by any means determine the relative rank of the branches. When an axis forks, for example, either or both of the branches may have a more complex costa and broader wings than the original axis, and the costa of a branch may increase in complexity with its growth in length. The differences are apparently due to nutritive causes and merely indicate that the costa and wings are variable with respect to the number of their component cells.

The plants of *M. decrescens* are whitish or yellowish green and apparently grow in dense mats. The living portion of the thallus may reach a length of 4–5 cm., while the width is mostly 0.9–1.3 mm. The wings are so strongly revolute that their margins sometimes meet, the thallus thus acquiring a cylindrical or subcylindrical form. The successive dichotomies may be as much as 1 cm. apart or as little as 1 mm., an individual thallus rarely showing both extremes. According to Stephani the ventral surface is naked, the hairs being restricted to the margin. In most cases this description applies, but occasionally a few scattered hairs arise from the ventral surface of the costa. The crowded marginal hairs, as he notes, occur singly and are usually straight. In well-developed plants a hair (FIG. 2, A) is found between every two marginal cells, and when the revolute wings approach each other closely the hairs form a delicate weft between them, making it difficult to study the features of the costa without spreading the wings apart. The hairs are mostly 0.2–0.4 mm. long and 10–20 μ in width, tending to taper from the base.

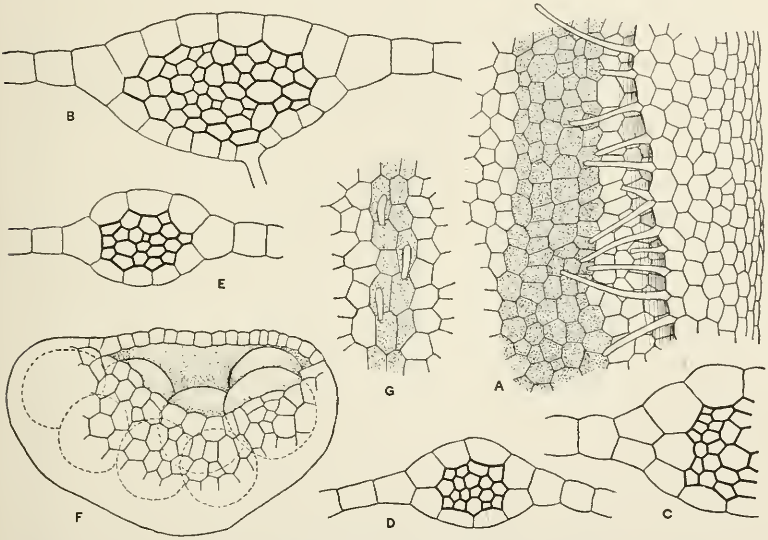

FIG. 2. METZGERIA DECRESCENS Steph.

A. Part of a slender thallus, ventral view, × 50; there are only two or three rows of cortical cells, the external stippled row on each side representing a bistratose transition-region between costa and wings. B–E. Transverse sections of costae, × 100. F. Male branch, × 100. G. Costa and adjacent alar cells of a male branch, showing slime-papillae, × 100. The figures were all drawn from the type material.

The alar cells have thin or slightly thickened walls, and trigones are either absent or minute and inconspicuous. Stephani gives the size of the cells as 54 × 45 μ. According to the writer's measurements the average size of the cells in the type specimen is about 45 × 34 μ, while the general average derived from the eight specimens listed above is 43 × 33 μ. At the same time one specimen gave an average as high as 55 × 35 μ, so that Stephani's figures are not excessive. The lowest average obtained was 36 × 32 μ. It should be remembered in this connection that, in species of *Metzgeria*, considerable variation in the size of the cells is to be expected, not only when different thalli, but also when different parts of the same thallus are compared. Data derived from cell-measurements must therefore be used with caution in distinguishing species.

The costa of *M. decrescens* (Fig. 2, B–E) yields some of the most distinctive characters of the species. It not only shows the marked variation in the number of cortical cells, to which attention has already been called, but it often shows in addition another feature unusual in the genus. In most of the *Metzgeriae* the transition between the unistratose wings and the multistratose costa is very abrupt, a condition clearly shown in many of the published figures. When, however, the costa is large and complex, as it is for example in *M. frontipilis*, the transition between the wings and the costa may be more gradual, a narrow band of large cells two or three cells thick being interpolated between the unistratose portion of a wing and the costa. In *M. decrescens*, although the costa is not particularly complex, both types of structure occur, just as they do in *M. frontipilis*. In some of the branches the abrupt transition is present (Fig. 2, E), in others the gradual transition (Fig. 2, B–D), and the latter is not necessarily associated with the more complex costae. When there is a gradual transition this is usually clearly apparent even when an intact thallus is examined. Under these circumstances the costa seems to be poorly defined, and the bistratose or tristratose band becomes evident by careful focusing, the outlines of the cells in the superimposed layers not corresponding.

The type material of *M. decrescens* shows male branches in abundance but no female branches. The male branches, which seem to be the only ventral branches present, have involute margins and are strongly incurved, although the apex does not approach the base very closely (Fig. 2, F). They measure about 0.45 × 0.3 mm. in well-developed examples and are wholly destitute of hairs, the only appendicular organs developed being the slime-papillae (Fig. 2, G). The alar cells are more delicate than those of a vegetative thallus and average only 25 μ in diameter. In some of the other specimens studied a few female branches with calyptras were found. These organs bore scattered hairs and attained a length in some cases of 3–3.5 mm., the diameter being 0.6–0.8 mm. Unfortunately the female branches themselves were so old and battered that their distinctive features could not be determined.

The three synonyms included under *M. decrescens* may now be considered. The first, *M. terricola,* was based on two specimens, one collected by Savatier on Desolation Island and the other by Dusén on Newton Island. According to Stephani *M. terricola* shows a variability in the number of cortical costal cells, comparable with what is found in *M. decrescens.* The wings of the thallus, moreover, are revolute in much the same way, while the cells are said to average about 54 × 36 μ, measurements which diverge but slightly from those given for *M. decrescens.* The following represent the most important differential characters indicated: the presence of a few setulae on the ventral surface of the thallus and the occurrence of the marginal hairs in pairs.

In Savatier's specimens, which may perhaps be regarded as the type, the costa is essentially like that of the type specimen of *M. decrescens;* and, although ventral hairs are sometimes present on the costa, this is equally true of *M. decrescens.* The marginal hairs, moreover, so far as the writer can determine, are invariably borne singly. In Dusén's material some of the thalli are like Savatier's, but others show crowded marginal cilia in pairs. The latter, however, are associated with costae that are bounded constantly, both dorsally and ventrally, by only two rows of cortical cells, while the cells of the revolute wings are considerably larger, averaging about 70 × 40 μ. In the writer's opinion the thalli with the geminate marginal hairs should be referred to *M. hamata,* although they evidently formed a part of the material from which the description of *M. terricola* was drawn. If these thalli are eliminated there is apparently nothing whatever to distinguish *M. terricola* from *M. decrescens.* The writer regrets that he has not seen Herzog's specimens of "*M. terricola,*" to which allusion has already been made (see page 274).

The second synonym, *M. longiseta,* was based on a specimen from the Straits of Magellan, the collector's name not being given. In his account of this species Stephani calls attention to the strongly convex thallus, the variable number of cortical costal cells, the long marginal hairs borne singly, and the alar cells averaging about 54 × 36 μ, four characters which *M. longiseta* clearly shares with *M. decrescens.* He mentions also the fact that the wings are two or three cells thick near the costa. This, as has been shown, is another characteristic feature of *M. decrescens,* although the original description does not allude to it. The differential characters of *M. longiseta* are apparently drawn from the marginal hairs, which are described as "hamate," and from the costa. The latter is said to be strongly convex dorsally and nearly plane ventrally and to have a thickness of five cells. The dorsal cortical cells, furthermore, are said to be convex and much larger than the internal and ventral cortical cells, which are said to be subequal in size. Unfortunately the type specimen does not support this description very convincingly. The marginal hairs are very rarely hamate, most of them being straight or irregularly curved and contorted; while the costa, as shown by cross sections, may project ventrally slightly more than dorsally. The dorsal cortical cells, moreover, measure about 50 μ in width, the ventral about 40 μ, and the internal cells, which may be in more than three layers, measure about 30 μ. These observations show that Stephani's differential characters are far from constant, and yet with the withdrawal of these his descriptions of *M. longiseta* and *M. decrescens* are almost identical.

Although the first two synonyms of *M. decrescens* are placed by Stephani among the *Pinnatae*, the third, *M. Dusenii*, is placed among the *Furcatae*. It is based upon material collected by Dusén on Desolation Island and the three original specimens examined have all been badly mixed with *M. frontipilis*. Stephani's description of *M. Dusenii* would seem to indicate that the species was much less variable in its costal features than *M. decrescens*, since the cortical cells are said to be in four rows both dorsally and ventrally. It is added that the dorsal surface is convex and the ventral smooth, that costal hairs are lacking, that the dorsal cortical cells are large and projecting, and that the ventral cells are much smaller. The original material shows at once the inconstancy of these features. Although some of the thalli show four rows of cortical cells on both surfaces, deviations from this number are frequent; some of the branches, for example, show only two or three such rows, while five rows of ventral cells were observed in at least one instance. Costal hairs, moreover, can be demonstrated by careful search in spite of their great infrequency, and they are really not much rarer than in the type of *M. decrescens*. The costal cells, finally, show deviations from the description. In a series of sections examined by the writer, the costa was found to be distinctly convex ventrally, while the ventral cortical cells measured 38 μ in width and were thus only slightly narrower than the dorsal cells, which measured 42 μ. Aside from the characters which have just been discussed the description of *M. Dusenii* agrees in all essential respects with that of *M. decrescens*, since the thallus is said to be strongly convex with naked wings and long marginal hairs borne singly, while the alar cells are said to average about 45 × 36 μ. The Desolation Island specimens are perhaps a trifle less robust than the type of *M. decrescens* from the Aysen Valley, and the branches tend to be shorter, but these differences are too slight and too inconstant to be of much significance.

It is interesting to note that Dusén's material from Newton Island, No. 113, has been differently determined by Stephani at different times. The specimen in the Boissier Herbarium bears the name *M. terricola,* while those at Stockholm and Upsala bear the name *M. Dusenii.* In the writer's opinion, as indicated above, these specimens are clearly the same and represent *M. decrescens.* It might appear from his determinations that Stephani recognized the identity of his *M. terricola* and *M. Dusenii* and wished to supplant one name by the other. Unfortunately this assumption is contradicted by his published writings.

3. METZGERIA CORRALENSIS Steph.

Metzgeria corralensis Steph. Bull. Herb. Boissier **7**: 933. 1899.
Metzgeria Lechleri Steph. op. cit. 942. 1899.

SPECIMENS EXAMINED: without definite locality or date, *Gay* (Mont., as *M. furcata,* and listed under this name by Montagne, **14**, p. 297); Corral, no date, *Krause* (B., TYPE); Arique, no date, *Lechler 652* (M., unnamed but probably representing the type of *M. Lechleri*); Valdivia, 1887–88, *Hahn* (B., as *M. Liebmanniana* and listed under this name by Stephani, **19**, p. 935); same locality, date and collector (B., apparently a part of the same collection as the preceding but bearing a manuscript name); Osarno Volcano, date and collector's name not given (M.).

Stephani places *M. corralensis* among the *Pinnatae* and describes the thallus as remotely pinnate. At the same time he makes no allowance for variability in the number of costal cells, as he did in *M. decrescens,* stating definitely that the dorsal cortical cells are in four rows and the ventral in eight. The type specimen shows that these numbers are too rigid. Although the dorsal cortical cells are usually in four rows (FIG. 3, A, B), the number really varies from two to five, and the ventral rows are frequently fewer than eight (FIG. 3, B). In spite of this variability a pinnate habit is no more apparent in *M. corralensis* than in *M. decrescens.*

The species varies in color from a pale yellowish green to a dull green and is fairly robust. According to Stephani the thallus sometimes attains a length of 4 cm. The width is mostly 1–1.5 mm. but may be as much as 2.5 mm. in well-developed plants. The wings are plane or somewhat convex and are mostly fifteen to twenty-five cells across in the type material, although Stephani gives the width as only twelve cells. According to his statements the alar cells measure 36 × 27 μ, and these figures agree pretty closely with the general average of 33 × 26 μ, obtained from the five specimens listed above. The cells, as he notes, are essentially thin-walled throughout, although vague indications of trigones are sometimes present.

In well-developed thalli the whole ventral surface, including both the costa and the wings, is covered over with crowded hairs, giving it a pubescent appearance. These hairs are mostly 0.1–0.3 mm. in length and 10–12 μ in diameter. Those along the margin, which are essentially like the others, sometimes spread widely and sometimes grow downward; they usually arise singly, as Stephani notes, but twinned hairs may occasionally be demonstrated. Between the densely pubescent ventral surface, which is doubtless typical for the species, and a smooth or nearly smooth condition, all gradations occur, although it is doubtful if a thallus is ever smooth throughout.

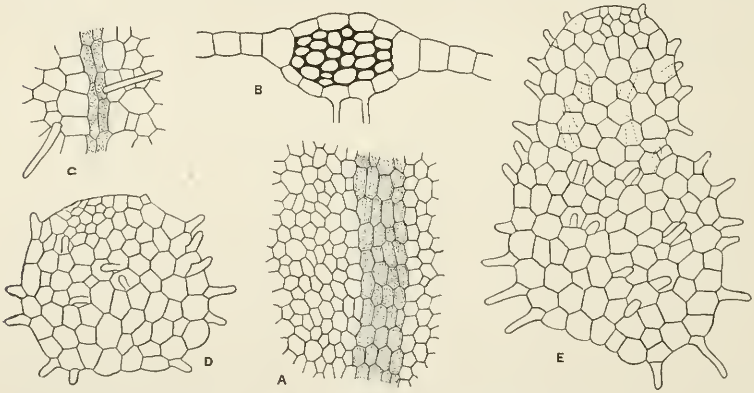

Fig. 3. Metzgeria corralensis Steph.

A. Part of a thallus showing costa and adjoining cells of wings, dorsal view, × 50. B. Transverse section of costa, × 100. C. Costa and adjoining alar cells of a male branch, showing ventral hairs, × 100. D. Gemma at time of separation, × 100. E. Germinating gemma, × 100. A, D and E were drawn from a specimen collected on the Osarno Volcano; B and C, from a specimen collected at Arique by Lechler.

In the specimens studied by the writer a few male branches are present and are mostly 0.2–0.35 mm. in length by 0.25–0.4 in width. The wings are involute and the costa so strongly incurved that the apex almost reaches the base, the branch thus acquiring a spherical or subspherical form. According to Stephani the surface is smooth, but this is rarely the case, from one to a dozen hairs being usually present (Fig. 3, C).

If Stephani's descriptions of *M. Lechleri* and *M. corralensis* are compared it will be seen that they agree in most important respects, even though he places *M. Lechleri* among the *Furcatae*. The most important differences that he brings out are derived from the costae and alar cells, the features of which in typical *M. corralensis* have already been discussed. According to his description the costa of *M. Lechleri* is bounded both dorsally and ventrally by four rows of cortical cells, while the alar cells have firm walls distinctly thickened at the angles. The study of Lechler's Arique specimens in the Mitten Herbarium, which agree in most respects with Stephani's description, brings out the fact that the cortical costal cells are inconstant in number, just as in *M. corralensis*. The alar cells, moreover, although slightly thickened, do not show conspicuous trigones; in fact it is usually difficult to make them out at all. Since the differences between the species thus break down, and since the Arique specimens are essentially like Krause's type, the writer feels convinced that the two species are synonymous.

The importance of gemmae in distinguishing species of *Metzgeria* has already been emphasized by the writer in another connection (**4**). In *M. corralensis* the gemmae are dorsal and are borne on ordinary vegetative branches, the growth of which is apparently unlimited. As in *M. crassipilis* (Lindb.) Evans of the eastern United States (see **4**, p. 282) and other species having dorsal gemmae, many thalli are not gemmiparous at all, while others produce the gemmae in great profusion. In the case of *M. corralensis* the early stages of development have not been studied, but their adult features will be described.

At the time of separation (Fig. 3, D) the gemmae vary somewhat in size but most of them are 0.18–0.27 mm. long and 0.16–0.24 mm. wide; they may be orbicular, but the width is usually a little less or a little more than the length. A gemma is six to eight cells across and has a single apical cell. What may be described as the dorsal surface is convex and usually shows from two to six short and rudimentary hairs. The gemma bears in addition from three to eight marginal hairs on each side, and these may be truly marginal or slightly displaced to the ventral surface, which seems otherwise to be perfectly smooth.

When a gemma germinates its apical cell continues (or resumes) its activities and gives rise to a flat, strap-shaped thallus which tends to be narrower than the gemma itself (Fig. 3, E) being often only four cells wide. While this is going on the hairs on the gemma increase somewhat in length, and similar superficial and marginal hairs appear on the flat extension. The superficial hairs are always more numerous on one surface than on the other and may be confined to one surface. Sometimes the more hairy surface of the extension is continuous with the hairy convex surface of the gemma and sometimes with the smooth concave surface, these observations apparently showing that the dorsiventrality of the gemma is not firmly fixed but that a reversal of the dorsiventrality may take place at germination.

The presence of superficial hairs on the gemmae of *M. corralensis* and on the young thalli to which they give rise are perhaps the most distinctive features of these structures. Except for these peculiarities the gemmae and young plants are much like those of *M. crassipilis* and *M. Liebmanniana.* The latter species, in fact, is closely related to *M. corralensis,* differing from it mainly in its greater size; and it is therefore not surprising that specimens of the Chilean species have been referred to *M. Liebmanniana.*

4. **Metzgeria divaricata** sp. nov.

Grayish or yellowish green, scattered or growing in depressed mats, more or less firmly attached to the substratum: thallus prostrate, repeatedly dichotomous but rarely branching ventrally, plane or slightly convex, well-developed thalli mostly 0.6–1.2 mm. wide, the forks mostly 2–8 mm. apart; costa bounded dorsally by two rows of cortical cells and ventrally by four; wings mostly eight to fifteen cells broad, the cells mostly 38 × 31 μ, the walls thin or slightly thickened and sometimes with more or less distinct trigones and nodular intermediate thickenings; hairs varying greatly in abundance; marginal hairs in the hairiest and most characteristic plants occurring in divaricate pairs, ventral hairs under these circumstances numerous on the wings and especially on the costa; hairs averaging about 0.15 mm. in length and 10–12 μ in width, often branched at the apex and acting as rhizoids: inflorescence dioicous: ♂ branches sometimes borne in considerable abundance, subspherical, usually bearing on the ventral surface from one to five scattered hairs, 0.33–0.36 mm. long and 0.33–0.45 mm. in width: ♀ branch broadly obcordate, 0.25–04. mm. long and 0.45–06. mm. wide, hairs abundant along the margin and also scattered over the ventral surface, especially in the median part; calyptra about 2 mm. long and 0.9 mm. wide, more or less hairy throughout but especially in the upper half: gemmae rarely abundant, marginal, borne on undifferentiated branches, oblong, flat or nearly so, usually with crowded rudiments of marginal and sometimes paired hairs slightly displaced to one surface.

SPECIMENS EXAMINED: Chile, without definite locality or date, *Neger 68* (B., as *M. conjugata,* and listed under this name by Stephani, **19**, p. 951); near Santiago, 1882, *Philippi 24* (B., as *M. furcata,* and listed under this name by Stephani, **9**, p. 941); Concepcion 1905–06, *Thaxter 90, G* (H., Y.); San Antonio, Pudeto River, Chiloé, July, 1908, *Halle & Skottsberg 257* (U., as *M. Lechleri,* and listed under this name by Stephani, **24**, p. 10). No. 90, collected by Professor Roland Thaxter, may be designated the type; No. 257, from Chiloé, is poorly developed and somewhat doubtful.

In *M. divaricata* and the species that follow the structure of the costa is far more constant than in *M. frontipilis, M. decrescens* and *M. corralensis.* This does not mean that an absolute constancy is to be expected. In *M. divaricata,* for example, the ventral cortical cells may be in five rows instead of four, even at some little distance from a fork; it simply means that deviations from the typical numbers are infrequent enough to be ignored.

As noted in the description the ventral hairs vary greatly in abundance. In the more extreme development of these hairs the entire ventral surface appears loosely pubescent, and the marginal hairs occur between every two marginal cells. In typical cases these marginal hairs are paired and spread so widely apart that they form a straight line perpendicular to the margin. As a rule the outer hair of each pair is truly marginal and the inner ventrally displaced. Sometimes, however, the outer hair is slightly displaced too, and a semblance of displacement is often brought about by the slight convexity of the wing-margins. When a long series of these paired and divaricate marginal hairs is present the thallus acquires a very striking and distinctive appearance (FIG. 4, A). Unfortunately the condition just described is not always realized. Sometimes, for example, one part of a thallus may be pubescent, while other parts produce hairs sparingly or not at all. An entire thallus, in fact, may be sparingly hairy throughout, and most of the marginal hairs present may be borne singly. Even under such circumstances, however, a prolonged search will usually bring to view an occasional pair of the characteristic marginal hairs.

Marginal gemmae occur abundantly on some of the plants collected by Neger but are apparently absent from all the other specimens. The gemmiparous branches are essentially like the others and present no evidence of limitation in growth. The gemmae are usually scattered, although a crowded series is sometimes to be observed, and the mother-cells of the gemmae arise directly from the marginal cells, just as in *M. furcata* (**4**, p. 277). At the time of separation the gemmae vary considerably in size, average examples measuring perhaps 0.3–0.4 mm. in length and 0.15–0.2 mm. in width. Most of them are oblong in form, six to eight cells across, and show an indistinct stalk and a single apical cell. Crowded rudiments of marginal hairs, slightly displaced to one surface, are usually present and not infrequently show a paired arrangement. Otherwise the gemmae are scarcely differentiated. In germination (Fig. 4, B–D) the young plant is at first nothing more than a slightly narrower extension of the gemma, although in one somewhat older example a rudimentary costa was present with a wing three cells wide on each side. No late stages of germination have been observed.

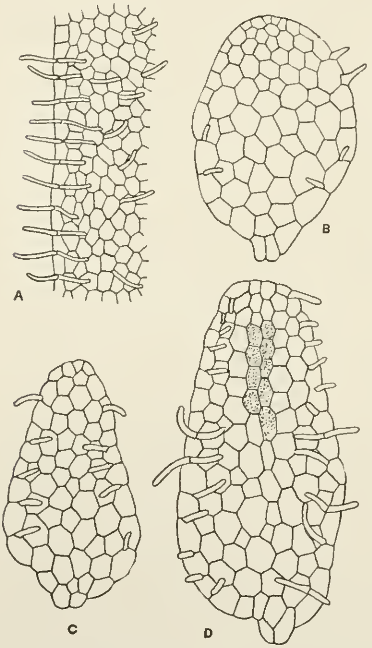

Fig. 4. Metzgeria divaricata Evans.

A. Marginal portion of a thallus-wing, ventral view, × 50. B–D. Germinating gemmae, × 100. A was drawn from the type material; B–D, from a specimen collected in Chile by Neger, No. 68.

The list of specimens cited brings out the fact that *M. divaricata*, apparently on account of its variability, has been confused with three other species of *Metzgeria*. In the structure of the costa with its two rows of dorsal and four rows of ventral cortical cells it agrees with *M. conjugata* and *M. furcata;* in having ventral hairs, sometimes produced in considerable abundance, it agrees with *M. corralensis*. It is, however, amply distinct from all three species. It differs from *M. conjugata* in being dioicous and in having gemmae and ventral alar hairs, while it differs from *M. furcata* in having paired marginal hairs. When strongly pubescent it resembles *M. corralensis* rather markedly but is distinguished by the more definite structure of the costa, by the occurrence of the marginal hairs in divaricate pairs, and by the marginal gemmae.

5. METZGERIA PATAGONICA Steph.

Metzgeria patagonica Steph. Bull. Herb. Boissier **7**: 940. 1899.

SPECIMENS EXAMINED: Newton Island, May, 1896, *Dusén 24* (M., U., TYPE).

The following additional station may be cited from the literature: Escapada Island, Skyring, *Skottsberg* (**24**, p. 11).

According to the original description of this well-marked species the wings of the thallus are strongly decurved and often revolute, but a supplementary note adds that the specimens are "etiolated" and that the normal structure is to be found only on the younger "innovations." In the material studied by the writer most of the thalli are perfectly plane and only a few of the branches show revolute margins. At the same time the plane thalli can hardly be regarded as abnormal; they do not present the appearance of being etiolated, and the presence of female branches in some abundance shows that the plants are by no means in a juvenile stage of development. The soluble yellow substance, to which Stephani calls attention in a later paper (**20**, p. 20), is very much in evidence when the specimens are soaked in water.

The thalli of *M. patagonica* are pale green, often deeply tinged with yellow, and grow in depressed mats. The width is mostly 1–1.5 mm. and the length may be as much as 3 cm. Measured in cells the wings are usually fifteen to twenty-five cells across. Although ventral branching sometimes occurs, dichotomous branching is far more common, the successive forks being mostly 1–5 mm. part.

Hairs are rarely abundant and many regions are nearly or quite free from them. The marginal hairs are straight and seem to be invariably borne singly. They are usually slightly displaced to the ventral surface, tending to extend at right angles to the wings, but they may be truly marginal and lie in the same plane as the wings. The hairs are about 10 μ in diameter and rather short, the length being usually only 0.1–0.12 mm. Although the wings are naked the costa sometimes bears loose and scattered clusters of hairs, essentially like the marginal hairs but sometimes a trifle longer. Apparently in either position a hair has the power of branching at the tip and acting as an organ of attachment.

The costa shows the same structure as that of *M. divaricata*, being bounded dorsally by two rows of cortical cells and below by four. The alar cells, according to Stephani, measure 54 × 40 μ, those near the costa being 72 × 40 μ. The writer's measurements give an average of 41 × 33 μ and do not indicate that the cells near the costa are appreciably longer than the others. The cells throughout have rather firm walls, which often show nodular intermediate thickenings as Stephani notes, but the thickened angles that he likewise emphasizes are difficult to demonstrate.

No male branches have been seen by the writer and the original description does not mention them. Female branches are often abundantly produced, and it is a noteworthy fact that a female thallus sometimes becomes gemmiparous shortly after it has borne the sexual branches. Some of the latter are small and undeveloped, but most of them are of fair size (Fig. 5, A), measuring perhaps 0.5–0.7 mm. in length and 0.9–1 mm. in width. The outline, which is broadly orbicular with a deep apical indentation, does not show clearly without spreading the branches out flat, owing to their strong concavity. The margin shows crowded hairs borne singly, each representing the outgrowth of a small cell situated between two larger cells, just as in the normal vegetative thalli of most *Metzgeriae*. On the ventral surface the thickened median portion bears a dense cluster of hairs, and a few other hairs are scattered over the unistratose portion.

Mention has just been made of gemmiparous plants, although Stephani does not allude to them. As a matter of fact the gemmae of *M. patagonica*, which are marginal in position, yield some of the most distinctive characters of the species. The gemmiparous branches are at first scarcely modified but rapidly decrease in width after the formation of the gemmae has been initiated. When the wings have been reduced to a width of four or five cells the growth of the branch comes to an end. The reduction in the width of the wings is often accompanied by a simplification in the structure of the costa, the rows of ventral cortical cells being only two or three. In the formation of the gemmae their mother-cells are derived directly from the marginal cells of the branch, without a preliminary cell-division. The gemmae may be scattered or crowded, a long series of adjoining marginal cells sometimes giving rise to a continuous row of gemmae. The latter tend to appear in acropetal succession and yet show many exceptions to this arrangement.

At the time of separation the gemmae are flat and unistratose structures, orbicular to oblong in outline, broadening out abruptly from a two-celled and often indistinct stalk, and showing a broad and rounded apex with a single apical cell. They are mostly 0.25–0.3 mm. long and 0.18–0.25 mm. wide, being composed of six to eight indefinite rows of cells. On each side six to eight hairs are usually present, and these are commonly (but not invariably) arranged in pairs. The hairs extend almost at right angles to the surface of the gemma and, when paired, spread in opposite directions. The majority are strongly curved and might often be described as hamate. Only the earliest stages of germination have been observed and in these the young plants have simply repeated the features of the gemmae, except that they have sometimes been a little narrower (Fig. 5, B). In other words they have remained flat and unistratóse thalli, showing no signs of dorsiventrality and tending to produce a succession of paired and divergent marginal hairs.

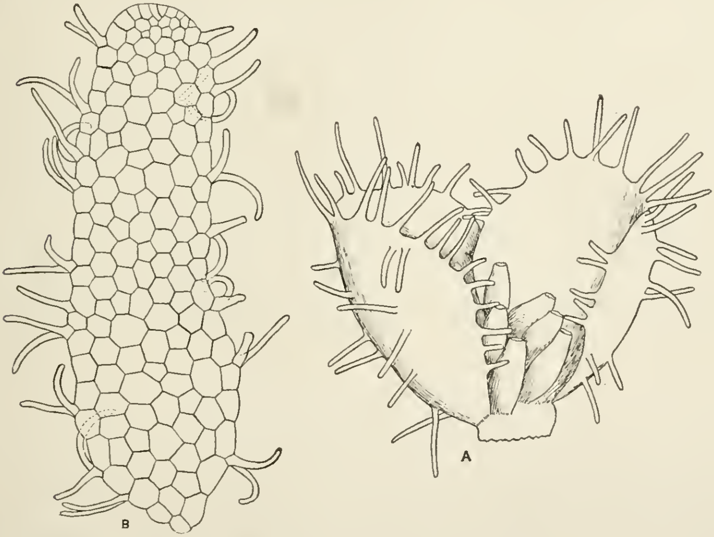

Fig. 5. Metzgeria patagonica Steph.

A. Female branch, × 50. B. Germinating gemma, × 100. The figures were both drawn from the type material.

Marginal gemmae with hooked hairs have been described in *M.*

uncigera Evans of the West Indies and Florida (**4**, p. 273), a species in which the vegetative thallus bears straight hairs arising singly. Dorsal gemmae with hooked hairs have been described in two West Indian species, *M. dichotoma* and *M. vivipara* Evans (**4**, pp. 285, 288), in both of which the vegetative thallus bears straight marginal hairs, again arising singly. In *M. vivipara* twinned hairs occur as a rare exception, the hairs being usually borne singly; in the other two species twinned hairs are apparently never found. *M. patagonica* shows a new combination of characters — marginal gemmae with curved or hooked hairs arising in pairs and a vegetative thallus with straight marginal hairs arising singly. It is this unusual association that separates the species most sharply from its allies.

Of course the structure of the costa allies *M. patagonica* with *M. conjugata* and *M. furcata,* as well as with the preceding species. In *M. conjugata,* however, no gemmae are produced and the marginal hairs of the thallus are normally borne in pairs; in *M. furcata* the hairs of the gemmae, if present at all, are straight and arise singly; while in *M. divaricata* the marginal hairs of both thallus and gemmae often arise in pairs but are straight. Aside from these differences *M. patagonica* can be distinguished from *M. conjugata* by its dioicous inflorescence and from the other two species by its lack of ventral hairs on the wings.

6. METZGERIA CHILENSIS Steph.

Metzgeria chilensis Steph. Bull. Herb. Boissier **7**: 937. 1899.

SPECIMENS EXAMINED: Quiriquina Island, near Concepcion, no date, *Dusén 179* (M., TYPE).

The following additional stations may be cited from the literature: Clarence Island, *Racovitza* (**22**, p. 4); Quicavi, Chiloé, *Skottsberg* (**24**, p. 10); Juan Fernandez, *Skottsberg* (**24**, p. 10); New Zealand, *Colenso* (**19**, p. 937). The Juan Fernandez specimen is clearly distinct from the true *M. chilensis;* the other specimens have not been seen by the writer.

The species was based on two specimens, one from Chile and the other from New Zealand. The Chilean specimen is naturally to be regarded as the type, but the original description was probably partly drawn from the New Zealand specimen, since it does not agree in all respects with Dusén's material.

The plants in the Mitten Herbarium are very fragmentary and grew in a loose depressed mat in admixture with other bryophytes. The thallus is mostly 0.5–0.9 mm. wide and attains a length of 1–1.5 cm. The wings, although described as almost revolute by Stephani, are flat or even slightly concave and are mostly six to twelve cells wide. The normal branching is dichotomous with the forks 2–10 mm. apart, but ventral branching is not exceptional.

The marginal hairs vary greatly in abundance. In some places they may be absent altogether; in other places, even on the same thallus, they may be as numerous as the marginal cells, a single hair arising between every two cells. In most cases the hairs are slightly displaced to the ventral surface, but they may be truly marginal, and it is not unusual for the apex to be branched and to act as an organ of attachment. The longest hair seen was 0.3 mm. long but most of them were 0.1 mm. or less in length, the average diameter being about 10 μ. The ventral surface of the wings is apparently wholly free from hairs, but the costa bears them in loose clusters or scattered and is rarely free from hairs for any great distance. These costal hairs are essentially like the marginal hairs but tend to be a little longer.

The costa is bounded both dorsally and ventrally by two rows of cortical cells, a type of structure found also in all the following species. The alar cells average about 35 × 27 μ, although Stephani's measurements gave 54 × 36 μ. The walls are slightly thickened and sometimes show minute trigones and occasional nodular intermediate thickenings.

According to Stephani the inflorescence is dioicous. The type specimen, however, is clearly autoicous, the male and female branches often occurring in close proximity. The male branches are mostly 0.3–0.4 mm. long and 0.25–0.3 mm. wide and are ellipsoidal in form, the margins being involute and the costa so strongly incurved that it approaches the base without reaching it. Except for the slime-papillae the surface is smooth. The female branches, which are more or less concave and obcordate in outline, are mostly 0.4–0.45 mm. long and 0.45–0.6 mm. wide. The marginal hairs grow out from small cells but are not numerous; the ventral hairs may be restricted to a cluster of six to twelve on the thickened median portion, but one to three scattered hairs may be present also on the wings. No gemmae have been observed.

The autoicous inflorescence will at once distinguish *M. chilensis* from all the other Chilean species. It agrees in this unusual feature with *M. conjugata*, but in that species the ventral cortical cells of the costa are in four rows and the marginal hairs often in pairs. The only other South American species to which an autoicous inflorescence has been assigned is *M. albinea* Spruce, which further agrees with *M. chilensis* in the structure of the costa. In *M. albinea,* however, the marginal hairs are in pairs. Aside from the inflorescence *M. chilensis* approaches the following species very closely.

7. Metzgeria decipiens (Massal.) Schiffn. & Gottsche.

Metzgeria furcata β. decipiens Massal. Nuovo Gior. Bot. Ital. **17**: 256. *pl. 28, f. 36.* 1885.
Metzgeria decipiens Schiffn. & Gottsche in Schiffner, Forschungsreise "Gazelle" **4**⁴: 43. 1890.
Metzgeria glaberrima Steph. Bull. Herb. Boissier **7**: 939. 1899.
Metzgeria nuda Steph. Kungl. Svenska Vet.-Akad. Handl. **46**⁹: 10. *f. 3a.* 1911.

Specimens examined: Valdivia, 1887, *Hahn* (S.); Corral, 1905–06, *Thaxter 1f, 2c, 78, 110, 122, 124, 138, 141* (H., Y.); valley of the Aysen River, 1897, *Dusén 283* (Möll., as *M. glaberrima,* and listed under this name by Stephani, **20**, p. 20); Puerto Chacabuco, 1908, *Halle 256* (St., as *M. glaberrima,* and listed under this name by Stephani, **24**, p. 10); near the mouth of the Rio Pudeto, Chiloé, 1908, *Halle 256* (St., as *M. glaberrima,* and listed under this name by Stephani, **24** p 10); Guaitecas Islands, 1897, *Dusén 394* (M., Möll., St., as *M. glaberrima,* and listed under this name by Stephani, **20**, p. 20); Port Gallant, Straits of Magellan, 1896, *Dusén* (N. Y., St., as *M. glaberrima*); Tuesday Bay, Straits of Magellan, 1876, *Naumann* (S., Y., listed by Schiffner, **16**, p. 43); Grappler Bay, Straits of Magellan, 1893, *Douglas* (H., Y.); Rio Azopardo, Tierra del Fuego, 1896, *Dusén 71* (U., as *M. glaberrima,* and listed under this name by Stephani, **21**, p. 10); Rio Olivia, Tierra del Fuego, 1902, *Skottsberg* (St., as *M. glaberrima,* and listed under this name by Stephani, **23**, p. 9); Cape Horn and Hermite Island, *Hooker* (M., as *M. furcata,* and listed under this name by Hooker and Taylor, **8**, p. 480); near Basil Hall, Staten Island, 1882, *Spegazzini* (Massal., Y., Type of *M. furcata β. decipiens*). The following three specimens from the Falkland Islands have likewise been examined: Port Stanley, 1902, *Skottsberg* (St., as *M. glaberrima,* and listed under this name by Stephani, **23**, p. 9); same locality, 1905, *Thaxter* (H., Y.); near Port Stanley, 1907, *Skottsberg 356* (U., type of *M. nuda*).

The following additional stations from the literature may be cited: Wellington and Desolation Islands, *Savatier;* and Hoste Island, *Hyades* (**2**, p. 246, as *M. furcata* var. *β. decipiens*).

The following stations for *M. glaberrima* may likewise be cited:

near Puerto Varas, *Dusén* (**20**, p. 20); Skyring and Dawson Island, *Skottsberg* (**24**, p. 10); Desolation Island, *Dusén* (**21**, p. 10); Ushuaia, Tierra del Fuego, *Skottsberg* (**23**, p. 9). Also the following stations beyond the boundaries of Chile: New Zealand and Australia, several collectors (**19**, p. 939); Antipodes Islands (**24**, p. 10).

As here understood *M. decipiens* is probably the commonest and most widely distributed *Metzgeria* in Chile. It exhibits a great deal of variation in size and particularly in width, in the number and distribution of its hairs and in the measurements of its alar cells. It shows, however, the following apparently constant features; a flat or slightly convex thallus; a costa bounded both dorsally and ventrally by two rows of cortical cells; a lack of ventral alar hairs; and a lack of gemmae. Another feature almost as constant is the presence of ventral vegetative branches. It is of course difficult to establish the absolute constancy of any characters in so variable a genus as *Metzgeria*, especially characters of a negative nature, but the writer has found no exceptions to the four first enumerated after a detailed study of the numerous specimens cited.

The plants are pale yellowish green and are sometimes scattered but usually form depressed and layered mats of considerable extent. They are frequently found on trees but are by no means restricted to such localities; in rare instances, in fact, they are epiphyllous in habit. The living portion of a thallus is usually 1–2 cm. long, while the width is mostly 0.8–1.2 mm. These figures represent the mean averages obtained from six specimens. The narrowest thallus seen, however, was only 0.2 mm. wide, while the widest was 1.8 mm. Measured in cells an average wing is usually thirteen to seventeen cells across; a very narrow wing, however, may be as little as two cells and a very wide one as much as twenty-seven cells. The ventral branches are sometimes so abundant that they largely replace the normal branches. When the latter occur to the usual extent the successive dichotomies are mostly 1–3 mm. apart. A ventral branch broadens out abruptly from a narrow stalk-like base and quickly acquires a normal width, often in fact just beyond the margin of the higher axis. Sometimes the branch spreads widely or obliquely; sometimes it grows in the same direction as the higher axis. Under the latter circumstances the axis is usually soon limited in growth; and, if the process is repeated, a more or less definite sympodium may be the result.

Hairs occur in two positions — along the margin and on the ventral surface of the costa. The marginal hairs (Fig. 6, A) are by far the more numerous and are sometimes very abundantly produced. In other cases, however, a prolonged search is necessary before any hairs at all can be demonstrated, and there are many intermediate conditions between these extremes. A thallus, in fact, may produce hairs abundantly in one part and be hairless or nearly so in another. When the marginal hairs are crowded a single hair usually arises between every two marginal cells, but sometimes the hairs arise in pairs more or less frequently. When borne singly they are either truly marginal or slightly displaced to the ventral surface. The hairs are usually straight and measure 0.15–0.3 mm. in length by 10–12 μ in width. In rare instances they are branched at the apex and act as organs of attachment. Costal hairs are usually exceedingly rare, and in many individual thalli none at all can be demonstrated, as Stephani notes under *M. glaberrima*. When they occur they are either scattered or in small irregular clusters and are essentially like the marginal hairs.

The alar cells vary considerably in size (Fig. 6, A–D), not only in different thalli but also (in some cases at least) in different parts of the same thallus. In Spegazzini's material from Staten Island, for example, the cells in most places averaged about $48 \times 36\,\mu$, while a branch of a thallus yielding these higher measurements in its other parts had cells averaging only $35 \times 29\,\mu$. Taking the mean averages of fourteen specimens the cells measure about $38 \times 29\,\mu$, the highest average being $48 \times 26\,\mu$ and the lowest $31 \times 22\,\mu$. Stephani's measurements of *M. glaberrima*, $36 \times 36\,\mu$, agree closely with the general average. It must of course be remembered that individual alar cells may deviate rather widely from these average measurements. The cells have thin or slightly thickened walls, and trigones are either minute or absent altogether.

The male branches of *M. decipiens* present few distinctive features. They are almost globular in form, the wings being involute and the costa so strongly incurved that the apex almost reaches the base (Fig. 6, E). The largest example measured was about 0.35 mm. in diameter. Hairs are entirely absent, but the usual slime-papillae are of course present.

The female branches (Fig. 6, F–I) are broadly obovate and vary from plane to convex when viewed from the ventral surface. Exclusive of the hairs they are usually 0.3–0.4 mm. in length and 0.45–0.75 mm. in width. Along the margin the hairs are crowded but apparently never in pairs, each hair representing the outgrowth of an ordinary marginal cell. On the ventral surface the hairs, if developed at all, are restricted to the thickened median portion, where from one to perhaps twenty may be present, the number being usually larger if

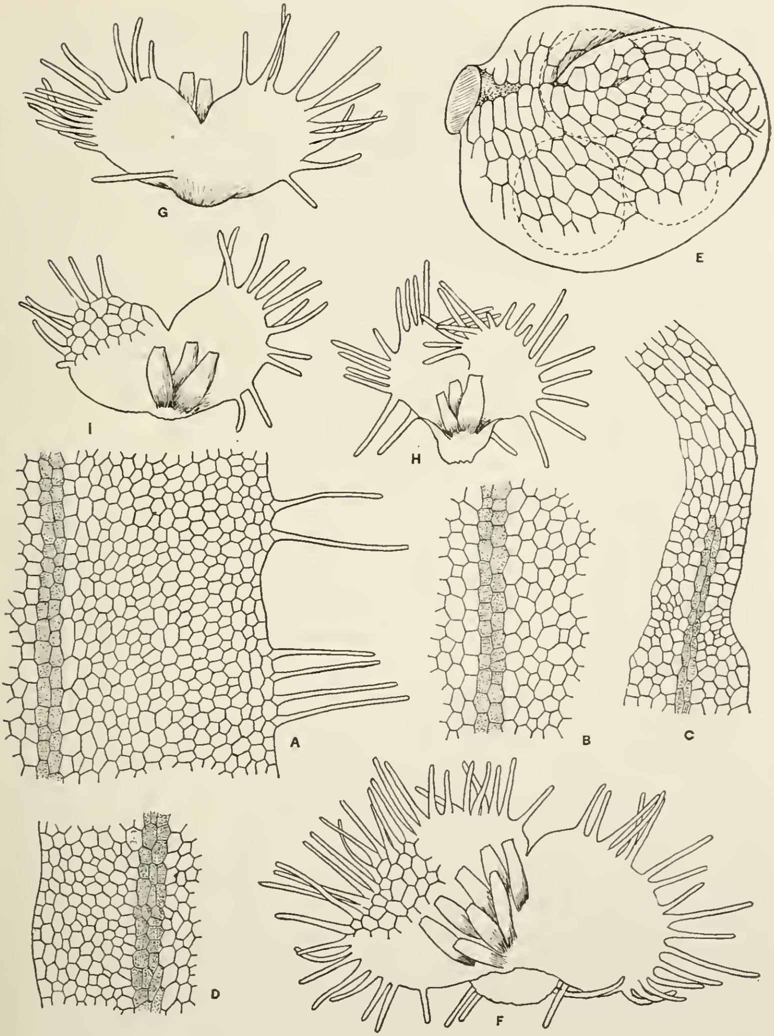

Fig. 6. Metzgeria decipiens (Massal.) Schiffn. & Gottsche.

A–D. Portions of thalli, ventral view, × 50. E. Male branch, × 100. F–I. Female branches, × 100. A, F, and G were drawn from a specimen collected by Naumann at Tuesday Bay; B and H, from a specimen of *M. glaberrima* collected on the Guaitecas Islands by Dusén, No. 394; C, from a specimen of *M. glaberrima* collected on Tierra del Fuego by Dusén, No. 71; D, E and I, from a specimen collected at Corral by Thaxter, No. 78.

fertilization has taken place. The calyptra at maturity is clavate, measuring about 1.2 mm. in length and 0.6 mm. in diameter in the upper part, exclusive of the hairs. The latter are densely crowded above the middle and more sparingly developed toward the base; some of them attain a length 0.4 mm.

On one of the specimens from Corral, No. 138, several capsules are present and give an opportunity for describing the valves, our knowledge of which in *Metzgeria* is still very incomplete. The mature capsule is dark brown and oval, measuring about 0.6 mm. in length and 0.4 mm. in diameter. The valves, when spread out flat, measure 0.6×0.3 mm. and are composed, as is uniformly the case in *Metzgeria*, of two layers of cells. Those of the outer layer (Fig. 7, A) are more or less subject to variation but in the more typical cases extend lengthwise and are two or three times as long as broad, a valve being mostly fourteen to sixteen cells across. The local thickenings of the cell-walls are conspicuous and are largely (but not wholly) confined to the inner longitudinal walls, that is, to the walls turned toward the middle of the valve. The median wall thus shows two rows of thickenings, which alternate with one another, whereas each other longitudinal wall shows only one such row. As a rule three or four thickenings are present in each cell; they extend from the surface through the thickness of the layer but are not prolonged on either tangential wall.

Although the cells of the inner layer (Fig. 7, B) do not exactly correspond with those of the outer layer, they are of about the same size and shape. With rare exceptions each cell shows from three to six transverse bands of thickening on the inner tangential walls, these bands being prolonged down the radial walls but not forming complete rings. Sometimes, however, the bands are less developed and do not extend wholly across the tangential walls, gradually fading out toward the outer boundary of the cell.

The spores are pale yellow, minutely punctulate, and 14–16 μ in diameter. The elaters are mostly 0.3–0.4 mm. in length and 6 μ in diameter in the middle, tapering gradually to the extremities. Each one bears the usual broad band of thickening extending its entire length.

If the account of the capsule-valves as given above is compared with the description of Andreas (**1**, p. 195) certain interesting differences become apparent. According to his statements the three rows of cells of the outer layer that come next to the edge of the valve have their thickenings definitely restricted to the inner longitudinal walls.

In the remaining cells, however, the thickenings are arranged more irregularly and the median wall of each valve is entirely free from them. In all probability these differences are specific in character, and it is natural to assume that the capsule-valves in *Metzgeria* may be as useful in distinguishing closely related species as in the related genus *Riccardia*. It is to be regretted that Andreas does not indicate the species from which his description was drawn.

Although no gemmae have been observed in *M. decipiens*, a single case of regeneration from a marginal cell has been demonstrated. The product of regeneration in this instance bore a strong resemblance to a gemma, but its true nature was made evident by the zone of dead cells separating it from the rest of the thallus. Attention may be called also to the ease with which the species reverts to a more juvenile condition. The narrow and relatively hairless thalli, which have been described, represent cases of such reversion, and these often reach a more extreme state by losing their costae altogether, thus becoming reduced to uniform, unistratose bands of cells (Fig. 6, C). The prevalence and long duration of these reversionary forms have added to the difficulties of recognizing and defining the species.

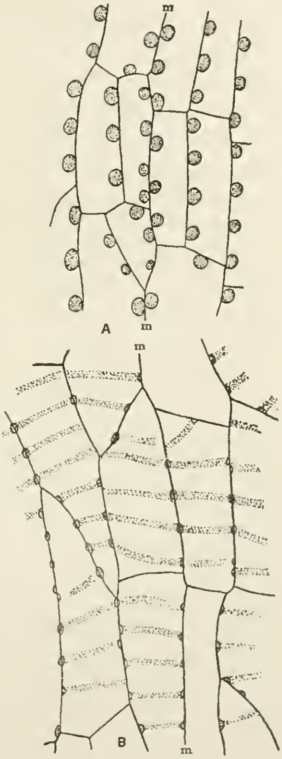

Fig. 7. Metzgeria decipiens (Massal.) Schiffn. & Gottsche.

A. Cells from outer layer of a capsule-valve, × 300; *m*, median wall of valve. B. Cells from the inner layer of a capsule-valve, × 300; *m*, median wall of valve. The figures were both drawn from a specimen collected at Corral by Thaxter, No. 138.

In reducing *M. decipiens* to doubtful synonymy under *M. nitida* (see p. 272) Stephani criticised Schiffner for basing a new species on material so poorly developed that it could not be definitely determined. In the writer's opinion this criticism is unjustified. In the first place *M. decipiens* was really based on *M. furcata* var. *decipiens* of Massalongo, and the figures drawn from Spegazzini's type specimen (**11**, *pl. 28, f. 36*) show female branches in abundance, some of them with young calyptras. Massalongo's description, moreover, in spite of its brevity, brings out some of the most distinctive characters of the species. In the second place Naumann's "Gazelle" Expedition specimen of *M. decipiens* is equally well developed and also shows characteristic female branches. It even illustrates the variability of the species to a certain extent, some of the thalli being almost destitute of hairs. These two specimens, which the writer has carefully examined, agree in all essential respects and certainly form an adequate basis for the proposal of a new species.

Under the original description of *M. glaberrima,* which is here included among the synonyms of *M. decipiens,* Stephani cited specimens from the Straits of Magellan, "Chile," New Zealand and Australia. Apparently he afterwards changed his mind regarding the New Zealand and Australian material, for, in 1911, he restricted the range of the species to southern Chile, Tierra del Fuego, Falkland and Antipodes Islands (**24**, p. 10). The natural inference from this would be that *M. glaberrima* as originally defined was an aggregate. If this should be established the "type-specimen" should presumably be one of those from the Straits of Magellan, since these are mentioned first. As collectors of the Magellan specimens Stephani named Speggazzini, Dusén and the "Exped. Gazelle." The actual specimens of Spegazzini and Naumann cited have not been seen by the writer. Dusén's Port Gallant specimen, however, agrees fully with Spegazzini's specimen of *M. furcata* var. *decipiens* and Naumann's specimen of *M. decipiens;* and, since it agrees with none of the other specimens of *Metzgeria* collected by Spegazzini and Naumann, it would almost seem as if Stephani had based his *M. glaberrima,* at least in part, upon the very specimens utilized by Schiffner in his description of *M. decipiens.* In any case Dusén's Port Gallant specimen is referable to *M. decipiens,* and the same thing is true of at least two other specimens collected by Dusén and definitely listed by Stephani under the name *M. glaberrima.* It therefore seems justifiable to consider the latter a synonym of *M. decipiens,* even if the original *M. glaberrima* included other distinct forms. The writer regrets that the New Zealand and Australian specimens cited by Stephani have not been available for study.

The type specimen of *M. nuda,* likewise included as a synonym, is sterile and far more poorly developed than the original material of *M. decipiens.* The thalli are not invariably naked, as the description states, although the hairs even when present are scantily developed. They occur on the margin and also ventrally on the costa. The alar cells average about 33 × 21 μ but are not always as small as this, averaging in one area as much as 41 × 33 μ. Since the absence of cilia is the only important feature distinguishing *M. nuda* from *M. decipiens,* and since this feature has been proved inconstant, the two species are clearly synonymous.

8. **Metzgeria epiphylla,** sp. nov.

Yellowish or whitish green, not becoming bluish after drying, scattered or in thin depressed mats, loosely adherent to the substratum: thallus prostrate, repeatedly dichotomous but also with ventral vegetative branches, flat or slightly convex, well-developed thalli mostly 0.6–0.8 mm. wide and rarely as much as 1 mm., the forks mostly 0.6–2.4 mm. apart; costa bounded both dorsally and ventrally by two rows of cortical cells; wings mostly eight to thirteen cells broad, the cells mostly 37 × 30 μ, the walls thin or slightly and uniformly thickened, sometimes with indistinct trigones; hairs varying in abundance; marginal hairs usually occurring singly but not infrequently in pairs, sometimes branched at the apex and acting as rhizoids, mostly 0.1–0.15 mm. long and 8–10 μ wide; ventral hairs sometimes lacking, sometimes sparingly developed on the costa and still more sparingly on the wings, similar to the marginal hairs: inflorescence dioicous: ♂ branches subspherical, smooth, 0.3–0.4 mm. long and 0.25–0.35 mm. wide: ♀ branch broadly obovate, 0.3–0.35 mm. long and wide, hairs abundant on the margin and usually on the ventral surface; calyptra about 1 mm. long and 0.45 mm. wide, the hairs abundant above the middle, few and scattered below: capsule brown, oval, mostly 0.5–0.6 mm. long and 0.35–0.4 mm. wide, the valves (when spread out) 0.6–0.75 × 0.2–0.25 mm.; spores pale brownish yellow and very minutely punctulate, 16–18 μ in diameter; elaters 0.3–0.4 mm. long, 6 μ wide in the middle and with a single broad spiral band running the entire length: gemmae sometimes abundant, arising on more or less narrowed and specialized branches with limited growth, marginal or submarginal and dorsal in position, orbicular to oval, plane or slightly convex and bearing a few short marginal hairs slightly displaced to the concave surface.

Specimens examined: Corral, 1896, *Dusén 82, 191* (U., as *M. australis,* and listed under this name by Stephani, **20**, p. 19); same locality, 1905–06, *Thaxter 10a, 108, 140* (H., Y.). No. 10a, collected by Professor Roland Thaxter, may be designated the type.

In its vegetative features *M. epiphylla* resembles *M. decipiens* so closely that it would be difficult to tell them apart if these features alone were relied upon. Both species, for example, show a flat or nearly flat thallus, branching both dichotomously and ventrally, and having a costa bounded on each surface by two rows of cortical cells. The costae, moreover, although usually naked, occasionally develop a few ventral hairs; the alar cells are almost identical in size and in the characters derived from their walls; and the marginal hairs exhibit a similar range in abundance, being sometimes numerous and sometimes very few and occasionally showing a twinned arrangement although usually occurring singly.

On the whole *M. epiphylla* (Fig. 8, A) is slightly smaller than *M. decipiens* and prefers living leaves as a habitat, although it occasionally grows on bark. *M. decipiens*, on the contrary, is much more at home on bark and other substrata than on leaves. One other vegetative difference to be noted, although more observations are necessary to prove its constancy, is the occasional presence of ventral alar hairs in *M. epiphylla* and their complete absence in *M. decipiens*.

The most trustworthy differential characters, however, are those derived from the sexual branches and the capsules, and these are supplemented by the presence of gemmae in *M. epiphylla* and their absence in *M. decipiens*. The male branches are much alike in the two species, except that those of *M. epiphylla* are even more strongly incurved, so much so that the apex usually comes in contact with the base. The female branches when normally developed are distinguished by their greater hairiness, the ventral hairs not being restricted to the thickened median portion, as in *M. decipiens*, but scattered over the entire surface. The capsules are mainly distinguished by differences in the character and distribution of the local wall-thickenings of the valves. In *M. decipiens*, as has been shown, the median wall of the outer layer has two rows of local thickenings, these being largely restricted to the inner longitudinal walls of the valve-cells. In *M. epiphylla* the median wall has no local thickenings or very small ones (Fig. 8, B), approaching in this respect the condition described by Andreas. On each side of this median wall two rows (or more rarely three) have the thickenings restricted to the outer longitudinal walls, while the remaining cells have them on the inner walls, as in *M. decipiens*. Each valve thus has two longitudinal walls with double rows of local thickenings. In the inner layer of the valves, transverse bands, instead of being conspicuous, are either lacking or very indistinct (Fig. 8, C), although the prolongations of such bands on the radial walls are still apparent.

Even in the absence of sexual branches and capsules, the presence of gemmae will at once serve to distinguish *M. epiphylla* from *M. decipiens.* The gemmiparous branches seem to be always narrower than the normal vegetative thalli, the reduction in width being confined to the wings, but at first no other signs of differentiation are evident. With the appearance of the gemmae (Fig. 8, D) the wings become still narrower and the branches curve away from the substratum, their growth in length being sooner or later brought to an end. In extreme cases the wings become reduced to a width of only two or three cells, but the growth may cease while the wings are considerably broader. No cases have been observed where a gemmiparous branch had reverted to a vegetative condition, and yet it would not be surprising if such a change occasionally took place. The gemmiparous branches are flat or slightly convex when seen from the dorsal surface and sometimes branch after the production of gemmae has begun.

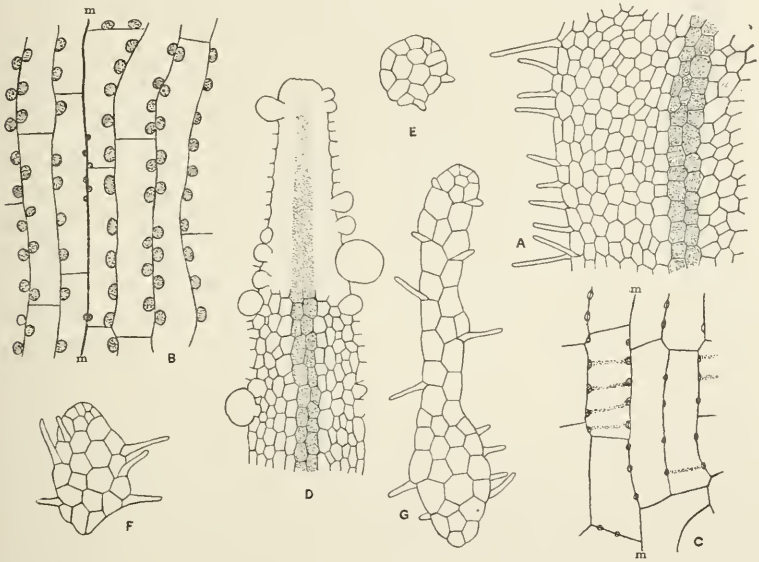

Fig. 8. Metzgeria epiphylla Evans.

A. Portion of a thallus, dorsal view, × 50. B. Cells from outer layer of a capsule-valve, × 300; *m,* median wall of valve. C. Cells from inner layer of a capsule-valve, × 300; *m,* median wall of valve. D. Gemmiparous branch, dorsal view, × 50. E, F. Gemmae about ready to separate, × 100. G. Germinating gemma, × 100. The figures were all drawn from the type material.

The gemmae which are first produced are strictly marginal, and in their development a marginal cell becomes directly the mother cell of the gemma. After the gemmae have been set free the empty mother cells with their ruptured outer walls can easily be demonstrated, and sometimes long and continuous stretches of such empty cells are present, indicating a copious formation of gemmae. Later on, with the narrowing of the gemmiparous branches, the cells of the submarginal row may in turn give rise to gemmae, setting them free dorsally. Apparently, however, the alar cells within this row and the cortical cells of the costa do not have this power.

The gemmae when set free are plane or slightly convex bodies, always small and relatively simple, yet varying somewhat in size and in the number of their component cells (Fig. 8, E, F). Most of them are orbicular to oval in outline, measuring 0.1–0.12 mm. in length by 0.09–0.1 mm. in width and being usually four cells across. A single apical cell is present and the stalk cells, although normally two, are often indistinct. On each side three or four short marginal hairs, borne singly and slightly displaced to the concave surface, can be detected; these are sometimes spreading and sometimes extend at right angles to the surface of the gemma. Upon germination the marginal hairs elongate, and the apical cell resumes its growth, giving rise to a flat thalloid extension only two or three cells wide and thus narrower than the gemma itself. In the case illustrated (Fig. 8, G) this extension had grown to more than twice the length of the gemma and had produced a series of scattered marginal hairs, slightly displaced to one surface. No later stages of germination have been observed.

9. Metzgeria violacea (Ach.) Dumort.

Jungermannia violacea Ach.; Weber & Mohr, Beitr. Naturk. **1**: 76. *pl. 1, f. 1–3.* 1805.
Fasciola violacea Dumort. Comm. Bot. 114. 1822 (in part).
Echinogyna violacea Dumort. Syll. Jung. 84. 1831 (in part).
Echinomitrium violaceum [*Echinomitrion violasceus*] Corda; Sturm, Deutschl. Flora **2**: 81. *pl. 22.* 1832 (in part).
Echinomitrium [*Echinomitrion*] *furcatum δ. violaceum* Hüben. Hep. Germ. 47. 1834 (in part).
Metzgeria violacea Dumort. Recueil d'Obs. sur les Jung. 26. 1835 (in part).
Metzgeria furcata δ. 2. *violacea* Nees, Naturg. Europ. Leberm. **3**: 489. 1838 (in part).
Metzgeria conjugata var. *β. violacea* Lindb. Acta Soc. F. et Fl. Fenn. **12**: 34. 1877.
Metzgeria angusta Steph. Bull. Herb. Boissier **7**: 944. 1899 (in part).
Metzgeria antarctica Steph. Sp. Hepat. **6**: 47. 1917.

SPECIMENS EXAMINED: near Arique, no date, *Lechler 633* (B., as *M. furcata* var. *violacea,* and listed as *M. furcata* by Stephani, **19**, p. 941); Corral, 1896, *Dusén,* mixed with *82* (U.); valley of the Aysen River, 1897, *Dusén 324* (Möll., St., as *M. hamata,* and listed under this name by Stephani, **20**, p. 20); Quellon, Chiloé, 1908, *Halle & Skottsberg 29* (St., as *M. chilensis,* and listed under this name by Stephani, **24**, p. 10); Punta Arenas, 1895, *Dusén 5* (U., as *Metzgeria* sp.); same locality and date, *Dusén,* no number (Möll., N. Y., as *M. angusta,* and listed under this name by Stephani, **21**, p. 10); same locality, 1905–06, *Thaxter 159* (H., Y.); same locality, 1907, *Von Schrenk* (B., type of *M. antarctica*); Isla di Navarino, Tierra del Fuego, 1902, *Skottsberg* (St.); Provenir, Tierra del Fuego, 1895, *Dusén 23* (U., as *M. angusta,* and listed under this name by Stephani, **21**, p. 10). The following specimens collected outside the boundaries of Chile may likewise be cited: without definite locality, Peru, *Lechler,* mixed with another species of *Metzgeria* (N. Y., as *M. furcata* var. *violacea*); San Carlos, Lake Nahuelhuapi, Argentina, 1897, *Dusén 456* (St., U., as *M. angusta,* and listed under this name by Stephani, **20**, p. 19); Dusky Bay, New Zealand, 1773, *Sparrmann* (Y., TYPE of *Jungermannia violacea,* specimen received from the Acharius Herbarium at Lund).

Specimens of *Metzgeria* showing a bluish or purplish coloration have long been familiar to students of the Hepaticae. As long ago as 1785 Dickson described the color of his *Riccia fruticulosa,* now known as *Metzgeria fruticulosa* (Dicks.) Evans (see **4**, p. 293), as "aeruginosus seu viridi-subcaeruleus," and Acharius, in 1805, stated that the present species had a "schöne Veilchenfarbe." The older writers evidently regarded these unusual hues as natural to the living plant, and Hübener, in 1834, associated the color with the presence of iron in the substratum (**9**, p. 47). A few years later, however, Funck showed that these ideas were untenable. In a letter addressed to Nees von Esenbeck (see **15**, p. 492) he discussed the blue color of *M. fruticulosa,* which he had found at Gefrees, in the Fichtel Mountains of Germany. His specimens grew on the young trunks of the Norway spruce and were distinctly green when he collected them. About six months after they were dried most of them had assumed a blue color. The soil where the trees grew was a disintegrated gneiss, without a trace of iron, and he suggested that there might be some connection between the color and the tannin in the bark. His opinion regarding the post mortem nature of the blue coloration has recently been confirmed by Miss Herzfelder (**7**, pp. 392–397), who worked mainly on *M. fruticu-*

losa. According to her statements no plants showing the blue or purple color are capable of revivication.

The coloration is by no means characteristic of the genus *Metzgeria* as a whole but is confined to certain definite species. It thus has a significance from the standpoint of taxonomy, even if lifeless specimens are the only ones that show it. So far as the writer's observations go the coloration is usually, if not invariably, associated with gemmiparous species and, in some cases at least, with species in which the gemmiparous branches show marked differentiation. The species may further be distinguished by a tendency toward reversion and by the long persistence of embryonic and juvenile stages of development. In extreme cases this persistence may be so pronounced that a large mat of plants will absolutely fail to show the normal features of the species to which it belongs. Most of the species in question are, moreover, usually sterile, and, even when male branches are present in some abundance, female branches are almost always extremely rare or absent altogether. On account of these various peculiarities the species of *Metzgeria* turning bluish or purplish have been the source of much confusion to students, and different observers have often reached divergent conclusions in regard to them.

The best known species in this category is *M. fruticulosa,* widely distributed in Europe and recently reported by the writer from the states of Washington and Oregon. *M. violacea* is a close relative of *M. fruticulosa,* so close that it can hardly be regarded as anything more than a "small" or "geographical" species. The original material of *Jungermannia violacea* was collected in 1773 at Dusky Bay, New Zealand, by A. Sparrmann, who accompanied Captain Cook on his second voyage. Strange to say there is no record of its having been collected there a second time, and most of the works dealing with the Hepaticae of New Zealand make no mention of it whatever. This is true, for example, of Hooker's well-known Handbook of the New Zealand Flora, published in 1867, and of Stephani's recent Species Hepaticarum.

The earlier writers, however, were more charitable toward the species. In 1815 its validity was recognized by Weber (**27**, p. 100), who regarded it as identical with Dickson's *Riccia fruticulosa,* reducing the latter to synonymy, in spite of its having been published earlier. For a while Weber's views prevailed to a certain extent, and European writers continued to use the name "*violacea,*" now in a specific and now in a varietal sense, always assuming as they did so that *J. violacea* and *Riccia fruticulosa* were one and the same thing. With the lapse of time the names "*violacea*" and "*fruticulosa,*" as applied to *Metzgeriae,* gradually fell into disuse, and the plants to which they were applied came to be regarded as unimportant forms of *M. furcata.* Lindberg, fortunately, did not share these views. He considered that *R. fruticulosa* represented a distinct and well-marked variety of *M. furcata* and that it was amply distinct from *J. violacea,* which he regarded as a corresponding variety of *M. conjugata.* It remained for the writer to restore Dickson's plant to specific rank, under the name *M. fruticulosa,* and the same recognition, with considerable hesitation, is given to *M. violacea* in the present paper.

Through the kindness of Professor Nordstedt of Lund, the writer has had the privilege of studying a part of the type material of *Jungermannia violacea.* In spite of its long preservation it soaks up readily in water and retains the vivid coloration to which it owes its name. It lacks sexual organs completely, as the published descriptions emphasize, but shows pointed and highly differentiated gemmiparous branches, to which numerous gemmae still remain attached. These specimens have been carefully compared with the long series of Chilean specimens listed above and do not seem to differ from them in any important respect. *M. violacea,* as here understood, is exceedingly variable; it shows marked reversions, and many of the plants examined exhibit a juvenile or even embryonic stage of development. The following account is therefore somewhat composite in character.

The more typical vegetative thalli vary from flat to convex, with the margins of the wings more or less revolute. The width is usually 0.5–0.8 mm., but narrower thalli are not infrequent and some attain a width of 1 mm. or slightly more. Measured in cells the wings are mostly ten to twenty cells wide. Ventral branching occasionally occurs, although the usual method is by forking, the forks being mostly 0.6–1 mm. apart and the entire thallus rarely exceeding a length of 0.5–1 cm. The alar cells, taking the mean average from five specimens, measure about $31 \times 25\ \mu$, the highest average obtained being $34 \times 27\ \mu$ and the lowest $27 \times 21\ \mu$. The walls are thin throughout and trigones are either absent altogether or minute and inconspicuous.

The variation in the number and distribution of the hairs is about as great as in *M. decipiens* and *M. epiphylla.* In other words a thallus may be hairless throughout the whole or the greater part of its extent, it may produce hairs in abundance, or it may present almost any intermediate condition between these extremes. The marginal hairs are not infrequently in pairs but usually arise singly. In fact, on some of the plants examined no twinned hairs could be discovered, although the hairs were fairly numerous. When the wings are distinctly revolute and the hairs abundant, a delicate weft is sometimes to be observed between the contiguous margins, much as in *M. decrescens,* but the hairs are just as likely to extend irregularly in all directions. Even when marginal hairs are present the thallus is often naked elsewhere; in other cases ventral hairs can be demonstrated on the costa and, still more rarely, on the wings. The hairs vary greatly in length, the majority measuring perhaps 0.08–0.12 μ in length; the diameter is mostly 10–12 μ. The costa, in ordinary well-developed thalli, is bounded both dorsally and ventrally by two rows of cortical cells.

In two specimens a few male branches were observed. They were smooth and almost spherical, the costa being so strongly incurved that the apex almost touched the base. Some of the branches were about 0.25 mm. in diameter but a few were somewhat larger, the largest one seen measuring 0.4–0.35 mm. The single female branch demonstrated was so disintegrated that its true features could not be determined. It bore a young calyptra with crowded hairs in the upper part and scattered hairs below the middle.

In most of the material gemmae are present in large numbers, and the gemmiparous branches (Fig. 9, A, B) show interesting modifications, comparable with those described under *M. epiphylla* but reaching a more advanced type of specialization and approaching in this respect the highly specialized gemmiparous branches of *M. fruticulosa.* Even when the vegetative branches are strongly convex and prostrate the gemmiparous branches are plane or nearly so and curve away from the substratum. At the same time the wings become narrower and narrower until, in extreme cases, they become reduced to a width of only two or three cells. No cases have been noted, however, in which the wings had entirely disappeared, and the growth of the gemmiparous branch often comes to an end while the wings are still four cells broad or more. With the reduction in the width of the wings, the cortical cells sometimes continue to show the usual arrangement in four rows, but the rows sometimes become increased to as many as six, both dorsally and ventrally, the rows under these circumstances being irregular and the cells themselves considerably reduced in size. Sometimes, especially when the formation of gemmae begins in a juvenile thallus, the gemmiparous branches may lose their costae and become reduced to narrow unistratose thalli only five or six cells broad; or, if the vegetative thallus itself lacks a costa, the gemmiparous branches may retain the same simple structure throughout their entire length. In other cases the gemmiparous branches may develop new costae (Fig. 9, A), sometimes retaining them as long as growth continues and sometimes losing them before growth is brought to an end. It will be seen from this account that the gemmiparous branches exhibit a wide range of variability.

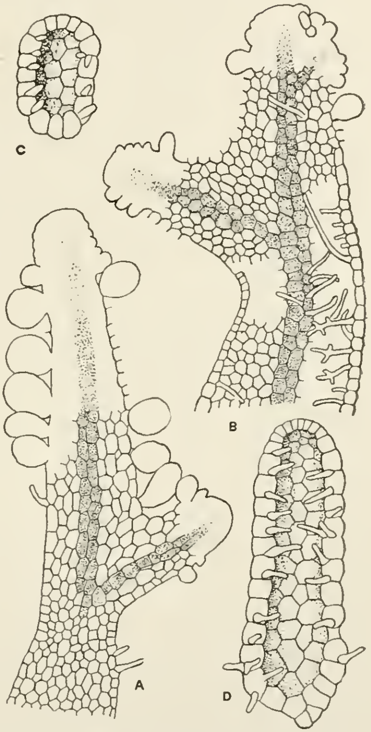

Fig. 9. Metzgeria violacea (Ach.) Dumort.

A, B. Gemmiparous branches, ventral view, × 50. C. Gemma about ready to separate, × 100. D. Germinating gemma, × 100. A was drawn from an unnumbered specimen labelled *M. angusta* and collected at Punta Arenas by Dusén; B–D, from a specimen collected at the same locality by Thaxter, No. 159.

The first gemmae to be produced are marginal and arise in acropetal succession, every marginal cell in extreme cases giving rise to a gemma. If the gemmiparous branch shows the more specialized features described above, some of the later gemmae may be given off dorsally from the submarginal alar cells and perhaps also from the cortical cells of the costa both dorsally and ventrally, the acropetal succession in such cases not persisting. In instances of extreme production the crowded gemmae extending in all directions almost conceal the tip of the slender gemmiparous branch, although even then the apical cell of the branch can usually be clearly distinguished.

At the time of separation the gemmae vary considerably in size, but an average example measures about 0.12–0.1 mm. and is five cells across. It is oblong in outline and strongly convex, the whole margin (including the single apical cell and the indistinct stalk) being revolute (Fig. 9, C). On each side three or four short rudiments of marginal hairs can be distinguished; these normally arise between every two marginal cells and may be borne singly or (more rarely) in pairs. Otherwise the gemmae show no cell-differentiation and are unistratose throughout.

In the early stages of germination the young plant simply repeats the features of the gemma and develops into a narrow strap-shaped thallus, strongly convex and bearing single or twinned hairs between every two marginal cells (FIG. 9, D). As the growth goes on the hairs of the gemma elongate and tend to equal those of the young plant. Even this early stage may be long-continued, and repeated dichotomies may take place before signs of further differentiation become apparent. The plant may, in fact, become gemmiparous almost immediately, and, in extreme cases, a gemma may form secondary gemmae before becoming detached. If differentiation proceeds normally the young plant gradually grows wider, develops a costa, and eventually shows the characteristic vegetative features of the species.

If the description just given is compared with the writer's earlier description of the gemmae and gemmiparous branches in *M. fruticulosa*, it will be seen that they correspond in most essential respects, and even in their vegetative features the two species are strikingly alike. In *M. fruticulosa*, however, the costa rather frequently shows three or four rows of ventral cortical cells, the gemmiparous branches sometimes lose their wings completely (becoming radial in character), and the gemmae are either plane or only slightly convex. In *M. violacea*, on the other hand, the costa of a vegetative thallus rarely shows more than two rows of ventral cortical cells (except just behind a dichotomy), the gemmiparous branches apparently never lose their wings completely (thus remaining dorsiventral), and the gemmae are distinctly convex. On the basis of these slight differences and the wide geographical separation of *M. fruticulosa* and *M. violacea*, it seems justifiable to admit the validity of both, at least provisionally.

Among the Chilean species *M. violacea* finds its closest allies in *M. decipiens*, which never produces gemmae, and *M. epiphylla*, which produces marginal and submarginal gemmae on specialized branches. The latter species is especially close, and the characters derived from the costa, the alar cells and the hairs are almost identical, except that the cell-measurements are a trifle higher. The following differential characters, however, suffice to distinguish the species under most circumstances. In *M. violacea* the plants usually grow on wood and develop a bluish coloration after being dried; the thallus is frequently convex; the gemmiparous branches reach a high stage of specialization, giving off gemmae from the cortical cells of the costa as well as from the alar cells; and the gemmae themselves are distinctly convex. In *M. epiphylla* the plants usually grow on leaves and do not develop a bluish coloration after being dried; the thallus is rarely distinctly convex; the gemmiparous branches, although specialized, develop gemmae only from alar cells; and the gemmae themselves are plane or only slightly convex.

Stephani's *M. angusta,* to which he referred some of Dusén's specimens of *M. violacea,* was based on material from Brazil, Venezuela, Trinidad, Mexico, Guatemala, Louisiana and Santo Domingo, as well as from Chile and Patagonia. He speaks of Dusén's specimens as exceedingly reduced, so that in all probability they are distinct from the other specimens cited. According to the description of *M. angusta* the wings are everywhere eight cells wide, the alar cells measure $54 \times 37\ \mu$, and the costa is setulose throughout on the ventral surface. It will be seen that this description does not apply very well to the specimens of *M. violacea.* The description of *M. antarctica* applies much better, except that the wings are usually much narrower than 0.7 mm., the measurement there given. It is unfortunate that Stephani made no mention in his description of the gemmae and gemmiparous branches, which certainly yield the most distinctive characters of the species.

10. METZGERIA MAGELLANICA Schiffn. & Gottsche.

Metzgeria magellanica Schiffn. & Gottsche in Schiffner, Forschungsreise "Gazelle" **4**^{4}: 43. *pl. 8, f. 6.* 1890.

SPECIMEN EXAMINED: Tuesday Bay, Straits of Magellan, 1876, *Naumann* (S., TYPE); known with certainty only from the type locality.

The type material of this interesting species, kindly sent for examination by Professor Schiffner, shows that it is amply distinct from *M. nitida,* under which Stephani included it as a synonym (see p. 272). The plants are a dull whitish green and grew in loose mats in admixture with other bryophytes, including a trace of *M. decipiens.* The thallus is normally so strongly convex that it approaches a terete condition, the revolute wings almost meeting below, as shown in the published figure. Of course, as would be expected, the convexity is sometimes less pronounced than this, and the thallus may even approximate a plane condition. The width when explanate is about 1 mm.; in the natural state it is usually 0.6–0.8 mm., and the length rarely exceeds 2 cm. Measured in cells the wings are mostly ten to eighteen cells across. Ventral branching is not rare, but the normal branching is dichotomous, the successive forks being usually 1–3 mm. apart.

Hairs vary somewhat in abundance and are apparently restricted to the margin, the ventral surface being entirely naked throughout. In many cases the margin is likewise hairless for long stretches, but at the other extreme the hairs may occur between every two marginal cells. They usually extend in the same direction as the wings, rarely being numerous enough to form a weft in the space between the margins. According to the original description the hairs often occur in pairs or even in three's. The writer, however, has been unable to verify this statement. So far as his observations go the hairs are invariably borne singly, arising in the usual way from small cells cut off from the marginal cells. In rare instances the marginal cells themselves may project directly as hairs, especially if a rhizoidal function is assumed, and under these circumstances two hairs may be situated side by side, but this is very different from the usual paired condition. Sometimes the hairs are short and spine-like with strongly thickened walls, yet this type of hair is exceptional, most of them being of the usual slender type and measuring 0.09–0.15 mm. in length by about 10 μ in width. They are truly marginal in position.

The costa, as described by Schiffner, is uniform in structure, being bounded both dorsally and ventrally by two rows of cortical cells. The alar cells are unusually small, averaging about $28 \times 24\ \mu$, although somewhat larger cells are often interspersed among the others. The walls are distinctly thickened and show indistinct trigones and occasional intermediate thickenings.

The male plants bear sexual branches in some abundance. The latter are oval to globular in form, measuring usually 0.3–0.35 mm. in length by 0.25–0.35 mm. in width and their cells are but slightly smaller than those of the vegetative thallus. Although the costa is strongly incurved the apex of the branch does not usually approach the base very closely. No appendicular organs are present except the slime-papillae.

The female branches are broadly obovate and deeply indented at the apex. They are mostly 0.3–0.35 mm. long by 0.45–0.6 mm. wide, and their concave halves approach each other so closely before fertilization that their margins are almost in contact. Ventral hairs are usually completely absent, but in two instances a single such hair was seen growing out from the thickened median portion. Marginal hairs, on the contrary, are fairly abundant, and represent outgrowths of small cells, just as in a normal vegetative thallus. They are mostly short and spine-like, with strongly thickened walls. The calyptras at maturity are mostly 1.5–2.5 mm. long and 0.7–0.85 mm. in diameter.

Their relatively short hairs are densely crowded in the upper part but more scattered below the middle.

Although *M. magellanica* is undoubtedly a close relative of *M. hamata*, as Schiffner states, it bears a strong superficial resemblance to small forms of the variable *M. decrescens,* owing to its subterete thallus with marginal hairs borne singly. Differences in the costa will at once serve to separate the two species. In *M. magellanica* the cortical cells are definitely in two rows both dorsally and ventrally, and the boundary between the costa and the unistratose wings is abrupt; in *M. decrescens,* although the cortical cells may be in only two rows both dorsally and ventrally, this condition is exceptional, the number of rows being usually more than two, and the boundary between the costa and the unistratose wings is often gradual, the two being separated by a narrow band two or three cells thick. *M. decrescens* is further distinguished by its larger alar cells with thinner walls, and by the sharp contrast in size between the cells of the vegetative thalli and those of the male branches.

11. METZGERIA HAMATA Lindb.

Metzgeria linearis Lindb. Acta Soc. Sci. Fenn. **10**: 494. 1875. Not *M. linearis* (Sw.) Aust.
Metzgeria hamata Lindb. Acta Soc. F. et Fl. Fenn. **12**: 25. *f. 25.* 1877.
Metzgeria leptoneura Spruce, Trans. Bot. Soc. [Edinburgh] **15**: 555. 1885.
Metzgeria nitida Mitt. Jour. Linn. Soc. Bot. **22**: 243. 1887.
Metzgeria australis Steph. Hedwigia **28**: 267. 1889.

SPECIMENS EXAMINED: Corral, 1905, *Thaxter 34* (H., Y.); Huafo Island, 1908, *Skottsberg 253* (U., as *M. albinea*, and listed under this name by Stephani, **24**, p. 10); Newton Island, 1896, *Dusén 113* in part (B.); Punta Arenas and Tuesday Bay, Straits of Magellan, 1876, *Naumann* (S., listed as *M. linearis* by Schiffner, **16**, p. 42); Staten Island, 1882, *Spegazzini 65* in part (Massal., Y., **11**, p. 257). The material from Corral is mostly in a juvenile condition, many of the thalli being narrow and etiolated and lacking costae completely. In a few cases, however, the distinctive features of *M. hamata* are clearly apparent.

The following additional Chilean stations may be cited from the literature: near Puerto Varas, *Dusén* (**20**, p. 20); Wollaston Island, *Hariot* (**2**, p. 246); Hermite Island, *Hooker* (**10**, p. 27).

The geographical distribution of *M. hamata* is very extensive in both hemispheres. In Europe it seems to be restricted to Ireland and western Great Britain with an extension northward to the Faroe

Islands. In Asia it occurs abundantly in the Himalayas and is found also in Japan, Java and Sumatra. In America its northernmost station, so far as known, is in Alaska. It reappears in the Allegheny Mountains, although rarely collected there, and seems to attain its most vigorous development in Jamaica and other West Indian islands. Although not yet known from Mexico it occurs in Guatemala and Costa Rica and has been reported in South America from British Guiana and Brazil and along the chain of the Andes from Colombia to Bolivia. In Chile, as noted above, its range extends far into antarctic regions. It has been cited also from New Guinea and New Zealand.

The following characters of *M. hamata*, emphasized by Lindberg in his descriptions, are perhaps the most important: the dioicous inflorescence; the convex to subterete thallus with revolute wings; the crowded marginal hairs, usually arising in pairs; the wings otherwise destitute of hairs; the costa bounded both dorsally and ventrally by two rows of cortical cells and bearing hairs on its ventral surface. These characters, in spite of the wide distribution of the species, are found with remarkable constancy. There is, to be sure, a considerable range of variation in the convexity of the thallus and in the abundance of the hairs, especially those of the costa, but this would naturally be expected. When the hairs are considered in more detail they are found to vary in certain of their features. In the more typical plants the hairs of a marginal pair diverge widely and are more or less strongly curved, the concavities of the curves being directed downward or away from the edge of the wing. In subterete thalli a fairly dense weft of hairs may thus be formed, partially concealing the costa. This typical condition, however, is by no means constant; in many thalli the hairs are either straight or irregularly curved, or contorted and extend in various directions (Fig. 10, A–E). When the hairs are sparingly developed, some of them may arise singly; when they are unusually crowded, some of them may be in three's or four's (Fig. 10, E).

The cells of the wings have delicate walls, sometimes with minute and inconspicuous trigones, and vary a good deal in size. It is not unusual, in fact, for the cells in one part of a thallus to be considerably larger than those in other parts, just as in *M. decipiens* and other species. According to the writer's measurements 50 × 37 μ would express the average size of the cells, although Stephani's figures, 65 × 50 μ, and Lindberg's, 50–65 μ, are both a little higher.

According to Lindberg the male branches, which seem to be rarely present, are smooth on the wings and bear a very few short hairs on

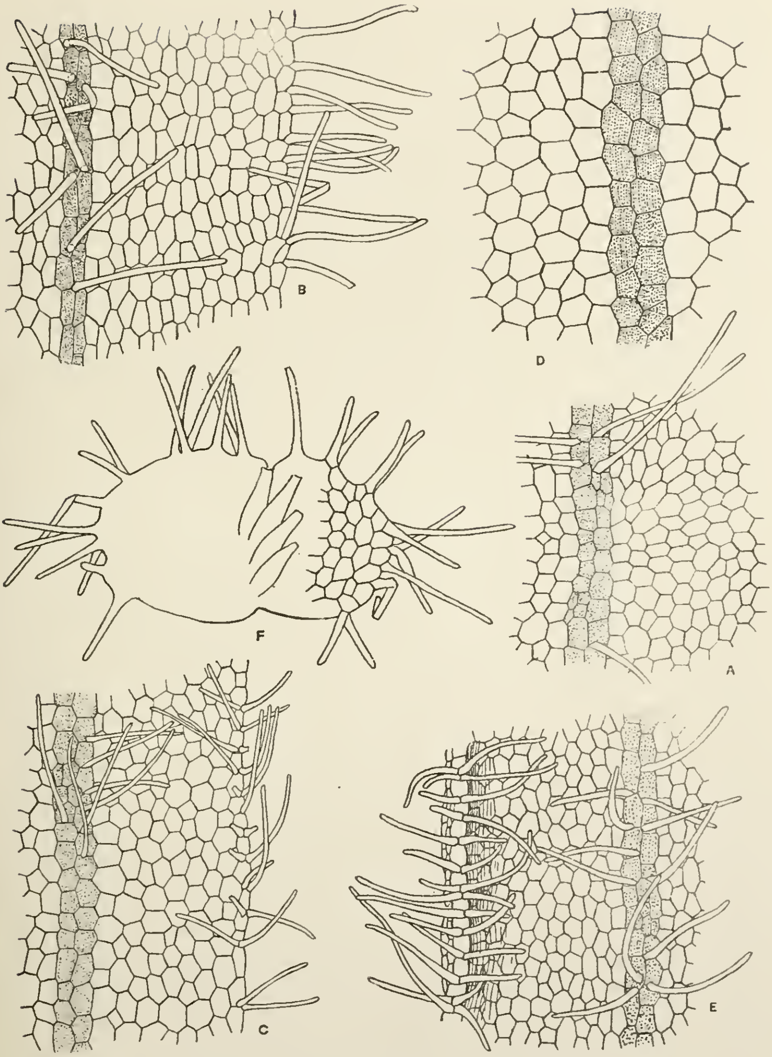

Fig. 10. Metzgeria hamata Lindb.

A–E. Portions of thalli, all except D ventral view, × 50. F. Female branch, × 50. A was drawn from a specimen collected at Punta Arenas by Naumann; B, from a specimen collected at Corral by Thaxter, No. 34; C, from the type material of *M. nitida;* D, from a New Zealand specimen of *M. nitida* collected by Colenso, No. 1100; E and F, from a specimen collected at Mabess River, Jamaica, by the writer, No. 306.

the costa. Stephani describes the branches as hairless throughout, and the writer has been equally unable to demonstrate hairs. It would be unwise, however, to draw definite conclusions from the relatively few male branches examined.

Female branches are much more common than male branches, and Lindberg's description brings out their most important features. He describes them as hairy along the margin and ventrally in the thickened median portion but as hairless elsewhere and adds that the marginal hairs occur singly and that they are very long, crowded, decurved and divaricate. The writer can confirm most of these statements but has demonstrated, in several cases, the occurrence of the hairs in pairs (Fig. 10, F). The calyptra, which is covered over with long hairs, presents few distinctive features; capsules have not yet been studied in detail; and gemmae are apparently never produced.

Stephani's record for the closely related species, *M. albinea*, was based on a specimen from Huafo Island, collected by Skottsberg. Since this specimen differs from *M. albinea* in being dioicous instead of autoicous, and since it shows the other distinctive features of *M. hamata*, it is included in the list of specimens given above. His record for *M. nitida* was based on a specimen collected by Naumann in the Straits of Magellan. In all probability it was an original specimen of Schiffner and Gottsche's *M. magellanica*, since this species is definitely cited as a synonym of *M. nitida*, but nothing to this effect is explicitly stated.

In the writer's opinion *M. nitida*, although recognized as valid by Stephani and others, is a synonym of *M. hamata*. Mitten's original description is brief and unsatisfactory, stating merely that the thallus is dichotomous; that the costa is bounded both dorsally and ventrally by two rows of cortical cells; that the margin bears a few cilia, arising singly or in pairs; and that the cells are hyaline, smooth, and four times as large as those of *M. furcata*. In a supplementary note the further information is given that the species is almost exactly like *M. furcata* in appearance, except that the larger and more translucent cells give it a shiny aspect.

The original description cites only two specimens: "Australia, Apollo Bay, *Sir F. von Mueller*," and "New Zealand, *Rev. W. Colenso*, on a specimen of *Homalia pulchella*, a 279." In the Mitten Herbarium the *M. nitida* cover contains a series of specimens from Australia, Tasmania, and New Zealand and also a few where no locality is indicated. One of the Australian specimens is labeled, "*Jungermannia 87*, Apollo Bay," and is presumably the first of the specimens originally listed. It may therefore be regarded as the type of the species. This specimen is unfortunately fragmentary and is nearly destitute of sexual branches, the few present being poorly developed. The thallus is almost plane, and the costa shows the four rows of cortical cells — two dorsal and two ventral — as called for in the description (Fig. 10, C).

The alar cells are in most regions rather large, measuring mostly 65–70 μ in length by 50–55 μ in width, but cells as short as 55 μ (or even slightly shorter) are not infrequent and may occupy considerable areas in thalli where most of the cells show the higher measurements. It will be seen that these figures are appreciably higher than those of the writer for typical *M. hamata*. Trigones are scarcely discernible. When the marginal hairs are abundant they occur in pairs, slightly displaced to the ventral surface, and there may be a pair between every two marginal cells; when the marginal hairs are scattered they usually occur singly, and long stretches of the thallus may be wholly free from hairs. The costal hairs tend to be less numerous than the marginal hairs but are sometimes crowded. At their best development the hairs are long and flexuous, attaining a length of 0.3–0.4 mm.

Several of the New Zealand specimens in the Mitten Herbarium were collected by Colenso but No. 279 is not present. There is, however, in the herbarium of the New York Botanical Garden, a specimen collected by Colenso and received from Kew, that closely agrees with the Apollo Bay specimen. This bears the number 1100. It has a slightly convex thallus, the margins being subrevolute, and the marginal hairs in exceptional instances arise in three's or even in four's. The alar cells of this specimen average about 70 × 55 μ (Fig. 10, D).

If these two specimens were the only ones to be considered it might appear as if *M. nitida* could be separated from *M. hamata* by its larger leaf-cells. Other specimens, however, from Australia and New Zealand, show that this distinction is inconstant. Although agreeing with the Apollo Bay specimen and No. 1100 in other respects these specimens have distinctly smaller cells. In one Australian specimen, collected by Hartmann, for example, they average about 49 × 40 μ; in another, collected by Lucas, about 54 × 40 μ; in a New Zealand specimen without the collector's name, about 42 × 36 μ, etc. It is clear, therefore, that the distinction in the size of the cells breaks down, and since no other more important and constant distinction has been brought forward, the two species are evidently identical.

Stephani's *M. australis*, which he at one time regarded as a synonym of *M. nitida* and which is here included among the synonyms of *M. hamata,* was based on a series of five specimens, one from Lord Howe's Island, collected by De Camera, and the others from various parts of Australia. In the Mitten Herbarium none of the Australian specimens listed by Stephani (in his original description) are represented, but a specimen collected by De Camera on Lord Howe's Island is included in the *M. australis* cover. This specimen is fragmentary and hardly determinable, but its marginal hairs are borne singly. It disagrees therefore with *M. hamata* but it disagrees equally well with Stephani's description of *M. australis,* according to which the hairs are normally borne in pairs. The other characters brought out are the following: a dioicous inflorescence; a convex thallus with abruptly recurved margins; ventral hairs restricted to the costa; cortical cells of costa in two rows both dorsally and ventrally; alar cells averaging about 45 μ. These are all characters of *M. hamata,* as Lindberg's description clearly shows, and no differential characters of importance are indicated. Whether the specimen from Lord Howe's Island in the Mitten Herbarium is identical with the one listed by Stephani could only be determined by a comparison. If they should be identical it would simply prove that his original *M. australis* was an aggregate.

In its convex thallus and in the structure of its costa *M. hamata* bears a certain resemblance to the smaller *M. magellanica.* In *M. hamata,* however, the marginal hairs are normally borne in pairs, the alar cells average about 50 μ in length and the costa is hairy below; while in *M. magellanica* the marginal hairs are borne singly, the alar cells average about 28 μ in length and the costa is naked.

It will be seen from the preceding pages that the following valid species of *Metzgeria,* although reported from Chile by earlier writers, are not here recognized as members of the Chilean flora; *M. conjugata, M. furcata, M. albinea, M. Liebmanniana,* and *M. pubescens.* In the case of the last three species the Chilean records have all been carefully investigated, usually by means of the actual specimens upon which they were based, and found to rest on incorrect determinations. The same thing is true of most of the records for the first two species, but one record for *M. conjugata* and three for *M. furcata* remain to be further considered.

The record for *M. conjugata* is the following: Chile, *Hahn* (see **19**, p. 951). The specimen in the Boissier Herbarium, upon which this record was based, bears the name *M. conjugata β violacea* and was collected at Valdivia. It agrees in all essential respects with a specimen in the Schiffner Herbarium, likewise collected at Valdivia by Hahn and coming originally from the Jack Herbarium. Both specimens are sterile and, although hardly in a condition to be determined, are surely not *M. conjugata*. Their distinct bluish coloration might seem to indicate *M. violacea*, but the complete absence of gemmae does not support this idea. The wings of the thallus, moreover, are broader than is usual in *M. violacea* and their margins are scarcely if at all revolute. A specimen in the herbarium of the New York Botanical Garden, which is said to have been collected in Peru by Lechler, adds to the uncertainty. This specimen is a mixture of *M. violacea* and a species strongly resembling the Valdivia specimens. The material of this species, however, shows scattered dorsal gemmae on broad thallus-branches and is thus clearly distinct from *M. violacea*. Unfortunately the plants are not only too fragmentary for description but their identity with Hahn's specimens, which bear no gemmae, can not be regarded as definitely established.

The records for *M. furcata* are the following: Cape Horn, *Hooker* (see **8**, p. 480, as *Jungermannia furcata*); Basket Island, *Spegazzini* (see **11**, p. 257); and Chiloé, *Skottsberg* (see **19**, p. 10). Hooker's material of "*J. furcata*" in the Mitten Herbarium, representing a part of the original collection, is made up very largely of *M. decipiens* (see page 296), although a slight admixture of *M. decrescens* is present (see page 279). Since Lindberg found *M. hamata* in the same collection (see page 315) it is possible that still other species may have been included. This possibility, however, is rather remote, and it seems justifiable to conclude that Hooker and Taylor's record was wholly based on incorrect determinations. Regarding the Basket Island and Chiloé records the writer can make no statements, since the specimens involved have not been available for examination.

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Index to Species.

The names of recognized Chilean species and the numbers of pages on which descriptions occur are printed in black-face type; the synonyms are printed in italics.

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(Continued on page 2 of cover.)

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Reprinted from Rhodora, Vol. 25, Nos. 293 & 294, May–June, 1923.

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NOTES ON NEW ENGLAND HEPATICAE,—XVII.[1]

Alexander W. Evans.

In the fifth series of these Notes[2] the writer recognized the genus *Ricciella* A. Br. as valid, separating it from *Riccia* L. on the basis of certain anatomical differences in the thallus. It has since been demonstrated that these differences are inconstant and that the genus *Ricciella* ought not to be maintained.[3] The four New England species referred to *Ricciella* should therefore be known as *Riccia crystallina* L., *Riccia fluitans* L., *Riccia membranacea* Gottsche & Lindenb. and *Riccia Sullivantii* Aust.

Another genus based on equally vague anatomical characters is *Neesiella* Schiffn., of which two species, *N. pilosa* (Hornem.) Schiffn.

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Rhodora **9**: 56. 1907.

[3] See Evans, Bryologist **25**: 81. 1922. See also Howe, North Am. Flora **14**: 11. 1923.

and *N. rupestris* (Nees) Schiffn., have been reported from New England.[1] This genus should be included in the genus *Grimaldia* Raddi, and the New England species should be known as *G. pilosa* (Hornem.) Lindb. and *G. rupestris* (Nees) Lindenb.[2]

In the present series of Notes the nomenclature of *Fossombronia brasiliensis* is considered, *Bazzania denudata* is recognized as a valid species and compared with the closely related *B. tricrenata*, certain species recently segregated from *Scapania nemorosa* are discussed, and a species of *Lejeunea* is reported for the first time from New England. In conclusion a few additions to local state floras are reported and a revised census of New England Hepaticae is given.

1. Fossombronia brasiliensis Steph. Mém. Herb. Boissier 16: 28. [Sp. Hepat. **1**: 382.] 1900. *F. angulosa* Aust. Hep. Bor.-Amer. *119*. 1873 (not Raddi). *F. salina* Lindb. Acta Soc. Sci. Fenn. **10**: 583. 1875 (*nomen subnudum*); Evans, Rhodora **3**: 9. 1901. In the place last cited *F. salina* was first definitely reported from Connecticut and from New England. A few years ago[3] a number of additional stations from a wide range of territory were recorded, extending the known distribution of the species into the West Indies. At the same time the very close relationship between *F. salina* and *F. brasiliensis* was emphasized, and it was pointed out that the only important difference between them (according to the published descriptions) was in the inflorescence, *F. salina* being monoicous, while *F. brasiliensis* was said to be dioicous. It was further pointed out that the name *F. brasiliensis*, on account of Lindberg's inadequate publication of *F. salina*, would have to be maintained, if it should ever be proved that Stephani's plant was really monoicous and that the two species were therefore synonymous. As a matter of fact Schiffner[4] had already demonstrated a monoicous inflorescence in *F. brasiliensis*, stating that the antheridia and archegonia were irregularly mixed together on the upper surface of the stem, and on the basis of his account the reduction of *F. salina* to synonymy would have been justified. In order to be quite certain of this reduction, however, the writer has examined three Brazilian specimens of *F. brasiliensis* from the Boissier Herbarium at Geneva, kindly sent for study by Professor Chodat.

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[1] See Evans, Rhodora **14**: 210, 1912; **16**: 64. 1914.

[2] See Bryologist **22**: 57. 1919. Also North Am. Flora **14**: 43. 1923.

[3] Bryologist **17**: 87. 1914.

[4] Oesterr. Bot. Zeitschr. **61**: 326. 1911.

These specimens are the following, the first being presumably the type of the species: Apiahy, *Puiggari 82*; Santa Catharina, *Ule 51*; and Rio de Janeiro, *Ule 108*. In the first two of these specimens spores are present and agree in all essential respects with those of *F. salina* from the United States and elsewhere. Any doubt regarding the identity of the two species is thus dispelled.

The known range of *F. brasiliensis* now extends from southern New England to Brazil. Many new stations have come to light during the past few years, of which the following are perhaps of particular interest: Kyle, Texas, *F. McAllister 1;* near Guadalajara, Mexico, *Barnes & Land 150*; Santa Ana, Isle of Pines, Cuba, *Britton & Wilson 15684*; Maricao, Porto Rico, *E. G. Britton 4103*; Port of Spain, Trinidad, *R. Thaxter*; and Arima, Trinidad, *Britton, Britton & Brown 2399.* In New England the species is still known with certainty only from Connecticut. In the writer's revised list of New England Hepaticae,[1] it is listed with a "—" sign from Rhode Island, on the basis of an old record for "*F. angulosa*" in Bennett's Catalogue. In June, 1922, Miss Annie Lorenz collected at Glocester in the same state a large sterile *Fossombronia* that probably represents *F. brasiliensis,* but it would be wisest not to report it definitely from Rhode Island until plants with capsules have been found.

2. Bazzania tricrenata (Wahlenb.) Trevis. Mem. Ist. Lomb. 13: 414. 1877. *Jungermannia tricrenata* Wahlenb. Fl. Carpat. 364. 1814. Other synonyms will be noted below. On rocks. Maine: tableland, Mt. Katahdin, 4300 ft. alt., *A. Lorenz* (new to Maine, the author's earlier record having been based on the following species). New Hampshire: Mt. Washington: *J. A. Allen, W. G. Farlow, Underwood & Cook, A. W. E.*; Mt. Monroe, *A. W. E.*; Lakes of the Clouds, *J. A. Allen, A. W. E.*; Mt. Adams, *W. G. Farlow*; Kings Ravine, *A. Lorenz 62, A. W. E.*; Crystal Cascade, White Mountains, *Underwood & Cook* (distributed in Hep. Amer. *53*, as *B. deflexa*); Carter Notch and Dome, *A. W. E.*; Flume, *C. C. Haynes, A. Lorenz & A. W. E.*; Bear's Cave, Franconia Notch, *E. Faxon*; Jackson, *J. A. Allen.* Vermont: Mt. Mansfield, *W. G. Farlow, A. W. E.* The species has been listed from New Hampshire and Vermont by the writer (Rhodora **5**: 171. 1903, as *B. triangularis*; **10**: 190. 1908; **15**: 23. 1913), while Miss Lorenz has definitely reported the Flume specimens (Bryologist **11**: 114. 1908). The specimens in Austin's

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[1] Rhodora **15**: 22. 1913. See also Rhodora **14**: 224. 1912.

Hep. Bor.-Amer. *80*, distributed as *Mastigobryum deflexum*, are likewise referable to *B. tricrenata*; they were collected on "rocks on the higher mountains" and probably came from New Hampshire. The species is known also from West Ranton, Newfoundland, *A. E. Waghorne 163, 164*, and from Mt. Albert, Gaspé County, Quebec, *J. A. Allen 27, J. F. Collins 4202* (see Evans, Bryologist **19**: 29. 1916), but most of the other records from eastern North America were based on the next species.

The wide range of variability exhibited by *B. tricrenata* has long been recognized. Its extreme forms are so different in appearance that they would undoubtedly be considered distinct species if they were not connected by imperceptible intergradations. In its more typical development, as represented by the figures of Macvicar[1] and Müller,[2] the characters are distinct and striking. The plants are pigmented with brown, sometimes very deeply so, and grow in compact mats or scattered among mosses. The individual stems tend to be suberect; they give off numerous flagelliform branches from the axils of the underleaves and occasional lateral branches of the *Frullania* type, the latter forming narrow angles with the stem. The ovate-triangular and persistent leaves are approximate or imbricate and are strongly convex, when seen from above; the dorsal base is rounded or subauriculate; and the apex shows three sharp teeth separated by narrow sinuses, the acroscopic tooth projecting slightly beyond the others. The underleaves are distant to approximate and quadrate-orbicular in outline; the apex is broad and truncate and shows four rounded to acute teeth more or less clearly; while the slightly bulging sides are entire or vaguely toothed. Diverging from this type are forms in which the leaves are distant, less convex, and acute or bidentate; while the underleaves may have only two or three vague teeth or be almost entire. It is not unusual, in fact, for a branch of a typical plant to exhibit divergent features of one sort or another.

The most thorough attempt to define and describe the numerous varieties and forms of *B. tricrenata* was made in 1838 by Nees von Esenbeck,[3] who discussed the species under the name *Herpetium deflexum*. He recognized five subdivisions of the first rank (or varieties), giving them the names α *tricrenatum*, β *implexum*,

[1] Student's Handb. British Hepatics 317. *f. 1–4.* 1913.

[2] Rabenhorst's Kryptogamen-Flora 6²: *f. 76. 79.* 1914.

[3] Naturgeschichte der europ. Lebermoose 3: 57–74. 1838.

γ *devexum*, δ *flaccidum*, and ε *pygmaeum*, but acknowledging their unstable character. Under the first of these he recognized subdivisions of a lower rank (forms and sub-forms), giving them the names α 1 *commune*, α 1*. *fuscum* and α 2 *elongatum*; under the second he recognized the subdivisions β 1 *laxius*, β 2 *innovans*, β 2* *julaceum* and β 3 *gemmiparum*; but under the others, γ, δ and ε, he distinguished no lower subdivisions. As synonyms of certain of these subdivisions he cited the following species, which had been either published by earlier writers or distributed in exsiccatae under manuscript names. *Jungermannia tricrenata* Wahlenb. (1814), under α 1; *J. triangularis* Schleich. (1805), *nomen nudum*, under α 1 and α 1*; *J. deflexa* Mart. (1817), under α 1*; *Pleuroschisma flaccidum* Dumort. (1831), under β 1; *P. parvulum* Dumort. (1831), under β 2; and *Jungermannia flaccida* Schleich. (1821), *nomen nudum*, under δ. He chose the name *deflexum* for the species, rather than *tricrenatum*, on account of an inaccuracy in the original description of *Jungermannia tricrenata*; but of course this would not now be considered a sufficient reason for invalidating Wahlenberg's species.

Nees von Esenbeck's subdivisions were taken over bodily in the Synopsis Hepaticarum (1845), where the species appears under the name *Mastigobryum deflexum* Nees. They were adopted also by Lindenberg and Gottsche in their monograph of *Mastigobryum*,[1] published a few years later, the subdivisions α 1, α 2, β 1, β 2*, γ, δ and ε being separately illustrated on their plate. The more typical condition of the species, as described above, is clearly shown by *f. 1–4*, which illustrate α 1 *tricrenatum commune*. Subsequent writers have either ignored Nees von Esenbeck's subdivisions altogether or have used his names very sparingly.

For many years the species continued to be known by the name *Mastigobryum deflexum*, but this name has gradually been superseded by other names. By those who recognize the genera of S. F. Gray the name *Bazzania tricrenata* is usually employed. In 1875, however, Lindberg[2] revived for the species the old specific name *triangularis* of Schleicher, forming the combination *B. triangularis* (Schleich) Lindb. He apparently dated the name from the year 1805, when Schleicher distributed specimens of *Jungermannia*

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[1] Spec. Hepat. *Mastigobryum* 108. *pl. 18.* 1851.

[2] Acta Soc. Sci. Fenn. **10:** 499. 1875.

triangularis in his Plant. Crypt. Helvetiae. Since it is now admitted[1] that Schleicher's *J. triangularis* is a *nomen nudum,* Lindberg's combination *B. triangularis,* of 1875, represents the first adequate publication of the specific name *triangularis* for the plant in question and should not be allowed to replace the name *tricrenata,* which clearly dates from 1814.

1900 Pearson[2] added to the nomenclatorial difficulties involved by recognizing both *B. tricrenata* and *B. triangularis* as valid species. He listed, as synonyms of the latter, *Jungermannia triangularis* Schleich. and *J. deflexa* Mart. According to Nees von Esenbeck, however, as already pointed out, both of these species are synonyms of his *Herpetium deflexum* α *tricrenatum,* under which he naturally cites, as another synonym, *J. tricrenata* Wahlenb. It would appear therefore that *J. triangularis* and *J. deflexa* should both be cited as synonyms of *Bazzania tricrenata,* when this is accepted as a valid species, and there is nothing in Lindberg's writings to indicate that he ever interpreted his *B. triangularis* in a different and more restricted sense. Pearson's *B. triangularis* of 1900 thus becomes a homonym of Lindberg's *B. triangularis* of 1875, in case each represents a distinct species.

The validity of Pearson's species, however, is not above question, and it is not at all certain that it represents a definite and clearly defined series of forms. According to his observations it differs from *B. tricrenata* in the following respects: the plants are smaller; the stems are more slender and usually, but not invariably, dichotomously "innovantly" branched; the leaves, which soon fall away, are proportionately shorter (except in the var. *flaccida*); the leaf cells are "rounder," with large and distinct trigones; and the underleaves are patulous and usually subentire. In the var. *flaccida* the leaves are described as narrower and often entire and apiculate. Except for the fact that the leaves are said to be caducous, instead of persistent, these differences might well come within the range of variability of such a species as *B. tricrenata,* and Pearson himself questions whether his *B. triangularis* may not be either the male plant or a mere variety of *B. tricrenata.*

As a matter of fact the specimens cited under *B. triangularis* do not all show the caducous habit. In the material from Tyn-y-groes

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[1] See Evans, Rhodora 10: 190. 1908.

[2] Hep. British Isles 130, 132. *pl.* 48, 49. 1900.

in Wales, for example (Carrington & Pearson, Hep. Brit. Exsic. *124*), which Pearson used for most of his illustrations, the leaves are distant and often greatly reduced in size but show no evidence of falling away. His other figures were drawn from specimens collected by Jack in Baden (Gottsche & Rabenhorst, Hep. Europ. *198*, *401*); the first was distributed under the name "*Mastigobryum deflexum* var. β *flaccidum* Nees" and the second under the name "*M. deflexum* β *implexum*." Both show caducous leaves to a greater or less extent and also differ from the Welsh specimens in other respects.

In 1912 Macvicar[1] followed the example of Pearson and recognized both "*Bazzania tricrenata* (Wahl.) Pears." and "*B. triangularis* Pears.," dating them from the year 1900. According to his account *B. triangularis* "can generally be separated in Britain without difficulty from *B. tricrenata*," and "the typical forms of the two plants never grow in the same patch." He described two principal forms of *B. triangularis* and a third, apparently less important, form. In the first the leaves are mostly distant, never falcate, and usually (but not always) acute, while the underleaves are oblong-quadrate and entire; in the second the leaves are approximate, sometimes falcate, and often two- or three-toothed at the apex; in the third the leaves are narrow, nearly flat, and frequently three-toothed. He brings out the additional fact that the cells of *B. tricrenata* are 24–30 μ in diameter, while those of *B. triangularis* are only 16–25 μ, but makes no allusion to the early falling away of the leaves. His illustrations clearly represent the first of his three forms, which is essentially like the Welsh plant figured by Pearson, while his second and third forms would agree better with Jack's Baden specimens.

In 1914 Schiffner distributed specimens of *Bazzania triangularis* (Schleich.) Lindb. and "*B. tricrenata* (Wahlenb.) Pears." in his Hep. Europ. Exsic. *637–650* and commented on them in the thirteenth series of his "Kritische Bemerkungen."[2] He expresses the opinion that these species are distinct in Scotland, but connected by transitional forms in the mountains of Central Europe. Under *B. triangularis* he issued Scotch specimens, illustrating Macvicar's first form, as forma *laxa*; French and Italian specimens, illustrating his second form, as forma *densior*; and Bohemian specimens, representing a new var. *intercedens*, stating, in regard to the last, that it might

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[1] Student's Handb. British Hepatics 317, 318. 1912.

[2] Privately printed at Gottesberg, Silesia.

perhaps be better referred to *B. tricrenata.* In connection with the Italian specimens of his forma *densior* he emphasized the fact that the leaves were very caducous and implied that this condition was distinctive of *B. triangularis.* Under *B. tricrenata* he distinguished, in addition to the typical form, the vars. *subintegristipula* Schiffn., *cavernarum* Schiffn. and *pratensis* Schiffn., the last two being proposed as new. It is unfortunate that he made no attempt to correlate these varieties with the subdivisions of Nees von Esenbeck.

In contrast to the views of Pearson, Macvicar and Schiffner, those of Stephani may be cited. In discussing "*Mastigobryum triangulare* (Schleicher)"[1] in 1908, he made no mention of "*Bazzania triangularis* Pears." but listed both *Jungermannia triangularis* Schleich., and *J. tricrenata* Wahlenb. as synonyms. He alluded to a wholly etiolated forma "*implexa*" but gave no description of it and even denied its varietal rank on the ground that it was merely dwarfed by unfavorable environmental conditions. Müller takes an intermediate position between these extremes. In 1913 he described a "var. *implexa* (Nees) under *Pleuroschisma tricrenatum* (Wahlenb.) Dumort.,[2] citing "*Bazzania triangularis* Pearson" as a synonym. In this variety he emphasized the scarcely convex and distant leaves, that easily become detached, and the squarrose orbicular underleaves; and he stated further that the variety was so distinct that it might at first sight be considered a valid species, except for the presence of intermediate forms connecting it with typical *P. tricrenatum.* He admitted, however, that these connecting forms were infrequent, even in Central Europe. Müller's figure of the var. *implexa* agrees on the whole with Lindenberg and Gottsche's figures of *Mastigibryum deflexum* β 1 *implexum laxius* (*f. 11–13*) and represents Schiffner's forma *densior* of *B. triangularis*, rather than his forma *laxa.*

It will be seen from the above citations that European writers are still at variance with regard to *B. tricrenata,* and that those who segregate off "*B. triangularis* Pears." do so somewhat tentatively. It will be seen further that those who do recognize *B. triangularis* include under it not only forms with caducous leaves but also slender forms with persistent leaves (the forma *laxa* of Schiffner). In the writer's opinion the presence of caducous leaves is a feature of considerable importance from a taxonomic standpoint. Such leaves represent a

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[1] Bull. Herb. Boissier II. **8**: 851. 1908.

[2] Rabenhorst's Kryptogamen-Flora 6^{2}: 270. *f. 80.* 1913.

form of vegetative reproduction, comparable with the gemmae found in other genera of the Hepaticae. It is admitted that the presence or absence of gemmae in certain cases affords a convenient method for distinguishing between closely related species. The gemmiparous habit of *Lophozia heterocolpa* (Thed.) M. A. Howe, for example, makes it possible to separate this species at a glance from *L. Muelleri* (Nees) Dumort., in which gemmae are unknown. If this reasoning is applied to caducous leaves (Bruch- or Brutblätter of Correns) their presence, if supported by morphological features of even a slight character, might well be made the basis for the segregation of plants showing this feature from a species in which the leaves are clearly persistent. In Schiffner's forma *densior* of "*Bazzania triangularis* Pears." and in Müller's var. *implexum* of *Pleuroschisma tricrenatum* these conditions are apparently realized. The forms designated by these names are clearly identical and differ from typical *B. tricrenata* not only in having caducous leaves but also in certain features of the leaves themselves. Instead of being strongly convex and narrowing rather abruptly from a broad and rounded or subauriculate base, these leaves are plane or only slightly convex and taper more gradually from a narrower and scarcely rounded base. In connection with the var. *implexum*, Boulay[1] makes the interesting observation that it descends from the higher mountains into the lower woody zone, while the typical form does not descend below the middle woody zone. There is thus a slight difference in altitudinal distribution to support the morphological differences.

If a species of the character just outlined is recognized, the choice of a name for it is beset with difficulties. "*B. triangularis* Pears." should apparently be typified by the forma *laxa* of Schiffner with persistent leaves, but the use of this name in any sense would lead to confusion on account of the older *B triangularis* Lindb. Nees von Esenbeck's *Herpetium deflexum* β *implexum* was probably a mixture of several forms, but his β 1 *implexum laxius* was apparently the same as Müller's *Pleuroschisma tricrenatum* var. *implexum*. Under β 1 Nees von Esenbeck, as shown above, included *Pleuroschisma flaccidum* Dumort. as a synonym, and Dumortier's description[2] certainly agrees with Müller's, except that no mention is made of caducous leaves. If it could be established that these were present

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[1] Muscinées de la France 2: 50. 1904.

[2] Syll. Jung. 71. 1831.

in Dumortier's plant, the specific name *flaccida* would become available; otherwise some other choice would have to be made.

According to our present knowledge the true *B. tricrenata* is largely restricted in eastern North America to the higher mountains of Quebec and New England. It is usually replaced at lower altitudes by a species in which the caducous habit of the leaves is even better marked than in the European "*Pleuroschisma tricrenatum* var. *implexum*." An account of this species follows.

(*To be continued.*)

NOTES ON NEW ENGLAND HEPATICAE,—XVII.[1]

ALEXANDER W. EVANS.

(*Continued from page 83.*)

3. BAZZANIA DENUDATA (Torr.) Trevis. Mem. Ist. Lomb. **13**: 414. 1877. *Mastigobryum denudatum* Torr., G. L. N. Syn. Hep. 216. 1845. *Jungermannia denudata* Torr. l. c., as synonym, not Nees. *Mastigobryum ambiguum* Lindenb. (in part) op. cit. 217. 1845. On rocks, more rarely on rotten logs. Maine: Greenville, *A. W. E.* (listed as *B. tricrenata* by the writer, RHODORA **14**: 17. 1912); Round Mountain Lake, Franklin County, and Jordan Mountain, Mt. Desert, *A. Lorenz.* New Hampshire; base of Mt. Washington, *J.*

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[1] Contribution from the Osborn Botanical Laboratory.

A. Allen; Flume, *James Herbarium*; Gorham and Franconia, *T. P. James*; Thompson's Falls, White Mountains, *Underwood & Cook 19*; the "Pool" and Shelburne, *W. G. Farlow*, Mt. Willard, *E. Faxon*; Mt. Prospect, Plymouth, *A. J. Grout*; Waterville, *A. Lorenz*; Ice Gulch, Randolph, and Howker's Trail, Mt. Madison, *A. W. E.* Vermont: Bolton, *A. W. E.*; Lake Dunmore, Salisbury, and Willoughby, *A. Lorenz*; Granville Notch, *C. A. Weatherby*; Downer's Glen, Manchester, *A. J. Grout*; Brandon, *D. L. Dutton 1378, 1577.* Massachusetts: Plainfield (part of the original material of *M. denudatum* from the Hooker Herbarium, now in the Mitten Herbarium); Middlefield, 1822, *Emmons 120* (specimen in the herbarium of the New York Botanical Garden, labeled "*J. denudata* sp. nov."); Mt. Greylock, *A. L. Andrews* (listed as *B. triangularis* by the collector, Rhodora **6**: 74. 1904); Everett Brook, Sheffield, *A. Lorenz*; Alandar, Berkshire County, *A. R. Northrop.* Connecticut: Salisbury, Beacon Falls,[1] Naugatuck, and Redding, *A. W. E.* (listed as *B. tricrenata* by Evans & Nichols, Connecticut Geol. & Nat. Hist. Surv. **11**: 64. 1908). General reports of the species from Massachusetts and Connecticut have been published by the writer, the last reference including also a general report from Maine (Rhodora **5**: 171. 1903, as *B. triangularis*; **10**: 190. 1908, and **15**: 23. 1913, as *B. tricrenata*).

Outside New England the following stations may be noted:—Newfoundland: Channel, *Howe & Lang*; Placentia Bay, *A. E. Waghorne 21, 22.* Nova Scotia: Louisburg, Cape Breton, *J. Macoun 94, 108* (listed as *B. triangularis* by the collector, Cat. Canadian Pl. 7: 33. 1902); Port Clyde, *J. Macoun 49*; Purcell's Cove, Halifax Harbor, *Howe & Lang 1542*; near Indian Brook, mountains north of the Barrasois River, valley of the Barrasois, and Cape Dauphin, Cape Breton, *G. E. Nichols 512, 592, 1141, 1322.* New York, Catskill Mountains, *C. H. Peck* (listed as *Mastigobryum deflexum* by the collector, Ann. Rept. Reg. Univ. New York **19**: 70. 1866); Rocky Falls, North Elba, Essex County, *C. H. Peck* 37 (listed as *B. deflexa* by the collector, Bull. New York State Mus. **6**: 177. 1899); Little Falls, *C. F. Austin*; Clareyville, *C. H. Peck 4*; Chapel Pond Brook, Adirondack Mountains, *E. G. Britton*; Undercliff, Essex County, *C. C. Haynes 338*; Little Moose Lake, Herkimer County, *C. C. Haynes* (listed as *B. triangularis* by the collector, Bryologist

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[1] A plant from this collection has been figured by the writer under the name *B. tricrenata*, Ann. Bot. **26**: 20. *f. 27.* 1912.

9: 62. 1906, and distributed as *B. tricrenata* [corrected label] in Am. Hep. *39*); East River Falls, above Lake Colden, and Lake Mohonk, *A. Lorenz.* Virginia: summit of White Top, 5678 ft. alt., *E. G. Britton 1*, J. K. *Small 52, 55, 56, 79* (listed as *B. deflexa* by Small & Vail, Mem. Torrey Club **4**: 193. 1894). West Virginia: Tibbs Run, Monongalia County, *C. F. Millspaugh* (listed as *B. deflexa* by the collector in Prelim. Fl. West Virginia 496); road to Cheat View, *E. M. Fling*; Spruce, Pocohontas County, *F. W. Gray 66.* North Carolina: Grandfather Mountain, *G. F. Atkinson 11579* (listed as *B. tricrenata* by Andrews, Bryologist **17**: 60. 1914—the other specimens cited here are all referable to the same species in his opinion); Roan Mountain, 6000 ft. alt., *A. L. Andrews 65.*

Soon after the publication of this species in the Synopsis Hepaticarum, Lindenberg and Gottsche[1] redescribed and figured it, but subsequent writers, with few exceptions, have considered its claims for recognition unfounded. As early as 1856 Sullivant[2] expressed the opinion that *M. denudatum* was probably a form of *M. deflexum*, and Austin,[3] in 1873, went one step farther by citing it as a simple synonym of *M. deflexum.* Most later students, especially in America, have followed Austin's examples. In 1888, however, Stephani[4] reported *M. denudatum* from Miquelon Island, south of Newfoundland, basing his record on specimens collected by E. Delamare and designating the species as peculiar to America. Pearson[5] cited this record two years later, under *Bazzania denudata*, but called attention to Austin's divergent views, and Macoun[6] repeated Pearson's citation in his last publication on Canadian hepaticology. Apparently Stephani afterwards changed his mind regarding *B. denudata*, since he makes no mention of it whatever in his monograph of the genus *Mastigobryum*, published in 1908, not even including it among the synonyms of his *M. triangulare.* In all probability he placed it in the same category as the forma "*implexa*," to which allusion has already been made. The fact that Trevisan recognized the species by forming the combination "*Bazzania denudata*" does not mean that he actually studied it. He merely transferred all the species of *Mastigobryum*, as given in the Synopsis, to the genus *Bazzania.*

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[1] Spec. Hepat. Mastigobryum 7. *pl. 1, f. 1–4.* 1851.

[2] In Gray, Man. Bot. Ed. 2, 702. 1856.

[3] Hep. Bor.-Amer. *80.* 1873.

[4] In Delamare, Renauld & Cardot, Fl. Miquelonensis 66. 1888.

[5] List Canadian Hepat. 9. 1890.

[6] Cat. Canadian Pl. **7**: 33. 1902.

In its variability *B. denudata* is a close rival of *B. trierenata*. It is perhaps advisable, therefore, to base our conception of the species on vigorous specimens, since these may be assumed to approach the typical condition more closely than delicate and poorly developed specimens. Even in well-developed material the plants grow in depressed mats, the individual stems being prostrate or slightly ascending but apparently never approaching a suberect position. The younger portions and sometimes the entire plants are green or yellowish green and do not show the brownish pigmentation of the cell-walls, which constitutes so striking a feature of *B. trierenata*. In the older portions a dull brownish hue occasionally becomes apparent, but this seems to be associated with age and death rather than with an active process of pigmentation.

The stems, so far as the living portions are concerned, are mostly 1–1.5 cm. long and measure (with the leaves) 1–2 mm. in width. At irregular intervals branches of the *Frullania* type, diverging at a wide angle, are produced; while flagelliform branches, arising in the axils of the underleaves, are rare or abundant according to circumstances. Occasionally a flagelliform branch gradually becomes transformed into a leafy branch as it increases in length, and a leafy branch may sometimes spring directly from the axil of an underleaf, showing that the distinction between leafy and flagelliform branches is by no means stable. Rhizoids are sparingly produced; in most cases they grow out from the basal cells of the reduced leaves on the flagelliform branches, but in very rare cases may take their origin from the basal cells of ordinary underleaves.

The leaves are distant to somewhat imbricate. They spread widely, usually at a right angle, and lie in approximately the same plane. In most cases the leaves are flat but they are sometimes more or less convex when viewed from above. They vary in form from short-ovate to oblong-ovate, measuring in most cases 0.6–0.8 mm. in length by 0.4–0.6 mm. in width, and are slightly or not at all falcate. The upper margin is more or less arched from a scarcely rounded base, while the lower margin tends to be more nearly straight, in rare cases showing a vague basal expansion. The apices are so variable that it is difficult to determine what represents the most typical condition. In some cases the leaf tapers gradually to an acute or obtuse point, but it is much more usual for the apex to be broad and rounded or truncate. Under these circumstances there may be no signs of apical teeth, and a long series of intermediate conditions may sometimes be found, even on a single individual, between this extreme and a three-toothed apex with sharp teeth separated by obtuse sinuses. The three-toothed condition, however, is rarely realized, most plants showing only one or two teeth, and these may be blunt or otherwise indistinct rather than acute. The leaf-cells average about 27 × 25 μ in the middle of the leaf; their walls are thin, and their trigones are small and often indistinct, usually with straight or slightly concave sides. The cuticle seems to be smooth throughout.

The underleaves are almost as variable as the leaves. They are distant to approximate and may be slightly imbricate in the vicinity of the shoot-apices. Sometimes they are subappressed, but it is much more usual for them to spread more or less widely from the axis. On well-developed plants they usually measure 0.2–0.3 in length and 0.3–0.45 mm. in width, the shape being broadly quadrate-orbicular. The base is almost straight and shows no indications of auricles; while the straight or slightly bulging sides are usually entire, although vague crenations or sharper teeth may be present in rare instances. The broad and truncate apex may show four rounded or obtuse teeth separated by distinct sinuses. In most cases, however, the teeth are fewer or lacking altogether, the apex then being entire or slightly emarginate.

Although the perianths of *B. denudata* are still unknown, female branches with unfertilized archegonia are not infrequent. Branches of this character were detected by Gottsche, who described the involucral leaves as ovate-cordate and crenulate at the apex with one or two teeth. Unfortunately the bracts and bracteoles of *B. tricrenata* and its allies do not attain their full size and development unless perianths and sporophytes are produced, so that Gottsche's account must not be accepted without reservations.

The most striking features of *B. denudata* are due to the production of caducous leaves and underleaves, and it is very unusual to find a patch of specimens in which this habit is not more or less in evidence. The throwing off of the leaves begins abruptly in most cases and then continues without interruption for a considerable period. Although in all probability the production of these leaves eventually brings the growth of the plant to an end, it is not unusual for an axis to fork two or three times after the caducous habit has been initiated.

Under such circumstances the forking and thread-like stems, tipped with rudimentary leaves but otherwise naked, except for the scanty vestiges left behind by the leaves and underleaves, present a very distinctive appearance. The caducous habit is sometimes more marked in the leaves than in the underleaves, and leafless stems with persistent underleaves are occasionally found. There are cases, too, where an axis recovers from the caducous habit and resumes its growth in a normal vegetative manner.

The caducous leaves are usually smaller than the ordinary leaves described above and may be reduced to a length of 0.2 mm. or even less, the caducous underleaves exhibiting a similar reduction in size. When a caducous leaf gives rise to a new stem the latter grows out directly, by a process of regeneration, from one of the leaf-cells, usually at or near the base. The stem elongates rapidly and produces a long series of minute leaves and underleaves, very similar to those on the flagelliform branches but somewhat firmer in texture and tending to spread more widely. Both leaves and underleaves are shortly bifid and essentially alike, the stem thus representing an almost radial structure and showing but little indication of the distinct dorsiventrality found in the normal leafy stems. The later stages in the development of these new stems have not been observed.

When typical plants of *B. tricrenata* and *B. denudata* are compared the differences between them are striking and have been brought out to a certain extent in the preceding account. In *B. tricrenata*, for example, the plants are more or less pigmented with brown, the stems tend to be suberect, the branches diverge at a narrow angle, and the persistent leaves are strongly convex; in *B. denudata*, on the contrary, the plants show no distinct brown pigmentation, the stems tend to be prostrate, the branches diverge at a wide angle, and the leaves are flat or only slightly convex and often caducous. When *B. denudata* is compared with "*Pleuroschisma tricrenatum* var. *implexum*" a closer approach is apparent, but in this latter plant the pigmentation is still present in a greater or less degree, the caducous habit is less marked and the caducous leaves themselves are less highly differentiated. It will be noted that "*Mastigobryum ambiguum* (in part)" is cited as one of the synonyms of *B. tricrenata*. This species was based on two specimens, as follows: "prov. Massachusetts (Asa Gray)" and "ad litora boreali-occidentalia (Hb. Hk.)." The first specimen has not been seen by the writer but there is little doubt of its identity with *B. denudata*; the second specimen (according to a fragment in the Mitten Herbarium) represents a closely allied but apparently distinct species, widely distributed in the Pacific coast region from Alaska to Washington. This species, for which the specific name *ambiguum* may be retained, will be considered in another connection.

4. Scapania nemorosa (L.) Dumort. Recueil d'Obs. sur les Jung. 14. 1835. *Jungermannia nemorosa* L. Sp. Plant. 1132. 1753. *Scapania nemorosa* is one of the commonest and most widely distributed of the leafy Hepaticae in Europe and North America. It is abundant in all the New England States, its range extending from the sea level to an altitude of five thousand feet or more. Although it attains its best development on moist rocks, it grows also on drier rocks, on banks in the woods, in swamps, and even on old logs; and it is not surprising that it occurs in numerous forms. Some of these are very different in appearance from one another, and yet it is difficult to distinguish them clearly on account of the existence of intermediate and intergrading forms. Within recent years, however, the attempt has been made to segregate out certain forms as distinct species. Of these segregates the following three occur in New England, and their claims for recognition may therefore be briefly considered: *S. Joergensenii* Schiffn., *S. Austinii* Warnst., and *S. recurvifolia* Warnst.

The first of these segregates, *S. Joergensenii*,[1] was based on material collected by the Norwegian botanist, E. Jörgensen, in the Blaamanden Mountains, near Bergen, Norway, at an altitude of 450–500 m. When Müller[2] published his monograph of the genus *Scapania* he gave a full description of *S. Joergensenii*, with illustrations, still citing the original material only and emphasizing the close relationship of the plant to *S. nemorosa*. He has since reduced it to varietal rank under *S. nemorosa* and has listed additional specimens from Alsace, Baden, Bohemia, the Fichtel and Harz Mountains of Germany, and the Thuringian Forest.[3] He has noted its occurrence also in North America, without citing definite stations, but the writer is able to supply the following from the specimens in the Yale Herbarium: Mt. Clinton, Mt. Pleasant and Tuckerman's Ravine, White Moun-

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[1] See Müller, Bull. Herb. Boiss. II. **1**: 607. 1901.

[2] Nova Acta Acad. Caes. Leop. Carol. **83**: 180. *pl. 23.* 1905.

[3] Rabenhorst's Kryptogamen-Flora **6**^{2}: 503. 1915.

tains, New Hampshire, *A. W. E.*; Crawford Bridle Path, White Mountains, *G. E. Nichols.* These stations are all near or above the timber line. As Müller points out the deep purple color is the only important feature distinguishing *S. Joergensenii* from *S. nemorosa*, and this feature by itself seems insufficient to justify a specific separation,

The second segregate, *S. Austinii*,[1] was based on No. 18 of Austin's Hep. Bor.-Amer., distributed as "*Scapania nemorosa*, var. 3" and described as very common "in shady places, on rocks and on the ground," no definite localities being cited. This specimen is referred to *S. nemorosa* without question by Müller, but Warnstorf criticises him for doing so and compares his *S. Austinii* with *S. curta* (Mart.) Dumort., rather than with *S. nemorosa.* The plant under consideration is frequent in southern New England, where it grows on shaded banks in woods, and at first sight looks very different from the typical form of *S. nemorosa* on moist rocks. It is characterized, according to its author, by its smaller size, by the small number of teeth on the leaf-lobes, and by the absence of wings on the keels. In the writer's opinion these features are associated with unfavorable environmental conditions and *S. Austinii* represents a juvenile condition of *S. nemorosa*, in which certain pecularities of the species fail to manifest themselves. It may be added that inconspicuous keels are occasionally present and that the gemmae, which are abundantly produced, are yellow, pyriform or elliptical, and unicellular, thus agreeing with those of *S. nemorosa* rather than with those of *S. curta.* Warnstorf's species, therefore, should be regarded as a synonym of *S. nemorosa* or perhaps as a variety.

The third segregate, *S. recurvifolia*,[2] was based on another specimen distributed by Austin in his Hep.-Bor.-Amer. This specimen is No. 16 and was designated "*Scapania nemorosa* var. 1." It was described as common on the "margins of rivulets, swamps, &c.," and was likewise referred to *S. nemorosa* without question by Müller. Warnstorf admits the close relationship of his species to *S. nemorosa* but emphasizes, as differential characters, its recurved and entire dorsal leaf-lobes and its thin-walled leaf-cells with poorly developed trigones. Here again the distinctive features, even if they were constant, are very slight and appear to be associated in some way

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[1] Hedwigia **63**: 79. 1921.

[2] Hedwigia **63**: 115. 1921.

with the environment. The writer, therefore, would regard *S. recurvifolia* as nothing more than a simple synonym of *S. nemorosa*. This conclusion is supported by the fact that the ventral leaf-lobes, as brought out by the description, are densely dentate and by the further fact that the gemmae are unicellular and conform closely to the *S. nemorosa* type.

In the same paper where Warnstorf described the last two segregates he reported the occurrence of the arctic *S. spitzbergensis* (Lindb.) K. Müll. in Connecticut, basing his record on a specimen collected by the writer at Branford. He intimated also that Müller's *S. nemorosa* forma *purpureolimbata*,[1] based primarily on a specimen collected by T. P. James at the Flume, New Hampshire, might be referable to the same species. The writer has examined these two specimens with care and finds that they lack the strongly convex dorsal lobes of *S. spitzbergensis* and also the coarsely toothed wings on the keels of the leaves; the keels in fact are almost invariably quite entire. There seems to be no reason, therefore, for separating these specimens from *S. nemorosa*, although they represent an unusually well-developed form. The only known American station for the true *S. spitzbergensis* is in Greenland.[2]

5. Lejeunea patens Lindb. Acta Soc. Sci. Fenn. **10**: 482. 1875. On trees and wet rocks. Pemetic Mountain trail, 600 ft. alt., Green Mountain Gorge, 800 ft. alt., and Southwest Harbor, 90 ft. alt., Mt. Desert, Maine, July, 1921, *A. Lorenz*. New to New England. In 1902 the writer[3] reported *L. patens* for the first time from North America, citing specimens from Newfoundland and Nova Scotia. It has since been collected in the mountains of North Carolina by Andrews.[4] In Europe it is one of the so-called "Atlantic" species, its known range extending along the coast from Norway to Ireland. It is closely related to *L. cavifolia* (Ehrh.) Lindb., so closely in fact that Müller and others regard it as a "small" species. At the same time it can usually be distinguished without difficulty. It differs, for example, in its paler color; in its more convex leaf-blades, spreading more abruptly from the lobules; in its smaller and more nearly orbicular underleaves; and in the crenulate margins of its leaf-lobes and underleaves.

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[1] Rabenhorst's Kryptogamen-Flora 6^2: 504. 1915.

[2] See Evans, Bryologist **14**: 87. 1911.

[3] Mem. Torrey Club **8**: 160. 1902.

[4] See Bryologist **24**: 53. 1922.

The following additions to local state floras, not already mentioned in the preceding Notes, may be recorded:—

For Maine: *Riccia arvensis*, Belfast (*A. Lorenz*).

For Vermont: *Jungermannia cordifolia*, Hartland (*A. Lorenz*); *Scapania dentata*, Manchester (*W. R. Taylor*); *S. glaucocephala*, Pawlet (*W. R. Taylor*).

For Rhode Island: *Cephaloziella Hampeana* and *Lophozia Mildeana*, Westerly (*A. Lorenz*).

The census of New England Hepaticae now stands as follows: total number of species recorded, 196; number recorded from Maine, 151; from New Hampshire, 154, from Vermont, 137; from Massachusetts, 121; from Rhode Island, 81; from Connecticut, 146; from all six states, 66.

Yale University.

Vol. III 1923 Part 3

PROCEEDINGS

OF THE

PORTLAND SOCIETY

OF

NATURAL HISTORY

ORGANIZED 1843

CONTENTS

PORTLAND, MAINE, U. S. A.
PRINTED FOR THE SOCIETY
1923

THE VEGETATION OF THE PENOBSCOT BAY REGION, MAINE

By ALBERT FREDERICK HILL

INSTRUCTOR IN BOTANY AND ASSISTANT CURATOR OF THE BOTANICAL COLLECTIONS, YALE UNIVERSITY

CONTENTS

I. INTRODUCTION

Location

The Penobscot Bay region in Maine is situated on the coast about midway between the eastern and western boundaries of the state. Although, in its strictest application, the term "Penobscot Bay" should be only used for the body of water at the mouth of the Penobscot River, in general it is applied to all the waters between Mount Desert Island on the east and White Head on the west, and to the adjoining land areas as well. This Penobscot Bay region, as it may be called, lies between meridians 68° 25′ and 69° 15′ west longitude and parallels 43° 50′ and 44° 35′ north latitude. It comprises approximately 1,200 square miles, nearly two-thirds of which is water. Of the land about one-half belongs to the mainland and the remainder to islands. The latter vary in size from the smallest ledges to some which contain as many as 30 square miles. Politically the region embraces some twenty-five townships, all of which border on the Bay, and which are situated in either Hancock, Knox or Waldo County (see map, Figure 1).

Physiography and Climate

The physiographic and climatic features of the Penobscot Bay region were described by the author in some detail in the introduction to an earlier paper (15) which dealt with the flora of the eastern part of the area. Consequently, in order to avoid repetition, only the more important points brought forward in the former discussion will be presented here.

In its topographical aspects, particularly its extremely irregular coast line and the presence of innumerable islands, the Penobscot Bay region illustrates the characteristic features of a drowned coast. The area represents a peneplain worn down from former highlands by pre-glacial

APR 11 1924

weathering and erosion. The few hills which have been able to withstand this denudation are prominent features of the landscape. The Camden Hills and Blue Hill on the mainland and the island of Isle au Haut are the more notable of these residual mountains or monadnocks. The exposed outer shores of the region are usually rocky and abrupt, often with sea cliffs and headlands, while in the more protected localities, beaches, mud flats and salt marshes occur. The water courses of the area are very insignificant, the Megunticook River in Camden and the Ducktrap River in Lincolnville alone justifying the name. Several so-called rivers, such as the Bagaduce and Weskeag, are in reality tidal estuaries. Lakes and ponds are fairly abundant, and are usually morainal in nature, although scoop lakes and barrier beach ponds are not uncommon.

The soils of the region are very meagre and often entirely lacking, especially at the higher elevations. They consist almost entirely of formations of glacial origin. Glacial till is everywhere abundant and well developed plains of outwash sands and gravels of glacio-fluviatile origin occur along the outlet of Megunticook Lake in Camden and Oyster River Pond in Rockport. A few kames are to be found at Sandy Point in Stockton Springs. Marine clay is the characteristic soil of the lowlands, together with a few postglacial deposits, such as beach sands and gravels or swamp muck and peat.

The rock structure still controls the topography of the region, owing to the paucity of the soil. These underlying rocks are predominantly silicious and acidic in nature. Granite is the most widely distributed rock, occupying fully one-half the entire area, and various micaceous schists and quartzites are of frequent occurrence. Limestones are well developed in the vicinity of Rockland and on Islesboro, but they are not typical. The Islesboro limestone is very impure, owing to the presence of many thin silicious layers, and is rated as "too silicious for commercial use". Of the

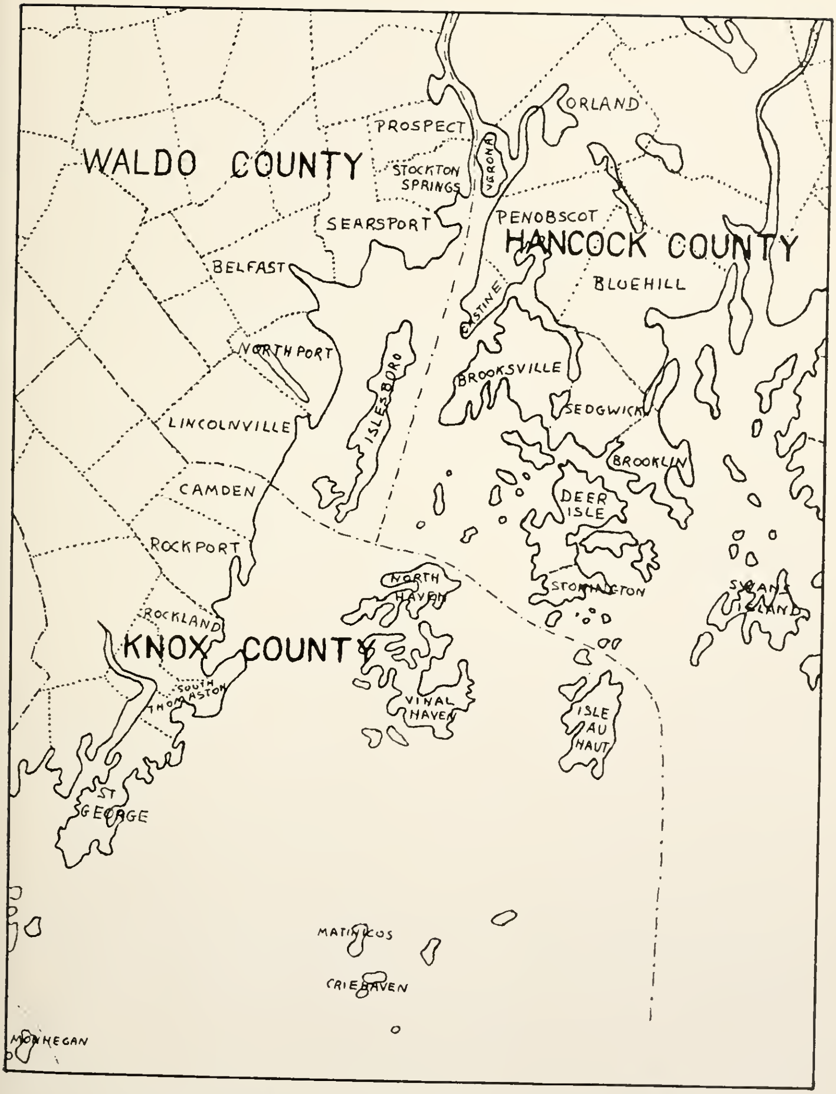

FIGURE 1. — Map of the Penobscot Bay Region, Maine, showing location of the townships which comprise the area.

two limestone members of the Rockland Formation, one is silicious and the other yields little or no basic soil, since it is highly crystalline, virtually a marble, and so decomposes with difficulty. Most of the other rocks of the area are also acidic, although locally small amounts of diabase, diorite, gabbro and serpentine may be found.

The climate of the region is that of any moist north temperate area with warm days and cool nights during the summer. The proximity of the ocean brings about much more equable conditions than are found inland, and this has a pronounced effect upon the vegetation in that the growing season is prolonged. Data from three U. S. Weather Bureau stations on the Maine coast (Eastport, Bar Harbor, Portland) for the ten years 1909-1919 show an average growing season of 166 days; while a similar average for inland stations (Orono, Millinocket, Greenville) is only 114 days. The prevalence of fogs renders the region excessively moist, with a consequent lowering of the temperature.

Previous Botanical Work

Although the island of Mount Desert on the eastern border of the Bay, and several areas to the westward, have been carefully studied botanically, the Penobscot Bay region of the Maine coast has been much neglected. Until recently the only work done has been of a desultory nature and entirely from the floristic point of view. In 1919 the author (15) published an account of the flora of a portion of the eastern part of the region, to which the reader is referred for references to any earlier works, but no ecological study of the vegetation has been attempted until the present time.

Acknowledgments

I wish at this time to express my great indebtedness to Professor George E. Nichols, who has been ever ready with advice and suggestions regarding the work; and to Dr. John

M. Stetson, who rendered invaluable aid in the securing of the photographs.

NOMENCLATURE AND ECOLOGICAL CLASSIFICATION

In the present work the nomenclature of the ferns and spermatophytes will follow that of the author's paper on the Vascular Flora of the eastern Penobscot Bay region (15); while that of the bryophytes will follow Evans and Nichols's Bryophytes of Connecticut (6). The nomenclature of the lichens is that of Mr. George K. Merrill, who has very kindly checked over all references.

The system of ecological classification to be used follows that outlined by Nichols (22). Briefly this system may be summarized as follows:

The fundamental unit of vegetation is the ASSOCIATION,—a plant community characterized by its essentially homogeneous physiognomy and ecological structure, and floristic composition at least as regards the dominant species. The vegetation of any given region comprises a complex of such associations. The individual associations may be classified according to their physiognomy and ecological structure, their geographic, and their successional relations.

Considered as to their physiognomy and ecological structure all associations which resemble one another in these respects may be referred to a common ASSOCIATION-TYPE. From the standpoint of the geographical relations two other vegetation units may be recognized: the CLIMATIC FORMATION which comprises a complex of associations occupying an area with uniform climate; and the PHYSIOGRAPHIC FORMATION which consists of a complex of associations which occur in areas which represent units in their relation to the larger physiographic features of the region.

In discussing the vegetation of the Penobscot Bay region, the climatic and physiographic formations will be outlined first and then the association-types. Under the latter the individual associations will be considered specifically and in their successional relations.

In an area occupied by a climatic formation, since the climate is essentially uniform, the nature of the vegetation is controlled by the character of the physiography. Everywhere in such a region there is a tendency for the vegetation to progress toward a uniform climax which represents a permanent condition.

Where the physiographic factors are favorable a permanent climax can develop which represents the most advanced type of vegetation that is capable of development on ordinary uplands in the particular region. This is the regional or climatic climax and associations of this kind, because they resemble one another ecologically even though they may differ slightly floristically, may be referred to a CLIMATIC CLIMAX ASSOCIATION-TYPE.

Frequently, however, unfavorable physiographic factors may have such a pronounced effect locally that the climatic climax is unable to develop and a permanent climax is reached lower down in the successional series. Associations of this type represent physiographic climaces and they may be referred to a PHYSIOGRAPHIC CLIMAX ASSOCIATION-TYPE.

II. PHYTOGEOGRAPHICAL RELATIONS OF THE PENOBSCOT BAY REGION

The Penobscot Bay region, which is merely a geographical unit, naturally is not distinct climatically, but rather represents a small portion of a larger climatic unit area. It should correspond, therefore in its climax vegetation to the climatic formation as a whole. Just which of the several formations of eastern North America the area under discussion is a part of, however, is not easily determined, owing to the peculiar characteristics of the general region of which New England and Penobscot Bay are a part. Moreover the nature and limits of these formations are still open to conjecture, as is evidenced by the varying treatment accorded them by phytogeographers. In the present paper an attempt will be made to clarify the relations of the various formations before assigning the Penobscot Bay region to any one of them.

It is a generally accepted conclusion in current ecological literature that there exist in eastern North America two great climatic unit areas, each of which is characterized by a particular type of climax forest. These forest areas comprise:

(1) the EASTERN DECIDUOUS FOREST which centers and attains its optimum development in the lower Ohio basin and the southern Appalachians, with the beech *(Fagus grandifolia)*, sugar maple *(Acer saccharum)*, chestnut *(Castanea dentata)*, tulip *(Liriodendron Tulipifera)*, sycamore *(Platanus occidentalis)*, red oak *(Quercus rubra)*, white oak *(Quercus alba)*, white ash *(Fraxinus americana)*, and several species of *Juglans* and *Carya* as the character trees. Of these the beech and maple are often cited as the most prominent. (See Cooper (4) in this connection).

(2) the NORTHEASTERN EVERGREEN CONIFEROUS FOREST, which centers and attains its optimum development in eastern Canada; with the balsam fir *(Abies balsamea)*, the black spruce *(Picea mariana)*, white spruce *(Picea canadensis)*, and paper birch *(Betula alba* var. *papyrifera)* as the character trees.

Between these two areas lies a broad zone where the ranges of the southern and northern climax trees overlap, thus creating an intermediate, telescoped type of vegetation — a tension zone in which the various species are in active competition. In general the limits of this TRANSITION FOREST REGION, as it is called, may be said to lie between the northern limits of the deciduous *Acer saccharum* and the southern limits of the coniferous *Abies balsamea* (see map, Figure 2). The Transition region, thus delimited, coincides to a remarkable degree with a distinct floristic region, the Canadian. However, even though the flora

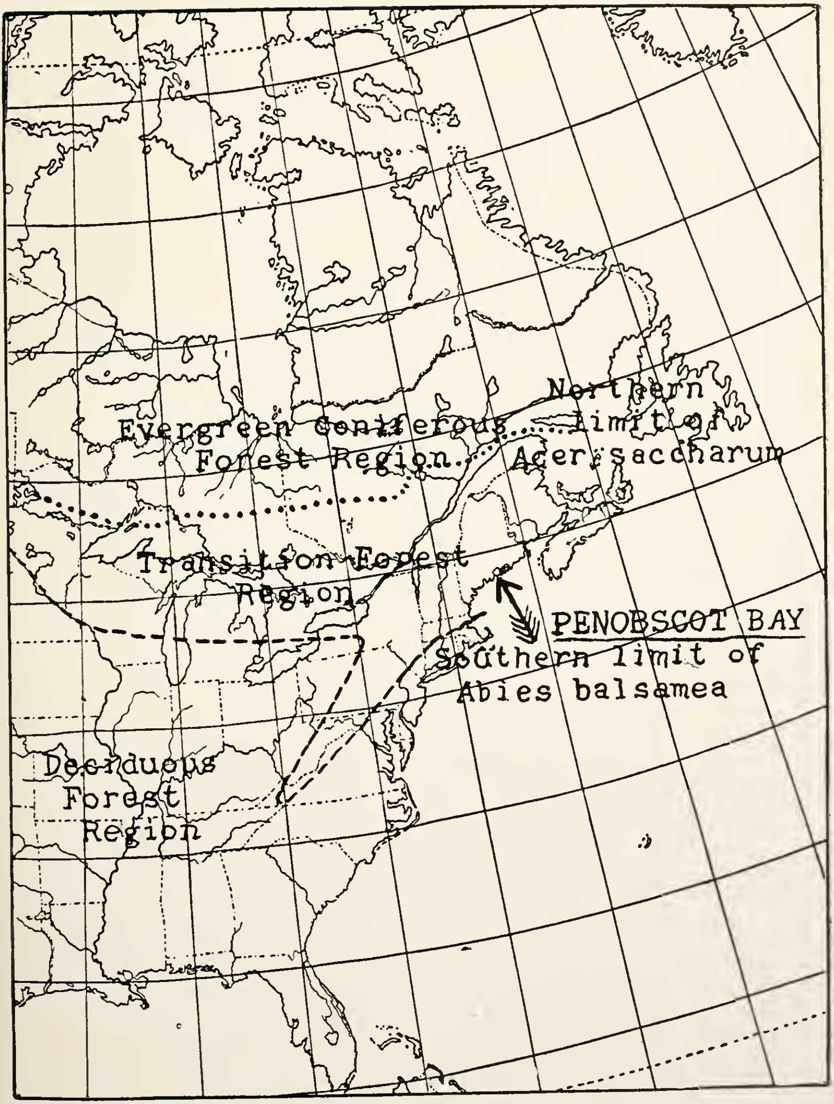

Figure 2. — Map of eastern North America, to show location of the Transition Forest Region, and of Penobscot Bay (after Nichols).

may be in part unique, ecologically at least it is doubtful whether this area should be considered as a distinct climatic formation. As Nichols (23) has pointed out it should rather be regarded as an extension of one or the other of the great forest areas mentioned above. As will be seen later, evidence from both the historical and developmental view-points indicate that it is a northern extension of the eastern deciduous forest. A study of the sequence of the post-glacial migrations, and the noteworthy fact that throughout the region the deciduous climax trees are able to supercede the coniferous in all physiographically favorable situations bear out this statement.

Combining as it does both northern and southern elements, the Transition Forest region presents a varied rather than a uniform type of vegetation. There are in the main, however, two readily recognizable subdivisions, each characterized by the nature of the climax forest which it supports. In the southern and western portions of the Transition region the climax forest consists primarily of sugar maple, beech, yellow birch *(Betula lutea)*, white pine *(Pinus Strobus)*, and hemlock *(Tsuga canadensis)*, while in the northeastern portion, in addition to these trees, there also occur balsam fir, black spruce, paper birch and red spruce *(Picea rubra)*.

In the opinion of the writer the proper interpretation of the forest areas of eastern North America necessitates the recognition of these two zones in the Transition region, and a modification of our ideas regarding the extent of the deciduous forest proper.

While the sugar maple and beech may be prominent members of the deciduous forest at the center of its best development, the most striking feature of such forests is the presence of trees like the chestnut, tulip, sycamore, black walnut *(Juglans nigra)*, butternut *(Juglans cinerea)*, and numerous hickories *(Carya* sp.) and oaks. This is the Aleghanian forest as defined by Bray (2) and it is this forest alone which the writer believes should be regarded as the eastern deciduous climax forest. The region which this type of forest occupies is distinct, both in its climate, and to a large extent in its soils. It has a rainfall-evaporation ratio[1] of from 80%-110%, according to Transeau (28), and in general is unglaciated and underlain by rich basic Silurian and Devonian rocks. From its area of greatest development in the Ohio basin and the southern Appalachians it extends northward to southern Michigan, Ontario, and western New York, with a branch running along the Piedmont region, east of the mountains, to the Hudson valley and southwestern New England. Numerous individual species have a similar range indicating that this region is a definite floristic as well as climatic unit area.

Immediately north of the deciduous forest region as thus delimited lies that part of the Transition region, which is more southern in its affinities and which may be termed the *Alleghanian-transition* zone. Here the climax forest is a mixture of sugar maple, beech, yellow birch, hemlock and white pine, the more striking trees of the typical deciduous forest being absent. The nature of such forests has been adequately treated by Whitford (30), Gates (12), Bray (2), and Nichols (21) and needs no discussion here. One point in connection with this zone, however, should be emphasized. Owing to the presence of unfavorable physiographic factors in many localities, the regional climax cannot be attained and the succession of vegetation stops at some physiographic climax. The white pine region of the lumbermen, so characteristic of the sterile sand plains of southern New England, is a good example of such a physio-

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[1] According to Transeau the determination of the rainfall-evaporation ratio affords a method whereby data concerning temperature, relative humidity, wind velocity and rainfall, all of which affect plant distribution, may be combined in a single number. This ratio is obtained by dividing the amount of rainfall at a given station by the depth of evaporation at that station. The resulting ratios when plotted on a map show climatic centers which correspond in general with centers of plant distribution.

graphic climax. This ecological concept, which is comparatively recent, recognizes the important role which edaphic and topographic factors play in the development of vegetation and permits the introduction of a permanent type of vegetation, different from the climax type of the region as a whole, but which must not be interpreted as constituting a distinct climatic formation, since, potentially at least, the regional climax is capable of development.

The characteristic jack pine country of the southern peninsula of Michigan is another example of a physiographic climax. This region has met with varied treatment at the hands of ecologists, but Harvey has recently shown (13) that it is definitely a part of the eastern deciduous forest climax, characterized locally by various physiographic climaces; and it should not be treated as a separate formation. In this connection he makes the valuable statement that "upon ecological grounds any region should be classified upon the basis of the highest ecological type which may find expression therein."

Whitford (30) earlier showed that the pine forests of northern Michigan are merely a stage in the development of the maple-beech-hemlock forest; and this latter must be considered the regional climax, even though it is not the most characteristic type of vegetation in all cases.

The second portion of the Transition region adjoins the northeastern coniferous forest and, as would be expected, shows a greater admixture of the northern coniferous species. In this section, which we can call the *Canadian-transition zone*, the climax forest is still composed of maple, beech, yellow birch, hemlock, and white pine, but with the addition, as prominent members, of the spruce, balsam fir and paper birch. This type of forest occupies much of northern New England, the Adirondack region in New York and the Maritime Provinces . A great part of this country seems at first sight to be predominantly coniferous, and has been classed as a portion of the northeastern coniferous forest by most phytogeographers. Nichols, however, has shown that in Cape Breton (23) the mixed deciduous evergreen forest is the regional climax and is attained on all physiographically favorable sites. The same condition obtains in northern Maine and adjacent New Brunswick (11) where similar forests occupy the better soils. On the poorer sites — the sterile slopes, swamps or poorly drained flats — a coniferous forest is dominant, but it constitutes a physiographic rather than a regional climax.

It might be argued that, since so much of the forest in such a region is coniferous, the climate must be such that a coniferous growth is favored and consequently the region should be considered as actually a part of the northeastern coniferous climax. The climate may be favorable for the balsam fir and spruces, but it is equally favorable for the deciduous climax trees, and these latter always win out in competition with the coniferous ones wherever edaphic and topographic factors are favorable, due, in part, to the inability of the conifers to successfully compete with the deciduous forms, owing to the nature of the trees themselves. In view of these facts it seems best to consider this portion of the Transition region as a northward extension of the deciduous forest formation, although, as in the preceding zone, there is a difference in the component species of the climax forest. The coniferous forest in this zone, as already stated represents merely a physiographic climax.

A study of the northward migration of plant life after the Glacial Period also leads us to classify the Transition region as deciduous rather than coniferous. We know from geological evidence that in all probability the climate directly preceding the Ice Age was much warmer than at present, with the result that southern broad-leaf species were able to exist as far north as Greenland, and this sort of vegetation was much more widespread. The advent of the ice sheet drove all existing life before it toward the south and this movement was halted only when the advance of the glaciers was checked. Upon the withdrawal of the ice the plants followed back to their old haunts, going in three waves as Adams (1) conceives it. First the arctic-alpine species, growing at the very edge of the melting ice, gradually moved northward until they reached their present distribution in the Arctic Circle, leaving behind relic species on the high mountain tops, the cold exposed shores and other favorable situations. Next followed the trees of the coniferous forest and the accompanying herbaceous vegetation, and these eventually attained the region of their present widespread distribution in the acid Laurentian area of eastern Canada. This group likewise left behind a much greater proportion of relic forms in favorable places. Finally the deciduous species began in their turn the northward migration and, although the climate had sufficiently ameliorated to permit their reaching the Maritime Provinces and the St. Lawrence valley, in many places they found the ground already pre-empted by the conifers. In favorable places they have been able to win out in the ensuing competition, failing to do so only where physiographic conditions were distinctly unfavorable for their growth. The result is the present day mixture of northern and southern forms, physiographic climax association-types, characterized by coniferous trees, occurring interspersed among examples of the regional climax association-type, in which deciduous species predominate. The nature of the vegetation in this zone and the successions leading to the climax association-type have been discussed in detail by Nichols (23) for Cape Breton Island.

Bearing in mind the statement of Harvey that ecologically a region should be classified upon the basis of the highest ecological type which may be developed, it is evident that the entire Transition region should be considered as one which climatically is capable of developing a deciduous climax, even though this potential climax fails of attainment in many localities. Consequently, with this interpretation in mind, there would be but two climatic formations in eastern North America: a coniferous forest extending southward from the arctic to the St. Lawrence valley; and a deciduous forest occupying the rest of the area.

Such a view-point, although ecologically correct, would, however, fail to recognize the existence of the Transition region, which, as already pointed out, is very distinct in both the nature of its climax forest and floristically as well.

It must be constantly borne in mind that we are concerned merely with the more conspicuous and extensive features of the vegetation as displayed by the various climax associations. Consequently it will be impossible to consider the minor local variations which often obscure the true conditions. It must be admitted that differences in topography and soil profoundly affect the vegetation and may even bring about physiographic climaces. However, these local variations in the physiographic factors, unless they are operative over extensive areas, are of prime importance only from the standpoint of floristic plant geography—the study of the distribution of individual species; and they are negligible in a survey of the distribution of masses of plants. These two viewpoints are both of value in the study of plant geography and they are not antagonistic, but simply approach the subject from different angles. The floristic plant geographer is interested primarily in the unusual occurrence of individual species, while his ecological co-worker is concerned with the usual and more general features of the vegetation as a whole.

To sum up, in the opinion of the writer, the following forest regions should be distinguished in eastern North America.

A. The Northeastern Evergreen Coniferous Forest Region. This area extends southward from the arctic tundra to the Great Lakes and the height of land, which borders the St. Lawrence valley on the north. For our purposes its southern limit may be assumed to coincide with the northern limit of the sugar maple (Figure 2). This region occupies the great Laurentian tableland of eastern Canada, a country of sterile acid granites with poor drainage. The climate may be judged from the rainfall evaporation ratios as given by Transeau (28), the amount of rainfall being equal to 150% and over of the evaporation. The climax forest consists of white and black spruce, balsam fir and paper birch.

B. The Eastern Deciduous Forest Region. This area centers in the Ohio basin and the southern Appalachians, sending a tongue northward along the Piedmont region east of the mountains. The northern limit of the area may be said to coincide with the southern limit of the balsam fir. The underlying rocks are for the most part Devonian and Silurian in nature and yield a rich basic soil. The rainfall-evaporation ratio is from 80%-110%. The climax forest of the region is composed of chestnut, tulip, black walnut, sycamore, beech, sugar maple, and several species of oak and hickory, constituting the "southern hardwood" forest of the lumbermen.

C. The Transition Forest Region. This area lies between the two above regions and shows characteristics of both. In extent it is situated between the northern limit of the sugar maple and the southern limit of the balsam fir, an area which about coincides with the distribution of one of its character trees, the yellow birch. The rainfall-evaporation ratio is from 110%-150%. The region shows a transition to the coniferous forest on the one hand; and to the deciduous forest on the other, although potentially the deciduous type must be considered as the regional climax. Two subdivisions may be recognized depending on the proximity of one or the other of the main forest regions

1. THE CANADIAN-TRANSITION ZONE. — this zone occupies the northeastern portion of the Transition region, characterized by the higher rainfall-evaporation ratios, and comprises the Maritime Provinces, northern New England,

the Adirondacks and scattered areas along the higher Appalachians. Much of this territory has sterile acid soils, a distinct glacial topography and usually poor drainage. The climax forest consists of sugar maple, beech, hemlock, yellow birch, white pine, balsam fir and spruces and constitutes the "spruce-northern hardwood" region of the lumbermen. The climatic climax is attained on the better sites, but on much of the area coniferous forests occur, which represent physiographic climaces due to local edaphic or topographic factors.

2. THE ALLEGHANIAN-TRANSITION ZONE. — this zone occupies the western and southern portions of the Transition region, an area with the lower rainfall-evaporation ratios. The climax forest consists of sugar maple, beech, yellow birch, hemlock, and white pine and constitutes the "northern hardwood" region of the lumbermen. Physiographic climaces are also frequent in this zone and are often widespread, as seen for example in the white pine region of New England and the jack pine region of Michigan and Wisconsin.

Due to the effect of local factors the vegetation in many localities may not coincide with any of the above groups. Coniferous species, for example, may be present in bogs in an otherwise purely deciduous region; and similarly southern forms may occur locally in a northern region. These exceptions to the usual order of things are interesting, however, only from the standpoint of the distribution of the individual species concerned, and they may be neglected in a consideration of the vegetation of the region under observation.

There are also instances where, within the limits of one climatic formation, there occur typical areas of a more northern climatic formation. Such a condition exists on the upper slopes of the higher mountains, such as Katahdin, the White Mountains, Adirondacks and some of the peaks of the southern Appalachians, where a deciduous or transition forest is forced, because of the altitude, to give way to a forest of the northeastern conifer type; and this in turn, on the highest summits, may even yield its place to alpine vegetation.

From these few cases it can be seen that the limits of the forest regions outlined above are not hard and fast and there is bound to be overlapping and an intermingling of various types. Such conditions are fairly local, however, and in general the vegetation in any given place may readily be assigned to one or another of the above formations.

The Penobscot Bay region of Maine lies within the Canadian Transition zone of the Transition Forest region. Its climax forest is that characteristic of the larger area — a mixed deciduous coniferous forest of sugar maple, beech, hemlock, yellow birch, balsam fir and spruce. The nature of this regional climax association-type, the climax forest, as it occurs in Cape Breton, and the successions which lead to it have been described in detail by Nichols (23) and need not be discussed here. Consequently we may proceed to a description of the regional climax as it occurs in the Penobscot Bay region.

III. THE CLIMAX FOREST OF THE PENOBSCOT BAY REGION

In the Penobscot Bay region the nature of the forest covering varies greatly and it is at first difficult to determine which of the several common types of woodland represents the actual regional climax association-type. On the islands and the outer portions of the mainland the prevailing appearance of the forests is coniferous, and it is only when we go back from the exposed shores to the more sheltered localities that we find deciduous trees appearing. Even here, however, the influence of various disturbing factors has so altered the nature of the vegetation that the cases where the deciduous trees of the regional climax predominate are comparatively infrequent and occur only where the combined physiographic and biotic factors are favorable.

Evidences of the nature of the original climax forest which formerly existed in this region are very meagre, since the entire country has been cut over repeatedly and no traces of virgin timber remain. There can be no doubt, however, but that deciduous forests of the climax type were once widespread over a great part of the Penobscot Bay area. All the information to be gained from local histories and the statements of the older inhabitants indicate clearly that the first settlers found huge forests of beech, maple, hemlock, spruce, pine and oak, which were early sought after by the lumbermen and destroyed, never to be replaced in their original glory. At the present time, however, there do occur several stands of second growth timber, which are reproducing themselves and must be considered as permanent. From these examples we are able to derive some idea of what the original conditions must have been like; and to prophesy as to the make-up of the climax forests of the future, if such are ever able to develop again.

The best instance of what we may call the typical climax forest of the region is located on the south side of Lake Alamoosook in the town of Orland. This stand of timber has never been cut over within the memory of the present inhabitants, although much of the hardwood has been culled out at various times. The majority of the trees, together with the shrubby undergrowth and the herbaceous species, still remain undisturbed and conditions in this tract more nearly approximate those in a virgin stand than anywhere else in the region. In this forest, which is pictured in Figure 3, hemlock is the most conspicuous species, both in numbers, for it comprises 50% of the trees, and in size as well, since the trunks in general measure from three to four feet in diameter. Next in abundance and size come the yellow birch and the red spruce, and with these are associated smaller numbers of the beech, sugar maple, red oak and pa-

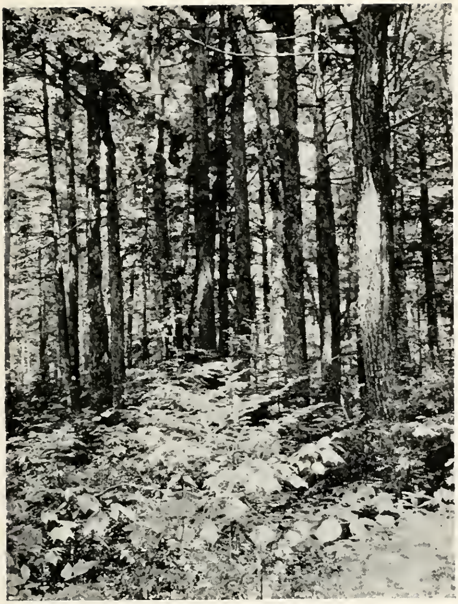

Figure 3. — Interior of climax forest at Lake Alamoosook, Orland; hemlocks and yellow birch with understory of fir, seedling hemlocks, hobble bush and mountain maple.

Figure 4. — Succession on granite, Naskeag Point, Brooklin; lichens, crevice plants (chiefly *Juncus Greenei*), heath mat with cladonias and polytrichum, and trees beginning to invade area.

per birch. The shrubby growth consists chiefly of mountain maple *(Acer spicatum)*, moosewood *(Acer pennsylvanicum)*, hobble bush *(Viburnum alnifolium)*, and hazelnut *(Corylus rostrata)*, with numerous seedling hemlocks and spruces and occasional reproduction of the other species. Considerable balsam fir is present, but only as small undeveloped trees less than ten feet in height.

Another tract of timber, situated along Craigs Brook in the same town, may also be considered as typical, although it is distinctly second growth and has not attained the age of the preceding stand. Here the beech and sugar maple are most abundant, with the yellow and paper birches and the hemlock less frequent, while the spruces are comparatively uncommon. As in the area just described, there is a definite second story, or layer, of balsam fir; and a shrubby growth which includes the yew *(Taxus canadensis)*, seedling oaks and hemlocks, as well as the characteristic shrubs mentioned above.

A third tract of climax forest, located on the southern slopes of Mt. Megunticook in Camden, shows similar conditions, although the trees are restricted to three species. Hemlocks comprise 60% of the individuals, and sugar maple and beech in about equal quantities make up the balance. A peculiar feature of this stretch of woods is the almost entire absence of shrubby undergrowth.

In all three of these areas the herbaceous plants are similar and it is interesting to note that these forms are more northern in their distribution than are the woody species. The following plants may be considered as characteristic of the climax forest:

Dryopteris spinulosa
Dryopteris Phegopteris
Lycopodium annotinum
Clintonia borealis
Maianthemum canadense
Oxalis americana
Viola incognita
Circaea alpina
Cornus canadensis
Monotropa Hypopitys

Coptis trifolia	*Pyrola chlorantha*
Rubus pubescens	*Mitchella repens*

Bryophytes are almost entirely lacking and the absence of a carpet of vegetation is noticeable at once, as is the open character of the forest as a whole.

The majority of the woods in the Penobscot Bay region, however, differ more or less in their composition from the examples cited above, which approach very closely the transitional climax forest as described for other localities. Often white pine and red oak are the most conspicuous members of a stand, or the white cedar or red maple may be prominent, while again pure stands of one species or another may occur. It would be impossible within the limits of the present discussion to take up all of the various types of woods which exist and the factors which are responsible for their occurrence. It will be sufficient to indicate what species are present in the forests; and the general requirements of these species.

An examination of some fifty tracts of typical well-developed upland woods was made to determine what trees were present. The white birch was found to occur in forty of the fifty areas, or in 80% of the cases. The following table shows the percentages for the other species.

Fagus grandifolia	60
Picea rubra	60
Quercus rubra	60
Tsuga canadensis	50
Betula lutea	50
Pinus Strobus	35
Acer rubrum	35
Abies balsamea (mature trees)	35
Acer saccharum	25
Thuja occidentalis	10
Betula populifolia	10
Fraxinus americana	10

Populus grandidentata	8
Picea canadensis	8

It will be evident from this table that the species which occur in 50% or more of these areas of woodland, chosen as typical of the Penobscot Bay region, are the character trees of the Canadian-Transition forest as a whole. The requirements of these character trees and of their associated species will be summed up as follows:

Betula alba var. *papyrifera.* As the figures indicate the paper birch is widespread throughout the area, and it occurs in nearly all stands save the very oldest. The tree is short lived, as compared with other hardwoods, for it is susceptible to decay and also to wind damage, since the roots do not anchor it at all firmly in the ground. It is intolerant of shade and so reproduces poorly when associated with hardwoods. In burned and lumbered localities, however, reproduction is very dense, and since most of the second and third growth woods are of this sort, the birch is the commonest tree to be found in the region.

Fagus grandifolia. The beech is a conspicuous species on well drained land where the soil is deep, especially in loamy soil. It is very tolerant and reproduces prolifically, trees of all ages being present in the stand. On cut over land and burned areas it exhibits good reproduction by sprout growth and may often be the only species present in such locations.

Picea rubra. The red spruce is able to grow on any sort of soil and in all situations, and it is very tolerant. It reproduces well on lumbered areas and in localities where there is little hardwood competition. A bare, moist, mineral soil or duff is the most favorable for reproduction, while the leaf litter of a hardwood forest prevents it. Once started, in a locality, however, the spruce is able to exist for years with almost no sunlight, and although usually outdistanced by hardwoods it persists and forms a characteristic second story in nearly all woods. If the hardwoods are removed anywhere the spruce at once begins to grow rapidly to full size.

Quercus rubra. The red oak is a prominent member of the deciduous forests, occurring either as individuals or in pure stands. It is often associated with white pine on recently burned or lumbered land. It reproduces well from seed in a light covering of leaves and also sprouts readily from the stump. It is fairly tolerant and so is able to persist after the other hardwoods have come in, and as it lives to a great age it is of frequent occurrence in the older stands.

Tsuga canadensis. The hemlock occurs on deep soil on the lowlands and lower slopes in protected situations. Mature trees are comparatively infrequent for the tree has been very extensively lumbered, and, although reproducing readily, growth is very slow. It is, however, very tolerant and the seedlings and young trees are able to flourish even in the dense shade of the climax forest.

Betula lutea. The yellow birch is very widely distributed, occurring in any sort of soil or location. It is perhaps more frequent on the richer, deeper soils, but owing to its shallow root system, it is also well adapted to thin soils. It seeds abundantly and the seeds can germinate in clearings or burned over areas, where the mineral soil is exposed, but the best reproduction occurs in the woods. Because of its tolerance the seedlings can develop readily in the deepest shade, and as a result the tree is abundant in second growth woods of all sorts.

Pinus Strobus. The white pine originally was very generally distributed, but it has been more sought after by the lumbermen than any other species and at present no old growth remains in pure stands and very little as isolated individuals in the forests. The tree thrives, however, on all but the driest soil and is a rapid grower where the light conditions are favorable. It is intolerant of shade, so in heavy woods the seedlings soon succomb, but in open places such as old fields or burned over areas, particularly those with a sandy soil, the pine reproduces readily and often forms pure stands, or else is associated with the red oak.

Acer rubrum. The red maple is frequent in moist soils at low elevations, although it is more characteristic of the swamp forests of the region. It is very conspicuous in second growth woods owing to its tendency of forming coppice and its ability to reproduce readily from seed. As it is fairly tolerant it can grow to maturity in dense hardwood stands.

Abies balsamea. The balsam fir, although more often occurring with the spruce in strictly coniferous woods, may be found in deciduous woods, though rarely as mature individuals. It reproduces prolifically in clearings and as it grows rapidly, at first, it plays a prominent part in the early stages of second growth woods. As the hardwoods increase in size they soon predominate over the fir, which is unable to successfully compete with them, owing to its intolerance and its relatively short life. The ecological relations of the fir in the deciduous forests have been discussed at length by Nichols (23).

Acer saccharum. The sugar maple, one of the character trees of the regional climax, like the hemlock, is restricted to the more favorable localities, where there is a deep, well drained soil and protection from the fogs and cold of the coast. In such places reproduction occurs readily, since the tree is a prolific seeder. Its reproduction is especially noticeable in the dense climax forests for the seedlings are very tolerant and can readily endure the heavy shade of the older maples, the beeches, birches and spruces. The tree is also abundant in the second growth on cut over land, largely owing to its ability to sprout from the stump.

The remaining five species, which occasionally are found with the climax trees, are of very little importance and usually represent relic species from an earlier stage in the succession of vegetation. The poplar *(Populus grandidentata)* and the gray birch *(Betula populifolia)* are pioneer trees in clearings and they rarely appear in the denser forests owing to their great intolerance. The white cedar *(Thuja occidentalis)* and the white ash *(Fraxinus americana)* are more typical of swamp forests, and in the upland woods are to be found only in extremely moist places. The white spruce *(Picea canadensis)* is primarily a pioneer in the revegetation of old fields and is unable to compete in the forest with deciduous trees, although it is of frequent occurrence in coniferous woods.

IV. THE PHYSIOGRAPHIC FORMATION-COMPLEX OF THE PENOBSCOT BAY REGION

A. PRIMARY FORMATIONS OF THE XERARCH AND MESARCH SERIES

1. Formations of Ordinary Well-Drained Uplands

In general the succession of vegetation leading up to the climax type is the same on all ordinary uplands, whether they be characterized by rock outcrops or glacial drift. Occasional differences do occur depending on the nature of the underlying rock, the succession on igneous rocks displaying slightly different features from that on sedimentary rocks. In the present discussion the succession on granite, the igneous rock of most frequent occurrence, will be outlined in detail. The succession on schists, the most abundant sedimentary rock, however, will be considered only in those respects in which it differs from granite, whenever these seem of sufficient importance to warrant it.

a. Association-types of igneous rock outcrops

Owing to the paucity of the soil covering and the consequent frequent occurrence of bare rocks, the Penobscot Bay region affords an extremely good opportunity for a study of the succession of vegetation in such a habitat.

Rock surface association-type

The first forms to appear on the bare surface of the rocks are the crustose lichens, which are adapted both by their habit and requirements to the severest and most unfavorable of habitats, such forms as *Rhizocarpon (Buellia) geographica, R. confervoides, Lecidia platycarpa, Lecanora polytropa* and *L. Hageni* being common. As a result of the activities of these plants the rock surface is etched away and a little soil formed in which a second group of lichens, the foliose species, can find a foothold. These are much more conspicuous and readily attract attention. They comprise various of the gray-green parmelias, including such forms as *Parmelia saxatilis, P. conspersa* and *P. sulcata*, which often form irregular patches several feet in diameter; and the striking yellow *Candelariella (Placodium) vitellina* and *Xanthoria (Theloschistes) parietina*, together with several species of *Umbilicaria* and *Gyrophora.* With these lichens are associated such xerophytic mosses as *Hedwigia ciliata* and *Grimmia apocarpa.* As soon as sufficient soil has accumulated the fruticose lichens come in. These consist of numerous species of *Cladonia*, chiefly *C. rangiferina, C. pyxidata* and *C. furcata; Stereocaulon coralloides*, and *Cetraria islandica.* The gradual growth of these forms soon result in a mat of lichens which eventually covers the surface of the rock, provided the slope is not too steep.

Crevice association-type

The crevices in rock outcrops, which are of common occurrence, support a type of vegetation which is more advanced from the very beginning, owing to the presence of particles of soil and the more sheltered environment, and, in addition to cladonias and other fruticose lichens, various herbaceous and shrubby plants early appear. Chief among these may be mentioned *Danthonia compressa*, *Lechea intermedia*, *Pyrus melanocarpa*, *Potentilla tridentata*, *Solidago bicolor*, *S. nemoralis* and the mosses, *Polytrichum commune* and *P. juniperinum*. In addition to these species, which are almost universally present, other forms may locally be prominent. One tract of granite has a crevice vegetation composed entirely of *Juncus Greenei* and *Polytrichum* (Figure 4). On an exposed serpentine hill on Little Deer Isle, the crevice plants are chiefly ferns, such as *Asplenium Trichomanes* and *Woodsia ilvensis*.

Heath-mat association-type

As the lichen mat, above referred to, develops it becomes more and more difficult to distinguish the crevice plants, for many of the species are now able to find a foothold in the larger amount of soil afforded by the mat and they rapidly spread over the surface. The lichens are still a prominent feature (Figure 5), but they are soon dominated by the higher plants, particularly the heaths and the resulting association is known as the heath-mat. *Juniperus communis* var. *depressa* is often conspicuous at this stage (Figure 6), while other characteristic species present on the mat include:

Herbaceous Plants

Pteridium aquilinum
Selaginella rupestris
Deschampsia flexuosa
Arenaria groenlandica
Potentilla tridentata
Lechea intermedia
Aralia hispida
Cornus canadensis
Lysimachia quadrifolia
Prenanthes trifoliata

Shrubby Plants

Pyrus melanocarpa
Rhododendron canadense
Kalmia angustifolia
Arctostaphylos Uva-ursi
Gaylussacia baccata
Vaccinium pennsylvanicum
Vaccinium Vitis Idaea var. *minus*
Viburnum cassinoides

FIGURE 5. — Heath mat stage on Great Pond Mountain, Orland; lichens still prominent; xerophytic spruce forest in background.

FIGURE 6. — Succession on granite, Oceanville, Deer Isle; mat of lichens and grasses with *Juniperus communis* var. *depressa*.

Trees

Picea rubra	*Betula alba* var. *papyrifera*

Coniferous forest association-type

As indicated above, isolated trees may be present on the heath-mat and rarely in crevices. As the depth of the soil and its water-holding capacity increase these trees spread gradually, often reproducing by layering, until gradually a coniferous forest develops. This does not occur uniformly, owing to local differences in physiography, so that even in a fully established forest there may be areas in which succession may not have proceeded beyond the heath-mat or even the rock surface stage.

This first coniferous forest to appear naturally grows in the rockiest places, where there is comparatively little soil present, only the thin layer of duff derived from the old heath-mat and the decaying needles. Often this layer can be lifted like a blanket from the surface of the rock. The forest is almost completely dominated by the red spruce (Figure 7), with a little white spruce and fir balsam, especially near the edges or bordering on open places. The trees grow very closely together with their branches interlacing, and the ground beneath them is nearly devoid of vegetation (Figure 8). This latter feature is characteristic of young coniferous woods elsewhere and has been attributed to various factors, such as insufficient light, dryness of the soil owing to the interception of moisture by the crowns, or the burial of the seeds under the covering of dead needles. Not only is there no herbaceous or shrubby vegetation, but the lower limbs of the trees themselves are dead or dying and usually festooned with the beard moss *Usnea barbata*. The trees of the stand are in general even-aged and the only young growth to be noted are occasional spindling spruces, which have germinated in the mineral soil, but have been suppressed by the dense shade. This type of forest is especially characteristic of the islands and seaward peninsulas of the mainland, where it grows in the most exposed situations even on the very edges of the rocky shores (Figure 19), where it must be subjected not only to cold fogs but to the constant drenching by wind swept spray as well. Many of the smaller rocky islands have as their entire vegetation a forest of this sort, which constitutes a physiographic climax and seems likely to persist indefinitely unless conditions are altered. The summits of the higher mountains, such as Great Pond Mountain in Orland, Isle au Haut, and Ragged and Megunticook Mountains among the Camden Hills also have a coniferous forest of this type.

Normally, however, this first rather xerophytic forest is not at all permanent. The death of the older trees and their removal, due to windfall, results in the admission of more light to the forest floor and the consequent appearance of a moss carpet. This in turn favors the coming in of herbaceous plants and shrubs, and the better development of seedlings. The suppressed little spruces, which were able to tolerate the deep shade, now grow rapidly under the stimulus of the renewed light. Reproduction, chiefly of balsam, takes place in these open places, and as is the case elsewhere the rapidity with which this species grows makes up for its lack of tolerance. As conditions become more and more mesophytic and a larger amount of soil accumulates, another type of coniferous forest (Figure 9) is gradually developed in which balsam fir is nearly as prominent as the red spruce, and other species are conspicuous members, chiefly the paper birch, white spruce, mountain ash *(Pyrus americana)*, mountain maple, moosewood, alder *(Alnus crispa* var. *mollis)*, hobble bush, withe-rod *(Viburnum cassinoides)* and yew. The most conspicuous feature of these woods is the profuse moss carpet, which comprises a great number of species of both mosses and liverworts. Prominent forms include:

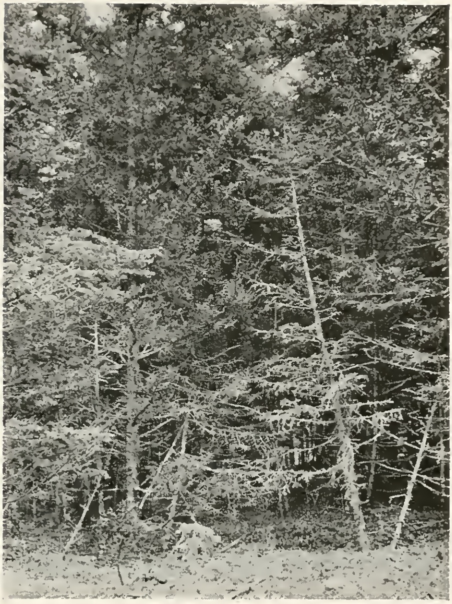

FIGURE 7. — Exterior of xerophytic coniferous forest, Naskeag Point, Brooklin; red spruce and fir balsam.

FIGURE 8. — Interior of same forest showing dead lower branches and lack of vegetation on forest floor.

Hylocomium proliferum
Hylocomium splendens
Rhytidiadelphus triquetrus
Dicranum scoparium
Ptilidium ciliare
Hypnum Schreberi
Stereodon cupressiformis
Ptilium crista-castrensis
Bazzania trilobata
Scapania nemorosa

Characteristic herbaceous species are

Dryopteris Linnaeana
Dryopteris spinulosa vars.
Lycopodium lucidulum
Maianthemum canadense
Clintonia borealis
Coptis trifolia
Ribes prostratum
Oxalis americana
Aralia nudicaulis
Cornus canadensis
Pyrola secunda
Moneses uniflora
Monotropa uniflora
Chiogenes hispidula
Trientalis borealis
Linnaea borealis var. *americana*
Solidago macrophyllus
Aster acuminatus

Where this coniferous forest occurs in rocky localities, as in the outer portions of the Penobscot Bay region, it seems to have reached a state of equilibrium with its environment and to be perpetuating itself. The new growth consists of the same species as the old forest and no further successional stages are in evidence. However we must consider it as constituting merely a physiographic climax, rather than as a distinct climax, as some authorities do, since in more favorable localities in the same region, such as the deeper soil of the glacial drift, there is a further transition to the regional deciduous climax. As reasons why the regional climax fails to develop on these rocky areas there may be given the following:

(1) *Shallowness of the soil.* While favorable for the superficial root systems of the spruce and fir, the thin layer of duff, which rarely exceeds a foot in depth cannot support such deeper rooted forms as the beech or sugar maple. The duff also dries out quickly and so lacks the necessary moisture for such a tree as the hemlock.

(2) *Lack of basic material.* Such mineral soil as may be present is derived from sterile acid granites, gneisses and quartzites, and does not afford the requisite amount of basic material necessary for most of the rich woods types.

(3) *Exposure.* The proximity of the ocean with the accompanying fogs and cold winds has the same limiting effect on the vegetation as increase in altitude or latitude, resulting in a local climate within a larger climatic unit area.

These factors which prevent the development of the regional climax are distinctly favorable for the coniferous forest and this latter type is widespread in the coastal region, where it forms at once the most prominent and striking feature of the landscape. The dense stands of spruce and fir, particularly on the islands, stand out in unexcelled beauty against the sky and water, and their pyramid outline deservedly entitles the region to be known as "the country of the pointed firs."

In a few instances there is developed in the Penobscot Bay region an upland forest in which the white cedar *(Thuja occidentalis)* is the predominant tree. This species is more characteristic of the swamp forests of the region, but it occasionally is found occupying hollows and other relatively moist sites on the uplands. The stands may be almost pure cedar, but usually considerable spruce and white birch is present. In rare cases this forest is developed on rocky ledges, usually of diorite, situated near the sea and in areas where there is abundant moisture from higher up on the slopes. It is an interesting fact that such stands almost invariably occupy the seaward slopes of the mountains and it is conceivable that the mountain summits intercept the fogs, which blow in from the ocean at all seasons, and precipitate them on these eastern slopes, thereby increasing the atmospheric humidity and the general moisture conditions.

Figure 9. — Coniferous forest, shore of Herricks Bay, Brooklin; spruce, balsam fir, white birch, mountain ash and *Alnus crispa* var. *mollis.*

Figure 10. — Succession on schist, Brooklin; crevice plants, huckleberry, gray birch and white pine.

b. Association-types of sedimentary rocks

The succession of vegetation described above, while particularly characteristic of granite, applies also to other igneous rocks. The succession on schists and other sedimentary rocks, however, differs in certain respects.

On a schist the crustose lichens are usually different species from those occurring on granite, such forms as *Rhizocarpon Oederi*, *Lecidia platycarpa* and *Lecanora cinerea* being conspicuous. The foliose and fruticose lichens and most of the herbaceous crevice plants, on the other hand, are those characteristic of the igneous rocks. More variations appear, however, among the woody forms. Associated with such ever present species as the huckleberry *(Gaylussacia baccata)*, the sheep laurel *(Kalmia angustifolia)*, red spruce and *Pyrus melanocarpa*, in the crevices and on the heath-mat, are the broom crowberry *(Corema Conradii)*, gray birch *(Betula populifolia)* and several species of pine. Of these latter the white pine (Figure 10) is the most frequent, but the red pine *(Pinus resinosa)* and the pitch pine *(Pinus rigida)* are not uncommon. The *Corema* is particularly striking in such localities (Figure 11), occurring in dense cushion-like patches scattered over the surface of the mat. These clumps originate in a crevice and spread slowly, sometimes attaining a diameter of several yards, but they never occupy the whole area of the mat. *Gaylussacia* has a somewhat similar tendency to form clumps, while *Kalmia*, *Pyrus*, and the trees occur as scattered individuals. Reproduction of the pines is abundant and in course of time the heath-mat is replaced by an open forest, the most xerophytic in the region.

This forest may be an almost pure stand of pitch pine, particularly where it occurs in the more exposed situations, as on Isle au Haut, or it may comprise a mixed growth of pitch pine and red pine. More often still these two species are associated with the white pine and also occasional specimens of the red spruce, red oak, and gray birch (Figure

12). The shrubby undergrowth in these latter woods is exceedingly dense and coarse, consisting of great mats of *Juniperus communis* var. *depressa*, *Myrica asplenifolia*, *Gaylussacia baccata*, *Vaccinium pennsylvanicum* and *V. canadense* and clumps of *Alnus crispa* var. *mollis*. *Corema* may persist for a while but soon dies out as the amount of shade increases. Characteristic herbaceous species of these xerophytic pine forests include:

Polytrichum commune
Pteridium aquilinum
Oryzopsis asperifolia
Danthonia compressa
Carex debilis var. *Rudgei*
Fragaria virginiana
Aralia nudicaulis
Gaultheria procumbens
Campanula rotundifolia
Solidago bicolor

The pitch pine forest is the only one of these three types which seems to have reached a state of equilibrium. It is one of the most distinct and sharply delimited association-types in the region and definitely constitutes a physiographic climax. In the other cases the xerophytic pine forest, as indicated by the presence of spruce, probably represents a pioneer stage and is destined to be replaced by the spruce-fir forest.

c. Association-types of uncompacted rocks

The succession of vegetation on the uncompacted rocks of the region — the glacial drift and marine clays — has proceeded much more rapidly than on the rock outcrops and has reached the final stages in nearly every instance. Consequently evidences of the initial stages are not at hand, but in all probability the succession was not unlike that already described. In the case of the marine clays, which occupy the lowlands near the coast the spruce-fir forest represents a physiographic climax; while on the deeper glacial soils succession continues beyond the coniferous forest stage.

FIGURE 11. — Edge of schist outcrop, Brooklin; clumps of *Corema Conradii* in foreground; *Kalmia angustifolia*, gray birch, white pine and red spruce.

FIGURE 12. — Forest on schists, Brooklin; white pine and gray birch with red spruce well established.

Development of the regional climax. Wherever soil conditions and topographic factors are favorable, deciduous trees soon begin to make their appearance, first among which is the yellow birch. Because of its shallow root system, well adapted to a comparatively thin soil, and its ability to germinate in the moss carpet, this tree easily becomes established in openings in the forest. As a consequence of this ability to grow both in the climax forest and a spruce forest as well, the yellow birch is one of the most widely distributed trees in the region. Owing to its tolerance it thrives in either situation. The beech follows the birch and like it does not require an extremely deep soil. These two trees are the only deciduous members of the regional climax forest which are at all frequent on the islands and the coastal portion of the mainland, where they occur as scattered individuals or occasionally form small stands in locally favorable situations.

As the leaf litter from these trees accumulates and the amount of humus increases, a seed bed is furnished for the sugar maple and hemlock. In localities where all the physiographic factors are favorable for their existence seedlings of these latter trees soon become frequent. Since they are very tolerant they grow rapidly in the shade of the other species and, when present in sufficient numbers, soon win out in competition with any conifers which may be present. The continual increase in leaf litter is proportionately unfavorable for the moss carpet, and this tends to disappear as the hardwoods increase, together with the herbaceous forms especially characteristic of such a habitat. The final stage in the succession on glacial till is a forest of the regional climax association-type. Figures 13 and 14 show such a mixed deciduous coniferous forest at Craigs Pond, in Orland. Theoretically such a forest should develop in all cases. Practically, however, the influence of various biotic factors has so altered the course of events that in only a few cases is the climax actually attained. Elsewhere secondary successions resulting from cultivation, fire, or lumbering have brought about changes in the character of the forest. A tract of woodland may consist of representatives of a single species, such as the beech, or of two or three species; and again trees, ordinarily of secondary importance, may play a prominent part and even dominate a given area. In consequence there is extreme variation between the different tracts of woods.

2. FORMATIONS OF WELL-DRAINED UPLANDS ALONG STREAMS

The rivers of the Penobscot Bay region are insignificant sluggish streams and have had very little effect in altering the topography of the country. Most of them are tidal in nature and the vegetation along their banks is of a lowland type. In only one instance has a river developed sufficient erosive action to carve out a valley for itself. The Ducktrap River in Lincolnville, along its lower course, flows through such a valley (Figure 15), which it has cut through a ridge of trap rock. Both of its banks are covered with a growth of spruce, fir, and hardwoods differing in no respect from the forests on ordinary uplands.

a. Association-types of boulder plains

The river has, however, been able to carry away the accumulated glacial debris along its course and has developed a well-marked boulder plain (Figure 16) with a characteristic flora growing between the rocks. The conspicuous pioneers in such a habitat are *Apocynum androsaemifolium* and the grasses, *Calamagrostis canadensis* and *Glyceria nervata*, while other abundant species include:

Juncus brevicaudatus
Iris versicolor
Radicula palustris
Hypericum ellipticum

Lysimachia terrestris
Lycopus americanus
Eupatorium perfoliatum
Eupatorium purpureum var. *maculatum*

Figure 13. — Climax forest of the regional type, Craigs Pond, Orland.

Figure 14. — Interior of Craigs Pond forest; beech, white and yellow birch, hemlock and spruce.

These plants tend to furnish an obstruction to the water and permit the deposition of sand and gravel, and gradually the soil among the boulders is built up higher and higher until shrubs and other herbaceous forms gain a foothold. Among these may be noted:

Scirpus atrovirens
Carex stipata
Salix cordata
Betula populifolia
Alnus incana
Thalictrum polygamum
Spiraea latifolia
Apios tuberosa
Mimulus ringens
Aster umbellatus

In one case a small alluvial island has been built up on the plain and this is entirely covered with a dense growth of *Calamagrostis canadensis* (Figure 15).

3. Formations of Well-drained Uplands along the Seacoast

The character of vegetation along the seacoast varies not only with the substratum, but with the degree of exposure as well. The possible seaward limit of vegetation is determined by the upper level of effective wave and ice action. In protected situations plants may extend to the water's edge, thus occupying all the area in which it is possible for them to develop. Succession on both rock outcrops and uncompacted rock in such places is entirely similar to that already described for ordinary uplands, and in the absence of unfavorable factors there may occur a complete development of the climax forest. On level rocky surfaces there is usually a sharp transition between the forest and the water. Occasionally, however, the rocks may drop off abruptly, forming miniature cliffs. When shaded by overhanging foliage the surface of these rocks may be cool and moist and support an abundant growth of bryophytes, such as species of *Philonotis*, *Dicranum*, *Mnium*, and *Scapania*, together with herbaceous forms like *Viola pallens*, *Sagina procumbens*, *Circaea alpina*, *Ilex verticillata* and several willows and alders. In drier, sunnier places the vegetation may consist of such species as *Festuca rubra*, *Poa compressa*, *Rosa humilis*, *Aquilegia canadensis*, *Myrica carolinensis*, *Rhus Toxicodendron* and various annual weeds. Lichens are frequent on these abrupt, sheltered shores and they comprise species like *Verrucaria maura* and *Verrucaria mucosa* growing where they are submerged at high water; *Verrucaria nigrescens*, just above the upper limit of the tides and *Lecanora subfusca* var. *campestris*, *Lecidea coarctata*, *Lecanora cinerea*, *Lecanora atra*, and *Rhizocarpon confervoides* anywhere above the limit of the highest tides.

In more exposed localities the action of sea, wind, and other factors have altered conditions and resulted in the formation of definite sea bluffs and headlands along eroding shores; and beaches of various sorts along depositing shores. The coastline of the Penobscot Bay region is so diversified that there is a great intermingling of these two types of shore. It may be said in general, however, that eroding shores are characteristic of salients, while depositing areas occur in reentrants.

a. Association-types of eroding areas along the coast

Association-types of rocky sea bluffs

Along the outer shores of the islands and the more exposed portions of the mainland sea bluffs have been developed by the action of the waves. These vary greatly in height, some extending but a few feet above the sea, while others tower to a height of several hundred feet as in the case of the cliffs on Isle au Haut and Monhegan. The vegetation of the sublittoral zone at the base of the bluffs, where the rocks run out beyond the low tide mark, consists of various red, green, and brown algae with a profuse growth of kelps in the deeper water.

In the littoral zone between the low and high tide levels the rocks are covered with masses of rockweed, species of *Fucus* and *Ascophyllum* (Figure 17). While these are perhaps more abundant near the low tide mark they may

Figure 15. — Ducktrap River at tide limit; boulder plain in right foreground; small flood plain island with *Calamagrostis canadensis* in left foreground.

Figure 16. — Boulder plain of Ducktrap River, Lincolnville.

reach well toward the high tide limit. On the rock surface where the seaweeds are absent several lichens may occur, notably *Verrucaria mucosa*, growing where it is submerged at every tide; and at a little higher level *Verrucaria maura*.

Occupying the area beyond the reach of the ordinary tides, but swept by spray during storms is another zone, the supralittoral. The lower portion of this is practically devoid of vegetation, but the upper portion is occupied by lichens, chiefly *Caloplaca elegans*, *Caloplaca murorum*, *Caloplaca baumgartneri*, and *Xanthoria parietina*. In the crevices of this area herbaceous plants first make their appearance. Characteristic forms include:

Hordeum jubatum
Carex hormathodes
Iris setosa var. *canadensis*
Sagina procumbens
Sedum roseum
Ligusticum scothicum
Coelopleurum actaeifolium
Plantago decipiens
Solidago sempervirens
Senecio sylvaticus

At the summit of the bluffs there is often developed a mat of prostrate or low shrubs, chief among which are the trailing juniper *(Juniperus horizontalis)*, common on bare rocks, and the crowberry *(Empetrum nigrum)*, where there is a peaty turf. This latter plant may form large mats which extend out from the edge of the turf and hang down over the face of the cliffs. Other conspicuous species occurring on the crests are the poison ivy *(Rhus Toxicodendron)*, bayberry *(Myrica carolinensis)*, bearberry *(Arctostaphylos Uva-ursi)*, mountain cranberry *(Vaccinium Vitis-Idaea* var. *minus)*, and *Juniperus communis* var. *depressa*. Between these shrubs grasses are common, chiefly *Festuca rubra*, *Danthonia compressa*, *Deschampsia flexuosa* and *Trisetum spicatum* var. *molle*, the latter two often growing in the *Empetrum* mat. Various halophytic seed plants, more common on beaches, may also be present, both on the crests of the bluffs and in crevices on the face. This area of prostrate shrubs does not always occur for its presence and extent is determined by the degree with which trees have occupied the crests. In the case of most cliffs the possible lower limit of tree growth as determined by wave action during the winter storms is located at the very edge and often the forest has been able to colonize the entire available surface. In such locations there is an abrupt transition between the coniferous woods and the bare rock face with no intermediate stages, a condition illustrated in Figure 19. More often, however, even though the trees extend to the edge of the bluffs, there is a narrow fringe of *Empetrum* present and overhanging the cliffs. Again, as in the condition described above, there may be a definite area at the summit where trees have failed to develop and the ground is occupied by the prostrate shrub association-type.

When trees are present on these sea cliffs they frequently show the effects of the constant exposure to which they are subjected by their gnarled or stunted growth, or in some other manner. On the Eastern Ear of Isle au Haut where the forest is exposed to an almost incessant buffeting of wind and spray, the trees back from the crest, in this case the white spruce, are so dense that, according to Norton (25), "a person of two hundred pounds weight may walk from the ground to the summit on the ends of the densely matted and tangled branches."

Association-types of headlands

Where conditions are very extreme the treeless zone extends back a considerable distance from the crest of the bluffs, and a barren headland results. The lower limit of possible tree growth in such an area may still be at the edge of the cliffs or even nearer the water, but the presence of various retarding influences, such as the nature of the rock surface, the steepness of the slope, and the degree of exposure, commonly prevent the occupation of the area by forests. Figure 18 pictures such a headland in which the forested portion is restricted and the trees show the effects of exposure.

FIGURE 17. — Rocky sea bluff, Swans Island; rockweeds at base of cliff.

FIGURE 18. — Portion of exposed headland, Hat Island, showing weather-beaten spruces.

The vegetation on these rocky headlands varies in different places. Where there is but little soil and rock outcrops or boulders are common, lichens may be abundant, especially foliose and fruticose forms, such as the parmelias, umbilicarias and cladonias. Grasses early make their appearance in such places, growing in crevices and pockets among the rocks. In less rocky areas they may carpet the whole headland. Conspicuous species are *Festuca rubra*, *Danthonia compressa*, *Agrostis hyemalis*, and *Poa pratensis* and associated with these such characteristic herbaceous forms as:

Arenaria lateriflora
Cerastium arvense
Potentilla argentea
Potentilla pennsylvanica
Epilobium adenocaulon
Anagallis arvensis
Veronica peregrina
Euphrasia stricta
Euphrasia purpurea var. *Randii*
Gnaphalium polycephalum

In the wetter depressions *Carex Oederi* var. *pumila*, *Carex Goodenovii*, *Juncus brevicaudatus* and *Vaccinium macrocarpon* are frequent. Eventually shrubs appear and the whole area may take on the appearance of the crests of the bluffs with sprawling mats of *Juniperus horizontalis* and *Empetrum* and great clumps of *Juniperus communis* var. *depressa*, *Myrica carolinensis*, *Prunus virginiana* and *Rosa virginiana*. Stunted spruces are occasional, and if the extreme conditions were modified, a coniferous forest would doubtless develop eventually.

Perhaps the most striking feature about the vegetation of the sea cliffs and headlands — and of the beaches and brackish marshes, to be described later — is the presence of many species of arctic and subarctic affinities. The extreme exposure of these habitats, the constant drenching with cold spray to which they are subjected and the frequent presence of fogs combine to render conditions much like those in boreal regions and afford a habitat where northern species can exist. The occurrence of this subarctic flora in this region has been discussed in an earlier paper (15), and it will be sufficient here merely to enumerate the more characteristic forms:

Juniperus horizontalis
Elymus arenarius var. *villosus*
Carex salina var. *kattegatensis*
Carex maritima
Iris setosa var. *canadensis*
Sedum roseum
Empetrum nigrum
Coelopleurum actaeifolium
Vaccinium Vitis-Idaea var. *minus*
Mertensia maritima

Association-types of sea bluffs in uncompacted rocks

Where wave action is cutting away a deposit of clay or glacial till, bluffs result which differ materially in their vegetative covering from the rocky bluffs described above. As long as the process of erosion is still active no plants can grow on the face of these bluffs. The only vegetation which appears is at the base and consists of a miscellaneous aggregation of "slump plants", which have slid down from the crest, together with various annuals, notable among which may be cited *Cirsium arvense*, *Oenothera muricata*, *Senecio sylvaticus* and *Erigeron canadensis.* When for some reason erosion ceases, grasses and alders rapidly invade the surface of the bluff and the latter spread with amazing swiftness, forming in a comparatively short time a dense thicket. Associated with *Alnus crispa* var. *mollis*, which is the alder commonly present in such places, are various of the herbaceous plants to be cited later (page 372) as characteristic of the moist edge of beaches. In some cases spruces and birches are invading the alders and eventually a coniferous forest will occupy the area.

The shore at the foot of these bluffs consists of a narrow rocky strip of boulders and cobbles, showing gradations to a shingle or a gravel beach. Unlike the latter, in this case the beach is the result of erosion and not deposition. The littoral zone, lying between the tide levels, is also covered

FIGURE 19. — Shingle beach at Dunhams Point, Deer Isle, showing gravelly lower beach, devoid of vegetation; coniferous forest on cliffs in background.

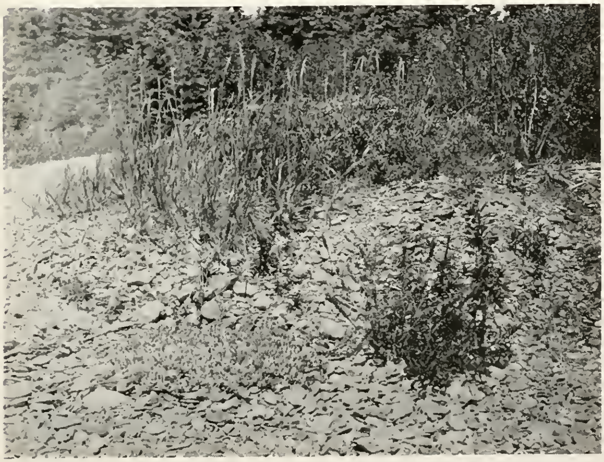

FIGURE 20. — Upper beach at same locality as that shown in Figure 19; *Mertensia maritima* and *Oenothera muricata* in foreground; *Elymus arenarius* var. *villosus, Lathyrus maritimus* and *Convolvulus sepium* var. *pubescens* in background.

with a profusion of large boulders, formerly present in the deposits, but which were too heavy to be transported away from their source. These are usually covered with a dense growth of rockweeds as is usual on rocky bottoms.

b. Association-complexes of depositing areas along the coast

Association-types of shingle beaches

Shingle beaches, composed of characteristic rounded wave-worn rocks of all sizes are of frequent occurrence in the region. They are usually found on the more exposed shores and in most instances are barrier beaches, cutting off small ponds or swamps from the ocean. On these beaches, as on sandy and gravelly ones as well, three more or less distinct zones are discernible. These comprise the lower beach, which lies between low and high tide marks and consequently is subjected to alternate submergence and exposure; the middle beach, which extends from the limit of summer tides to that of the winter storms; and finally the upper beach, which ordinarily is not submerged at any period of the year.

The *lower beach* is usually steep and absolutely devoid of vegetation. The rocks of which it is composed are constantly being rolled back and forth by the waves and this incessant motion naturally prohibits any plant growth (Figure 19). At its lower limit this beach may tend to become sandy or gravelly.

The *middle beach* is in general similar to the preceding in structure. The rocks however are not in motion during the growing season, since it is free from waves in the summer, and consequently some vegetation is able to develop. The most conspicuous plant on such a beach is the sea lungwort *(Mertensia maritima)* growing in great prostrate clumps, while the beach pea *(Lathyrus maritimus)* and the wild morning glory *(Convolvulus sepium* var. *pubescens)* are also common.

The *upper beach*, especially in the more exposed places is likewise very stony and resembles the middle beach in both its structure and vegetation (Figure 20). In the case of barrier beaches there is a well developed crest on this beach. Growing on the seaward side of this crest, where the boulders and cobbles are larger, are the species mentioned above; while on the leeward side, where the rocks are ordinarily smaller, other forms are frequent. Prominent among these may be mentioned:

Ribes hirtellum
Rosa humilis
Geranium Robertianum
Rhus Toxicodendron
Oenothera muricata
Achillea Millefolium

Where a shingle beach borders on an upland of glacial till there is a tendency for soil to accumulate on the upper beach and as this process proceeds many other species make their appearance, such as:

Equisetum arvense
Elymus arenarius var. *villosus*
Urtica dioica
Rumex pallidus
Rumex Acetosella
Cakile edentula
Ligusticum scothicum
Coelopleurum actaeifolium
Scutellaria galericulata
Galium Aparine
Bidens frondosa
Cirsium arvense

The upper beach is never very extensive and it may be entirely lacking. Often there is a sharp transition to a brackish pond or marsh and again to an upland forest. In some instances the forest has encroached upon the shingle, but it never forms a distinctive covering.

Association-types of gravelly and sandy beaches

In the more protected reentrants along the shore, gravel and sand beaches are formed. The pitch of these beaches is much less sharp than in the case of shingle beaches and often they are nearly level and so extend for considerable distances seaward. Almost invariably they are composed of coarse gravel or fine pebbles, save near the upper edge

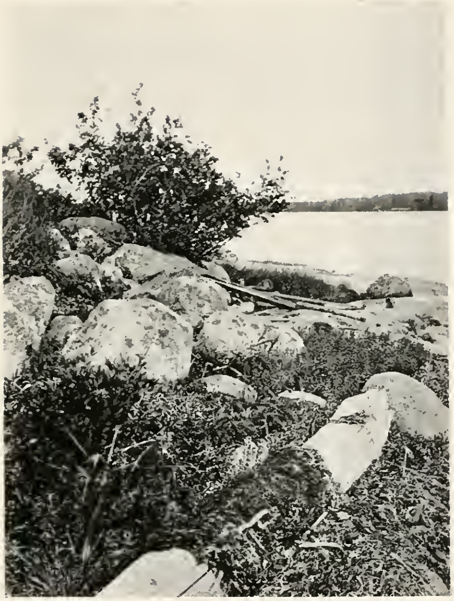

FIGURE 21. — Driftwood area on middle beach, Naskeag Point, Brooklin; *Ligusticum Scothicum*, *Arenaria peploides* var. *robusta*, *Agropyron repens*. *Alnus crispa* var. *mollis* in background.

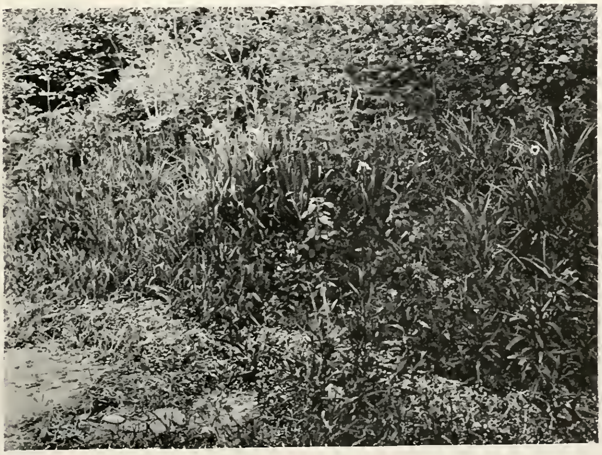

FIGURE 22. — Swampy margin of beach at edge of uplands, Naskeag Point, Brooklin; *Iris versicolor, Thalictrum polygamum, Carex stipata, Agropyron repens*, etc.

where considerable sand may be present. A true sand beach is rare enough to be a curiosity and dune development is entirely absent.

The lower beach. As in the preceding type a lower beach is present, which ordinarily is devoid of vegetation. Occasionally, just below high tide level, rocks may occur on the beach and these afford enough protection from wave action so that various halophytic seed plants can gain a foothold between them and give rise to a miniature salt marsh. This is especially true where the beach overlies a clay soil and the ground between the stones is somewhat muddy. Common species in such areas, which are inundated at every tide, include:

Puccinellia paupercula var. *alaskana*
Spartina patens
Carex maritima
Juncus Gerardi
Suaeda maritima
Limonium trichogonum
Glaux maritima var. *obtusifolia*
Plantago decipiens

The middle beach. Vegetation is much more abundant on the middle beach and the presence of large amounts of driftwood aids the plants in securing a foothold in the gravel and sand (Figure 21). Many of the species found here are those characteristic of sand beaches in other regions, namely:

Ammophila arenaria
Elymus arenarius var. *villosus*
Agropyron repens
Rumex pallidus
Chenopodium album
Salsola Kali
Atriplex patula var. *hastata*
Arenaria peploides var. *robusta*
Cakile edentula
Lathyrus maritimus

The upper beach. As in the case of shingle beaches the upper beach is rarely of any size, occurring usually as a narrow fringe bordering on the uplands. In addition to the plants cited as characteristic of the middle beach the following species are common:

Equisetum arvense	*Ribes hirtellum*
Rumex Acetosella	*Oenothera muricata*
Polygonum allocarpum	*Plantago major* var. *intermedia*

In a few instances, such as the Carrying Place on Swans Island, a well developed upper beach is present. In this locality the vegetation is predominated by *Elymus arenarius* var. *villosus*, and associated with it are *Lathyrus maritimus*, *Cakile edentula*, *Rumex pallidus*, *Convolvulus sepium* var. *pubescens* and *Myrica carolinensis*.

A characteristic feature associated with many of the sand and gravel beaches is the presence of an extremely moist area where the beach adjoins the upland. Such places are practically miniature swamps and should properly be considered with the other lowland association-types. They are, however, of such general occurrence in connection with beaches as to warrant describing them at this time. Water leaching down from above keeps these areas constantly supplied with moisture. Where the substratum is sandy or gravelly this water does not accumulate on the surface but is readily absorbed, owing to the porous nature of the soil. The vegetation in such places is extremely characteristic (Figure 22), and consists of species also present in lowlands away from the coast. Prominent forms which almost invariably occur are:

Calamagrostis canadensis	*Thalictrum polygamum*
Carex crinita	*Impatiens biflora*
Carex stipata	*Cicuta maculata*
Iris versicolor	*Heracleum lanatum*
Alnus crispa var. *mollis*	*Scutellaria galericulata*
Rumex crispus	*Mentha arvensis* var. *canadensis*
Lathyrus palustris var. *pilosus*	*Cuscuta Gronovii*

Where the substratum consists of clay, or ledges are present, drainage is impeded and water tends to collect in little

Figure 23. — Succession in abandoned pasture. Naskeag Point, Brooklin; grasses, daisies, *Potentilla tridentata* and blueberries in foreground; junipers, spruces and firs in background.

Figure 24. — Forest of white spruce in former pasture, Dunhams Point, Deer Isle.

pools. These usually become brackish, owing to the addition of salt water from the spray and in consequence support a different sort of vegetation. Characteristic species in such places include forms which are typical of brackish marshes rather than fresh swamps, such as:

Carex salina var. *kattegatensis*
Carex maritima
Scirpus campestris var. *paludosus*
Spergularia leiosperma
Ranunculus Cymbalaria
Potentilla pacifica

B. SECONDARY FORMATIONS OF THE XERARCH AND MESARCH SERIES

1. Formations Due to Human Activity

a. Association-types due to cultivation

In many places tracts of land, which have been under cultivation at one time or another, are abandoned and almost immediately these begin to revert to a wild state and a series of successions ensue, which lead to a climax type of vegetation.

Association-types of fallow fields

When a plowed field is abandoned it is overrun the succeeding year by herbaceous species, many of which were present as weeds while the field was under cultivation. These form a dense growth which may persist for several years. Common forms include:

Polygonum tomentosum
Polygonum Persicaria
Spergula arvensis
Capsella Bursa-pastoris
Raphanus Raphanistrum
Trifolium repens
Prunella vulgaris var. *lanceolata*
Galeopsis Tetrahit var. *bifida*
Ambrosia artemisiifolia
Chrysanthemum Leucanthemum var. *pinnatifidum*
Leontodon autumnalis
Solidago nemoralis

Soon various grasses begin to invade the area and as these become more and more firmly established they replace the herbs as dominant forms. Conspicuous species are *Poa pratensis*, *Agrostis alba*, *Agrostis hyemalis*, *Anthoxanthum odoratum* and *Phleum pratense.* Gradually a solid turf is formed and this furnishes a habitat for other herbaceous plants, such as *Fragaria virginiana*, *Trifolium procumbens*, *Rhinanthus Crista-galli*, *Euphrasia americana*, *Anaphalis magaritacea* and *Hieracium pratense.* In this condition the area closely resembles the abandoned fields to be described below; and the further stages in development are also similar.

Association-types of abandoned fields

When a pasture or hay field is abandoned it grows up chiefly to grasses, as indicated above. In some instances, where there is but little soil, the prominent species are *Festuca rubra* and *Danthonia spicata*, and with them various polytrichums and lichens. The first change to be noted in the vegetation of these abandoned fields is the appearance of shrubs and seedling trees, a condition illustrated by Figure 23. Among the conspicuous species may be mentioned *Juniperus communis* var. *depressa*, the sweet fern *(Myrica asplenifolia)*, blueberries *(Vaccinium pennsylvanicum* and *V. canadense)*, gray birch, paper birch, and in the moister places *Alnus crispa* var. *mollis.* Where this latter species occurs it always spreads very rapidly and soon forms a solid thicket, which prevents the invasion of other woody forms. In other cases the shrubs are destined to be succeeded by coniferous trees, which seed in from neighboring areas. The species of most frequent occurrence is the white spruce, which often forms pure stands, one of which is shown in Figure 24. Another common tree is the tamarack *(Larix laricina)*, which exhibits a surprising ability to colonize these old fields. Still again the red spruce and balsam fir may be present. As the conifers increase in number and in

FIGURE 25. — Late stage in abandoned pasture, Brooklin: spruce and fir dominant and killing out juniper.

FIGURE 26. — Grove of white pine in old field near Fish Hatchery, Orland.

size the shrubs are gradually killed out. Figure 25 shows an old pasture which has been nearly overgrown by red spruce, fir, and larch, with a little juniper fringing the open places. The first of the shrubs to disappear is the sweet fern, then the juniper and finally the blueberries which, however, are sometimes able to persist until there is almost a complete forest covering. The birches are able to survive and grow to maturity with the other trees, eventually forming a part of the resulting woodland, though much outnumbered by the conifers. Ultimately the area is covered with a spruce-fir forest similar to that already described for ordinary uplands.

In some localities where the soil is sandy and there are seed trees present in the vicinity, the white pine is the chief colonizer of these old fields. This species comes in very rapidly even during the grass stage and usually results in even-aged stands of the sort shown in Figure 26, which consist almost entirely of pine, with perhaps a little birch in mixture. Such areas were probably much more frequent in former times when the pine was more abundant.

b. Association-types due to fire

The nature of the existing vegetation in the Penobscot Bay region has been more profoundly altered by fire than by any other single agency. Not only have changes been brought about in the species present, but in some cases the soil itself has been so altered that the whole character of the plant covering has been changed. The severity of a fire, and its consequent effect on plant life, depends on its nature. A light surface fire, running through the leaf litter, is not as disastrous as a crown fire which sweeps through the whole forest and destroys all growth. Future development in an area after a fire depends partly on the kind of stand, but more especially on the condition of the humus. A deciduous forest is not as easily burned as a coniferous one, and usually not as severely, since the leaf litter is less inflammable than dry needles and there is also a larger amount of green shrubby undergrowth. The succession of vegetation after a fire differs, depending on whether the humus is only slightly injured, or completely destroyed.

Association-types where humus is little injured

When a climax forest is burned the first noticeable result is the profuse growth of herbaceous species that appears the season after the fire. Some of these are forms which formerly grew on the forest floor, such as *Cornus canadensis*, *Clintonia borealis*, *Maianthemum canadense* and *Linnaea borealis* var. *americana;* while others are new species which are able to invade the area owing to the increase in light. Conspicuous among these are several of the golden rods *(Solidago bicolor*, *S. nemoralis* and *S. puberula)*, *Aster lateriflorus*, *Erechtites hieracifolia*, *Lactuca canadensis* and the fireweed *(Epilobium angustifolium)*, this latter plant forming dense masses and often carpeting the entire area. Shrubs also may be present, chief among which are the raspberry *(Rubus idaeus* var. *canadensis)*, the bush honeysuckle *(Diervilla Lonicera)*, red berried elder *(Sambucus racemosa)* and gray birch. Meanwhile certain of the trees have begun to sprout from the root collar and give rise to a dense coppice growth. This is particularly true in the case of the paper birch and to a lesser degree of the red maple and beech. The birch, also, seeds in freely and owing to its rapid growth soon develops a characteristic forest. Associated with it are a few other light-loving and rapid growing trees, the bird or fire cherry *(Prunus pennsylvanica)*, and the "popple", a term used in Maine to denote both the large-toothed aspen *(Populus grandidentata)* and the quaking aspen *(Populus tremuloides)*. This birch-popple forest is of widespread occurrence throughout the region, and is almost always an indication of a previous burn. After a time conifers begin to come in underneath the hardwoods and form a definite layer society, as is shown in Figure 27. The wood may remain in this condition for a considerable period of time, 40-60 years, according to Dana (5), but sooner or later the conifers become dominant. Recent studies of Toumey's (27) on the relation of gray birch to the regeneration of white pine are of interest in this connection. These studies suggest that a stand of birch is never sufficiently dense to cause the death of the pine by shading. The latter tree is able to come in and show a fair amount of growth in all cases. The rapidity of growth, however, is dependent upon the density of the birch, a falling off of the growth rate of pine accompanying an increase in the number of individuals of the birch. This is due to competition for soil moisture and nutrients rather than to shading. The growth of spruce and fir under birches in the Penobscot Bay region may well be analagous. The conifers are able to persist and show some growth but are retarded from complete development by the root competition. It is only when the shorter lived birches begin to die that this competition is lessened enough to allow the conifers to complete their growth and become dominant. As these latter increase in prominence any popple, which may be present, drops out, since it is very intolerant of shade. Some of the birches, however, may persist and occupy a prominent place, not only in the coniferous forest, but also in the climax forest which may follow. The appearance of conifers after a burn is entirely dependent on the presence of seed trees in the immediate vicinity, since all young growth is killed by the fire, and the trees do not possess the ability to sprout from the roots. The birches, on the other hand, not only have this ability, but in company with the popple, possess very light winged seeds which can be blown great distances. As a result these trees are invariably present on burned areas. The cherry, which is widely distributed by birds, is also almost sure to be present in such places.

Association-types where humus is absolutely destroyed

In the case of fires where the soil layer is thin, as in the xerophytic coniferous forests on the islands and hill-tops, and after extremely severe fires in deciduous woodland, the humus covering may be entirely destroyed and the bare rock surface exposed. Where this occurs on steep slopes subsequent rains may wash away every vestige of the old soil and particles of mineral matter as well, rendering it practically impossible for vegetation to get a new start. On more level surfaces a series of successions develop not unlike those already outlined under primary successions. There may not be the same regularity in the process, for here and there over an area some soil may have persisted and this will naturally affect the nature of the succession.

One departure from the usual course of events following a fire is of frequent enough occurrence to warrant mention. If either white or red pines are present nearby they soon invade a burn and come to play an important part in its future development (Figure 28). They may replace the birch-popple stage from the first, but usually accompany these trees for a while, eventually outstripping them and becoming dominant. Very often red oak is associated with the pine in such cases. Where the soil is very shallow and conditions extremely xerophytic a scrub forest of pine and oak may result (Figure 29) which is seemingly permanent and may constitute a physiographic climax. Occasionally the oak occurs alone in such localities (Figure 30). On better soils the trees develop into good sized specimens and a growth of spruce and fir comes in beneath them. In such situations these conifers are destined to supersede the pine and oak as dominant species, although the latter do not drop out entirely but remain as scattered individuals. Occasionally the coniferous forest may be followed by one of the climax type in which the pine and oak are still present.

Figure 27. — Spruce and fir coming in under white birch on area formerly burned, Northport.

Figure 28. — Succession after a burn, Orland; red pine and gray birch invading grasses and shrubs.

Association-types of blueberry barrens

Blueberry barrens, because of their economic value, are of steadily increasing prominence in the Penobscot Bay region, particularly in the eastern portion, and they will be considered in some detail. The development of these barrens shows a series of changes in the reverse direction from these previously described. In this case the start is made with a forest already present on the land. This is cut off and the land burned over. The result is the destruction of the original stand and of the humus as well. The usual growth of herbaceous plants and shrubs springs up and eventually a birch-popple wood comes to occupy the area. This wood is burned over in its turn and this process may be repeated several times. The continual destruction of the sprouts weakens and kills the roots, and more and more humus is destroyed. Finally it becomes impossible for trees to compete with the hardier plants and a barren results. In such localities only a few scraggly growths of red maple, white and gray birch and cherry sprouts are to be found. Shrubs and herbs, however, are conspicuous. Together with masses of blueberry bushes are such conspicuous species as:

Pteridium aquilinum
Carex scoparia
Myrica asplenifolia
Rubus idaeus var. *canadensis*
Lechea intermedia
Epilobium angustifolium
Aralia hispida
Kalmia angustifolia
Gaultheria procumbens
Gaylussacia baccata
Lysimachia quadrifolia
Diervilla Lonicera
Solidago sp.
Anaphalis margaritacea

The blueberries are by far the most abundant plants in these barrens and the species represented are *Vaccinium pennsylvanicum* and its variety *nigrum*, and *Vaccinium canadense.*

The productivity of the barrens is maintained by burning the land periodically. This is usually done in the spring immediately after the snow disappears, when the tops are dry, but the soil is still wet and so serves as a protection for the roots. The burning is said to improve the berries and also serves to keep down the development of shrubs, for nature is constantly struggling to gain the upperhand and start a succession of vegetation in the proper direction. About one-third of the barren is burned each year, while berries are gathered on another third, and the remainder lies idle. The season that an area is burned over the bushes sprout out and grow a few inches. The second year they bear a full crop of berries, but the bushes are not large enough to furnish sufficient fuel for a fire which will completely clear the ground. The third year the crop falls off, but there is sufficient vegetative growth so that the patch can be burned again.

Newly burned forest land bears a better crop than the older barrens because the soil is richer and there is a greater amount of ash on it. Consequently there is a too common tendency to convert more and more of the forests which are less profitable financially into blueberry land, rather than to trouble to properly care for the existing barrens.

c. Association-types due to lumbering

The nature of the vegetation following the cutting off of woodland is dependent on the character of the original growth and whether or not the area is burned over following the removal of the trees.

In the case of hardwood forests many of the component species possess the ability to sprout from the stump, so that often a second growth of such species results almost immediately. This is particularly true in the case of the beech and there are many pure second growth stands of this tree. In general, however, the removal of the deciduous trees, and the consequent increase in light favors the rapid development of the conifers, which were present in the under-

Figure 29. — Succession after a burn, Mt. Battie, Camden; red and white pine and red oak on slopes of mountain.

Figure 30. — Succession after a burn, Great Pond Mountain, Orland; red oak and bearberry.

growth. These trees grow to maturity and succeed the hardwoods as the dominant species.

Where coniferous forests are cut over and the ground cleaned up the usual tendency is for a broadleaf wood of gray and white birch, poplar and red maple to develop. This is apt to be so dense that at first seedlings of the conifers are unable to grow. Eventually, however, as in the case after a fire, the spruce and fir will again become dominant.

The presence of slash left on the ground after lumbering operations is a constant fire menace, since the dead branches and twigs furnish fuel for a very hot fire which utterly destroys the humus. As noted above, it is only occasionally and with difficulty that vegetation is able to reclothe such an area.

The most striking feature of the vegetation after a forest has been cut over is the presence of clearings in which several distinct stages may appear before the trees become reestablished. The first of these consists of herbaceous species such as:

Pteridium aquilinum
Panicum implicatum
Carex debilis var. *Rudgei*
Polygonum cilinode
Epilobium angustifolium
Aralia hispida
Solidago nemoralis
Aster lateriflorus
Erechtites hieracifolia
Lactuca hirsuta

These are followed almost immediately by a dense growth of raspberries which may completely cover the area. Other shrubby species frequently associated with the raspberries include:

Betula populifolia
Ribes prostratum
Rubus alleghaniensis
Prunus pennsylvanica
Acer rubrum
Sambucus racemosa

This "bramble association", as Gates (12) terms it, is best developed after the slashing of a coniferous wood, where the ground is left covered with branches. The thickets formed by these species in such areas are so dense that the popple and birch do not become established and conifers are able to succeed the brambles directly.

C. PRIMARY FORMATIONS OF THE HYDRARCH SERIES

The formations of the hydrarch series include lakes and ponds, which differ from one another only in the matter of size; and swamps of several different kinds. These two groups are not absolutely distinct and usually show intergradations, the lakes and ponds in general tending to become filled up and converted into swamps through the action of various agencies.

As already indicated (page 308), the lakes and ponds of the Penobscot Bay region are for the most part of glacial origin, occurring either as morainal lakes which are connected in some manner with glacial debris, or as scoop lakes which occupy depressions scooped out of the underlying rock itself. Other ponds are coastal in nature, occurring behind barrier beaches, while a fourth group has resulted from the cutting off of indentations along the shore of a larger lake by the formation of a bar or sand spit.

The swamps may originate through the filling in of a lake or pond, in which case they are known as lake-swamps; or they may result from the seepage of perennial springs in locations where the topography prohibits pond formation. These latter are known as spring-swamps. A third type—the precipitation swamp — which is common in more northern regions and depends on direct atmospheric precipitation for its water supply, is practically absent from the Penobscot Bay region. Coastal swamps, however, developed by the deposition of sediment in shallow places along the shore are of frequent occurrence.

1. Formations of Lakes, Ponds, and Swamps Inland

The nature of the vegetation in lakes, ponds and swamps inland depends on the character of the drainage and the

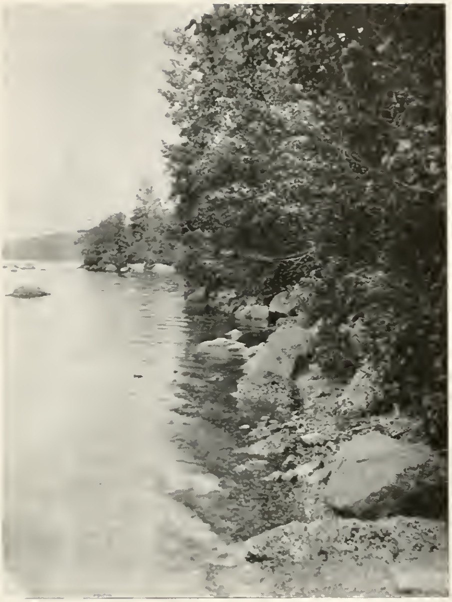

FIGURE 31. — Shore of Lake Alamoosook, Orland, showing absence of aquatic vegetation.

FIGURE 32. — Shore of Torrey Pond, Deer Isle, looking east; sedges with *Carex filiformis* predominant, shrub zone and upland coniferous forest.

permanency of the water supply. A well-drained area differs from an undrained one in several respects; the place where it is developed; the amount of underlying peat; the acidity of the soil; and the character of the plant covering. The permanency of a lake or pond is controlled by the relation between the topography and ground water level. Where this relationship is such that water is present in a closed basin throughout the year, a permanent lake or pond is formed. Where water is present during the spring, but absent at other seasons due to the lowering of the water table or evaporation, a periodic pond results. In places where the topography favors swamp formation and there is abundant surface water throughout the summer due to a high water table, a permanent swamp occurs. Swampy areas which dry out during the summer may be found, but these periodic swamps do not have as distinctive a type of vegetation as do the other types of lowland mentioned.

a. Association-types of permanent well-drained lakes, ponds, and lake-swamps

The succession of vegetation starting in a well-drained lake or pond and leading to the formation of a forested area has been one of the stock illustrations of ecologists for many years and need not be discussed in detail. Briefly six well-recognized stages occur, namely: (1) submersed aquatics; (2) aquatics with floating leaves; (3) aquatics with aerial leaves — these three stages comprising the lake series; (4) sedges; (5) shrubs; (6) swamp forest — the latter three making up the swamp series.

Association-types of the lake series

The nature of the aquatic vegetation in the ponds and lakes of the Penobscot Bay region varies with the character of the shores and bottom. In ponds with gravelly bottoms there is apt to be no vegetation. Sandy bottoms on the other hand support a few very characteristic species, while muddy shores have a much larger variety. Along rocky shores, especially in the larger lakes, such as Alamoosook in Orland (Figure 31) and Megunticook in Camden, the action of waves and ice tends to keep out any plants save perhaps the submersed and floating aquatics. The following list of species are of most frequent occurrence:

Equisetum fluviatile
Typha latifolia
Sparganium americanum
Potamogeton Oakesianus
Potamogeton natans
Sagittaria latifolia
Dulichium arundinaceum
Eleocharis palustris
Scirpus validus
Cladium mariscoides
Carex filiformis
Acorus Calamus
Pontederia cordata
Eriocaulon septangulare
Juncus militaris
Nuphar variegatum
Nymphaea odorata
Potentilla palustris
  var. *villosa*
Sium cicutaefolium
Lysimachia terrestris
Nymphoides lacunosum
Utricularia vulgaris
  var. *americana*
Lobelia Dortmanna

The submersed and floating aquatics cited in this list are usually to be found in all ponds, but the species of the third stage vary in different localities. Perhaps the most frequent plant is *Carex filiformis*, which covers extensive areas and often invades the zone of water lilies (Figures 32 and 33). With it are usually associated *Potentilla palustris* var. *villosa* and *Equisetum fluviatile.* Again the pickerel weed *(Pontederia cordata)* or the bulrush *(Scirpus validus)* may predominate. In a few instances *Cladium mariscoides* and *Juncus militaris* are the most important species. The cat-tail *(Typha latifolia)* is occasional, but this plant is more typical of small periodic or brackish ponds. On the western side of the Bay the buck bean *(Menyanthes trifoliata)* is extremely abundant in the shallow water along muddy pond shores, where it forms extensive mats, sometimes to the exclusion of all other species. On the eastern side of the Bay, however, this plant is practically absent.

Figure 33.—Shore of Torrey Pond, Deer Isle looking west; telescoping of floating aquatic and sedge stage: shrub stage in foreground; sphagnum bog at end of pond.

Figure 34.—Lagoon on south side of Lake Alamoosook; Orland with zonation of vegetation; pickerel weed in foreground, followed by open water, floating aquatics, pickerel weed, cat-tails, *Calamagrostis canadensis*, red maple, willows and alders; low forest in background.

Association-types of the swamp series

Sedge stage. The continued growth of the sedges present in the previous stage gradually results in the building up of the substratum slightly above the level of the water and affords a support for a large number of other grass-like forms, characteristic among which may be mentioned:

Calamagrostis canadensis
Poa triflora
Glyceria canadensis
Eleocharis tenuis
Scirpus cyperinus
Scirpus atrocinctus
Carex stricta
Carex lurida
Juncus effusus vars.
Juncus canadensis

Associated with these are numerous herbaceous species which are equally characteristic of spring swamps and will be considered under that heading. The sedge stage is very apt to be telescoped by other stages and even obliterated entirely. At best it is of short duration, shrubs invading it almost from the start and soon replacing the grasses and sedges as the dominant forms.

Shrub stage. The most important shrub in these lake-swamps is the alder *(Alnus incana)* which is almost universally present. Other conspicuous species include:

Salix discolor
Myrica Gale
Spiraea latifolia
Pyrus melanocarpa
Amelanchier laevis
Rosa nitida
Rosa virginiana
Ilex verticillata
Nemopanthus mucronata
Chamaedaphne calyculata
Kalmia angustifolia
Rhododendron canadense
Vaccinium corymbosum
Viburnum cassinoides

Swamp forest stage. The end of succession in a well-drained pond or swamp is a swamp forest which in most instances represents a physiographic climax. The component trees of this forest are usually the red maple, white cedar and red spruce, and associated with them the ashes *(Fraxinus americana* and *F. nigra)*, larch *(Larix laricina)* and balsam fir in smaller numbers. These trees appear first as scattered individuals in the shrub stage, but eventually come to cover the whole area. During this process the shrubs are not killed out but remain to form a part of the abundant undergrowth characteristic of such woods. Various herbaceous species, common in the two preceding stages, also occur and with them such other forms as:

Athyrium Filix-femina
Osmunda regalis
Taxus canadensis
Glyceria nervata
Bromus ciliatus
Carex Goodenowii
Carex leptonervia
Carex intumescens var. *Fernaldii*
Carex scabrata
Arisaema triphyllum
Habenaria fimbriata
Thalictrum polygamum
Hamamelis virginiana
Scutellaria lateriflora
Viburnum dentatum
Solidago canadensis

In situations where, for some reason, the substratum is less wet than ordinarily the trees of the swamp forest may be replaced by others. The spruce and fir may increase in abundance until they become dominant; and in very favorable places deciduous trees of the regional climax may come in. The typical climax forest is, however, never attained in such places. A wooded swamp along the outlet of Craigs Pond in Orland is illustrative of this mixture of lowland and upland types, comprising the following species: hemlock, white cedar, red oak, beech, red maple, moosewood, and *Fraxinus pennsylvanica*, with an undergrowth of mountain maple, *Hamamelis virginiana* and *Viburnum alnifolium.*

The normal succession in well-drained ponds and swamps outlined above may be taken as representative for the entire region, although the several stages may not always be developed. Telescoping of the various zones is extremely frequent and often one or more stages may be entirely omitted. In many lakes, as shown in Figure 31, there is only a narrow border of shrubs between the water and the forest.

In a few instances all the stages are present in their most typical development. About Maces Pond in Rockport this zonation of vegetation is particularly striking. In the deeper water occur the submerged and floating aquatics, with the water lily *(Nymphaea odorata)* conspicuous. As we proceed shorewards this area is succeeded by a broad zone of pickerel weed, bordered on its landward side by a narrower one of cat-tails. A well-marked sedge stage follows this, consisting of *Carex rostrata*, *Carex lurida*, *Scirpus atrocinctus* and *Calamagrostis canadensis* with *Sium cicutaefolium*, *Chelone glabra* and *Bidens cernua* as prominent herbaceous species. A solid zone of *Myrica Gale* makes up the shrub stage, and this in turn gives way to a swamp forest in which red maple predominates with *Viburnum dentatum* and *Sambucus canadensis* the principal shrubs in the undergrowth. A similar zonation on a smaller scale is shown in Figure 34 which pictures a small lagoon on the south side of Lake Alamoosook in Orland. This area has been cut off from the larger lake by a sand bar and is rapidly becoming filled with vegetation.

Association-types of cedar swamps

In localities which are favorable to the growth of the white cedar *(Thuja occidentalis)* this species is apt to predominate in the swamp forest, sometimes to the entire exclusion of all other trees. A cedar swamp of this nature occupies an extensive area on Beauchamp Point in Rockport and may be described as characteristic. About 90% of the trees are cedars and the remainder comprise scattered individuals of larch, white spruce, and red maple. The shrubby vegetation includes:

Taxus canadensis
Salix discolor
Myrica carolinensis
Alnus incana
Ilex verticillata
Acer pennsylvanicum
Cornus stolonifera
Ledum groenlandicum

The most striking feature of this swamp is the great profusion of bryophytes which not only carpet the forest floor and the numerous rotten logs, but extend well up the base of the trees. Conspicuous forms are:

Bazzania trilobata
Trichocolea tomentella
Riccardia latifrons
Ptilium crista-castrensis
Calliergon cordifolium
Rhytidiadelphus triquetrus
Climacium americanum
Mnium punctatum
Thuidium delicatulum
Hylacomnium splendens
Ptilidium pulcherrimum
Stereodon cupressiformis

Other genera, such as *Lepidozia*, *Lophocolea*, *Sphagnum*, *Cephalozia*, *Dicranum* and *Chrysohypnum* are also frequent, as are several lichens, chiefly *Peltigera*, *Lobaria* and *Usnea*.

Characteristic herbaceous species include:

Dryopteris Thelypteris
Osmunda cinnamomea
Carex flava
Carex trisperma
Symplocarpus foetidus
Smilacina trifolia
Cypripedium hirsutum
Coptis trifolia
Drosera rotundifolia
Viola incognita
Chiogenes hispidula
Mitchella repens

b. Association-types of periodic lakes and ponds

Periodic ponds are more closely allied to well-drained than to undrained areas, since the drying out which they undergo during the summer accomplishes essentially the same result as might otherwise be effected by drainage. The vegetation in these periodic ponds differs from that of permanent ponds chiefly in the absence of the aquatic forms. Water is present for too short a period for these to develop and swampy conditions prevail almost from the outset. The most characteristic species in these "bog-holes" which occupy mucky depressions in fields and pastures, is the cat-tail (Figure 35) and with it are found:

Sparganium diversifolium
Glyceria nervata
Eleocharis obtusa
Eleocharis tenuis
Juncus effusus var. *Pylaei*
Juncus brevicaudatus
Hypericum virginicum
Lysimachia terrestris

Figure 35. — Periodic pond, Naskeag Point, Brooklin; cat-tails and *Eriophorum tenellum* prominent; larches in background.

Figure 36. — Margin of undrained pond in sphagnum bog, Swans Island; *Chamaedaphne calyculata* and *Pyrus melanocarpa* advancing into pond; water lilies abundant.

Scirpus atrocinctus	*Galium Claytoni*
Eriophorum tenellum	*Bidens cernua*

Usually a fringe of shrubs or even trees borders such a periodic pond, forms like *Alnus incana, Ilex verticillata, Rhododendron canadense, Kalmia angustifolia* and the larch being common.

c. Association-types of permanent undrained lakes, ponds, and lake-swamps

Association-types of ordinary bogs

The succession of vegetation in undrained areas differs from that in well-drained ponds chiefly in the ultimate development of a bog, a swampy area characterized by the predominance of ericaceous shrubs and the abundance of sphagnum. Bogs are fairly common on the islands and the eastern side of the Bay, but they are infrequent inland and along the western border.

The early stages in the filling up of an undrained pond are similar to those outlined for well-drained areas, such aquatic plants as *Nymphaea odorata, Nuphar variegatum, Utricularia vulgaris* var. *americana, Utricularia intermedia* and the various potamogetons being common. It is in the sedge stage that differences are first evident. The most striking feature in the development of a bog is the formation of a floating mat. This results from the vigorous growth of plants along the margin of the pond, which tend to push out from the shore and eventually produce a raft-like mass of vegetation. In some cases sedges, chiefly *Carex filiformis* and *Carex rostrata*, are pioneers in this mat formation, growing with their rhizomes so interlaced as to afford considerable strength to the mat. Shrubs, however, are of far greater importance in the Penobscot Bay region in building up such a floating mat. The most conspicuous pioneer species is the sweet gale *(Myrica Gale)* while other frequent forms include the cassandra *(Chamaedaphne calyculata)* and *Pyrus melanocarpa* (Figure 36). The rootstalks and branches of these shrubs furnish a frame work on which various sphagnums find a foothold and develop in great profusion. The important role which these mosses play in bog formation has been emphasized by most writers and summed up in detail by Cooper (4) and Nichols (23).

The continual growth of the mat lakewards and the accompanying filling up of the pond from within finally results in the complete elimination of any open water. At first the continuous mat, thus formed, may still overlie water, in which case it constitutes a quaking bog, but as more and more debris falls down from the under side of the mat the bottom is built up and sooner or later the mat becomes grounded. When this has occurred the bog is drier than at any previous time during its formation.

During the course of its development the sphagnum mat becomes colonized with various other plants. In cases where sedges are the pioneer plants these may at first dominate an area of considerable extent on the mat itself, but later they are invaded by shrubs. Where shrubs are the pioneers the mat from the very first supports a vegetation consisting of both sedges and low shrubs growing together. In either case as the mat becomes drier, larger shrubs begin to come in and eventually trees, such as the larch and black spruce *(Picea mariana)*. Each individual bog varies somewhat as to its component species, but the following list comprises the plants ordinarily present:

Herbaceous Species

Lycopodium inundatum
Eriophorum callitrix
Eriophorum virginicum
Rynchospora alba
Carex exilis
Carex trisperma
Carex paupercula var. *irrigua*
Smilacina trifolia
Calopogon pulchellus
Pogonia ophioglossoides
Drosera rotundifolia
Drosera longifolia
Sarracenia purpurea
Utricularia cornuta
Solidago uniligulata

FIGURE 37. — Floating mat in bog, Stockbridge Pond, Swans Island, showing low, wet depressions in floating mat.

FIGURE 38. — Stockbridge Pond bog, at edge of upland forest; *Myrica Gale* and *Carex rostrata* in foreground; larch, red spruce and red maple in background.

Carex filiformis
Carex rostrata
Xyris montana
Aster nemoralis
Aster radula

Shrubs

Myrica Gale
Pyrus melanocarpa
Nemopanthus mucronata
Ledum groenlandicum
Chamaedaphne calyculata
Kalmia Polifolia
Gaylussacia dumosa var. *Bigeloviana*
Vaccinium macrocarpon
Vaccinium Oxycoccus
Lonicera caerulea vars.
Viburnum cassinoides

Trees

Larix laricina
Picea rubra
Picea mariana
Acer rubrum

In general the bogs fall into two classes depending on whether or not the mat completely fills the depression in which the bog occurs, the case where a pond still occupies the center of the depression being of most frequent occurrence. The bogs at Stockbridge and Sadler ponds on Swans Island may be described as typical of such a condition. The ponds in these bogs have the usual aquatic species and about their margin a fringe of *Chamaedaphne calyculata*, *Myrica Gale* and *Pyrus melanocarpa* which are the chief species concerned in the steady encroaching of the mat on the pond itself. The floating mat is distinctly of the quaking type with sphagnum predominating, and growing in it numerous sedges and low shrubs. The commonest sedges are the various species of *Carex*, cited in the above list, *Rhynchospora alba*, and *Eriophorum virginicum*, while associated with them are most of the herbaceous plants, such forms as *Calopogon*, *Pogonia*, *Sarracenia*, *Drosera rotundifolia*, *Solidago* and *Aster* being conspicuous. The characteristic shrubs on the mat, in addition to the three already mentioned as pioneers, include *Kalmia*, *Gaylussacia*, and *Lonicera* and the cranberries *(Vaccinium macrocarpon* and *V. Oxycoccus)*. A striking feature of the mats is the presence of numerous depressions (Figure 37) which are filled with aquatic sphagnums. The vigorous growth of these has prevented the encroachment of less hydrophytic species and the consequent building up of the mat to the general level. These depressions are very wet and mucky and in addition to the mosses usually contain a few very characteristic forms, of which *Lycopodium inundatum*, *Xyris caroliniana*, *Drosera longifolia* and *Utricularia cornuta* may be cited as examples. Bordering on this more or less open portion of the bog is a zone in which larger shrubs, such as *Viburnum*, *Ledum*, *Nemopanthus* and the red maple occur and this is followed by a narrow fringe of black spruces and larches adjoining the upland (Figure 38).

In the other type of bog the mat has completely filled the depression and usually becomes grounded. In these mature bogs it is no longer possible to make out any zonation to the vegetation, the sedges, shrubs, and trees growing intermingled (Figure 39). The bog forest, consisting chiefly of black spruce, larch and red maple, covers large portions of such bogs and ordinarily represents a physiographic climax, since the substratum is too wet for other woodland types to come in. Where there are somewhat better conditions of drainage a coniferous forest of red spruce and fir may succeed and in such cases it is possible to observe bog and upland species growing side by side.

The marginal ditches, so common a feature of bogs elsewhere, are comparatively rare in the Penobscot Bay region. Where they do occur their vegetation resembles that of a well-drained swamp in which such shrubs, as *Ilex verticillata*, *Rosa virginiana*, *Rosa nitida*, *Spiraea latifolia* and *Rhododendron canadense* predominate, while the most frequently occurring herbaceous forms are *Osmunda cinnamomea* and *Calla palustris*.

Association-types of raised bogs

The bogs discussed in the preceding paragraphs all be-

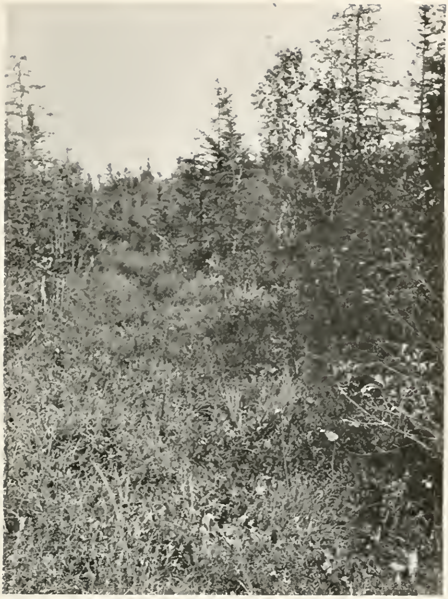

Figure 39. — Bog at Brooklin in tree stage; larch, red spruce, gray birch and *Viburnum cassinoides; Sarracenia purpurea* in open places.

Figure 40. — Spring swamp of the open swamp type. Dunhams Point, Deer Isle; *Scirpus cyperinus* prominent.

long to the type which originates through the filling in of a water-filled depression. A second type of bog results from the gradual building up of vegetation on a comparatively flat surface. This is the raised bog so characteristic of the Maine coast east of Penobscot Bay, and of the Maritime Provinces (see Nichols, 23, 24). The sphagnums which play the prominent part in the formation of such a bog require a very large amount of water, more than can be supplied from the ground. This additional moisture is obtained directly from atmospheric precipitation, a phenomenon which gives the name of precipitation swamps to these areas. In the course of the development of a raised bog there is usually a more or less definite sequence of stages, comprising a bog meadow, wet bog and dry bog, the latter constituting the climax association. In the Penobscot Bay region there is but a single instance of a bog which can be undoubtedly attributed to the raised type and in this case the vegetation has reached the dry bog stage. In the "Bog" in Rockland the ground is covered with a compact growth of the usual ericaceous shrubs with a few subordinate herbaceous species. The area covers over a square mile of territory and is about four feet higher in the center than near the margins, thus exhibiting in its convex surface one of the chief characteristics of raised bogs. Toward the northern end it merges with a deciduous swampy wood while at the southern edge the damming of a small stream which flows out of the bog has altered the vegetation thereabouts to such an extent that it exhibits the features of a filled-in bog with a definite zone of aquatics and a sedge and shrub stage.

d. Association-types of spring swamps

Many of the swamps in the Penobscot Bay region owe their origin to the presence of seepage water from the ground water table. These spring swamps may occur on wet slopes along streams where they are subject to occasional inundation, or at the edge of beaches. The latter have already been described (page 372). Naturally in all such localities aquatic species are absent and the pioneer vegetation usually consists of grasses and sedges.

The amount of water present determines the nature of the first association-type to occupy the area. Where it is inundated for a considerable period or the supply of seepage water is very plentiful a marsh or open swamp results (Figure 40). The characteristic species in such a locality are:

Onoclea sensibilis
Poa triflora
Glyceria canadensis
Scirpus georgianus
Scirpus rubrotinctus
Scirpus cyperinus
Carex crinita
Carex stipata
Carex lurida
Juncus effusus vars.
Senecio Robbinsii
Iris versicolor
Polygonum sagittatum
Thalictrum polygamum
Cardamine pennsylvanica
Impatiens biflora
Epilobium densum
Cicuta maculata
Mentha arvensis
Chelone glabra
Eupatorium perfoliatum
Eupatorium purpureum var. *maculatum*

Carex stricta is occasionally present along streams (Figure 41), but this species, so characteristic of open swamps in other regions, is of little ecological significance here. The distribution of *Scirpus rubrotinctus* and the Joe-Pye-Weed (*Eupatorium purpureum* var. *maculatum* in the Penobscot Bay region is interesting and suggests that of the buck-bean mentioned above (page 394). These species are extremely abundant on the western shores of the Bay, occurring in almost every swamp, while they are practically absent from the eastern side.

In situations where the plants of the spring swamps are free from inundation, save in the early spring, and the ground is fairly dry during the rest of the growing season a dense, turf-like vegetation develops. These "swales" are characterized by the dominance of grasses and sedges of a

Figure 41. — Well-drained swamp along outlet of Norton Pond, Lincolnville.

Figure 42. — Permanent swamp of the wet meadow type, Naskeag Point; Brooklin; dark area in center is *Juncus balticus* var. *littoralis*.

lower habit than those in open swamps (Figure 42). The common species in these wet meadows include:

Dryopteris Thelypteris
Dryopteris noveboracense
Agrostis alba
Agrostis alba var. *vulgaris*
Calamagrostis canadensis
Glyceria nervata
Eriophorum tenellum
Carex scoparia
Carex echinata
Carex rosea
Carex flava
Juncus balticus var. *littoralis*
Luzula campestris var. *multiflora*
Habenaria psycodes
Liparis Loeselii
Geum rivale
Hypericum virginicum
Hydrocotyle americana
Veronica scutellata

The character and the succession of the vegetation in meadows is often altered owing to the fact that they are usually cut over for hay each year. If left to themselves both the above types of swamp become colonized by shrubs. These, indeed, may be present from the very first and areas with a mixture of shrubs and grasses and sedges are very frequent (Figure 43). The most important shrub is the alder *(Alnus incana)*, while other common species are:

Salix discolor
Salix humilis
Amelanchier laevis
Spiraea latifolia
Rosa virginiana
Ilex verticillata
Cornus stolonifera
Vaccinium corymbosum

Eventually the swamp is invaded by trees and a swamp forest results of the same character as that already described as the culminating association-type in lake-swamps.

e. Association-types of poorly drained swamps

The conditions thus far described for the formation of the hydrarch series apply only to the clearly marked extremes of pond and swamp vegetation. It must not be assumed that every locality in the lowlands can be assigned to one or another of these types. Wherever there are intermediate conditions of drainage, as in poorly-drained areas, there occur intermediate conditions in the vegetation. Such places show similarities to ordinary swamps on the one hand and bogs on the other, and also grade into the uplands.

This mingling of species of several different association-types is particularly marked where trees occupy the area. One such poorly-drained tract on Naskeag Point in Brooklin (Figure 44) may be described as typical. The ground in this locality is slightly undulating, with shallow depressions in which water may be present for a good part of the summer, alternating with higher places. The characteristic trees present are the larch, balsam fir, red spruce and white cedar, with an undergrowth of *Rhododendron canadense, Kalmia angustifolia, Viburnum cassinoides, Ledum groenlandicum* and *Nemopanthus mucronata.* In the low wet places sphagnum, particularly *Sphagnum palustre,* is abundant and growing with it are the snowberry *(Chiogenes hispidula)* and cranberry *(Vaccinium macrocarpon).* An adjacent portion of the forest floor may be slightly higher and here the sphagnums are absent while *Cornus canadensis, Linnaea borealis* var. *americana, Gaultheria procumbens, Lycopodium annotinum* and *Aralia nudicaulis* are the most conspicuous species.

Another frequently occurring association-type is found in localities which are poorly-drained, but have water present only at infrequent intervals. After a rain, water collects in pools and may be abundant enough to submerge the vegetation, but this surface water evaporates during dry weather and the area may become quite dry. In such situations there is a scattered growth of shrubs alternating with grasses and sedges and considerable sphagnum. By far the most common species is the steeple-bush *(Spiraea tomentosa),* which is so universally present as to be a good indicator of this type of habitat. *Alnus incana* is also frequent, as are the following herbaceous forms

Figure 43. — Permanent swamp on Naskeag Point, Brooklin; *Dryopteris Thelypteris*, cat-tails and shrubs prominent.

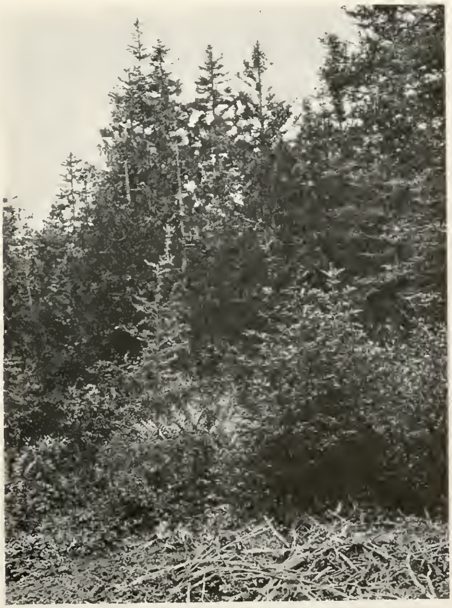

Figure 44. — Poorly drained swamp in Brooklin with mixture of swamp and upland trees.

Osmunda Claytoniana
Scirpus atrocinctus
Juncus effusus vars.
Habenaria clavellata
Spiranthes Romanzoffiana
Microstylis unifolia
Polygonum Hydropiper
Ranunculus repens
Drosera rotundifolia
Lycopus uniflorus

Trees such as the red spruce and larch may be present as isolated individuals.

A third type of poorly-drained swamp is found on the summits of the hills and other exposed rock surfaces, where it occupies little hollows and depressions in the rock. In some cases the bottom of these may be muddy and there is a vigorous growth of rushes, particularly *Juncus brevicaudatus*. More often sphagnums are present and these alter the character of the vegetation in the hollows. During a rain the sphagnums absorb moisture and remain saturated long after all water has been evaporated from the rest of the rock surface. This enables several species to maintain a foothold, which otherwise would be unable to do so. Among such plants may be mentioned *Eriophorum tenellum*, *Eleocharis tenuis*, *Carex canescens* var. *disjuncta*, *Carex trisperma* and the cranberry, together with several shrubs, *Rhododendron canadense*, *Myrica Gale*, *Nemopanthus mucronata* and *Spiraea latifolia*, which seem quite out of place on a rocky hill top side by side with species like *Kalmia angustifolia*, and *Gaylussacia baccata* (Figure 45). These miniature bogs may even support a stunted growth of trees, as shown in Figure 46. In this instance red spruce, larch and gray birch are prominent.

2. Formations of Lakes, Ponds, and Swamps Along the Seacoast

The formations along the seacoast belonging to the hydrarch series comprise the barrier-beach ponds, salt marshes, and brackish marshes. In these areas the plant life is influenced to a varying degree by the sea. From the standpoint of physiography they are all examples of depositing shores, the associations of eroding shores having been considered in connection with the xerarch formations (page 364).

a. Association-types of barrier-beach ponds

The development of barrier-beaches across the mouth of some reentrant of the shoreline results in the formation of a pond, which ordinarily is salt or brackish, since it is constantly fed by seepage through the beach. The vegetation in these salt ponds differs markedly from that of fresh-water ponds, particularly in the aquatic species. Here the most characteristic forms are the eel grass *(Zostera marina)* and the ditch grass *(Ruppia maritima)*, which often occupy the whole area, together with various pond-weeds, such as *Potamogeton pectinatus* and *Potamogeton bupleuroides.* Where the shores are muddy a typical salt marsh is usually present (Figure 47). On rocky or gravelly shores, however, other species are more frequent. On the seaward side, in the areas of greater salinity, grow forms which can tolerate the salt, such as *Scirpus americanus*, *Scirpus campestris* var. *paludosus*, *Eleocharis palustris* and *Spartina Michauxiana.* Along the landward side, on the other hand, where seepage from the adjacent uplands renders conditions much fresher are found many species more characteristic of fresh-water areas. These commonly include:

Typha latifolia
Poa triflora
Scirpus occidentalis
Juncus canadensis
Iris versicolor
Myrica Gale
Alnus incana
Polygonum Hydropiper
Spiraea latifolia
Galium Claytoni

b. Association-types of salt marshes

The rocky and abrupt character of most of the shores in the Penobscot Bay region naturally precludes the formation of salt marshes which are dependent on the deposi-

Figure 45. — Poorly drained depression on summit of Great Pond Mt., Orland; incipient bog with sphagnum and shrubs.

Figure 46. — Boggy depression on summit of Mt. Battie, Camden; *Scirpus cyperinus*, *Eleocharis tenuis* and *Eriophorum viridi-carinatum*, with shrubs and trees in background.

tion of sediment in shallow places. Consequently these marshes are much less frequent than on less rugged portions of the Atlantic coast, and where they do occur they are much less extensive. In this region they attain their best development behind barrier-beaches and along the tidal rivers on the western side of the Bay (Figure 48).

As is the case elsewhere the first species to appear in the building up of a salt marsh is the salt thatch *(Spartina alterniflora)*. This coarse grass lines the banks of the tidal creeks in situations where it is submerged at every high tide. Back from the edges of the creeks the surface of the marsh is higher and there is a zone in which the salt meadow grass *(Spartina patens)* predominates. Frequently this is present in a pure stand, but in other cases the following species may be associated with it:

Triglochin maritima
Salicornia europaea
Suaeda maritima
Limonium trichogonum
Plantago decipiens
Solidago sempervirens

The shoreward edge of the marsh where the substratum is still higher is characterized by a zone in which the black grass *(Juncus Gerardi)* is the chief species. Often in localities where the salinity is reduced this species may be replaced by *Juncus balticus* var. *littoralis* (Figure 49). In this rush zone are found such forms as:

Agrostis alba var. *maritima*
Puccinellia paupercula var. *alaskana*
Hordeum jubatum
Agropyron repens
Scirpus nanus
Scirpus campestris var. *paludosus*
Carex maritima
Juncus bufonius
Atriplex patula var. *hastata*
Spergularia canadensis
Ranunculus Cymbalaria
Potentilla pacifica

Of these species *Scirpus campestris* var. *paludosus*, *Carex maritima* and *Ranunculus Cymbalaria* occur in the wetter, muddier places.

Of more frequent occurrence are the incipient salt marshes which are formed on muddy shores (Figure 50). These are rarely of any great extent, consisting of scattered individuals or groups of such species as *Suaeda maritima, Glaux maritima* var. *obtusifolia*, *Limonium trichogonum* and *Plantago decipiens*, with larger patches of the *Spartinas, Juncus Gerardi* or *Carex maritima*. These latter may cover considerable territory by means of their creeping rootstalks and furnish enough obstruction to the water so that considerable silt is deposited about them. During the winter, however, all traces of such embryonic marshes are wiped out. They occur on the upper portion of the lower beach, the lower portion being either bare or occupied by eel grass and rockweed. The mud flats which are found at the head of many of the bays (Figure 50) have a vegetation consisting chiefly of *Zostera*, which is left stranded at each receding tide, and various algae.

c. Association-types of brackish marshes

It is impossible to draw any sharp line between a salt marsh and a brackish marsh for in many instances they are continuous and support the same species, the differences in salinity being too slight to effect the vegetation. In the higher portions of the brackish marsh, however, several species may occur which are not found in a typical salt marsh. Among these may be mentioned:

Hierochloe odorata var. *fragrans*
Elymus virginicus
Carex hormathodes
Carex leptalea
Carex salina var. *kattegatensis*
Scirpus validus
Juncus pelocarpus
Aster novi-belgii

The brackish marsh intergrades on its landward side with fresh swamps and this transition area may contain species of the brackish marsh side by side with such non-halophytic plants as:

Figure 47. — Salt marsh bordering on barrier-beach pond, Harrimans Point, Brooklin.

Figure 48. — Salt marsh along Weskeag River, South Thomaston, a tidal estuary.

Dryopteris Thelypteris
Festuca rubra
Carex scoparia
Iris versicolor
Myrica Gale
Rosa virginiana
Spiraea latifolia
Lathyrus palustris var. *pilosus*
Heracleum lanatum
Vaccinium macrocarpon

In one locality, the so-called "Cranberry Marsh", located at North Point on Swans Island there is an interesting transition between a salt marsh and ordinary uplands. This area is situated behind a barrier-beach and its vegetation occurs in several well-marked zones. Directly adjacent to the beach is a small pond filled with *Ruppia*, *Potamogeton* and various green algae. Adjoining this is an extensive, extremely muddy and slimy portion of the marsh with an almost solid carpet of *Suaeda maritima* and occasional clumps of *Plantago decipiens* and *Triglochin maritima.* Directly bordering on this zone is an extensive thicket of *Myrica Gale* which in turn is followed by a boggy meadow consisting of various *Carices* with *Eriophorum virginicum*, *Rynchospora alba*, *Vaccinium macrocarpon* and such shrubs as *Spiraea latifolia*, *Myrica carolinensis*, *Ilex verticillata*, *Rosa virginiana* and *Alnus crispa* var. *mollis.* Trees are also present, chiefly larches and red maples and numerous specimens of *Picea rubra* have invaded the area from the adjacent upland. These have increased noticeably during the last twelve years and are reproducing readily. The whole area apparently represents a former barrier-beach pond which has been gradually filled in by vegetation. This process has been facilitated by the fact that there is no seepage through the beach, the surface of the marsh, being well above the mean high tide level. Only at the edge of the beach where it is exposed to spray do salt marsh conditions exist. Vegetation has advanced up to the point where salinity is too great and one stage has succeeded another on this area until now it is dominated by shrubs. These have been able to invade the ground ordinarily covered by the salt marsh grasses and are kept out of the remainder of the marsh only by the extreme halophytic conditions which prevail there.

V. COMPARISONS WITH OTHER REGIONS

The vegetation of the Penobscot Bay region of the Maine coast shows a marked resemblance to that of other localities within the Canadian transition zone of the Transition Forest region, for which data are available. Unfortunately comparatively little ecological work has been done in this area and almost none so far as the succession of vegetation is concerned. Some idea of the nature of the climax forest can be gained from the publications of foresters, but these are primarily economic in character and do not consider at all the dynamics of the vegetation. The most valuable works in this connection are those of Chittenden (3), Fernow (7, 8), Frothingham (9), Hawley and Hawes (14), Macoun (17) and Murphy (20). Papers of an ecological nature which deal with the area, in addition to those previously referred to, include those by Ganong (10), Howe (16), Moore (18, 19), and Transeau (29). The most striking feature brought out by these papers is the similarity in the climax forests of the several regions described. Whether it be the Maritime Provinces, northern New England, the Adirondack Mountains of New York, or the Penobscot Bay region of Maine, the climax association-type is a mixed coniferous deciduous forest with sugar maple, beech, hemlock, yellow birch, spruce and balsam fir the predominant trees. This is the culminating type of vegetation on areas of optimum drainage, deep loose soils and moderate slopes.

Not only does the Penobscot Bay region agree in its climax forest—the regional climax association-type—with the rest of the larger area of which it is a part but also in respect to the various physiographic climaces which occur. The development of the spruce-fir forest on the thin soils of the islands and the outer portions of the mainland is sim-

FIGURE 49. — Detail of salt marsh shown in Figure 47; from right to left, zones of *Spartina patens*, *Carex maritima*, *Juncus balticus* var. *littoralis* and *Calamagrostis canadensis*.

FIGURE 50. — Muddy shores of Herricks Bay, Brooklin; *Zostera marina* on tidal flats in background; rockweeds on rocks on lower beach; incipient salt marsh with *Spartina alternifolia* on upper part of lower beach.

ilar to that which occurs in southern Nova Scotia, as described by Transeau (29). That this type of forest in Nova Scotia, just as in Maine, should not be considered the regional climax is evident since, as Transeau himself states, the successions leading to the coniferous forest "are typical only of the region directly influenced by the coastal conditions" while inland a mixed conifer-hardwood forest occurs. Furthermore Fernow (8) states that the coniferous forest, which usually occurs on the thin soil of the granite ridges, and along the coast comprises only some 20% of the woodlands of Nova Scotia, the remainder being of the mixed spruce-hardwood type.

In New England the spruce-fir forests are divided by the foresters into four general types: (1) spruce swamp, (2) spruce flat, (3) mixed hardwood and (4) spruce slope. Of these the spruce swamp and spruce slope clearly represent physiographic climaces, the former occupying the poorly-drained, low-lying areas with an acid, mucky or peaty soil; while the latter occurs on the shallow rocky soils of the upper slopes. Both these types are of frequent occurrence in the Penobscot Bay region. The mixed hardwood forest constitutes the climax type, while the spruce flat is intermediate between the swamp and the hardwood type. That the mixed hardwood rather than the spruce forest represents the regional climax association-type is evident from the statement of the foresters that the spruce attains its best development in the former type of woods. The spruce forest certainly should not be considered as constituting a regional climax type in places where it may be predominant, if the spruce is unable to become dominant over the deciduous species in other localities which are the most favorable for its development.

A comparison of the Penobscot Bay region with Cape Breton brings out the fact that the vegetation is not as diversified as in the latter area. There are no forests which can be definitely classed as belonging to the northeastern coniferous forest region, since the altitude is nowhere great enough to effect the development of this particular climax. There is also an absence of the characteristic vegetation of ravines, flood plains and open valleys or intervales, since these topographical forms are lacking. In other respects the two regions are very similar, the chief difference being the much larger percentage of spruce over balsam fir in the coniferous forests.

The Penobscot Bay region, as would be expected, shows an even greater similarity to the island of Mount Desert which lies on the eastern border of the Bay. An ecological investigation of this island is under way at the present time and some preliminary observations have already been published (see Moore 19, 20). Five chief associations are recognized: the spruce, white pine, cedar, pitch pine and gray birch-aspen together with several minor associations, one of which is the spruce-northern hardwood. All of these types are to be found in the adjacent Penobscot Bay region where the first four constitute physiographic climaces; and the gray birch-aspen wood represents a stage of the secondary succession after a fire or lumbering. The spruce-northern hardwood forest is of more frequent occurrence than on Mount Desert, but only in the localities well back from the coast.

Hawley and Hawes (14) in their map of the forest regions of New England make Penobscot Bay the boundary on the coast between the white pine region, which extends to the western border, and the spruce region, which begins on the eastern border of the Bay. In the opinion of the writer the white pine region should not be considered as distinct, for it represents merely a physiographic climax on sandy sterile soils in an otherwise deciduous area. But if it is so recognized, the region should not be extended as far east along the coast as Penobscot Bay. The forests on the western side of the Bay are of the same nature as those of the eastern side, which are classed as "spruce" by Hawley and

Hawes. Not only should the entire Penobscot Bay region be thus designated as belonging to the "spruce" region, but also most of the territory between the Kennebec and Penobscot Rivers, at least along the coast. As a matter of fact all this "spruce" region of New England, with the exception of the upper slopes of Mt. Katahdin and the higher White and Green Mountains, should better be classed as "spruce-northern hardwoods", since this type of forest is the regional climax for the area.

VI. SUMMARY

The Penobscot Bay region in Maine is situated on the coast about midway between the eastern and the western boundaries of the state. The region is a rugged one with the characteristics of a drowned coast. The soils are chiefly of glacial origin but are very meagre, and the underlying rocks control the topography. The latter are predominantly acidic, granite being of most frequent occurrence. The climate is that of any moist maritime north temperate region.

From the standpoint of its vegetation the Penobscot Bay region is a part of the Canadian-transition zone of the Transition Forest region, the northernmost of the two zones of the intermediate area between the eastern deciduous and the northeastern coniferous forest regions. The climax forest of this zone, and of the Penobscot Bay region as well, is a mixed forest of both deciduous and coniferous species, the "spruce-northern hardwoods" of the lumbermen. The characteristic trees include *Acer saccharum*, *Fagus grandifolia*, *Tsuga canadensis*, *Betula lutea*, *Pinus Strobus*, *Abies balsamea*, *Picea mariana* and *Picea rubra*. The shrubby undergrowth consists primarily of *Acer pennsylvanicum*, *Acer spicatum* and *Viburnum alnifolium;* while on the forest floor many northern herbaceous species occur. This forest, which constitutes the regional climax association-type, is the culminating type of vegetation on ordinary uplands where the various physiographic factors are favorable. Elsewhere, owing to the effect of factors which preclude the development of the regional type, the succession of vegetation may be halted lower down in the successional series and physiographic climaces result.

The succession on igneous rocks passes through a rock surface, crevice, and heath mat stage to a spruce-fir forest which constitutes a physiographic climax. This is very frequent on the islands and the outer shores of the mainland. On glacial drift such a forest may be followed by one of the regional climax type. On sedimentary rocks the succession is quite similar save for the introduction of a pine forest following the heath mat. Where this consists of pitch pine it represents a physiographic climax, but if white or red pines are present these latter trees are usually succeeded by a spruce-fir forest.

Succession on uplands along the coast varies depending on whether the locality is on an eroding or a depositing shore. Sea bluffs are frequent and often have a characteristic growth of prostrate shrubs at their crest, though the coniferous forest may extend to the very edge of the cliffs. If the exposure is extreme, barren headlands may occur with a carpet of grasses, or low shrubs, and rarely of stunted trees. Beaches are either of the shingle or gravel type, the former often occurring as barrier beaches, and their vegetation displays no unusual features.

Secondary successions on uplands resulting from cultivation, fire or lumbering are extremely common and have greatly altered the nature of the vegetation. Old fields and pastures are eventually reclaimed by a forest of spruce and fir or in sandy places by white pine. After a fire the fireweeds, which spring up the first year, are followed by a birch-poplar wood which may persist for some time but is later succeeded by a coniferous wood. A fire which destroys the humus reduces the area to the rock surface stage and vegetation is forced to make a fresh start. Blueberry barrens, maintained by frequently burning over a locality, are of increasing prominence. After a hardwood is cut off it is followed by either a sprout growth or by conifers. A coniferous forest is usually succeeded by a bramble stage and a birch-poplar wood before conifers again return.

Succession in lowlands is similar to that in other regions, several different types occurring: well-drained lakes and lake-swamps with stages leading to a swamp forest, or rarely a cedar swamp, as a physiographic climax; undrained ponds in which a bog forest constitutes a physiographic climax; spring swamps, either open swamps or wet meadows, which ultimately may be covered by a swamp forest; and poorly-drained areas, which show intermediate conditions between swamps, bogs and uplands. The vegetation of lowlands along the shore,—barrier beach ponds, salt and brackish marshes—is like that of similar areas elsewhere.

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PHASE REVERSAL IN PROTOPLASM AND EMULSIONS

THE reversal of phases in oil emulsions by electrolytes was discovered by Clowes.[1] Clowes worked with olive oil emulsions in which the aqueous phase was a soap solution, the soap being added directly or formed through saponification of the oleic acid in the olive oil by an aqueous phase of NaOH. Clowes found that, when the salt of a bivalent cation ($CaCl_2$) is in excess in the aqueous phase, the emulsion is of the water-in-oil type, and when the hydroxide of the monovalent cation Na is in excess, the emulsion is of the oil-in-water type. Clowes came to some very interesting and far reaching conclusions on the basis of his experiments. It does not appear that he worked with emulsions in which the stabilizing agent is some colloid other than soap.

Clowes saw in the behavior of oil and water emulsions (in which soap is the emulsifier) an explanation of changes in protoplasmic permeability. It is now believed (by some biologists) that monovalent cations increase permeability of the plasma membrane, while bivalent cations decrease permeability. The hydroxide of the monovalent cation Na produces in an oil emulsion (with a soap stabilizer) a system in which the continuous phase is water. Such a system would be readily permeable to water soluble substances. Salts of bivalent cations, such as $CaCl_2$, produce an emulsion in which oil is the continuous phase. Such a system would be impermeable to water soluble substances.

APR 11 1924

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[1] Clowes, G. H. A., ''Protoplasmic equilibrium,'' *Jour. Phys. Chem.*, 1916, xx, 407-451.

On the basis of the similarity of the reactions of oil emulsions and of protoplasm to mono- and bivalent cations, Clowes has conceived of living protoplasm in contact with water as a system which is, within the protoplasmic mass, a dispersion of proteins, lipoids, etc., in water, and, at its surface, a system of the reverse type, in which water is dispersed in an external continuous fatty or lipoid phase. Clowes does not, however, regard the surface layer of protoplasm as a system in which the aqueous phase is wholly discontinuous, but rather as a system in which the continuous lipoid phase is permeated by water channels, *i.e.,* as an emulsion which is near the reversal point.

Clowes has assumed that the stabilizer active in the supposed protoplasmic emulsion is either soap or a substance which is like soap in its reaction to mono- and bivalent electrolytes. While soaps are present in protoplasm it does not seem likely that they are the emulsifier which determines the behavior of the supposed living emulsion when other possible emulsifiers such as proteins and lipoids are present in much greater quantities.

I had the pleasure of discussing phase reversal in emulsions with Mr. Hatschek, of London. Mr. Hatschek called my attention to the fact that if the emulsifier in an oil emulsion is some colloid other than soap, for example, gum arabic, the emulsion will not reverse when a bivalent electrolyte is added to it. With the kind permission of Mr. Hatschek I have repeated and extended his preliminary experiments.

The manner of making the stabilizers and the emulsions, with also the methods employed in determining the type of system, will all be fully described in a subsequent publication.

Oil emulsions in which sodium oleate or sodium stearate is the emulsifier are of the oil-in-water type and are reversible with $BaCl_2$.

Oil emulsions with casein, gliadin, cholesterin, or cephaelin as the aqueous phase, are of the water-in-oil type and are reversible with NaOH.

Oil emulsions in which saponin (senegin, smilacin), gelatose, gum arabic, albumin, lecithin, or a plant extract is the emulsifier, are oil-in-water systems which are *not* reversible with $BaCl_2$.

It is of interest to note that of three proteins, all present in protoplasm, the most abundant one, albumin, does not permit reversal, while the two others do; and of two lipoids, both constituents of living matter, one, lecithin, does not, and one, chloresterin, does permit reversal. Further, the plant extract (obtained by grinding and pressing fresh spinach), which one might expect to approach somewhat the chemical make-up of protoplasm, does not permit reversal.

Who can tell what the emulsifier in the supposed living emulsion actually is?

Since the hypothesis of Clowes rests on the assumption that the emulsifier in protoplasm is of that type which forms an emulsion which is reversible with $BaCl_2$ or NaOH, and since certain of the substances here experimented with as emulsifiers, are very abundant in protoplasm but form emulsions which are not reversible with $BaCl_2$ or NaOH, one is forced to conclude that, in view of the fact that we are totally ignorant of the actual nature of the active emulsifier in living matter, a theory of the mechanism of permeability changes which is based on the behavior of only one group of emulsions, must be regarded as a purely speculative hypothesis which rests on very uncertain evidence.

It is of further interest to note that NaCl will not reverse any of the reversible emulsions here studied, yet it is this salt which causes (in the opinion of some investigators) such a pronounced increase in the permeability of protoplasm.

Quite aside from the experimental facts here given, it should be pointed out that the hypothesis of Clowes, like so many other interesting speculations on protoplasmic behavior in general and on permeability changes in particular, rests on two very fundamental assumptions (in addition to the one above discussed) in support of which there is no substantial evidence.

It is assumed by Clowes, and indeed by most biologists as well, that protoplasm is an emulsion in which a reversal of phases is of common occurrence. The emulsion hypothesis of protoplasmic structure is still adhered to by many biologists in spite of the fact that there is in all physical chemistry no *conclusive* evidence that any lyophilic colloid, of which protoplasm is one, is a liquid-liquid system. That the dehydrated lyophilic colloids starch and cellulose are crystalline has been shown to be true by the work in Roentgen ray spectography of Herzog. Although this does not necessarily tell us what the hydrated colloid is like, the consensus of opinion among colloid chemists seems to be that the dispersed particles of the hydrated colloid, in a gelatin sol for example, are solid. In the process of hydration there apparently takes place a breaking down of larger crystalline aggregates into smaller ones, which may even approach the gelatine molecule in size. I believe that I am not misinterpreting the writings of McBain, Freundlich, Proctor[2] and Bachmann when I state they are of this general opinion.

Regardless of the physical nature of the colloidal particles—and after all, as Hatschek has pointed out, the distinction between liquid and solid becomes somewhat vague with particles approaching ultramicroscopic dimensions—there is no evidence that a reversal of phases takes

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[2] Proctor, H. R., The structure of elastic jellies, *Phys. and Chem. of Colloids, Rep. Faraday Soc. and Phys. Soc.*, London, 1921, 40-43.

place in the process of gel formation from the sols of lyophilic colloids. On the contrary, the work of Bachmann and Zsigmondy and of McBain has shown that in gelatin and in soaps, and therefore probably in many other if not all lyophilic colloids, *there is no reversal of phases in the formation of a gel,* but merely an aggregation of the colloidal particles—the dispersion medium in the sol is still the dispersion medium in the gel. The conception of a reversal of phases in the process of gelation owes its origin to the earlier supposition that the lyophilic colloids are liquid-liquid, "emulsoid" systems, an idea which is not now held by such chemists as Donnan, Freundlich, McBain and Zsigmondy. One wonders, therefore, how far we dare go in our phase reversal speculations on the mechanism of permeability changes and similar vital phenomena.

The full account of the experimental data here briefly reported will include a discussion of the remarkable behavior of the emulsion with a gelatose emulsifier. This is an emulsion of the oil-in-water type and is reversible, in the *same* direction with the hydroxide of either the bivalent cation Ba or the monovalent cation Na, but not with the salt of either cation. There will also be published data on the possible influence of acidity on phase reversal. That pH value is a factor in phase reversal is apparently true in certain cases, but that it is the determining factor in other cases is certainly not true. H-ion concentration must affect the ability of an emulsion to reverse through acting on the emulsifier—possibly the hydration power of the emulsifier—consequently, the effect of pH will differ in emulsions with different emulsifiers, and this the experiments show to be true.

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Reprinted from the Bulletin of the Torrey Botanical Club, Vol. 50, September, 1923.

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The altitudinal distribution of plants on Mt. Gedeh, Java*

William Seifriz

(WITH PLATES 15-17 AND SEVEN TEXT FIGURES)

Mt. Gedeh is in the "Preanger Regent" of western Java. At its foot lies the village of Singdanglaja, some five hours' journey by rail and coach from Buitenzorg. Gedeh, with Pangerango, the "princely mountain," and Sela, form a trio of volcanic mountain peaks. Of these Gedeh alone is semi-active. It was last in eruption in 1899. At present the hot springs gush-

Fig. 1. Mt. Pangerango from Gedeh. The slope of Pangerango makes clear how rapid a change in altitude plants have to contend with. Water covered rice fields can be faintly seen in the valley just over the lower edge of Pangerango.

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* Contribution from the Osborn Botanical Laboratory.

ing from the mountain side and the several fumaroles in the crater emitting fumes of sulphur are the only indications that Mt. Gedeh is a volcano in the dormant state. Mt. Pangerango (FIG. 1), whose beautiful conical form commands admiration, and Mt. Sela are both extinct. The botanical explorations described on the following pages refer primarily to Mt. Gedeh, though some mention is made of plants of interest found on the two neighboring peaks.

Midway up the slope of Mt. Gedeh is the government experimental station of Tjibodas ("white river"). The laboratory, cottage, and garden at Tjibodas serve as a base for botanical excursions into the mountain forests beyond. The Tjibodas Garden contains numerous interesting plants, notably the renowned grass trees, *Xanthorrhoea Preissii* (PLATE 15, FIG. 1). These liliaceous trees are natives of the Australian savannahs. The twin specimens in the Tjibodas Garden are familiar to botanists through the illustration in Haberlandt's "Botanische Tropenreise." The trees have doubled in size since Haberlandt saw them thirty years ago.

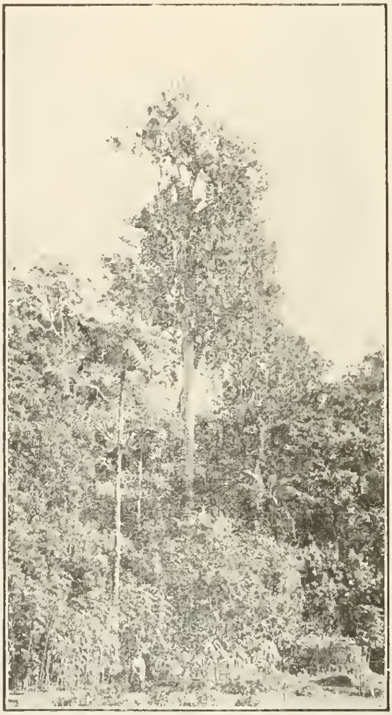

FIG. 2. The superb rasamala, *Altingia excelsa*. This tree (in the center background) is 150 feet high. Note the straight uniform trunk. The tree-fern is an *Alsophila*, 42 feet high.

Back of Tjibodas, extending to the summits of Mts. Gedeh, Pangerango, and Sela, is a virgin forest of supreme beauty, with a flora unsurpassed, if indeed it is approached, by that of any other similar region in the world. One of the most striking features of plant life in this mountain rain-forest is the marked change in type of vegetation as one ascends. At Tjibodas, at an altitude of 4,600 feet, the palms, bamboos, fig trees, and bananas, characteristic of the lowlands, still occur, but are soon displaced by oaks, chestnuts, *Podocarpus* and tree-ferns. Gnarled, moss-covered trees then follow, only later to disappear. And finally, after attaining an altitude of 9,400 feet, a scant alpine flora, characterized by the Javanese edelweiss, is reached.

The following brief description of the altitudinal distribution of plants in the virgin forest on Mt. Gedeh will, I trust, give some idea of the distribution of the plant life and of its luxuriance and beauty.

Java was divided into four "Gewächszonen" by Junghuhn, the foremost naturalist of the Dutch East Indies, and these vegetative zones he divided into "Gebiete." The first zone of Junghuhn is the hot region from the sea-coast to an altitude of 2,000 feet; the second, the temperate region from 2,000 to 4,500 feet; the third, the cool region from 4,500 to 7,500 feet; and the fourth, the cold region from 7,500 to 10,000 feet. These last two vegetative zones of Junghuhn, from 4,600 feet, the altitude of Tjibodas, to 9,400 feet, the crater of Mt. Gedeh,* which are the ones that concern us here, can be divided into five distinct subzones.

I. THE RASAMALA SUBZONE

(4,600–5,500 feet)

The first subzone, at Tjibodas, is characterized by its big trees—superb giants many of them are. The monarch of all is the rasamala, *Altingia excelsa* (*Liquidambar Altingiana*) (FIG. 2), whose smooth, grayish white trunk arises out of the wealth of vegetation at its base as straight as a ship's mast. These fine trees reach a height of 175 feet and a maximum diameter, near the base, of 8 feet (FIG. 3). When buttresses are formed the base may flare to a diameter of 12 feet. The trunk maintains a diameter of fully 2½ feet for 75 to 100 feet from the ground at which point it first branches. So characteristic a tree of this region is *Altingia* that it may well lend its name to the subzone.

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* The summit of Mt. Pangerango is 9,800 feet.

The rivals of the rasamala in size are the oaks and chestnuts. The oaks, of which there are several species (e.g., *Quercus spicata* and *Q. Pseudo-molucca*), are in some respects strikingly different from our American oaks. The trunks rise like great columns before they branch to form the crown, and the fruits are of a colossal size compared to an American acorn. Botanists do not always appreciate how characteristic a tree of the tropics the oak is. We become accustomed to regarding *Quercus* as a temperate genus. The chestnuts are likewise of great size. The two characteristic species are *Castanea Tungurrut* and *C. argentea.*

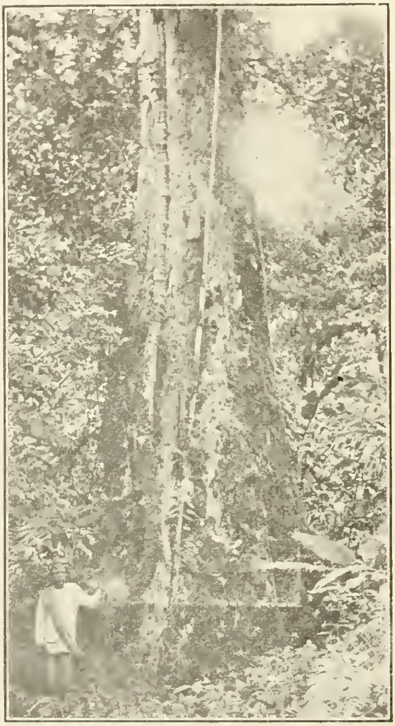

FIG. 3. The trunk-base of the rasamala. The large liane (on the left), marked with successive rings, is a *Piper*, possibly *P. baccatum.* The smaller liane, extending up the trunk, is *Ficus disticha.* The large leaves of a banana, *Musa acuminata*, can be seen in the lower right corner.

Conspicuous among the big trees of the first subzone on Mt. Gedeh are the figs, whose composite trunks assume tremendous size. There are nine species of fig on Gedeh (more than sixty in all Java), the largest of which is *Ficus involucrata.* In connection with the epiphytic habit of fig tree seedlings it is of interest to note that Chodat,* as a result of his recent investigations in South America, has discovered that "the young *Ficus* from its first implantation behaves as a *saprophyte.*"

The medium sized and smaller trees of the first subzone are

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* Chodat, Robert: La Végétation du Paraguay, Geneva, 1920.

of many kinds. There are numerous species of *Eugenia* and *Litsea*, three of *Viburnum*, two of *Turpinia*, and one each of *Euonymus* (*E. javanicus*), *Ilex* (*I. spicata*), and *Olea* (*O. javanica*). The small tree *Pithecolobium montanum* is one of the few Leguminosae to be found in these mountain forests. We shall meet a second tree member of this family on the very summit of Gedeh. Another tree of this and the second subzone which is worthy of special note is *Vernonia arborea*. This tree is one of the Compositae, yet it may be 80 feet high and 2½ feet in diameter (FIG. 4).

FIG. 4. The trunk of *Vernonia arborea*. This 80 foot tree is one of the Compositae.

The fig, *Ficus Ribes*, is an interesting small tree because it affords a striking example of a rather common fruiting habit among tropical trees, namely, cauliflory. *Saurauja* (*S. pendula*, *S. nudiflora*, and five other species), whose white flowers with thick, waxy petals are often seen strewn over the path, is an example of incomplete cauliflory. The flowers are borne not only on the surface of the tree trunk and larger limbs but at the tips of slender twigs as well. Such a semi-cauliflory characterizes several other Javanese trees.

The foregoing list of first subzone trees is very incomplete and gives at best but a number of representative species. Of trees alone there are nearly two hundred species on Mt. Gedeh; of shrubs and herbs over three hundred and fifty species; and of lianes some sixty or more, totaling at least six hundred species of plants exclusive of the ferns, mosses and fungi.

Lianes are numerous in the first subzone. The family Vitaceae is well represented among the smaller climbers

The slender and warty vine, *Vitis papillosa*, is of interest because of its multitude of aerial roots which often swing clear for fifty feet or more from the crown of some huge tree and present a striking picture when one comes upon a barricade of them lighted up by the sun. *Smilax odoratissima* is the catbrier of these forests. *Agalmyla parasitica* (which is *not* parasitic) is an interesting epiphytic climber frequently met with. The tubular flowers are of a brilliant scarlet with long protruding stamens of purple. The leaves of this vine when in the cool of the shade project outward perpendicularly to the support, but droop once the sun strikes them. The petioles and leaves are thick, succulent, and turgid, suggesting the mechanism by which the raising and lowering of the leaves is accomplished. Another creeper found frequently upon the trunks of trees is the aroid, *Scindapsus hederaceus*, readily distinguished by its broad, winged petioles. This vine and its sister genus *Rhaphidophora* are the only two climbing Araceae found in any great abundance in the mountain rain-forest. Among the large lianes are *Uncaria* and *Embelia* (*E. pergamacea*), the latter often attaining great length (as much as 250 feet).

So numerous are the plants that make up the undergrowth of the first subzone that it is an almost hopeless task to attempt to give a representative list of them. A single bamboo, *Dinochloa scandens*, is still to be found at this altitude. Of the many palms which characterize the tropical vegetation of Java as a whole, but three comparatively inconspicuous genera occur in the mountain forest. These are the slender and graceful *Pinanga Kuhlii* and the two rattan palms, *Calamus* and *Plectocomia* (*P. elongata*). The two latter genera are climbing palms with long extended leaf rhachides armed with vicious recurved thorns by means of which the plants often attain a height of 75 feet or more, thus reaching up into the second story of the forest. One of the Pandanaceae, *Pandanus Lais*, is very common in the undergrowth of the first subzone.

Showy flowers are much more abundant at Tjibodas than is usually the case in a tropical rain-forest, although less frequent in the forest interior. They seek the bright areas along the trail and the open formations of the higher zones. In the closed formation of the first subzone the most striking flower is that of the ginger, *Amomum*. Its brilliant scarlet blossom is often found protruding from the ground, growing quite alone in the very center of the trail. Dense thickets are formed by the rank growth of the tall vegetative shoots of this plant. Associated with this ginger is another species, *Phaeomeria solaris*, whose flower also appears just above the surface of the soil some distance from the leafy shoots of the plant. The blossom is of a rich orange-red color and as large as a small head of cabbage. Other but terminal-flowered gingers will be met with in the next subzone. The blossom of *Arisaema filiforme* (a jack-in-the-pulpit) is an attractive though somber colored flower, especially interesting because of its unusually long spadix which droops out of the spathe to a length of eight inches. The three jaunty bells of the tiny weed, *Argostemma montanum*, form a dainty white flower cluster which is abundant along the trail. *Cestrum elegans* is a small tree-shrub with red pendent flowers.

Of the phanerogamous epiphytes the orchids are the most numerous. Those most frequently met with are species of *Dendrobium* and *Bulbophyllum*. *Liparis*, *Eria*, and *Appendicula* are somewhat less numerous, although *A. ramosa* is rather abundant. Certain species of *Dendrobium* are remarkable because all the individuals in any one locality blossom simultaneously.* The epiphytic "pines," *Tillandsia* and *Caruguata*, which are so striking and characteristic a feature of the epiphytic vegetation of tropical America, are not to be found in Java—indeed, not in all the eastern tropics.

Ferns, both as part of the vegetation of the forest floor and as epiphytes are exceedingly abundant. The ferns as a group are widely distributed throughout the mountain rain-forest, occurring in all subzones, though in varying abundance. Common terrestrial forms of the first subzone are, *Pteridium aquilinum*, *Pteris longipes*, numerous species of *Dryopteris* (e.g., *D. truncata*), and the interesting *Diplazium proliferum*, which develops a bud, often of huge size, at the base of each pinna. This habit of proliferating is not infrequent among the ferns of this region.

A noteworthy fern is the enormous *Angiopteris evecta*, found in moist spots, especially bordering streams, and occurring in many forms. This fern commands attention because of its colossal 15–18 foot fronds which spread out over the trail.

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* See Seifriz, William: The gregarious flowering of the orchid *Dendrobium crumenatum*. Am. Jour. Bot. **20**: 32–37. 1923.

Another interesting fern is the stout *Polypodium Feei*, with its mass of prominent sori completely covering the back of a fertile frond. It grows in great profusion among the rocks near the base of waterfalls. A variety of this same fern—a most adaptable and widely distributed species—is again found on the dry lava floor of the crater of Mt. Gedeh.

Tree-ferns are infrequently met with along the trail in the lower subzones. They seek the more open forest formations at higher altitudes or the sunny yet moist ravines.

The epiphytic ferns with the tree-ferns distinguish a tropical fern flora from a temperate one. The characteristic epiphytic fern of the first subzone on Mt. Gedeh is the magnificent bird's nest fern, *Asplenium nidus* (PLATE 15, FIG. 2). This huge fern, with a spread of sometimes as much as 15 feet, may be seen perched like a large bird with out-spread wings, upon a small limb far out in space, or it may be found near the ground completely encircling a tree trunk, then resembling a fancy flower basket. Occasionally one is seen apparently floating free in the air, and only on close examination is the bent slender twig supporting it discovered (PLATE 16, FIG. 1).

The nest shape of *Asplenium nidus* forms an ideal catch-all for falling leaves and detritus, a natural basket always full of rich organic matter. This fine substratum in turn supports yet other epiphytic ferns. Some of these are of very good size, such as *Stenolepsis tristis* and *Nephrolepsis acuminata*, with fronds often 6–8 feet in length (PLATE 16, FIG. 1). This latter fern is one of the most graceful in the forest.

While *Asplenium nidus* is the characteristic fern and epiphyte of the first subzone, other epiphytic ferns are numerous. Chief among these is *Polypodium Heracleum*, a rival in size though not in abundance of *Asplenium nidus*. The large, deeply cleft fronds of the *Polypodium*, measuring as much as 7 feet in length and 18 inches in width, surround a tree very much as does the bird's nest fern. This remarkable genus is the only one which has representative species in all the subzones, from Tjibodas to the crater of Gedeh.

The long grass-like fern *Vittaria elongata* drapes the trees and lianes in an attractive manner (FIG. 3). Several polypodiums, e.g., *P. obliquatum*, are common as epiphytes. And one should not neglect the less conspicuous but beautiful and delicate little filmy ferns, species of *Hymenophyllum* and *Trichomanes*. The smallest of the hymenophyllums we shall find at a higher altitude.

Mosses exist, but are to be found in much greater abundance in the second and fourth subzones. Species of liverworts are not numerous, although fine patches of the large *Dumortiera hirsuta* are frequent.

Fungi (with conspicuous fruits) are seldom met with. This is rather generally true of the tropics. A few species of the woody and leathery forms of the Polyporaceae and an occasional gill fungus are all that are superficially evident. Diligent search does, however, reveal other and interesting species, often of brilliant color.

Of lichens the number of species is exceedingly great. I have seen trunks of the great rasamala completely covered with encrusting lichens which give to the tree the appearance of an elaborate mosaic. The Graphidae are especially attractive. One feels that nature must have some story to tell in their queer markings if one but knew the key. Indeed, they look every bit as intelligible as the hieroglyphics of the Malay language. Forty-seven species of lichens were collected from the first subzone. The genera *Graphis*, *Pertusaria*, and *Sticta* are especially well represented.*

II. THE PODOCARPUS SUBZONE

(5,500–7,000 feet)

At an altitude of about 5,500 feet there is a pronounced change in the general appearance of the mountain forest. One realizes immediately that the woods have assumed a different dress. Everything is moss-covered (PLATE 16, FIG. 2). It is surprising with what suddenness the transformation takes place, and one wonders what differences in climatic factors can exist which produce so marked and so sudden a change between the region just left and that which lies beyond. So profuse is the moss drapery that one is inclined to term this the moss zone. Such a designation would, however, be inaccurate, as subsequent investigation will show.

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* For a full account of the lichens and mosses collected in the Tjibodas forest see, The altitudinal distribution of lichens and mosses on Mt. Gedeh, Java, to be published in The Ecologist, January, 1924.

Here, in the second subzone, which we have just entered, the vegetation first really assumes the aspect of a tropical rain-forest. Lianes are more numerous. The undergrowth is less orderly (but by no means a "jungle," a word which is so often and so erroneously used to characterize tropical vegetation). Trees, rocks, and soil are moss-bedecked; and all is reeking wet, actual bogs being met with under foot.

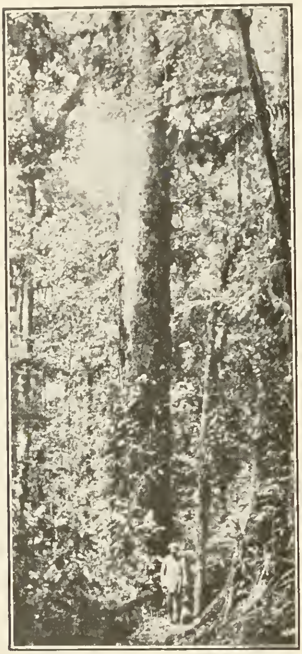

FIG. 5. The monarch of the second subzone, *Podocarpus imbricatus*. The vine on the trunk some 20 feet from the ground is *Epipremnum pinnatum*. The native shown is Sapiin, the veteran plant collector of Tjibodas, who knows the Sundanese name of every seed-plant in these mountain forests.

Some plant forms of the first subzone are still abundant, but others are no longer seen and new forms take their place. The great rasamala is rare. *Podocarpus* is its successor (FIG. 5). This tree is the only conifer, in fact the only gymnosperm, indigenous to Mt. Gedeh. Three species of *Podocarpus* are to be found, *P. imbricata* (*P. cupressina*), *P. neriifolia*, and *P. amara*. While this genus extends into the two adjacent zones, especially the upper one, it is in this second subzone that it is most abundant and reaches its maximum size, fully 5 feet in diameter.

Podocarpus is the monarch of the second subzone, as was *Altingia* of the first, but other very large trees are also numerous. Especially fine is *Engelhardtia* (*E. serrata* and *E. spicata*). This big tree resembles the rasamala in size and shape, but its small lanceolate leaflets give to its lofty crown a different and lacy appearance. Another large tree common to this and the adjoining third subzone is *Schima Noronhae*, the "poespa" of the Javanese. Its good-sized, showy flowers are often seen sprinkling the ground with spots of white and yellow. The figs, oaks, and chestnuts are still present and of great size. One repeatedly stops to admire the huge, tall, straight trunks of these superb giants of the mountain forest.

The small trees of the second subzone include *Meliosma nervosa*, *Elaeocarpus Acronodia* (and four other species of this genus), *Michelia montana* of the magnolia family, *Macropanax dispermum* of the Araliaceae, and *Pygeum latifolium*, a rosaceous tree (PLATE 16, FIG. 2).

Lianes are abundant. A conspicuous climber is the spiny *Fagara scandens*, one of the Rutaceae. The huge stubby spines tipped with sharp thorns give to this vine a vicious appearance. Isolated specimens of the climbing aroid *Epipremnum pinnatum* are met with.

Of epiphytes, the beautiful bird's nest fern, *Asplenium nidus*, still flourishes. The climbing pandanaceous epiphyte *Freycinetia* is first met here. The smaller epiphytes of this second subzone are chiefly orchids, ferns and mosses. An attractive orchid frequently seen in *Schoenorchis juncifolia*, with long, drooping stems and spindling, awl-shaped leaves, resembling a *Freycinetia* in miniature.

The forest floor assumes quite a different aspect in the second subzone owing to a greater abundance of light. Tropical forests are not as dark as most people who have never visited them believe; indeed, more light penetrates a tropical mountain rain-forest than enters a temperate closed deciduous forest, and a great deal more than reaches the ground in a Maine pine wood. The forest canopy of the second subzone is an open one. Trees are fewer than in the first subzone and the undergrowth flourishes proportionately better.

The rattan and Pinango palms are more numerous here at 6,000 feet than they were a thousand feet lower. Numerous species of Zingiberaceae are present. The two first subzone gingers, *Amomum* and *Phaeomeria solaris*, are still frequently met with. The coarse weed, *Cyrtandra repens*, with large, white, tubular flowers is widely spread in this as it is in the two adjoining subzones.

Terrestrial ferns grow in great luxuriance (PLATE 16, FIG. 2). *Polypodium nigrescens* is an interesting example which immediately attracts attention not only because of itshuge, coarse fronds but because of the exceedingly prominent sori which, when seen on the dorsal side of the frond, are at first suspected of being insect galls. Another interesting species of fern is the epiphytic climber, *Oleandra neriiformis*, whose sprawling fronds reach far out from the tree trunk on which they grow somewhat in the manner of the epiphytic *Freycinetia*. The slender, hairy *Polypodium setigerum* is a graceful epiphytic fern. But to give a representative list of the ferns to be found in a Javan mountain forest would be a tremendous task.

Lycopodiums and selaginellas are likewise numerous. *Lycopodium Phlegmaria* is an interesting epiphytic species looking, with its tiny lanceolate leaves, more like a phanerogamous creeper than a member of the Pteridophyta.

The epiphytic growth of bryophytes is luxuriant. Every tree is moss-bedecked (PLATE 16, FIG. 2). The most abundant and typical festooning moss of the second subzone is *Papillaria fuscescens*, readily distinguished by its long, pendent streamers and small alternate "leaves" standing out at right angles to the stem. The moss *Mniodendron divaricatum* is a constant companion under foot from the first to the third subzone. Its little upright shoots, resembling miniature palms, are scattered over the ground and rocks along the trail until the highest altitudes are reached. Occurring epiphytically with the profuse growth is one of the many species of the liverwort *Plagiochila* (e.g., *P. Belangeriana*). A small terrestrial hepatic is *Fimbriaria Zollingeri*.

Very few lichens are to be found in this moss-covered zone, though a few gelatinous species are present. The absence of lichens is probably due, in part, to the moderate amount of light which penetrates the interior of this subzone, and, in part, to lack of space upon which to grow. They are crowded out by the widespread mossy covering.

As the upper limits of the second subzone are reached the giant specimens of *Podocarpus*, *Engelhardtia*, and *Schima* are no longer to be found. Only relatively small examples of these genera are now present (PLATE 16, FIG. 2). The average diameter of trees in the upper half of the second subzone is not over 12 inches as compared with diameters of 5 feet (*Podocarpus*) and 4 feet (*Engelhardtia*) in the first half of the zone.

As the border line between the second and third subzones is reached small bogs are not infrequent. Growing in these one may find the pitcher plant, *Nepenthes melamphora*, with brilliant, purplish red, pendent pitchers. One wonders why a plant such as *Nepenthes* occurs in a locality so poor in insect life as the upper mountain regions of these forests. The pitcher of *Nepenthes* is a nicely planned mechanism for attracting, catching, and digesting insects, but of little use in the high altitudes of the third subzone where insect life is sparse. When the pitchers of *Nepenthes* are emptied they are found to contain but few and only small insects. As the plant thrives wonderfully well, an organic diet appears unnecessary. A further point of interest in connection with *Nepenthes* is the extreme polymorphism of the species. In the bogs where the plant is met with under foot in the third subzone, it is of a very compact form not rising over 8 inches from the ground. In other and drier regions of this zone *Nepenthes* occurs as a liane reaching a maximum length of 25 feet. The tendrils are extended leaf midribs. On the vines few, sometimes no, pitchers are formed. Numerous transitional forms occur between the two extreme types.

III. THE HERBACEOUS SUBZONE

(7,000–8,000 feet)

The transition from the second to the third subzone is gradual. The change in type of vegetation with increase in altitude is noticeable throughout the second subzone, the upper limits of which begin to assume third subzone characters. The epiphytic pandanaceous *Freycinetia* and the tall herb *Strobilanthes cernuus*, typical third subzone species, begin to appear in the upper limits of the second subzone, while second subzone genera, such as *Podocarpus* and the bird's nest fern, *Asplenium nidus*, last far into the third subzone.

The third subzone is open in character. The undergrowth, therefore, receives more light. Being at a high altitude the zone is frequently enveloped in clouds, and being, further, just below the gap between Gedeh and Pangerango, it is protected from wind. The zone is, consequently, very moist. Abundant light and moisture permit a luxuriant flora of tender herbs.

The trees of the third subzone are not distinctive. The open forest formation is made up of tree genera which are characteristic of the two neighboring zones. The second zone genera *Quercus* and *Schima* are abundant, and *Podocarpus* occurs occasionally. The high altitude trees *Symplocos*, *Polyosma*, *Astronia*, and *Rapanea* first make their appearance here.

The most characteristic liane and epiphyte of the third subzone is the climbing *Freycinetia*. This grotesque plant, of which there are two species on Gedeh, is widely distributed. Sometimes only a single leafy shoot reaches far out into space. More often a number of sprawling branches hang over the trail like so many ferocious dragons blocking the way. Frequently the growth is so dense as to form a solid mass 15–20 feet in diameter high up on a tree trunk.

But it is the herbaceous undergrowth which characterizes the third subzone. Areas exist which are literally flower gardens. Several species of *Impatiens* are very abundant. The exquisite, pansy-like blossoms of these plants are found in delicate shades of pink and purple. The most common species is the pink-flowered *I. platypetala*. Frequently the purple-spotted pink flowers of *I. cyclocoma* are seen, and also the white, purple-centered blossoms of *I. hirsuta*. Less abundant is *I. choneceras* with a white flower, from which projects a short spur.

The liliaceous *Disporum chinense* (*D. pullum*), first cousin to the American Solomon's seal (*Polygonatum*), with dangling purple bells, is common in the undergrowth of this flowery zone. One of the commonest blossoms is the slender white, tubular flower of *Ophiorrhiza longiflora* (Rubiaceae). Begonias (e.g., *B. isoptera*) are very numerous, likewise the urticaceous herb *Elatostemma*. This latter plant is interesting because of the force with which the male flowers open. When a male bud (the species is monoecious) opens, the stamens fly back one at a time with great suddenness and force, scattering the pollen in a miniature cloud; indeed, the generic name tells the story, "stamen hurler."

Strobilanthes cernuus is a tall, succulent herb forming dense thickets in the second as well as the third subzone. The native name is "bobokuan" ("boku," articulation). It is a most unattractive, rank weed, but its flowers are exquisite little things. They are very small, shaped like tiny rose buds. The petals are white, pencilled along their outer edge with brilliant green.

The presence of one of the gingers, *Hedychium coronarium*, is first noted by its sweet perfume, scenting the air from far. *Curculigo curvata*, of the *Amaryllis* family, forms nearly pure stands in the undergrowth. A large yellow raspberry, *Rubus alpestris*, tempts one to taste it only to find that it is frightfully sour.

The notch between the peaks of Gedeh and Pangerango, where the third subzone ends at an altitude of nearly 8,000 feet, is the home of one of the most exquisite of all tropical plants, the tree fern. The tree fern, although always associated with the tropics, is in reality subtropical. It is not found with such truly tropical plants as the cocoanut. On the contrary, it occurs at relatively high altitudes, where the temperature is moderate. As a group, the ferns are generally regarded as shade loving plants, but I am inclined to believe that it is not their apparent shade loving proclivities which determine the regions in which ferns in general

FIG. 6. The crown of an *Alsophila*.

thrive, but rather their moisture requirements. The tree fern, for good development, requires *abundant* light as well as ample moisture and a cool temperature. Specimens found in the dark interior of the mountain rain-forests are invariably poor, and never have I seen a good stand of tree ferns but that the crowns were above all the surrounding vegetation, exposed to direct sunlight.

In the gulch at Kandang Badak, where the above mentioned climatic conditions prevail, there is an excellent growth of tree ferns. *Alsophila glauca* var. *densa* and *Cyathea orientalis* are the two characteristic tall species. The genus *Dicksonia*, which does not exceed a height of 10 feet as compared with a maximum of 50 feet for the other two genera, is represented by a single species, *D. Blumei*. When well developed the crown of the tree fern represents the most beautiful and delicate of all tropical foliage (FIG. 6).

Gleichenia, like the tree fern, requires ample light for its best development, but is an exception among ferns in that it thrives well in very dry soil. This fern is usually found in exposed sunny localities. Thus, it is very abundant in the open formation of the third subzone, where two species are common, a small, wiry one, *G. linearis*, and a large, coarse species, *G. volubilis*, which often sends out prostrate leafless shoots as much as 20 feet in length. Both form impenetrable thickets.

Mosses are much less abundant here in the third subzone than they were in the second. Their absence is due probably to the open, sunny, and therefore less moist nature of this region. Lichens, on the other hand, are more numerous. The cosmopolitan *Usnea* occurs in great abundance. This lichen is typically, the world over, a genus of high altitudes or latitudes.

The evidence that Mt. Gedeh is not a dead volcano is to be had along the trail in the third subzone, where two springs of steaming hot water gush forth and give rise to the brook "Tjipanas."* In the extremely hot water (about 130° F.)† of these springs there grows in great luxuriance a species of the

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*"Tji" is a Malay prefix signifying "river". "Panas" the newcomer soon adds to his vocabulary; it means "hot".

† One often reads of higher temperatures of springs in which plants are growing, but the maximum temperature from a reliable source is not over 65° C. (150° F.).

alga *Oscillatoria*, which forms a jelly-like mass, rather resembling blubber, some two inches in thickness. Only the surface layer of this mass is green.

IV. THE VACCINIUM SUBZONE

(8,000–9,000 feet)

The climb to the crater of Mt. Gedeh or to the summit of Mt. Pangerango is made in about two hours from the cabin at Kandang Badak situated in the notch between the two peaks. The transition from the third to the fourth subzones is very abrupt on Gedeh and Pangerango. Tree ferns grow in great abundance almost to the very ridge at the notch where the third subzone ends. Above this point no tree fern is again met with. *Castanea*, *Quercus*, and *Engelhardtia*, among the big trees of the lower subzones, and persisting as smaller trees to the very edge of the fourth subzone, are now no longer seen. *Podocarpus* and *Schima Noronhae* are still present, but in reduced size, and greatly in the minority as compared with the other species. With change in kind there takes place a pronounced change in size and form of the trees. The maximum height here is not over sixty feet, and while some gnarled trunk may be more than a foot through, the average diameter of the trees is but 8 inches. Especially noticeable is the irregular shape of the trees of this zone (PLATE 17, FIGS. 1, 2). Whether the gnarled and twisted form of high altitude trees is due to the purely mechanical effect of wind or to trying physiological conditions such as high evaporation and low light intensity, under which the plants must grow, is still an unsettled question.

The characteristic genus of the fourth subzone is *Vaccinium*. In the upper half of the zone it forms pure stands (PLATE 17, FIG. 2), but in the lower half other typical high altitude trees are present. Among these are, *Polyosma ilicifolia*, *Astronia spectabilis*, *Symplocos sessilifolia*, *Weinmannia*, *Eurya japonica*, and *Rapanea avenis*, the last a typically high altitude tree resembling *Vaccinium*. The type of leaves of the last two genera is an instance of a very common characteristic of alpine plants, namely, the reduced size, leathery texture, and waxy surface of the leaves.

A tree of unusual interest, occurring near the summit of Mt. Sela, is the maple *Acer niveum*, which attains a maximum height of 100 feet. It is the only maple in Java.

Among the large lianes at this altitude are *Vaccinium varingiaefolium*, (*V. Teysmanni*), *Lonicera Loureiri*, and *Schefflera lutescens.*

The genus *Vaccinium* is remarkable because of extreme polymorphism; it exists as a tree, shrub, or liane, and ma[illegible] terrestrial or epiphytic. Five species occur on Mt. [illegible] *varingiaefolium*, *V. coriaceum*, *V. lucidum*, *V. laurifolium* [illegible] *ellipticum*. *V. varingiaefolium* is the most polymorphic [illegible] all. It may be shrub, tree or liane and may grow terres[illegible]lly or epiphytically. As a liane it was formerly known as *V. Teysmanni.* In this form it is found in the lower half of the fourth subzone (PLATE 17, FIG. 1). In the upper section of the zone it occurs only as a tree to the almost complete exclusion of all other tree species. So far as I am aware botanical science is totally ignorant of the cause of such polymorphism. In the case of the pitcher plant *Nepenthes*, a conceivable factor is moisture, since the dwarf form is found in bogs and the liane form grows on dry soil. The same factor may possibly play a part in determining the form of *Vaccinium varingiaefolium*, since the liane is found only in the relatively moist lower half of the fourth subzone, while in the much drier upper section the species occurs as a tree. *Schefflera lutescens* may also occur as tree or liane.

The shrub *Rhododendron* is very abundant in this open, high altitude forest. There are three species: *R. retusum* with red flowers, *R. cilium* with large yellow flowers, and *R. javanicum* (the most common) with very large, orange-red flowers. This last species is especially interesting because of its presence here at 9,000 feet as a terrestrial shrub, although equally abundant as an epiphyte at Tjibodas 4,000 feet lower.

Herbs of the third subzone types are still numerous in this higher region. Especially noticeable is the blue color of flowers and fruits. Very prominent are the cobalt and pale green blues. The berries of the shrub *Lasianthus lucidus*, a rubiaceous plant, are of the former color, while the clusters of berries of *Dichroa febrifuga*, one of the Saxifragaceae, are a rich dark blue. The flowers of this plant are of a striking pale blue color. But the finest of the blue flowers is that of the orchid *Dendrobium Hasseltii.* Indeed, while I am inclined to give first place to *Impatiens platypetala* as the most beautiful of all the mountain flowers, *Dendrobium Hasseltii* holds a close second place. This orchid is quite common in these high, foggy regions.

The parasite *Balanophora elongata* is a curious plant. The only aerial portion is the thick, short, flower-spike of brick-red [illegible]*nophora* grows parasitically on the roots of *Vac-* [illegible] *Albizzia*, the latter a tree whose acquaintance we [illegible]on make. The subterranean portion of the parasite is [illegible]e of host and parasite tissue. This composite tissue is very [illegible]rd and much resembles a piece of stag horn coral.

Terrestrial ferns are less numerous at this altitude. *Polystichum biaristatum* and *Plagiogyria glauca* are the most common. The coarse *Lomaria vestita* forms pure patches. *Nephrodium tuberosum* (*N. hirsutum*) is worthy of special note because of its large root tubercles. The epiphytic ferns are more numerous, especially species of *Polypodium*—for example, *P. obliquatum*, the smaller *P. hirtellum*, the climbing *P. rupestris*, and the smallest of polypodies, *P. cucullatum*. The thick, leathery, 15 inch leaves of *Elaphoglossum* one would hardly suspect as being those of a fern. Among the "filmy" ferns is the tiniest of all ferns, *Hymenophyllum paniculiflorum*, whose delicate lacy frond measures less than an inch in length. The lycopodium, *L. volubile*, is very prolific at this altitude.

Mosses are again exceedingly abundant in the lower half of the fourth subzone. Every tree and vine is covered with a thick mat of reeking wet moss (PLATE 17, FIG. 1). That is, there is here a second "moss zone." It is evident that "moss zone," which has been used by ecologists as a descriptive term in connection with mountain rain-forest regions, may be inaccurate.

The mosses of the fourth and second subzones differ strikingly in type. Those of the second subzone are mostly festooning types, loose in form, growing in long, pendent streamers. In the higher and more windy fourth subzone the mosses are all of a compact, tufted type, well adapted to hold water. A comparison of the two photographs, PLATE 16, FIG. 2, and PLATE 17, FIG. 1, will help visualize the pronounced difference in moss type of these two zones. An enumeration of genera would further emphasize the marked altitudinal distribution of mosses on Mt. Gedeh. Of thirty-two species collected and identified no species and only two genera are common to both the second and the fourth subzones.

The fourth subzone extends to the summit of Pangerango with no pronounced change in type of vegetation, except at the very top where there is a small alpine plant community, barely more than an acre in area. The plants of this little alpine garden consist of shrubs, herbs, and grasses. Of shrubs there are dwarf *Vaccinium*, *Rapanea*, *Eurya*, and *Gaultheria*. The fruit of the bush *Vaccinium* resembles that of the American blueberry, and, though edible, is insipid.

Among the flowers of this small alpine pasture one of the prettiest is *Hypericum Leschenaultii*, much resembling the evening primrose of American pastures. Another reminder of fields at home is the buttercup, *Ranunculus javanicus*. Then there is a dandelion-like plant, *Sonchus asper*, the pale blue violet *Viola serpens*, the weed *Plantago major*, and a wild strawberry. Indeed, one could well imagine himself in a New England pasture. The small yellow, tubular flower of *Primula imperialis* deserves mention because it was singled out by the Dutch naturalist Junghuhn as "Queen among all the herbs which inhabit the summits of the mountains." So exalted a position for *Primula imperialis* is hardly deserved when *Impatiens platypetala* is near.

The view from the summit of Pangerango is one of the finest in all Java. Water-covered rice fields, one of the most charming and characteristic features of oriental tropical agriculture, lie close to the mountain base (FIG. 1), and beyond groves of cocoanut palms are distinguishable. Other mountain peaks stand silhouetted against the soft color of the morning sky. One is looking over the "Preanger Regent," the most picturesque province of all Java.

The trail to the crater of Mt. Gedeh differs from that to the summit of Mt. Pangerango, just described, in two striking particulars: first, the fourth subzone of Gedeh is divided into halves, distinguished by several prominent characteristics; and second, there is on Gedeh a fifth subzone of considerable area with a very distinctive flora.

The trees of the lower half of the fourth subzone on Gedeh are covered with a profuse growth of moss. Thick, water-soaked wads of moss pad every trunk. Suddenly, about midway in the zone, the moss covering disappears, and the trees are bedecked with lichens instead. An idea of the completeness of the change can be had by comparing the photographs on PLATE 17.

Both sections of this high altitude subzone receive ample precipitation, but the upper half is considerably more open in character and more wind-swept. The complete absence of mosses in the upper part of the zone is probably due to the effect of dessicating winds at the higher altitude, where even compact, tufted mosses would be unable to retain moisture. The presence of lichens in the upper half of the zone and their absence in the lower section is possibly due, in part, to better illumination and, in part, to lack of mosses in the upper region. Certain it is that the profuse moss covering of the lower half of the subzone leaves no spot where a lichen might subsist.

Having reached a second lichen flora it is instructive to compare the lichens found at the higher altitude with those of the first subzone at Tjibodas. Of sixty-seven species of lichens collected none are common to both the first and the fourth subzones, with one possible exception. Among the fourth subzone lichens are four species of *Parmelia*, a *Phaeographis*, and a *Cetraria* (*Nephromopsis*); the latter is the most common lichen at this altitude, growing luxuriantly in large, fluffy, cream-colored patches.

V. THE EDELWEISS SUBZONE

(9,400 feet)

On emerging from the last stand of trees which ends the fourth subzone on Mt. Gedeh (PLATE 17, FIG. 2), quite a different type of vegetation confronts one. Plant life is sparse. Only one genus of tree exists and it averages not over 12 feet in height. The two characteristic plants of the alpine flora of the fifth subzone are the shrub, *Anaphalis javanica* (one of the Compositae), and the small tree *Albizzia montana* (FIG. 7). The former, with flowers of soft grayish-white color, is the edelweiss of Java. Other plants typical of this open alpine formation on the lava floor of the old crater of Gedeh are the crinkly leaved tree-shrub *Myrica javanica*, the dwarf *Rhododendron*, the dwarf *Vaccinium varingiaefolium*, and the shrub *Gaultheria leucocarpa* with tiny pale pink flowers, white berries, and leaves of a pronounced and very agreeable winter-green odor when crushed. The leaves of *Gaultheria* exhibit a characteristic of alpine plants, standing perpendicularly to and closely surrounding the stem. Some few ferns are still found at this altitude, and lycopodiums are quite abundant, for example, *L. gedeanum.*

This fifth subzone is essentially the last distinctive vegetative region on Mt. Gedeh. There is, however, a small area immediately surrounding the present crater of Gedeh and extending a short distance down into the crater, which can be regarded as an upper subdivision of the fifth subzone, for here the plants are fewer in number and all greatly dwarfed. The vegetation which is scattered over this waste surface of lava consists of isolated and small stunted specimens of edelweiss, *Vaccinium, Rhododendron, Myrica,* and another *Gaultheria* species, *G. fragrantissima.*

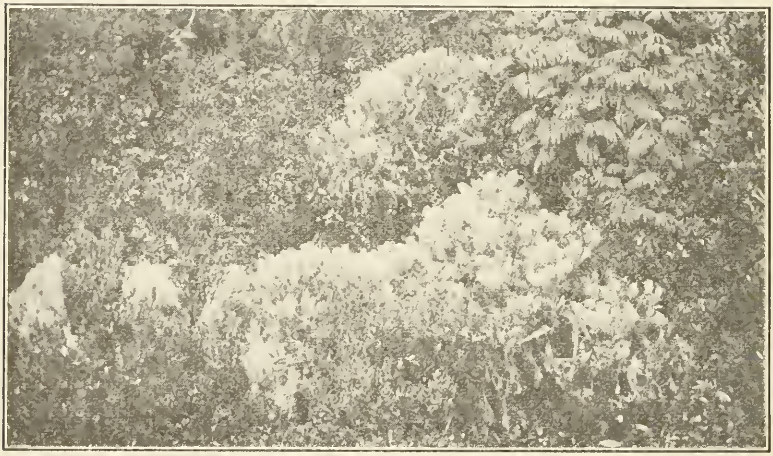

Fig. 7. The Javanese edelweiss, *Anaphalis javanica.* The foliage in the right background is that of a young *Albizzia montana.* The tiny leaves in the left center background are *Myrica javanica.* The shrubs in front of the edelweiss, center and left, are dwarf *Vaccinium varingiaefolium.*

Of the multifarious ferns ubiquitously present from the first to the fifth subzone, only one, a dwarf variety of the remarkably adaptable species, *Polypodium Feei,* remains to occupy the rocky lava floor of the old crater of Gedeh. Representatives of this genus are found in every zone from an altitude of 4,600 to one of 9,400 feet.

Within the confines of the huge old crater of Gedeh there occurs, in addition to the present semi-active crater, another small, secondary but extinct crater which harbors a flora all its own. This little plant community owes its existence to its well protected situation and to the abundance of water which drains into it from the summit of Gedeh. Here, on the bottom of the small crater pit, there is a rank growth of the sedge, *Gahnia javanica*, scattered in the form of huge hillocks.

There is probably no tropical mountain rain-forest in the world which possesses a greater wealth of plant life than that at Tjibodas on Mt. Gedeh. I can imagine no walk more delightful and full of interest than from the laboratory at Tjibodas to the crater of Gedeh and the summit of Pangerango. The Tjibodas virgin forest, as compared with other similar regions, presents an outstanding diversity of vegetative types. While, in certain respects, the flora of Java is surpassed by that of Ceylon, and by the vegetation in certain parts of India, in neither case, nor anywhere in the tropics, so far as my knowledge extends, is there within so limited and so readily accessible a region such a multiplicity of genera and such extremes of plant forms—a thousand or more species—from bananas to edelweiss.

I wish to express my indebtedness to Dr. C. A. Backer of the Buitenzorg Herbarium for his kindness in identifying many plants collected by me. Without Dr. Backer's generous assistance so complete a description of the vegetative zones as is here given would not have been possible.

Description of plates 15-17

PLATE 15

FIG. 1 (at left). The grass trees, *Xanthorrhoea Preissii*, in the Tjibodas Garden. These liliaceous trees are natives of the Australian savannahs.

FIG. 2 (at right). The stately bird's nest fern, *Asplenium nidus*.

PLATE 16

FIG. 1 (at left). An *Asplenium nidus* suspended at the end of a slender branch. Note other epiphytic ferns growing out of the base of the *Asplenium*.

FIG. 2 (at right). The upper limits of the second subzone. The larger trees (the maximum size at this altitude) are *Engelhardtia*. The smaller trees are *Pygeum*, *Elaeocarpus*, *Meliosma*, and *Schefflera*. *Disporum* is abundant on the forest floor (lower right corner). The terrestrial ferns are chiefly *Dryopteris heterocarpa*. *Asplenium caudatum* is the (epiphytic) fern with long slender fronds to the right of the coolie. One of the most abundant mosses in the profuse epiphytic moss growth is *Papillaria fuscescens*, the typical festooning moss of the second subzone.

PLATE 17

FIG. 1 (above). The moss section of the fourth subzone. The largest tree (left center) is *Schima Noronhae*. The smaller trees are *Polyosma*, *Symplocos*, and *Rapanea*. The liane is *Vaccinium varingiaefolium* (*V. Teysmanni*). Few *Vaccinium* trees are to be found in the lower half of this zone. Note the thick padding of moss. The moss covering the large tree is *Sematophyllum pinnatum*. Suspended from the liane are the tiny epiphytic ferns, *Polypodium cucullatum* and *Hymenophyllum paniculiflorum*.

FIG. 2 (below). The lichen section of the fourth subzone. Note the complete absence of moss. This is the last stand of trees on Mt. Gedeh. The trees are almost entirely *Vaccinium varingiaefolium*, the same species which grows as a liane a few hundred feet lower (see FIG. 1).

SEIFRIZ: PLANTS ON MT. GEDEH, JAVA

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Se[illegible], W.

An emulsion of oil dispersed in water is a system which is readily permeable to water-soluble substances, and an emulsion of water dispersed in oil is a system which is poorly or not at all permeable to water-soluble substances. Since Na (in the form of the hydroxide and in the emulsions with which Clowes worked) produces an emulsion of the former type, and (in the opinion of Osterhout) increases protoplasmic permeability, and since Ca produces an emulsion of the latter type and decreases the permeability of protoplasm, Clowes conceives of the living membrane as a fine emulsion which is in a state of equilibrium at or near the reversal point. In the presence of Na the emulsion at the surface of protoplasm would tend more toward the oil-in-water type, and in the presence of Ca it would approach the water-in-oil condition, never being fully of the one or the other type while the cell is living. Clowes looks upon living protoplasm in contact with water as a system which is, within the protoplasmic mass, a dispersion of proteins, lipoids, etc., in water and, at its surface, a system of the reverse type of structure in which water is dispersed in a continuous fatty or lipoid phase. The dispersion at the surface is not, however, complete, but rather a system in which the fatty continuous phase is permeated by water channels, i.e., it is at the reversal point. This sponge or honey-comb structure of the surface layer of protoplasm Clowes considers as capable of being modified by calcium salts, anesthetics, etc., in such a way that a system is formed in which the water communications are decreased or completely cut off. Salts of monovalent cations, on the other hand, would tend to produce a system in which the water channels are more extensive.

Clowes' hypothesis is based on three assumptions: first, that protoplasm is, in its colloidal nature, an emulsion; second, that this emulsion is capable of phase reversal; and third, that the emulsifier active in protoplasm is either soap or a substance which behaves as does soap when in the presence of certain mono- and bivalent cations. Without intending to assert that the first assumption is untrue, it is nevertheless well to point out that we are totally ignorant of the actual physical nature of the ultramicroscopic particles of the living colloid. This being the case, any convenient hypothesis can be postulated. One cannot, therefore, deny the possibility of protoplasm being a colloidal emulsion, that is, a system in which liquid, ultramicroscopic particles, in a high state of dispersion, are suspended in a liquid medium. The actual physical nature of the colloidal particles of the living system we cannot yet hope to determine,but after all, as Hatschek (8) points out, the distinction between liquid and solid becomes rather vague with particles approaching ultramicroscopic dimensions.

Regardless of the physical nature of the living colloidal particles, there is no evidence upon which to base the assumption that a reversal of phases takes place in protoplasm. Protoplasm is a lyophilic colloid. Phase reversal was formerly thought to be the process by means of which lyophilic colloidal sols, "emulsoid" sols, become gels (jellies). The researches of Bachmann (1) and Zsigmondy (14), which have been substantiated by a different method of investigation by McBain (10), have shown that in gelatin (Bachmann) and soap (McBain) no reversal of phases takes place in the transformation of the gelatin sol and the soap sol into their gels.

It is not my desire here to question further the emulsion theory of protoplasmic structure. I do, however, wish to emphasize the fact that the ideas that protoplasm is, in its *colloidal* nature, an emulsion, and that this living emulsion is capable of phase reversal, are pure assumptions. But we shall, with Clowes and others, tentatively assume that protoplasm is a colloidal emulsion in which a reversal of phases is a physical possibility provided that the other prerequisite conditions, such as the type of emulsifier, are favorable. It is with this last assumption, namely, the type of emulsifier, that we are here primarily concerned. That Clowes' hypothesis is highly interesting and that it opens up a new line of speculation on the mechanism of permeability changes, goes without saying. The question is, how far is the theory applicable?

ACKNOWLEDGMENT. I had the pleasure of discussing the hypothesis of Clowes with Mr. Hatschek of London. I objected to Clowes' analogy on the grounds of the first two of the three assumptions named above. Mr. Hatschek then called my attention to the third assumption, namely, that if some emulsifier other than soap is used, the oil-in-water emulsions will not reverse no matter how much salt of a bivalent cation is added. This was demonstrated by a simple test-tube experiment in which olive oil was emulsified in a weak aqueous solution of saponin. An excess of $BaCl_2$ failed to cause a reversal. It was this demonstration and subsequent discussion which ultimately led to the research work here published. I wish not only to acknowledge the fact that the original suggestion on which this article is based comes from Mr. Hatschek, but I also desire to express my indebtedness to him for turning over to me the notes on his preliminary experiments.

I wish also to make known my indebtedness to Prof. H. S. Uhler of the Department of Physics of Yale University, who so kindly placed a small laboratory and all necessary physical instruments at my disposal.

METHOD. All of the emulsions worked upon were prepared by adding 25 cc. of oil to 25 cc. of an aqueous solution of the emulsifier. The mixture was put into a 150 cc. flask and vigorously shaken intermittently. This method of preparing an emulsion is that of Briggs (4), and consists in giving the mixture of oil and aqueous solution ten violent shakes by hand, then allowing the emulsion to rest for half a minute, when it is again shaken. This procedure is repeated nine times.

The oil used was the commercial "Pompeian" olive oil. The emulsifiers were all aqueous solutions. Where the organic stabilizer is insoluble in water, it was dissolved in some suitable solvent, such as alcohol, and a colloidal dispersion made by pouring a small quantity of the alcoholic solution into water. The emulsifiers were the following: the two soaps, sodium oleate and sodium stearate; gelatose; gum arabic; the glucosides: saponin, senegin and smilacin; the proteins, albumin from egg, albumin from blood, casein and gliadin; the lipoids, cholesterin and lecithin, the alkaloid, cephalin; and an extract from plant tissue. To these solutions was added a small crystal of thymol except in those cases where the solution itself is aseptic.

The electrolytes used in reversing or in attempting to reverse the emulsions were NaOH, NaCl, Na_2SO_4, $BaCl_2$, $CaCl_2$ and $Ba(OH)_2$. The emulsions were thoroughly shaken after each addition of salt or alkali. While no attempt was made to obtain in every case precise quantitative measurements, yet the reversal point in all instances was determined with reasonable accuracy. To ascertain the amount of electrolyte necessary to cause reversal was not the main objective, but merely to determine whether or not a reversal is at all possible with certain emulsifiers and certain ions.

We shall first concern ourselves with the type of emulsifier. Two electrolytes only will, at the beginning, be considered in reference to reversibility. The question whether other electrolytes have the same influence as do NaOH and $BaCl_2$, will be taken up after the question of the type of emulsifier is disposed of. A further problem which developed during the earlier experiments, namely, the possible influence of the degree of acidity of the emulsions on their type and reversibility, is to be discussed in a subsequent publication.

Three methods were followed in determining the type of emulsion: 1, electrical conductivity; 2, color; 3, microscopical examination.

The electrical conductivity method is based on the principle that since water is the continuous phase in an oil-in-water emulsion, the emulsion will conduct a current of electricity, while an emulsion of the reverse type, since oil is the continuous phase, will not conduct an electric current. This method was first proposed by Clayton (5, p. 114) and, has more recently been used with success by Bhatnagar (2). The type of emulsion prevailing is ascertained by the reading of an ammeter. The reversal point can be determined with considerable precision. The method also has the advantage over the color method of telling in a remarkable way what is happening in the emulsion. A higher or lower reading, the rising or falling of the needle, and particularly the fluctuations of the ammeter needle, are all indicators of what is taking place in the emulsion.

An Arrhenius or Ostwald conductivity cell can be conveniently used for making the conductivity measurements, but equally satisfactory and much less expensive is a simple apparatus consisting of two electrodes of platinum foil 1 cm. wide and 10 cm. long supported by two glass rods 2 cm. apart. With this apparatus the emulsions to be tested are poured into small glass vials, measuring 3 cm. in diameter and 9 cm. high with a volume of 68 cc. The platinum electrodes are allowed to project into the vials any convenient distance, but the same distance in every case—in these experiments to a depth of 5 cm. in the emulsion. The current used in this work was a 52 volt direct current. The ammeter employed was a milliammeter reading to one milliampere, with a range of 150 milliamperes. For readings in excess of 150 milliamperes a shunt was inserted in the circuit which raised the value of the milliammeter scale tenfold.

The readings of the oil-in-water type of emulsions varied from 3 milliamperes in the case of the soap (sodium sterate) emulsions, to, with one exception, 100 milliamperes in the case of the gelatose emulsions. In those soap (sodium oleate) emulsions in which the aqueous phase is a 1M NaOH solution, the current reached the high value of 420 milliamperes. Higher amperage is obtained in all emulsions which have been repeatedly reversed by alternate additions of mono- and bivalent electrolytes.

The color method for determining the type of emulsion consists in adding a stain which is soluble in but one of the two phases. For this purpose the oil soluble dye Sudan III may be used. When the emulsion is of the oil-in-water type the color is a pale pink. When the emulsion is of the water-in-oil type its color is a brilliant red, since the oil is then the continuous phase.

The microscopic method of determining the type of emulsion consists simply in making a microscopic examination of a sample of the emulsion. This method is not as convenient as the other two but should always be employed to determine the precise state of an emulsion, especially when it is incompletely reversed. It sometimes happens that the electrical conductivity points clearly to an emulsion of the oil-in-water type, while the color indicates equally clearly that the system is of the reverse type. Only a microscopical examination reveals the true state of affairs.

Experimental. *Sodium oleate.* The first emulsion studied was the same as that with which Clowes worked, namely, an emulsion in which the emulsifier is sodium oleate. The sodium oleate is formed as a result of saponification of the oleic acid in the olive oil by the NaOH in the aqueous phase of the emulsion. The emulsion is made by shaking 25 cc. of olive oil with the same volume of the aqueous phase. Molar and M/10 NaOH were used. The emulsion is quickly formed and is of the oil-in-water type. The dispersed oil droplets measure from mere specks of less than $\frac{1}{2}\mu$, which are in active Brownian movement, to globules 50μ in diameter. The viscosity of the emulsion is 5.7 as compared with a value of 1 for water. The current which will pass through such an emulsion at 52 volts is 420 milliamperes in the case of 1M NaOH, and 100 milliamperes when M/10 NaOH is the aqueous phase. On the addition of $BaCl_2$ the current falls. One would expect a rise in amperage when the concentration of electrolytes in the continuous aqueous phase is increased, and this is what takes place in those oil-in-water emulsions which do not reverse. The fall in current in a soap emulsion indicates a reduction in the volume of the electrolytic phase which is available as a conductor for the current. This reduction, as evidenced by the fall in amperage, is an indication that the emulsion is reversing. Complete reversal of the M NaOH emulsion takes place when 1.2 cc. of M $BaCl_2$ has been added. The M/10 NaOH emulsion is reversed with 0.3 cc. of M $BaCl_2$, or 3 cc. of M/10 $BaCl_2$. The milliammeter reads 0.00 after complete reversal has taken place. A very slight reading, of some 3 milliamperes, may be obtained when the color of the emulsion plainly indicates that there has been reversal. This is due to an excess of aqueous phase which has not been caught in the water-in-oil emulsion. If the emulsion is allowed to stand for a short time, less than a minute, when the excess of free water settles in a small layer at the bottom, no reading of the ammeter is to be had.

Sodium stearate. This emulsion was prepared by adding the soap directly to the aqueous phase. A M/1,000 concentration of sodium stearate ($NaC_{18}H_{35}O_2$) was used. A good emulsion is formed in which the oil particles measure from 1 to 30 μ. The emulsion creams very slowly. Its viscosity is 100 as compared with 1 for water. The emulsion is an oil-in-water one, and is readily reversible with $BaCl_2$. Its electrical resistance is high, the current passing through it, at 52 volts, being but 3 milliamperes. It is very sensitive to electrolytes, requiring but 0.2 cc. of a M/1,000 concentration of $BaCl_2$, and but 2.0 cc. of a M/10,000 concentration of $BaCl_2$ to reverse it. The water-in-oil emulsion thus obtained by reversal can be readily reversed to its original type by adding NaOH. It was possible, by alternate additions of $BaCl_2$ and NaOH, to reverse a sodium stearate emulsion nine times. High concentrations of the two electrolytes were used to avoid too great a dilution of the emulsion. One drop, 0.033 cc., of M $BaCl_2$ is sufficient to reverse the original emulsion.

Gelatose. This emulsifier was prepared by boiling 10 grams of gelatin in 100 cc. of water for ten hours in a reflux condenser. The hot sol was filtered through a tight plug of cotton wool. The solution thus obtained is non-gelatinizable. A so-called WH Gold Label brand of gelatin (supplied by Paul Putmann, Inc., New York) was used. Gelatose and olive oil produce an oil-in-water emulsion with a viscosity 30 times that of water. The amperage of the gelatose emulsion varies from 92 to 116 milliamperes, averaging about 100. Reversal cannot be produced in this emulsion by as strong a concentration as 10 cc. of M $BaCl_2$. As the volume of the aqueous phase in 50 cc. of emulsion was, in all cases, 25 cc., the final concentration of $BaCl_2$ in the system was $1000 \times \frac{10}{35} = 286$ millimoles. This concentration, at which neither reversal nor "breaking" of the emulsion takes place, is more than 3,500 times that necessary to reverse the soap (sodium stearate) emulsions mentioned above, and about 15,000 times as great as the concentration which Bhatnagar (3) finds necessary to cause reversal in the emulsions with which he worked.

Saponin, senegin and smilacin. These saponin solutions were made from Merck preparations. The saponin, senegin and smilacin were dissolved in water at concentrations of 1 in 500. Each of these glucosides produce oil-in-water emulsions which cannot be reversed by $BaCl_2$.

Gum arabic. Ten grams of a fine, white, powdered gum arabic were dispersed in 100 cc. of water. With this solution as an emulsifier the resulting emulsion is of the oil-in-water type. The amperage of the original emulsion is, with a 52 volt current, 78. On the addition of 0.1 cc. of M $BaCl_2$ the current rises to 81 milliamperes; and finally to 250 milliamperes when 10 cc. of M $BaCl_2$ have been added. The oil-in-water emulsion with a gum arabic emulsifier is, therefore, irreversible with $BaCl_2$.

Albumin. Two kinds of albumin were used, albumin from blood and albumin from egg, both Merck products. Albumin readily forms an oil-in-water emulsion in which the oil particles measure from 1 to 50μ. The emulsion creams slowly, a barely noticeable aqueous layer being formed at the bottom in 5 minutes. The viscosity of an emulsion made from 1 per cent blood albumin is 9; from $\frac{1}{2}$ per cent egg albumin it is 4.6, as compared with 1 for water. The amperage at 52 volts is, in 1 per cent blood albumin, 91, and in $\frac{1}{2}$ per cent egg albumin, 39 milliamperes. An emulsion with either of the two albumins as the emulsifier cannot be reverted by 10 cc. of M $BaCl_2$ in 50 cc. of emulsion.

Casein. Casein well shaken in water and allowed to stand for an hour gives a fine colloidal dispersion which readily emulsifies olive oil. The emulsion formed is a water-in-oil one, and suddenly becomes stable during the sixth or seventh interval of shaking, i.e., after 60 or 70 shakes. The dispersed water particles are from less than $\frac{1}{2}$ to 30 μ in diameter, and exhibit no Brownian movement. The emulsion is very thick, the viscosity being too high to conveniently measure with a capillary viscosimeter. No current will pass through the original emulsion at 52 volts. The emulsion reverts readily with NaOH. One drop (0.033 cc.) of M NaOH will bring the emulsion to the reversal point. Two drops will cause complete reversal into an oil-in-water emulsion. If to this emulsion one drop of M $BaCl_2$ is now added, the emulsion immediately reverts to its original type, i.e., to a water-in-oil one, the ammeter reading being again 0.00. By alternately adding 1 or 2 drops of M NaOH and M $BaCl_2$, it was possible to reverse an emulsion with a casein emulsifier eight times.

Gliadin. This alcohol soluble protein, which comes from wheat gluten, was kindly given me by Dr. Thomas B. Osborne of the Connecticut Agricultural Experiment Station. The solution received was a 5 per cent concentration of gliadin in 70 per cent alcohol. Two cubic centimeters of this were dispersed in 98 cc. of water. The colloidal solution thus obtained was used as the emulsifying agent. The resulting emulsion is a water-in-oil one. The emulsion forms very quickly, usually within the first ten shakes. The color of the original emulsion is red (the oil phase being stained with Sudan III), indicating clearly that oil is the continuous phase. If the emulsion is not completely formed a slight (3 milliampere) reading of the ammeter may be obtained. Ordinarily, however, the ammeter registers zero.

A water-in-oil emulsion with 0.1 per cent gliadin as the aqueous phase, is readily reversed by 0.3 to 0.5 cc. of M/10 NaOH into an oil-in-water emulsion, with a milliamperage of 6 or 7. Two-tenths cubic centimeter of M/10 $BaCl_2$ will again reverse the emulsion into its original form, with a zero reading of the ammeter; and 0.5 cc. of M/10 NaOH will throw it back again to an oil-in-water emulsion with a milliamperage of 10. By keeping the emulsion near the reversal point it can be reversed again and again by very small quantities of salt and base. When thus kept near the reversal point, 0.07 to 0.1 cc. of M/10 $BaCl_2$ will produce complete reversion into a water-in-oil system with which no reading of the milliameter can be obtained, and 0.15 to 0.3 cc. of M/10 NaOH will cause reversal in the opposite direction with a milliamperage increasing with each reversal, i.e., with increasing concentration of electrolytes in the aqueous phase. At the eleventh reversal the milliamperage was 60.

Lecithin. Lecithin is a lyophilic "lipoid" readily dispersed in water. The lecithin used came from Merck. One gram was dispersed in 100 cc. of water. This sol makes a very good emulsifying agent. The emulsion formed is of the oil-in-water type, the oil particles of which vary from 1 to 8 or 10μ (relatively few larger) in size, the smaller ones being in active Brownian movement. The milliamperage of the emulsion, with a 1 per cent lecithin aqueous phase, is 30. Ten cubic centimeters of M $BaCl_2$ raise the amperage to 320 milliamperes, which means that the emulsion is still of the original oil-in-water type. The oil emulsion with lecithin emulsifier is, therefore, irreversible with $BaCl_2$.

Cholesterin. Cholesterin is generally included among the "lipoids". It is more true to the character of fatty substances than is lecithin, being lyophobic. An aqueous colloidal dispersion of cholesterin was made by first dissolving 2 grams in 100 cc. of absolute alcohol boiled in a reflux condenser, and dispersing 1 cc. of this 2 per cent alcoholic solution in 99 cc. of water, and finally filtering. This 0.02 per cent aqueous dispersion of cholesterin emulsifies olive oil very quickly into a water-in-oil emulsion of high viscosity.

It is remarkable how precisely these cholesterin emulsions will emulsify at exactly the same point in the process of shaking when the emulsions are made from the same lot of material. Of three cholesterin emulsions made up at the same time two emulsified on the 55th shake and one on the 58th. The pauses between every tenth shake were, in these three emulsions, $\frac{1}{2}$ minute in the first case, 1 minute in the second case, and 5 minutes in the third case. The length of the pause, if above a certain minimum, is apparently of little or no influence.

No current, at 52 volts, passes through the original water-in-oil cholesterin emulsion. The emulsion is readily reversible with NaOH. One drop (0.033 cc.) of M NaOH, or 0.3 cc. of M/10 NaOH, is sufficient to reverse the emulsion. $BaCl_2$ will reverse the oil-in-water emulsion obtained with NaOH, back into the original type, and NaOH will again cause reversal into an oil-in-water emulsion.

Cephalin. The alkaloid cephalin was used in a concentration of 1:500 as an emulsifier. With this solution as the aqueous phase a good water-in-oil emulsion is obtained. Complete reversal results on the addition 1.0 to 1.5 cc. of M/10 NaOH. This oil-in-water emulsion can be reversed back to the original form by 0.3 cc. of M/10 $BaCl_2$. One cubic centimeter of the M/10 NaOH will again reverse the emulsion, and 2.0 cc. of M/10 $BaCl_2$ will again bring it back. As the emulsion is reversed again and again higher concentrations of the salt and the base are necessary to cause complete reversal. Finally, the emulsion "breaks," that is, separates into two layers, of oil and water respectively.

Plant extract. A quantity of fresh spinach was run several times through a coarse and then a fine mincer. The pulp thus obtained was subjected to high pressure. A large quantity of plant juice, consisting of protoplasm and cell sap, is pressed out. This plant extract will remain in a state of colloidal suspension for two or three days. It then precipitates. Such an extract from spinach, diluted to one-half, forms, with olive oil, a good oil-in-water emulsion, the oil particles of which are from 1 to 50μ in diameter, averaging some 5 or 10μ. The emulsion has a viscosity of 10.7 as compared with 1 for water. The current obtained with 52 volts is high, being 235 milliamperes. Small quantities of M/10 to 10 cc. of M BaCl will not cause this emulsion to reverse.

THE INFLUENCE OF OTHER IONS ON REVERSIBILITY. We have seen how highly speculative a theory may be when formulated on the behavior of one type of emulsion. Equally misleading would it be to look no further than the effect of a single group of ions.

In considering the reversibility and irreversibility of the emulsions, the influence of only two electrolytes $BaCl_2$ and NaOH, has so far been considered, the former being used to reverse the emulsions of the oil-in-water type and the latter to reverse those of the water-in-oil type. The hydroxide of barium and the chloride of calcium were also tried upon the oil-in-water systems, and two salts of sodium were tried upon the water-in-oil emulsions. In every case $CaCl_2$ had the same effect on the emulsions as did $BaCl_2$, reversing the reversible ones and having no effect on the irreversible ones. This was also true for $Ba(OH)_2$, with one exception, to be considered shortly.

The fact that the hydroxide of barium will reverse the sodium oleate emulsion in which the aqueous phase is the hydroxide of sodium, is interesting because of its bearing on the relative importance of cations and anions on reversibility. One-tenth cubic centimeter of saturated $Ba(OH)_2$ (which titrated 0.194 M) has no apparent effect on 50 cc. of sodium oleate emulsion in which M/10 NaOH is the dispersion medium. Two-tenths cubic centimeter of the $Ba(OH)_2$ will reverse $\frac{1}{4}$ of the total volume of the emulsion: 0.4 cc. will reverse slightly more than half: and 0.7 cc. will reverse the entire 50 cc. of the emulsion into one of the water-in-oil type. A high concentration of NaOH is now necessary to bring the emulsion back into the oil-in-water type. One cubic centimeter of 10 M NaOH will reverse the emulsion into its original form. The concentration of NaOH in the system is still not too high to prevent a third reversal of part of the total volume of the emulsion. One cubic-centimeter of saturated $Ba(OH)_2$ will reverse $\frac{3}{5}$ of the already twice reversed emulsion. That portion of the emulsion which has been reversed for the third time is a good water-in-oil emulsion (microscopically examined), of high viscosity.

Barium hydroxide will not only reverse all the emulsions which $BaCl_2$ will, but will also (partially) reverse one upon which $BaCl_2$ has no apparent effect, namely, the emulsion in which gelatose is the emulsifier. A saturated aqueous solution of $Ba(OH)_2$ (0.194 M) will reverse slightly more than half of the volume of the gelatose emulsion. That portion of the total volume which has been reversed into a water-in-oil system does not separate out into a separate layer distinct from the remaining oil-in-water emulsion, but instead, the two systems are dispersed one within the other. The amperage of the partially reversed emulsion is higher than that of the original, thus indicating that no reversal has taken place. The color of the emulsion, however, has become deep red (the oil phase being stained with Sudan III). One would, therefore, with color alone as the criterion, say, without hesitation, that the emulsion has reversed into one of the water-in-oil type. Only a microscopical examination reveals the true state of affairs, namely, that both types of emulsion exist.

The most remarkable fact about the reversal of the emulsion with a gelatose emulsifier is that the hydroxide causing reversal may be either that of a mono- or bivalent cation. NaOH also partially reverses the emulsion just as does $Ba(OH)_2$.

When an emulsion with a gelatose emulsifier is microscopically examined after 6 cc. of M/10 NaOH has been added it is seen to consist of the two types of emulsions, as just described. Further addition of the hydroxide causes no further reversal but, on the contrary, a *return* to the original oil-in-water system throughout the mixture.

Leaving the unusual behavior of the emulsion with a gelatose emulsifier out of consideration, it can be stated that both the chloride and the hydroxide of barium and of calcium have the same effect in reversing oil emulsions.

When salts of sodium are added to water-in-oil emulsions which are reversible with NaOH, *no* reversal takes place. Neither NaCl nor Na_2SO_4 will cause any of the emulsions to reverse. It is quite evident, therefore, that it is not the cation Na which is alone responsible in causing reversal. Nor can we say that it is the anion OH which is alone the active ion in reversing water-in-oil systems, otherwise the hydroxide of any cation should do, yet $Ba(OH)_2$ does not reverse water-in-oil systems, but, on the contrary, behaves like $BaCl_2$ in reversing oil-in-water emulsions.

The inability of NaCl to reverse the emulsions which can be reversed with NaOH, is of special interest because of its bearing on the biological significance of Clowes' hypothesis. It is this salt, NaCl, which has been the classical example to illustrate the effect of a monovalent cation on the permeability of protoplasm, and with $CaCl_2$ furnishes the fundamental evidence on which the theory of antagonism is based. If NaCl has no apparent effect on the reversibility of oil emulsions, the hypothesis of Clowes loses much of its weight.

Clowes (6, p. 423) states that while NaCl does not reverse the water-in-oil emulsions it "undoubtedly promotes the formation of emulsions of oil in water." If this is true, the effect is certainly exceedingly slight. When 5 M NaCl is slowly added to a water-in-oil emulsion in which gliadin is the emulsifier, no change is at first to be noted, either in the (red) color or in the electrical conductivity of the original emulsion. Not until 5 to 7 cc. of 5 M NaCl have been added to a water-in-oil emulsion, with gliadin as stabilizer, is a slight reading of the milliammeter to be had. But the emulsion is still red, and therefore primarily of the water-in-oil type. A microscopical examination reveals the presence of a water-in-oil emulsion in which are scattered larger regions of pure water, indicating a tendency toward separation of the two phases. That NaCl tends rather to cause separation of the water and oil than to promote the formation of an oil-in-water emulsion, is indicated further by the behavior of soap emulsions in the presence of NaCl.

It occasionally happens that an emulsion made with soap (0.001 M $NaC_{18}H_{35}O_2$) as the emulsifier, is of the water-in-oil type, instead of the usual oil-in-water form. This is the case when the soap solution has stood for several days. There takes place a change in acidity, in pH value, which seems to be an influencing factor. No matter what the type, the sodium stearate emulsion is very sensitive to electrolytes. When of the usual oil-in-water type (made with a freshly prepared soap solution), a drop or two of M/10 $BaCl_2$ is sufficient to cause complete reversal. If of the oil-in-water type (made from an old soap solution), very little NaOH is also necessary to cause reversal. If NaCl tends to promote the formation of a system of the oil-in-water type one would expect that this influence would be readily detectable in so sensitive an emulsion as is the one with a sodium stearate stabilizer. Such is not the case, however. Two cubic centimeters or 5 cc. of 5 M NaCl does not prevent the formation of a water-in-oil emulsion in which (an old and therefore less alkaline solution) of sodium stearate is the emulsifier, even though the emulsion is very sensitive to NaOH.

Na_2SO_4 is as ineffective as NaCl in causing reversal of the emulsions studied.

Discussion. If speculations on the behavior of the protoplasmic membrane are to have any value, it would appear desirable to ascertain if the reversal of phases by electrolytes of mono- and bivalent cations is a phenomenon common to all emulsions.

It was pointed out in the introduction of this article that Clowes' hypothesis rests on three assumptions. For the purpose of discussion the first two of these assumptions were considered as valid. The third assumption has to do with the type of emulsifier. The question which we can put to ourselves is this, Is the emulsifier that is active in protoplasm an emulsifier that will permit reversal of phases in the living emulsion (assuming with Clowes that protoplasm is an emulsion) when the salt or hydroxide of a mono- or bivalent cation is added? A brief review of the foregoing experimental data is sufficient to show that an answer to the question at hand is impossible.

That protoplasm contains soaps we know, but their proportion, compared with that of "lipoids" and proteins, is small. It seems unlikely that soap is the emulsifier that is the determining one in the behavior of the hypothetical protoplasmic emulsion. All experiments on permeability tend to emphasize the presence of proteins and "lipoids" in the plasmatic membrane. If the emulsifier active in protoplasm is a "lipoid," then the question arises whether it is like lecithin, in which case reversal could not happen, or like cholesterin in which case reversal could take place. Lecithin is more abundant in plant tissue, and cholesterin in animal tissue. Whether the "lipoid" is free and functions as such is doubtful. Osborne (10) finds that of a maximum content of 30 per cent of "lipoid" in egg yolk very little is free, the greater portion being chemically bound with proteins.

The abundance of proteins in protoplasm makes it highly probable that the predominating emulsifier is a protein. But this does not simplify our problem. If the emulsifier is an albumin then reversal is not possible, while if it is casein or gliadin, or a protein behaving like them, then reversal is possible. Who can say what the actual nature of the substance is which keeps the supposed protoplasmic emulsion in a state of equilibrium?

Clowes' hypothesis suffers not only from the fact that emulsions with certain kinds of emulsifiers will not reverse, but also from the fact that those emulsions which do reverse do so on the addition of the hydroxide but not the chloride of sodium. The fact that NaCl will not reverse any of the emulsions is of importance in its bearing on the behavior of protoplasm, because it is with NaCl that such pronounced changes in protoplasmic permeability have been observed by many biologists.

In view of the extremely slight if any tendency of NaCl to produce the formation of water-in-oil emulsions, and especially, in view of the inability of NaCl to reverse any of the emulsions here reported upon, it must be evident that Clowes' hypothesis can not be considered to cover the mechanism of the changes in protoplasmic permeability by sodium chloride at least.

Clowes has given us some interesting suggestions. If it should be found that protoplasm is, in its colloidal structure, an emulsion, and that this emulsion is maintained by an emulsifier which permits a reversal of the liquid phases making up the system, then and only then can the speculations of Clowes serve as the foundation of a theory of the mechanism of permeability changes in the protoplasmic membrane. Before we attempt to visualize so complex a vital phenomenon on the basis of so simple a mechanical process as phase reversal in emulsions, it is only the part of wisdom to thoroughly investigate the assumptions on which our analogy rests.

SUMMARY

1. Olive oil emulsions in which one of the soaps, sodium oleate or sodium stearate, is the emulsifier, are oil-in-water systems which are reversible with $BaCl_2$.

2. Oil emulsions with casein, gliadin, cholesterin, or cephalin as the aqueous phase, form water-in-oil systems which are reversible with NaOH.

3. Oil emulsions in which saponin (senegin, smilacin), gelatose, gum arabic, albumin, lecithin, or plant extract, is the emulsifier, form oil-in-water systems which are not reversible with $BaCl_2$.

4. Since the hypothesis of Clowes, on the mechanism of permeability changes in the plasma membrane, rests on the assumption that the emulsifier in protoplasm is of that type which form an emulsion that is reversible with $BaCl_2$ or NaOH and since certain of the substances here experimented with as emulsifiers, are very abundant in protoplasm but form emulsions which are not reversible with $BaCl_2$ or NaOH, one is forced to conclude that, since we are totally ignorant of the actual nature of the emulsifier in protoplasm, a theory of the mechanism of permeability changes which is based on the behavior of only one type of emulsion in the presence of certain ions, must be regarded as a purely speculative hypothesis which rests on very uncertain evidence.

5. $CaCl_2$ and $Ba(OH)_2$ are both like $BaCl_2$ in their influence on the emulsions investigated, with one exception.

6. NaCl will not reverse any of the emulsions here investigated. The effect of NaCl on the emulsions is to cause "breaking," that is, to cause a separation of the two liquid phases. There is little evidence to support the belief that NaCl tends to promote the formation of oil-in-water emulsions.

7. In view of the striking difference in the reaction of emulsions to NaCl and to NaOH, there seems to be little reason to believe that the behavior of oil emulsions when treated with NaOH serves as a satisfactory basis of an explanation of the mechanism of permeability changes occasioned in the plasma membrane by NaCl.

8. Since both the chloride and the hydroxide of barium and the chloride of calcium will reverse certain oil-in-water emulsions, and since the chloride of sodium will not reverse certain water-in-oil emulsions which

the hydroxide of sodium will reverse, and since the hydroxide of both sodium and barium will (partially) reverse one particular emulsion, one is forced to conclude that valency of the cation is not alone the determining factor in phase reversal. Nor does it seem possible to formulate any general rule regarding the relative potency of cations and anions in causing reversal.

9. The behavior of emulsions varies with and is dependent upon the type of emulsifier.

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NEW YORK
BOTANICAL
GARDEN

Reprinted from Rhodora, Vol. 25, November, 1923.

SECOND REVISED LIST OF NEW ENGLAND HEPATICAE.[1]

Alexander W. Evans.

In 1903 the writer[2] published a preliminary list of New England Hepaticae, in which 123 species were reported. Of these, 75 were accredited to Maine, 81 to New Hampshire, 67 to Vermont, 76 to Massachusetts, 65 to Rhode Island, 94 to Connecticut, and 31 to all six of the New England States. From 1902 to 1912 a number of noteworthy species were discussed in this journal in a series of Notes on New England Hepaticae, many of the species representing additions to the flora. This series comprised ten numbers, the first appearing in November, 1902, and the last in November, 1912. In 1913 the writer[3] published a Revised List of New England Hepaticae, in which much of the information found in these Notes was incorporated. In this list 177 species were reported, 123 being accredited to Maine, 130 to New Hampshire, 109 to Vermont, 97 to Massachusetts, 77 to Rhode Island, 134 to Connecticut, and 53 to all six states.

Since the appearance of the Revised List the series of Notes has been continued, seven additional numbers having been published, as follows: the eleventh in April, 1914 (**16**: 62–76); the twelfth in June, 1915 (**17**: 107–120); the thirteenth in April and May, 1916 (**18**: 74–85, 103–120. *pl. 120 + f. 1–40*); the fourteenth in December, 1917 (**19**: 263–272); the fifteenth in September, 1919 (**21**: 149–169. *pl. 126 + f. 1–14*); the sixteenth in December, 1921 (**23**: 281–284); and the seventeenth in May and June, 1923 (**25**: 74–83, 89–98). In these Notes considerable new information regarding the distribution of the New England species is given, and this is included in the Second Revised List found below. As in the preceding lists the sign + indicates that an herbarium specimen has been seen, the sign — that a printed record has been found. In accordance with the prevailing views on the classification of the Hepaticae more families are recognized in the new list than in the earlier lists. Of these families the first four belong to the order Marchantiales, the next eleven to the Jungermanniales, and the last to the Anthocerotales.

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Preliminary Lists of New England Plants,—XI, Hepaticae. Rhodora **5**: 170–173. 1903.

[3] Rhodora **15**: 21–28. 1913. Full references to the first ten numbers of the Notes are given here.

RICCIACEAE.	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Riccia arvensis Aust.	+	+	+	+	—	+
“ Austini Steph.					—	+
“ Beyrichiana Hampe				+		+
“ crystallina L.			+	+		+
“ dictyospora M. A. Howe						+
“ fluitans L.	+	+	+	+	+	+
“ Frostii Aust.			+			
“ hirta Aust.						+
“ membranacea Lindenb. & Gottsche						+
“ sorocarpa Bisch.				+		+
“ Sullivantii Aust.	+	+	+	+	+	+
Ricciocarpus natans (L.) Corda	+	+	+	+	+	+
SAUTERIACEAE.						
Clevea hyalina Lindb.			+			
REBOULIACEAE.						
Asterella tenella (L.) Beauv.	+	+	+	+	+	+
Grimaldia fragrans (Balb.) Corda			+	+	+	+
“ pilosa (Hornem.) Lindb.			+			
“ rupestris Nees			+			
Reboulia hemisphaerica (L.) Raddi	+	+	+	+	+	+
MARCHANTIACEAE.						
Conocephalum conicum (L.) Dumort.	+	+	+	+	+	+
Lunularia cruciata (L.) Dumort.	+		+	+	+	+
Marchantia polymorpha L.	+	+	+	+	+	+
Preissia quadrata (Scop.) Nees	+	+	+	+	+	+
RICCARDIACEAE.						
Metzgeria conjugata Lindb.	+	+	+	+	—	+
“ crassipilis (Lindb.) Evans			+	+		+
“ furcata (L.) Dumort.	+	+	+			+
“ pubescens (Schrank) Raddi	+	+	+			
Pallavicinia Flotowiana (Nees) Lindb.	+	+	+	+		+
“ Lyellii (Hook.) S. F. Gray	+	+	+	+	+	+
Riccardia latifrons Lindb.	+	+	+	+	+	+
“ multifida (L.) S. F. Gray	+	+	+	+	+	+
“ palmata (Hedw.) Carruth.	+	+	+	—	—	+
“ pinguis (L.) S. F. Gray	+	+	+	+	+	+
“ sinuata (Dicks.) Lindb.				+	+	+
PELLIACEAE.						
Blasia pusilla L.	+	+	+	+	+	+
Fossombronia brasiliensis Steph.					—	+

PELLIACEAE	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Fossombronia cristula Aust.				+		+
“ foveolata Lindb.	+	+	+	+	+	+
“ Wondraczekii (Corda) Dumort.		+	+	+		+
Pellia epiphylla (L.) Corda	+	+	+	+	+	+
“ Fabroniana Raddi		+	+			+
“ Neesiana (Gottsche) Limpr.	+	+	+	+		+
CALOBRYACEAE.						
Scalia Hookeri (Lyell) S. F. Gray		+				
LOPHOZIACEAE.						
Chiloscyphus fragilis (Roth) Schiffn.	+	+		+		+
“ pallescens (Ehrh.) Dumort.	+	+	+	+	+	+
“ polyanthos (L.) Corda	+	—	—	—	—	+
“ rivularis (Schrad.) Loeske	+	+	+	+	+	+
Geocalyx graveolens (Schrad.) Nees	+	+	+	+	+	+
Gymnomitrium concinnatum (Lightf.) Corda	+	+				
“ corallioides Nees	+	+				
Harpanthus Flotowianus Nees		+				
“ scutatus (Web. & Mohr) Spruce	+	+	+	+	+	+
Jamesoniella autumnalis (DC.) Steph.	+	+	+	+	+	+
Jungermannia cordifolia Hook.	+	+	+			+
“ lanceolata L.	+	+	+	+	—	+
“ pumila With.	+	+	+	+	—	+
“ sphaerocarpa Hook.	+	+				
Lophocolea alata Mitt.				+		+
“ bidentata (L.) Dumort.	—		—	+	—	+
“ heterophylla (Schrad.) Dumort.	+	+	+	+	+	+
“ minor Nees	+	+	+	+	+	+
Lophozia alpestris (Schleich.) Evans	+	+	+	+		+
“ attenuata (Mart.) Dumort.	+	+	+	+		+
“ badensis (Gottsche) Schiffn.		+	+			+
“ barbata (Schmid.) Dumort.	+	+	+	+		+
“ bicrenata (Schmid.) Dumort.	+	+	+	+	+	+
“ confertifolia Schiffn.	+	+	+			
“ excisa (Dicks.) Dumort.	+	+			+	+
“ Floerkii (Web. & Mohr) Schiffn.		+	+			
“ grandiretis (Lindb.) Schiffn.			+			
“ Hatcheri (Evans) Steph.	+	+				
“ heterocolpa (Thed.) M. A. Howe	+	+	+			
“ incisa (Schrad.) Dumort.	+	+	+	+	—	+
“ inflata (Huds.) M. A. Howe	+	+	+	+		+
“ Kaurini (Limpr.) Steph.	+	+	+			
“ Kunzeana (Hüben.) Evans	+	+				

LOPHOZIACEAE.	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Lophozia longidens (Lindb.) Macoun	+	+	+			+
" longiflora (Nees) Schiffn.	+	+				
" lycopodioides (Wallr.) Cogn.	+	+				
" marchica (Nees) Steph.	+	+	+			+
" Mildeana (Gottsche) Schiffn.	+	+	+	+	+	+
" obtusa (Lindb.) Evans	+					
" porphyroleuca (Nees) Schiffn.	+	+	+	+		+
" quinquedentata (Huds.) Cogn.	+	+	+			+
" ventricosa (Dicks.) Dumort.	+	+	+	+	—	+
Marsupella aquatica (Lindenb.) Schiffn.	+	+				
" emarginata (Ehrh.) Dumort.	+	+	+	+		+
" sparsifolia (Lindb.) Dumort.		+				
" sphacelata (Gieseke) Dumort.		+	+			
" Sullivantii (DeNot.) Evans	+	+	+	+		+
" ustulata (Hüben.) Spruce	+	+				
Mylia anomala (Hook.) S. F. Gray	+	+	+	+	—	+
" Taylori (Hook.) S. F. Gray	+	+	+			
Nardia crenulata (Sm.) Lindb.	+	+	+	+	+	+
" crenuliformis (Aust.) Lindb.				+		+
" fossombronioides (Aust.) Lindb.						+
" geoscyphus (DeNot.) Lindb.	+	+		+		+
" hyalina (Lyell) Carringt.	+	+	+	+		+
" obovata (Nees) Lindb.	+	+	+			
" obscura Evans	+	+	+	+		+
" scalaris (Schrad.) S. F. Gray	+					
Pedinophyllum interruptum (Nees) Schiffn.						+
Plagiochila asplenioides (L.) Dumort.	+	+	+	+	+	+
" Austini Evans		+	+			+
Sphenolobus exsectaeformis (Breidl.) Steph.	+	+	+			+
" exsectus (Schmid.) Steph.	+	+	+	+		+
" Hellerianus (Nees) Steph.	+	+	+	+	—	+
" Michauxii (Web. f.) Steph.	+	+	+	+		+
" minutus (Crantz) Steph.	+	+	+	+		
CEPHALOZIELLACEAE.						
Cephaloziella bifida (Schreb.) Schiffn.	+		+	+		+
" byssacea (Roth) Warnst.	+	+	+	+		+
" elachista (Jack) Schiffn.	+	+	+	+	+	+
" Hampeana (Nees) Schiffn.	+	+	+	+	+	+
" myriantha (Lindb.) Schiffn.	+	+	+	+	+	+
" papillosa (Douin) Schiffn.				+		+
" spinicaulis Douin						+
" Sullivantii (Aust.) Evans	+	+		+		

CEPHALOZIACEAE.	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Bazzania denudata (Torr.) Trevis.	+	+	+	+		+
“ tricrenata (Wahlenb.) Trevis.	+	+	+			
“ trilobata (L.) S. F. Gray	+	+	+	+	+	+
Calypogeia fissa (L.) Raddi	+	+		+		
“ Neesiana (Massal. & Carest.) K. Müll.	+	+	+	+		+
“ paludosa Warnst.	+	+	+	+	+	+
“ sphagnicola (Arn. & Perss.) Warnst. & Loeske	+	+	+			+
“ suecica (Arn. & Perss.) K. Müll.	+	+	+			+
“ Sullivantii Aust.	+	+		+	+	+
“ Trichomanis (L.) Corda	+	+	+	+	+	+
Cephalozia bicuspidata (L.) Dumort.	+	+	+	+		+
“ catenulata (Hüben.) Spruce	+	+	+	+	—	+
“ connivens (Dicks.) Lindb.	+	+	+	+	+	+
“ curvifolia (Dicks.) Dumort.	+	+	+	+	+	+
“ fluitans (Nees) Spruce	+	+	+	+	+	+
“ Francisci (Hook.) Dumort.	+	+		+		
“ Loitlesbergeri Schiffn.		+				+
“ Macounii Aust.	+	+				
“ macrostachya Kaal.	+	+	+	+	+	+
“ media Lindb.	+	+	+	+	+	+
“ pleniceps (Aust.) Lindb.	+	+	+			+
Lepidozia reptans (L.) Dumort.	+	+	+	+	+	+
“ setacea (Web.) Mitt.	+	+	+	+		+
“ sylvatica Evans	+	—		+	+	+
Odontoschisma denudatum (Mart.) Dumort.	+	+	+	+	—	+
“ elongatum (Lindb.) Evans	+	+				
“ prostratum (Sw.) Trevis.				+	+	+
PTILIDIACEAE.						
Anthelia Juratzkana (Limpr.) Trevis.		+				
Blepharostoma trichophyllum (L.) Dumort.	+	+	+	+		+
Ptilidium ciliare (L.) Nees	+	+	+	+	—	+
“ pulcherrimum (Web.) Hampe	+	+	+	+	+	+
Temnoma setiforme (Ehrh.) M. A. Howe	+	+	+			
Trichocolea tomentella (Ehrh.) Dumort.	+	+	+	+	+	+
SCAPANIACEAE.						
Diplophyllum albicans (L.) Dumort.	+					
“ apiculatum (Evans) Steph.	+		+	+	+	+
“ gymnostomophilum Kaal.	+		+			
“ taxifolium (Wahlenb.) Dumort.	+	+	+	+		+
Scapania apiculata Spruce	+	+				
“ convexula K. Müll.	+					
“ curta (Mart.) Dumort.	+	+	+	+		+

SCAPANIACEAE.

	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Scapania dentata Dumort.	+	+	+	+		+
“ glaucocephala (Tayl.) Aust.		+	+			
“ hyperborea Jörgensen	+	+				
“ irrigua (Nees) Dumort.	+	+	+			+
“ nemorosa (L.) Dumort.	+	+	+	+	+	+
“ Oakesii Aust.	+	+	+			
“ paludicola Loeske & K. Müll.	+	+	+			+
“ paludosa K. Müll.	+	+	+			+
“ subalpina (Nees) Dumort.	+	+				
“ umbrosa (Schrad.) Dumort.	+	+				
“ undulata (L.) Dumort.	+	+	+	+	+	+

RADULACEAE.

	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Radula complanata (L.) Dumort.	+	+	+	+	+	+
“ obconica Sulliv.	+		+	+		+
“ tenax Lindb.	+	+	+	+	—	+

PORELLACEAE.

	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Porella pinnata L.	+	+	+	+	+	+
“ platyphylla (L.) Lindb.	+	—	+	—	—	+
“ platyphylloidea (Schwein.) Lindb.	+	+	+	+	+	+

LEJEUNEACEAE.

	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Cololejeunea Biddlecomiae (Aust.) Evans	+	+	+	+	—	+
Frullania Asagrayana Mont.	+	+	+	+	+	+
“ Brittoniae Evans	+	+	+	+	+	+
“ eboracensis Gottsche	+	+	+	+	+	+
“ inflata Gottsche						+
“ Oakesiana Aust.	+	+	+			
“ plana Sulliv.					—	+
“ riparia Hampe		+	+	—		+
“ saxicola Aust.						+
“ Selwyniana Pears.	+	+	+			
“ squarrosa (R. Bl. & N.) Dumort.					—	+
“ Tamarisci (L.) Dumort.	+			+		+
Jubula pennsylvanica (Steph.) Evans	+	+	+	+	—	+
Lejeunea cavifolia (Ehrh.) Lindb.	+	+	+	+	—	+
“ patens Lindb.	+					+
Leucolejeunea clypeata (Schwein.) Evans		+		+		+
“ unciloba (Lindenb.) Evans					+	

ANTHOCEROTACEAE.

	Me.	N. H.	Vt.	Mass.	R. I.	Conn.
Anthoceros carolinianus Michx.						+
“ crispulus (Mont.) Douin		+	+	+		+
“ laevis L.	+	+	+	+	+	+
“ Macounii M. A. Howe	+	+				+
“ punctatus L.	+	—	—	+		+
Notothylas orbicularis (Schwein.) Sulliv.	+	+	+	+	—	+

Notes on the Preceding List.

It will be seen that this Second Revised List includes 196 species, a gain of 19, or nearly 11 per cent. over the first Revised List. From Maine 151 species are now reported, a gain of nearly 23 per cent.; from New Hampshire, 154 species, a gain of about 18 per cent.; from Vermont, 137 species, a gain of nearly 26 per cent.; from Massachusetts, 121 species, a gain of nearly 25 per cent.; from Rhode Island, 82 species, a gain of about 6 per cent.; from Connecticut, 147 species, a gain of nearly 10 per cent.; and from all six states, 67 species, a gain of about 28 per cent. The increases during the last ten years are naturally less striking than those between 1903 and 1913 (see Rhodora **15**: 26).

The list includes the following additions to local state floras, made during 1923: *Riccardia latifrons* for Rhode Island, the record being based on specimens collected by the writer at Westerly; *Pellia Neesiana* for Vermont, based on specimens collected by Miss Lorenz at Ripton; and *Lejeunea patens* for Connecticut, based on specimens collected by Miss Lorenz at Thomaston. The writer has likewise collected *Riccardia multifida, Chiloscyphus pallescens, Harpanthus scutatus* and *Cephalozia curvifolia* at Westerly, so that the Rhode Island records for these species are now given the + sign.

If the Second Revised List is compared with the first a number of differences become apparent. Some of these represent additions and others changes in names, the latter being largely due to modifications in the interpretation of genera and species. For the sake of convenience the differences between the lists are summarized below, with references to the Notes, the Roman numeral in each case indicating the number in the series and the Arabic numeral the page.

Additions: *Riccia Frostii* (XIV, 264); *Clevea hyalina* (XI, 62); *Grimaldia rupestris* (XI, 64, as *Neesiella rupestris*); *Fossombronia cristula* (XII, 107); *Scalia Hookeri* (XIV, 266); *Harpanthus Flotowianus* (XIV, 268); *Lophocolea alata* (XII, 111); *Lophozia grandiretis* (XI, 63); *Nardia fossombronioides* (XVI, 281); *N. obscura* (XV, 159); *Cephaloziella spinicaulis* (XII, 117); *Bazzania denudata* (XVII, 89); *Calypogeia fissa* (XIV, 271); *Cephalozia Loitlesbergeri* (XV, 168); *C. macrostachya* (XII, 114); *Diplophyllum gymnostomophilum* (XI, 71); *Scapania hyperborea* (XVI, 282); *S. Oakesii* (XIII, 75); *S. paludicola* (XIII, 77); *Porella platyphylloidea* (XIII, 109); *Lejeunea patens* (XVII, 97).

CHANGES OF NAMES: *Ricciella crystallina, R. fluitans, R. membranacea* and *R. Sullivantii* (of the first Revised List) are replaced in the genus *Riccia* (XVII, 74); *Neesiella pilosa* and *N. rupestris* are included in the genus *Grimaldia* (XVII, 75); *Fossombronia salina* is superseded by *F. brasiliensis* (XVII, 75); *Plagiochila Sullivantii* (of list) is now *P. Austini* (XI, 68); *Calypogeia tenuis* is now *C. paludosa* (XII, 119); *Cephalozia serriflora* again becomes *C. catenulata* (XII, 112); *Diplophylleia albicans, D. apiculata* and *D. taxifolia* are placed in the genus *Diplophyllum* (XI, 74); *Scapania gracilis* (of list) is included under *S. nemorosa* (XIII, 75); *Porella rivularis* (of list) is included under *P. platyphylla* (XII, 109).

YALE UNIVERSITY.

Reprinted from Rhodora, Vol. 25, November, 1923.

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CERCIS CANADENSIS IN CONNECTICUT.[1]

G. E. Nichols.

About fifteen years ago one of my students brought into the laboratory a twig of redbud, *Cercis canadensis,* which he had collected "somewhere on West Rock." West Rock is a trap ridge about 400 feet in height, situated on the outskirts of New Haven and site of the famous Judges' Cave. It is included in the New Haven city park system, but for the most part is in a natural condition, being very largely covered with second growth woodland. Since the redbud had not been recorded as a native plant northeast of New Jersey, it was assumed at the time that the specimen in question must have come from a planted tree; but subsequent inquiries from the superintendent of city parks elicited the information that no redbuds had ever been planted in the park, which covers an area of about 200 acres, and until recently the source of the specimen remained a mystery.

One day last May, however, as I was driving along the crest of the Rock, through woods that gleamed white with masses of blossoming dog-wood, my eye was caught by a mass of an entirely different color—the rose-pink of the redbud. The mystery was solved.

There they were, a clump of half a dozen good-sized individuals, ranging from half an inch to nearly two inches in diameter and up to about a dozen feet in height, together with two or three smaller plants.

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[1] Contribution from the Osborn Botanical Laboratory

The entire group occupies a piece of ground less than three feet in diameter, and very likely has originated through root suckering from a single plant. How the original plant got there is another question; but from the location of the station—near the summit of a rocky ridge which has never been inhabited, and fifty feet from the nearest road, from which it is separated by a tangle of wood and thicket—it seems certain that the plant was not introduced by human agencies. Moreover, the redbud here occupies essentially the same sort of habitat which it favors on trap ridges in eastern Pennsylvania: a moist, rocky depression in oak-hickory woods, where it grows associated with such other woody plants as basswood and butternut, silky cornel and high bush blueberry, bittersweet and grape. In short, I have no hesitation in accepting this Connecticut station for the redbud as representing a northeastward extension in the known natural range of the species, notwithstanding the fact that it apparently fails to propagate itself further by seed.

Yale University.

Reprinted from Bryologist, Vol. XXVI, November, 1923.

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NOTES ON NORTH AMERICAN HEPATICAE—X[1]

Alexander W. Evans

In a recent paper on New England Hepaticae[2] the writer discussed the variable *Bazzania tricrenata* (Wahlenb.) Trevis. and presented reasons for recognizing the closely allied *B. denudata* (Torr.) Trevis. of eastern North America as a valid species. In the present paper similar claims are made for *B. ambigua* (Lindenb.) Trevis. of western North America, and another related species from the mountains of Virginia and North Carolina is proposed as new. In connection with these two species and in order to give a more complete idea of the distribution of *B. tricrenata* in North America, the known stations outside eastern Canada and New England are enumerated.

In describing the genera *Targionia* and *Marchantia* in the North American Flora the writer reported certain extensions of range, without citing the specimens upon which the records were based. These specimens are listed below. The paper calls attention also to three species that ought to be reduced to synonymy, reports a species of *Mylia* as new to North America and records the genus *Lophozia* for the first time from Florida.

1. Targionia hypophylla L.; Evans, N. Am. Fl. **14:** 31. 1923.

Collected on a damp bank, in the winter of 1921–22, near the city of San Salvador, by Paul D. Standley (*No. 19590*); specimen received from the U. S. National Herbarium. Not before reported from Central America.

2. Marchantia breviloba Evans, Trans. Connecticut Acad. **21:** 265. *f. 9.* 1917; N. Am. Fl. **14:** 64. 1923.

Collected on soil along a stream, in 1920, near Furey, Haiti, by E. C. Leonard (*No. 4430*); specimen received from the U. S. National Herbarium. Previously known only from Jamaica.

3. Marchantia paleacea Bertol.; Evans, N. Am. Fl. **14:** 64. 1923.

Collected on March 13, 1922, near Kyle, Texas, by F. McAllister (*No. 1*). Previously known in the United States only from Arizona.

4. Lophozia Mildeana (Gottsche) Schiffn.

Collected on a moist clayey bank, on March 24, 1923, fifteen miles southwest of Sanford, Florida, by S. Rapp (*No. 94*). Species and genus new to Florida. According to the published records the nearest known station for the species is

APR 11 1924

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Notes on New England Hepaticae,—XVII. Rhodora **25:** 74–83, 89–98. 1923.

near Easton, West Virginia, where it was discovered about twenty years ago by A. L. Andrews.[1]

5. MYLIA CUNEIFOLIA (Hook.) S. F. Gray, Nat. Arr. Brit. Pl. **1**: 694. 1821. *Jungermannia cuneifolia* Hook. Brit. Jung. *pl. 64.* 1814; *Leptoscyphus cuneifolius* Mitt. Jour. Bot. **3**: 358. 1851. *Aplozia cuneifolia* Dumort. Hep. Eur. 55. 1874. *Coleochila cuneifolia* Dumort. Hep. Eur. 106. 1874. *Clasmatocolea cuneifolia* Spruce, Trans. Bot. Soc. Edinb. **15**: 440. 1885. *Leioscyphus cuneifolius* Steph. Bull. Herb. Boissier II. **5**: 218. [Sp. Hepat. **3**: 18.] 1905.

Collected on the bark of trees, in June, 1923, on Mt. Mitchel (5711 ft. alt.) and Mt. Pisgah (5649 ft. alt.), North Carolina, by P. O. Schallert (*Nos. 5, 25,* both in part). New to North America.

This distinct species has long been considered one of the great rarities of the European flora. Its occurrence in the United States is therefore of much interest from the standpoint of plant distribution. The original specimens of Hooker's *Jungermannia cuneifolia* were collected in the vicinity of Bantry, Ireland, by Miss Ellen Hutchins, over a century ago, and the species is now known from perhaps half a dozen additional Irish localities. In 1832 Corda[2] reported it from near Friedland in Bohemia, but his record has not been confirmed and is no longer accepted by hepaticologists. It was not until 1898, in fact, that a thoroughly trustworthy station outside of Ireland was made known. In that year Kaalaas announced the discovery of the species, under the name *Clasmatocolea cuneifolia,* near Fossan, Stavanger Amt, Norway. In the following year Macvicar[3] extended the known range of the plant by reporting it from Moidart, West Inverness, Scotland, and has since added a few other Scotch stations.[4] Except in Ireland, Scotland and Norway no European localities are known, and the species is thus seen to be "Atlantic" in its range.

Since *M. cuneifolia* is totally unlike *M. Taylori* (Hook.) S. F. Gray and *M. anomala* (Hook.) S. F. Gray in its general appearance and since its sexual organs are still unknown, the affinities of the species remained more or less doubtful for many years. In 1889, however, a closely allied species, *M. antillana* Carringt. & Spruce,[5] from the island of Guadeloupe was described, and in this the flattened bilabiate perianth characteristic of the genus *Mylia* was demonstrated. It thus became evident that S. F. Gray was correct in including *Jungermannia cuneifolia* in his genus *Mylia* (which is the same as Mitten's genera *Leptoscyphus* and *Leioscyphus*) and that Spruce was in error when he provisionally referred the species to his genus *Clasmatocolea.*

Small depressed mats of *Mylia cuneifolia* are occasionally found, but it is much more usual for the stems to occur in intricate admixture with other hepa-

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[1] See BRYOLOGIST **8**: 65. 1905. The species is here listed as *L. marchica* (Nees) Steph., which at that time was understood in a broad sense, including *L. Mildeana* among its synonyms. For the distinctions between the two species, see Evans, Rhodora **12**: 199. 1910.

[2] In Sturm, Deutschl. Fl. Jungerm. 94. *pl. 28.* 1832.

[3] Jour. Bot. **37**: [6]. 1899.

[4] See especially Trans. Bot. Soc. Edinb. **25**: 188. 1910.

[5] Bescherelle & Spruce, Bull. Soc. Bot. France **36**: clxxvii. *pl. 4.* 1889

tics, usually species of *Lejeunea* (in its broad sense), *Frullania* and *Plagiochilla.* In the North Carolina material *Frullania Asagrayana* Mont. and a small sterile *Plagiochila* with caducous leaves are present in some abundance. On account of its minute size the *Mylia* is often difficult to detect in these admixtures, an individual stem being almost invisible to the naked eye. Full and accurate descriptions of the species are given in recent European manuals,[1] and the following account is largely a compilation. The European material studied by the writer was collected by Macvicar at Moidart, some of it having been distributed in Schiffner's Hepaticae Europaeae Exsiccatae, No. 250, as *Leptoscyphus cuneifolius*.

A more or less distinct brown pigmentation is usually present in both leaves and stems. The latter are mostly simple but occasionally give off one or more ventral intercalary branches from the axils of the underleaves. According to Kaalaas, who gave an unusually full description of the species in citing it as a Norwegian plant, the stems may attain a length of 1 cm. as a maximum, but a length of only 3–5 mm. is much more usual. The diameter averages about 0.05 mm. Rhizoids are very scantily produced and seem to be restricted to the bases of the underleaves.

The slightly concave leaves, which spread somewhat from the stem, are usually far apart and show an almost transverse insertion. When well developed they measure 0.15–0.2 mm. in length, but considerably smaller leaves are not infrequent. Although the shape is variable, a tendency to broaden out from a narrow base is usually apparent, giving in most cases obovate or obcuneate outlines, with a rounded, truncate or slightly emarginate apex. The leaf-cells average about 18 μ in diameter and vary but little in size in the different parts of a leaf. They are distinguished by their smooth cuticle, pigmented walls and well-defined trigones, often with convex sides.

According to the older descriptions the underleaves of *M. cuneifolia* are acutely bifid. This condition, however, as the later descriptions testify, is very rarely attained. Most of the underleaves are narrowly to broadly lanceolate, with an acute or acuminate apex and perfectly entire sides. Occasionally a blunt tooth is present on one side or even on both. The underleaves spread more or less widely from the stem and average about 0.1 mm. in length and 0.05 mm. in width. As Kaalaas states each underleaf adjoins a lateral leaf on one side of the stem but is distant from the lateral leaf on the other side. He adds that there may be actual coalescence between the underleaf and the lateral leaf, but the writer has been unable to confirm this statement.

In the absence of sexual organs the species reproduces itself vegetatively by means of caducous leaves, which are sometimes thrown off so copiously that the stems appear almost leafless, except for the persistent underleaves. Schiffner has described the process very clearly.[2] He interprets the caducous leaves as "Bruchblätter," rather than "Brutblätter," in the terminology of Correns, because there is no predetermined zone of separation, the leaves breaking off in

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[1] See especially Macvicar, Student's Handb. British Hepatics 231 (with figures). 1912.

[2] Oesterr. Bot. Zeitschr. **57:** 457. 1907.

such a way that the basal row of leaf-cells is left attached to the stem, either wholly or partially. The new plants arise either from the marginal cells or from the cells along the line of separation, the latter origin being the more frequent, but it is unusual to find more than one new plant attached to a single leaf. The new stem grows out in the same plane as the leaf and soon develops rudimentary leaves of its own, each consisting of only a few cells. The method of vegetative reproduction just described is similar to that found in *Bazzania denudata* and some of its allies.

There are no other North American species with which *M. cuneifolia* is likely to be confused. The lanceolate underleaves might perhaps bring to mind those of *Harpanthus scutatus* (Web. & Mohr) Spruce, and D. Moore[1] once expressed the opinion that the *Mylia* might perhaps turn out to be a species of *Harpanthus*, if sexual plants should ever be discovered. Aside from the underleaves, however, the two species have little in common. *Harpanthus scutatus* is a larger and greener plant, the leaves are distinctly bifid with sharp lobes, and vegetative reproduction is by means of gemmae borne on the reduced leaves of specialized shoots.

6. BAZZANIA TRICRENATA (Wahlenb.) Trevis.

In listing stations for this species from eastern North America[2] the writer had seen no specimens from farther south than New Hampshire and Vermont. He has since had the opportunity of studying, at the New York Botanical Garden, some of the material distributed by Sullivant in the Musci Alleghanienses, under the name *Herpetium deflexum*. This material, Nos. 252 and 253, was issued as vars. 1 and 2. The habitat is given as, "In montium editiorum saxis irroratis," referring presumably to the mountains of North Carolina. In the writer's opinion both specimens represent a rather slender form of the true *B. tricrenata* and thus extend markedly the known range of the species to the southward. Other specimens from the mountains of Virginia and North Carolina, representing similar slender forms, are cited in the list below, and this is followed by a list of specimens from western North America. The species is still unknown from the more central parts of the continent.

VIRGINIA: summit of White Top Mountain, *Small 54* (in part).

NORTH CAROLINA: Yonahlossee Road, side of Grandfather Mountain, *Andrews 52;* summit of Jones Knob, *Andrews 24;* Mt. Pisgah, *Schallert;* Grandfather Mountain, *Schallert 19* (in part).

ALASKA: Aats Bays, *Frye 935;* Augustine Bay, *Frye 543, 571, 590* (in part); Exchange Cove, *Frye 278;* mouth of Hidden Inlet, *Frye 63, 86;* Lake Bay, *Frye 210* (in small part); Port Alice, *Foster 786* (in part); Port Wells, 1899, *Trelease 1531;* Ratz Harbor, *Frye 298;* Shipley Bay, *Frye 762;* Sitka, 1894, *U. S. Fish Commission;* Snug Harbor, *Rigg 1221;* Tam Gas Harbor, *Frye 213* (in small part); Verdure Creek, *Frye 23* (in part). Most of these stations have already been listed by the writer.[3]

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[1] Proc. Roy. Irish Acad. II. **2:** 646. 1877.

[2] Rhodora **25:** 76. 77. 1923.

[3] See especially Bull. Torrey Club **41:** 598. 1915.

British Columbia: Asulkan Valley, *Brinkman 230, 251, 252a;* Chilliwack Lake, 1901, *J. M. Macoun 9;* Lewis Island, northeast of Percher Island, *Frye 1149, 1161, 1166.*

Some of the specimens listed grew on rocks, as in eastern North America, while others grew on logs or tree-trunks.

7. Bazzania ambigua (Lindenb.) Trevis. Mem. Ist. Lomb. **13:** 414. 1877. *Mastigobryum ambiguum* Lindenb. (in part); G. L. N. Syn. Hep. 217. 1845.

The history of this species is much like that of *B. denudata* and has already been briefly narrated by the writer.[1] Soon after its publication it was redescribed and figured by Lindenberg and Gottsche,[2] but subsequent writers, almost without exception, have either ignored it altogether or included it among the synonyms of *B. tricrenata.* Lindenberg based his species on two specimens—one from Massachusetts and the other from our northwest coast. Since the second specimen evidently served for Lindenberg and Gottsche's figures of *Mastigobryum ambiguum* and since it agrees with a widely distributed plant of the Pacific coast region it seems justifiable to typify the species by this specimen, rather than by the specimen from Massachusetts, which probably represented *B. denudata.* A list of the specimens examined by the writer follows. To these may be added a portion of the type-material in the Mitten Herbarium, now in the possession of the New York Botanical Garden. The species prefers tree-trunks and logs but occasionally grows on rocks.

Alaska: Aats Bay, *Frye 908;* Augustine Bay, *Frye 590* (in part); Exchange Cove, *Frye 279;* Farragut Bay, *Brewer & Coe 620* (in small part); Hot Spring, *Trelease 1489* (in small part); Lake Bay, *Frye 210;* Morse Cove, *Frye 452;* Nichols Bay, *Frye 368;* Point Malmsbury, *Frye 982;* Port Alice, *Foster 785, 786* (in part, a somewhat doubtful form); Port San Antonio, *Frye 606;* St. John Harbor, *Foster 865;* Shipley Bay, *Frye 763, 774;* Sitklan Island, *Frye 50;* Swifts Cannery, *Frye 690;* Tam Gas Harbor, *Frye 119, 134, 136, 148;* Wrangell, *Foster 2472* (in part).

British Columbia: Comox (or Hastings), *J. Macoun* (distributed in Can. Hep. *16*, as *B. deflexa*); Lewis Island, northeast of Percher Island, *Frye 1162-1164;* Port Renfrew, *Miss Gibbs 35, 52, 60, 139, 158;* same locality, *Miss Hone 247;* Revelstoke, *J. Macoun 241;* Skidegate, Queen Charlotte Islands, *Spreadborough 83167* (in part); Swanson Bay, *Frye 1131, 1133;* Ucluelet, *J. Macoun 14, 15, 45, 46, 49, 54, 82, 106* (some of these specimens are not typical and approach "*Pleuroschisma tricrenatum* var. *implexum*").

Washington: Cascade Mountains, *O. D. Allen 19;* Montesano, *Grant 2048;* upper valley of the Nisqually River, 1895, *O. D. Allen 8* (with perianths and capsules); Pacific Beach, *Foster 1407, 1450;* South Bend, *Frye 2040;* Aberdeen, *Foster 907;* Hamilton, Foster.

Oregon: Silverton, *Foster 1315.*

Most of these specimens have already been recorded by the writer or others under the name *B. tricrenata* (or one of its synonyms). Some of the published

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[1] Rhodora **25:** 94. 1923.

[2] Spec. Hepat. *Mastigobryum* 9. *pl. 3* (upper part). 1851.

published descriptions. It is unfortunate that well-developed bracts of *B. denudata* are still unknown.

The perianth of *B. ambigua* is narrowly ovoid, measuring about 3 mm. in length and 1 mm. in diameter. Three rounded keels are present and these are separated above the middle by grooves. The contracted mouth is minutely and irregularly spinulose-denticulate.

The valves of the brown capsule measure about 1 × 0.5 mm. The cells of the outermost layer are in more or less distinct longitudinal rows and average about 28 μ in length by 14 μ in width. The thickenings, usually one to three in each cell, tend to be restricted to alternate longitudinal walls, the intervening longitudinal walls and the transverse walls being free from thickenings or nearly so. The cells of the innermost layer are somewhat longer but scarcely narrower than those of the outermost layer. On the inner tangential walls distinct or poorly developed thickenings in the form of half-rings can be distinguished. The minutely punctulate, brownish green spores are 12–14 μ in diameter, and the elaters, each with two brown bands of thickening, are rounded at the ends and measure 200–250 μ in length by 8–10 μ in diameter.

Vegetative reproduction in *B. ambigua*, by means of caducous leaves, is a very striking phenomenon, and many tufts show numerous examples of long slender branches with neither leaves nor underleaves except at the apex. The process is essentially the same as in *B. denudata*, where it has already been described,[1] so that it will be unnecessary to enter again into the details.

Some of the specimens collected by Macoun on "rocks near the sea," at Ucluelet, British Columbia, are decidedly aberrant, owing probably to their exposed habitat. They are deep brown in color, they exhibit the caducous habit to some extent, and their leaves are narrow. They show in consequence a strong superficial resemblance to European specimens that have been referred to "*B. triangularis* Pears." or. perhaps better, to "*Pleuroschisma tricrenatum* var. *implexum* K. Müll." In certain cases, however, branches with narrow leaves are found on plants which bear also branches with the broader bidentate leaves characteristic of *B. ambigua*, so that the determination of Macoun's more doubtful specimens as *B. ambigua* seems allowable.

8. **Bazzania nudicaulis** sp. nov.

Collected May 28, 1892, on rocks, summit of White Top Mountain, Virginia (5675 ft. alt.), by J. K. Small (*No. 54*, in part); also August 3, 1919, on rocks, High Bluff of Roan Mountain, North Carolina (over 6000 ft. alt.), by A. L. Andrews (*No. 65*); also June 16, 1923, on rocks (and tree-roots), Grandfather Mountain, North Carolina (5964 ft. alt.), by P. O. Schallert (*No. 19*, in part). No. 65 from Roan Mountain may be considered the type.

Scattered or growing in depressed mats, often in admixture with other bryophytes, varying in color from pale yellowish brown to dark brown or almost black: stems mostly 1–2.5 cm. long and (with the leaves) 0.7–1.5 mm. wide; lateral branches infrequent, diverging at a rather wide angle; ventral branches

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[1] Rhodora **25:** 93. 1923.

sometimes sparingly produced and sometimes more abundant, usually flagelliform but occasionally similar to the lateral branches; rhizoids absent altogether or very sparingly produced, apparently restricted to the minute leaves of the flagelliform branches: leaves distant, 0.5–0.65 mm. long and 0.3–0.45 mm. wide when well developed but often considerably smaller, obliquely to widely spreading, plane or somewhat convex, ovate to ovate-lanceolate, usually scarcely rounded at the dorsal base but sometimes distinctly rounded or even subcordate, both upper and lower margins somewhat arched, apex narrowed and very variable, sometimes undivided and acutely or obtusely pointed, sometimes with two or (rarely) three short and sharp or blunt teeth, separated by acute to rounded sinuses; leaf-cells averaging about 25 × 20 μ in the median portion and 16 μ in width along the margin, trigones of fair size but inconspicuous, with slightly concave to straight sides, cuticle smooth throughout: underleaves distant, quadrate-orbicular, mostly 0.4–0.45 mm. long, exauriculate at the base, the sides slightly bulging and the apex truncate, sometimes emarginate and sometimes with three or four crenations: sexual branches not seen; vegetative reproduction by means of caducous leaves and underleaves, usually abundantly produced.

The throwing off of leaves and underleaves as "Bruchblätter," which is so striking a phenomenon in *B. ambigua* and *B. denudata*, is even more pronounced in *B. nudicaulis*. Many of the plants, in fact, are wholly leafless for long stretches and present the appearance of fine wires, yellowish or brownish in color and more or less interwoven. In some cases large and fairly well-developed leaves become separated from the axis, but the caducous habit, as in *B. denudata*, is more uniformly associated with branches bearing smaller leaves. The majority of such branches arise laterally and conform to the normal *Frullania* type, but it is not unusual for a ventral branch to assume the caducous habit, instead of developing as a flagelliform axis with minute and persistent leaves. No cases have yet been observed, however, in which a ventral branch changed its character during the course of its development.

In spite of its somewhat more robust habit *Bazzania nudicaulis* bears a certain superficial resemblance to *Mylia cuneifolia*. Both species are characterized by distant leaves, well-developed underleaves and a more or less marked pigmentation, and both exhibit a vigorous vegetative reproduction by means of caducous leaves or Bruchblätter. Here, however, the resemblance ends. The branches in the *Mylia* seem to be always ventral, the leaves are almost transversely inserted and tend to broaden out toward the apex, while the underleaves are narrow and usually undivided and sharp-pointed. In the *Bazzania*, on the other hand, lateral branches can always be demonstrated, the leaves are incubous and narrow toward the apex, while the underleaves are broad and truncate.

As Schiffner has pointed out the caducous leaves of *Mylia cuneifolia* give rise to new plants by the regeneration (or germination) of marginal or basal cells. In *Bazzania nudicaulis* and other species of *Bazzania* with caducous leaves the regenerative process seems to be less restricted, a new plant often springing from a cell in the interior of a leaf. Such a cell may even be situated in the apical half of a leaf, although a position nearer the base is more frequent. Regeneration from marginal cells is apparently rare and has not been seen by the writer. The new plants of *B. nudicaulis*, so far as observed, arise singly and are essentially like those of *B. denudata*.[1]

Although the regenerative process just described is usually first initiated in leaves that have fallen away, this is by no means invariably the case. Several instances have been noted in which leaves, while still attached to the axis, have given rise to new plants. Leaves of this character have been situated on plants in which the growing points have been injured. The inhibitory influence on regeneration exerted by the growing points has thus been removed, just as it normally is when leaves become separated.[2]

In distinguishing *B. nudicaulis* from its allies there are three species or varieties with which it should be particularly compared, namely, *B. denudata*, *B. tricrenata*, and the European plant known as "*Pleuroschisma tricrenatum* var. *implexum*."

It has already been shown that the species shares with *B. denudata* the habit of vegetative reproduction by means of caducous leaves. In *B. denudata*, however, the plants are pale and unpigmented; the leaves are slightly larger than in *B. nudicaulis* and tend to lie in one plane, thus giving the shoots a decidedly flattened appearance; the leaf-apices (in spite of their great variability) are usually broad and rounded or truncate; and the morphological distinctions between persistent and caducous leaves are fairly sharp. In *B. nudicaulis* the shoots rarely appear flattened, the leaf-apices are usually narrow, and morphological distinctions between persistent and caducous leaves are scarcely apparent.

In its typical development *B. tricrenata* is strikingly different in appearance from *B. nudicaulis*, but certain slender forms approach the new species more closely. This is particularly true of the forms occurring in the high mountains of Virginia and North Carolina, and some of these are actually found mixed with two of the specimens of *B. nudicaulis* cited above. At the same time the writer has tried in vain to find any organic connection between the two, and there is little difficulty in telling them apart. Aside from their persistent habit the leaves of *B. tricrenata* are usually more or less imbricated, they narrow more abruptly from a relatively broader base, and rarely spread at as wide an angle as in *B. nudicaulis*. The underleaves, moreover, occasionally show sharper teeth, and sexual branches are not infrequent. Even in cases of exceptionally poor development, where most of the branches bear minute and scattered leaves, an occasional stem with larger and more imbricated leaves can usually be demonstrated.

The "var. *implexum*," which has not yet been detected with certainty in America, has been discussed elsewhere by the writer.[3] It is somewhat larger than *B. nudicaulis*, its leaves are often contiguous or slightly imbricated, their apices frequently show two or three sharp teeth, and male branches are produced in some abundance. It agrees with the American plant in being more or less pigmented and in reproducing vegetatively by means of caducous leaves.

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[1] See Rhodora **25:** 94. 1923.

[2] See, in this connection, Buch, Overs.Finska Vetensk.Soc. Förh. **62** (Afd. A, No. 6): 2. 1920.

[3] Rhodora **25:** 81–83. 1923.

Aside from the differences already mentioned, however, the caducous habit of the "var. *implexum*" is never developed to so surprising an extent as in *B nudicaulis.*

9. LEPTOCOLEA CARDIOCARPA (Mont.) Evans, Bull. Torrey Club **38**: 268. *pl. 12, f. 1–3.* 1911. *L. Jooriana* (Aust.) Evans, Ibid. **38**: 270 1911

In discussing the species of *Leptocolea* found in Porto Rico, the writer[1] recognized both *L. cardiocarpa* and *L. Jooriana* as valid but pointed out their very close relationship. The only important distinction brought out was in the inflorescence, *L. cardiocarpa* being described as autoicous and *L. Jooriana* as paroicous. A few years ago the autoicous *L. cardiocarpa* was reported for the first time from the United States, on the basis of specimens collected by Rapp near Sanford, Florida. The paroicous *L. Jooriana* had long been known from several of the Southern States.

It now appears that the supposed distinction between *L. cardiocarpa* and *L. Jooriana* is inconstant. The first suspicion that this was the case came from the study of gemmiparous material of *L. Jooriana*, likewise collected at Sanford by Rapp. It was found that one of the gemmae, upon germinating, gave rise to a simple shoot, which almost immediately bore a male spike with imbricated bracts, similar in all essential respects to the male spikes of *L. cardiocarpa.* The suspicion became a certainty from the study of additional material from the same locality, where both paroicous inflorescences and elongated male spikes were sometimes found on a single individual. It therefore becomes necessary to reduce *L. Jooriana* to synonymy as indicated above.

10. FRULLANIA INFLATA Gottsche; G. L. N. Syn. Hep. 424. 1845. *F. mexicana* Lindenb. op. cit. 425. 1845. *F. Rappii* Evans, BRYOLOGIST **15**: 22. *f. 1–9.* 1912.

In 1912, the writer proposed *F. Rappii* as a new species, basing it on material collected by S. Rapp at Sanford, Florida. In comparing it with other autoicous members of the genus its very close relationship with *F. inflata* was pointed out, but what seemed to be a trustworthy distinction was drawn from the local thickenings of the walls of the leaf-cells. In *F. Rappii* these included not only trigones but also intermediate thickenings, the latter being especially numerous in the lobules but occurring also to some extent in the lobes. In *F. inflata* the only thickenings present were supposed to be the trigones.

It has since been demonstrated, through the studies of Miss Haynes and the writer, that the distinction just noted is far from constant. Although the leaves of some of the more lax specimens of *F. inflata* from northern localities seem to show a complete lack of intermediate thickenings in the walls of their cells, careful search will usually reveal an occasional such thickening in the lobules, even in cases where none are present in the lobes. In specimens from more southern stations there is a tendency toward an increase in the number of lobular thickenings, while similar thickenings make their appearance in the lobes, until the condition characteristic of *F. Rappii* is reached. Since the other slight distinctions

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[1] Bull. Torrey Club **38**: 261–271. 1911.

between the species prove to be equally uncertain, it becomes necessary to reduce *F. Rappii* to synonymy under *F. inflata* as indicated above.

In 1915 the writer reported *F. mexicana* from Arizona and New Mexico, the specimens from the latter state having been previously referred to *F. inflata*.[1] In recognizing the validity of *F. mexicana*, its very close relationship to *F. Rappii* was emphasized, and it was shown that the two species agreed closely in the character and distribution of the local wall-thickenings in the lobes and lobules. The distinctions brought out between them were relatively slight, and the species were kept apart largely on account of their wide geographical separation. With the inclusion of *F. Rappii* among the synonyms of the widely distributed *F. inflata*, the supposed distinctions between the Florida species and *F. mexicana* and between the latter species and *F. inflata* lose their significance and come within the limits of variability to be expected. The reduction of *F. mexicana* to synonymy follows as a matter of course.

Another closely allied autoicous species is *F. saxicola* Aust.,[2] under which Müller has recently included the European *F. cleistostoma* Schiffn. & Wollny as a synonym.[3] This species, in North America, is known only from Connecticut, New Jersey and Texas, while in Europe it seems to be confined to the vicinity of Meran in the Tyrol. The beak of the perianth in *F. saxicola* is completely blocked by papillae growing out from the inner surface, while the beak in *F. inflata* was supposed to be free and open. Miss Haynes, however, has called the writer's attention to the fact than even in *F. inflata*, especially in material from southern localities, the beak may show a few internal papillae, although these are rarely visible until the beak has been split lengthwise and spread out flat. The distinction between the beaks thus proves to be quantitative rather than qualitative in character. Since the other distinctions between the species are not very striking the reduction of F. *saxicola* to synonymy under *F. inflata* might likewise seem to be indicated, but the writer hesitates to make this reduction positively until more and better material of *F. saxicola* is available for study.

The type specimens of *F. inflata* were collected by Beyrich "in America septentrionali ad Whastite Red River" and are presumably in the Gottsche Herbarium at Berlin. Several stations for the species have been recorded by the writer from time to time, but in order to give a comprehensive idea of its known range in North America a complete list of the specimens examined is given below.

CONNECTICUT: Brookfield, *Evans;* Salisbury, *Lorenz*. DISTRICT OF COLUMBIA: Georgetown, *Coville* (distributed as *F. virginica* in Underwood & Cook's Hep. Amer. *68*). NORTH CAROLINA: Winston-Salem, *Chapman 613*. GEORGIA: Flint River Swamp, Sumter County, *Harper 2042 f*. FLORIDA: Sanford and vicinity, *Rapp* (including the type of *F. Rappii*). ALABAMA: Mobile, *Mohr*. MISSISSIPPI: without definite locality, *Hall*. OHIO: Fairfield County, *Miller*.

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[1] BRYOLOGIST **13:** 36. 1910.

[2] See Rhodora **12:** 202. 1910.

[3] Rabenhorst's Kryptogamen Flora **6**^{2}**:** 631. 1915.

MINNESOTA: Granite Falls, *Anderson 52;* Carlton, *Conklin* (distributed in Miss Haynes's Amer. Hep. *94*). LOUISIANA: Baton Rouge, *Joor.* St. Martinsville, Lafayette and several other localities, *Langlois.* TEXAS: Austin, *Underwood, McAllister.* NEW MEXICO: Cloudcroft, Sacramento Mountains, *Wooton.* ARIZONA: Mt. Lemmon, Catalina Mountains, *Johnson;* Madera Canyon, Santa Rita Mountains, *Bartram 263*.. MEXICO: without definite locality or collector's name (type of *F. mexicana* in the Lindenberg Herbarium at Vienna).

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FOURTH SERIES

VOL. XIII, No. 6, pp. 111–130 NOVEMBER 6, 1923

VI

NOTES ON THE HEPATICÆ OF CALIFORNIA[1]

BY

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The Hepaticæ of California were ably described in 1899 by Howe[2], who recognized eighty-five species and several distinct varieties. During the twenty-four years that have since elapsed, ten additional species from California have been recorded in the literature. Of these the following were proposed as new: *Aplozia pendletonii* Pearson, *Cephalozia patulifolia* Steph., *Fossombronia hispidissima* Steph., and *Scapania perlaxa* Warnst. The others are all northern species with an extensive geographical distribution.

Within the past few years Mrs. E. C. Sutliffe, of the California Academy of Sciences, has interested herself in the Hepaticæ and has collected diligently in several parts of the state. Her careful collections, supplemented by the collections made by various other students, have added eight more species to the flora of California. These and the additions already recorded in the literature are noted in the present report. Attention is likewise called to certain changes in nomenclature that affect the species of California, and a few species are critically discussed. Perhaps the most important

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[1] Contribution from the Osborn Botanical Laboratory.
[2] Mem. Torrey Club 7. 1899.

November 6, 1923.

of these are the species of Fossombronia, to which Mrs. Sutliffe has devoted particular care, but it must be admitted that our knowledge of these species is still far from adequate. In the arrangement of the notes Howe's sequence is followed throughout, and all page-references are to his work, unless otherwise noted.

1. **Riccia lescuriana** Aust. (p. 15)

It has recently been shown by Howe[3] that the correct name for this species is *R. beyrichiana* Hampe.

2. **Riccia minima** L. (p. 23)

Most writers now apply to this species the later name, *R. sorocarpa* Bisch. The reasons for doing so have been discussed by the writer.[4]

3. **Riccia americana** M. A. Howe (p. 24)

According to the later views of its author[5] the species should be considered a synonym of *R. austini* Steph.

4. **Riccia fluitans** L.

Lily Lake, Marin County, September, 1921, Mrs. Sutliffe. New to California. This widely distributed species has been reported also from the neighboring states of Nevada and Arizona and is described by Howe (p. 33).

5. **Neesiella rupestris** (Nees) Schiffn.

This species, which (in the writer's opinion) should be known as *Grimaldia rupestris* (Nees) Lindenb., has recently been reported from California by Conklin[6], the record being based on the following specimen: Santa Anita Canyon, San Gabriel Mountains, Los Angeles County, June, 1921, George L. Moxley 997. Through the kindness of Dr. Conklin the writer has had the privilege of examining this specimen and

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[3] Bryologist 20: 34. 1917.
[4] See Rhodora 12: 195. 1910.
[5] North Am. Flora 14: 17. 1922.
[6] Bryologist 25: 23. 1922.

would refer it to *Cryptomitrium tenerum* (Hook.) Aust. (p. 45), rather than to the Grimaldia.

6. **Asterella violacea** (Aust.) Underw. (p. 53)

In the opinion of the writer[7] this species is a synonym of *A. bolanderi* (Aust.) Underw.

7. **Asterella gracilis** (F. Web.) Underw. (p. 56)

The writer[8] has recently discussed the synonymy of this species and shown that it should bear the name *A. ludwigii* (Schwaegr.) Underw.

8. **Lunularia cruciata** (L.) Dumort. (p. 60)

At the time Howe published his description of this introduced species it was known in North America in a gemmiparous condition only. A few years later Miss Julia T. Shinn[9] announced the discovery of fruiting material at Niles, California, and Mrs. Sutliffe, in the past year, has collected additional fruiting specimens in Mill Valley, Marin County. They grew, according to her label, "on damp banks beside steps forming a street."

9. **Sphærocarpos californicus** Aust. (p. 65)

Through the careful work of Miss Haynes[10] it has been proved that this species is a synonym of *S. texanus* Aust., which antedates *S. californicus* by two years.

10. **Riccardia major** Lindb. (p. 72)

In accrediting *R. major* to California Howe compared the species with *R. pinnatifida* (Nees) Trevis. and stated that the latter was distinguished by its "softer, flatter thallus, without indication of a unistratose margin," by "its looser texture,"

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[7] See Contr. U. S. Nat. Herb., 20: 303. 1920.
[8] Contr. U. S. Nat. Herb., 20: 269. 1920.
[9] Torreya 2: 124. 1902.
[10] Bull. Torrey Club 37: 223. 1910.

and by its dioicous inflorescence and smooth calyptra, the last two characters being quoted from other writers. In 1900 Schiffner[11] discussed "*Aneura pinnatifida* Nees" at length and showed that the species was an aggregate, based partly on tropical material and partly on European material. The tropical material, in his opinion, represented a species closely related to *R. multifida* (L.) S. F. Gray, while the European material agreed in great part with *Riccardia sinuata* (Dicks.) Trevis., a species antedating Nees von Esenbeck's species by a number of years. Schiffner therefore recommended that *Aneura pinnatifida* should no longer be recognized as a species and that the European specimens of the so-called *A. pinnatifida* should be definitely referred to *R. sinuata.* He showed further that the inflorescence of *R. sinuata* was autoicous (instead of being dioicous) and that the calyptra was covered over with inflated or tubular surface-cells (instead of being smooth), thus agreeing in these respects with *R. major* as described by Howe.

In connection with *R. sinuata* Schiffner discussed *R. major* and reached the conclusion that the two species were very close allies. At the same time he pointed out certain slight distinctions between them and suggested that they be recognized as distinct species, at least provisionally. His differential characters were drawn in part from the sporophyte and in part from the gametophyte. Six years later he[12] showed that the sporophytic differences were less constant than he had supposed but still insisted on the importance of the gametophytic differences and continued to regard *R. major* as a valid species. According to his account *R. sinuata* is a true aquatic; the thallus is rigid, fleshy and brittle and shows a bipinnate or tripinnate branching; the main axis is six to 10 cells thick, and the most delicate branches are never fewer than four or five cells thick; while the axis and leading branches broaden out at the apex. *R. major,* on the other hand, is a swamp plant rather than a true aquatic; the thallus is thinner and less rigid than in *R. sinuata* and shows a simply pinnate or rarely bipinnate branching; the main axis is only five cells thick on the more robust specimens, and the branches are only three

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[11] Lotos 48: 357-382. 1900.
[12] Oesterr. Bot. Zeitschr. 56: 170. 1906.

or four cells thick; while the axis and branches never broaden out at the apex.

It will be seen that Schiffner's differential characters are based on variable features, and this is made still more evident by his remarks on a specimen of *R. major* collected by Howe at Duncan's Mills, Sonoma County, California. In this specimen the main axis is described as six cells thick and is said to broaden somewhat at the apex, thus showing (as Schiffner himself admits) an approach to *R. sinuata.* It is not surprising therefore that his conclusions regarding *R. sinuata* and *R. major* have not been universally accepted by European hepaticologists. Müller,[13] for example, does not accept them at all; in his opinion the differential characters are insufficient even for the establishment of a variety and he cites *A. major*[14] "mit ruhigem Gewissen" as a simple synonym of *A. sinuata* (Dicks.) Dumort. Macvicar,[15] on the other hand, accepts *A. major* as a valid species distinct from *A. sinuata.* At the same time he states that "it is doubtful how far" it "is permanently distinct" and cites a specimen from Sussex in which some of the thalli are bi- or tripinnate.

From the data in the literature and from the study of a large series of specimens the writer is inclined to regard *R. major* as a poorly developed form or variety of *R. sinuata,* rather than as a distinct species, its peculiarities being apparently associated with an unfavorable environment. It may be added that some of the material from California represents the more typical form of *R. sinuata,* the thalli being often tripinnate and the main axis seven to nine cells in thickness. This is true, for example, of the two specimens collected by Mrs. Sutliffe in 1922 at the following stations: Big Carson Canyon and Mt. Tamalpais, both in Marin County.

11. **Fossombronia hispidissima** Steph. Mém. Herb. Boissier 16: 35. 1900

Mill Valley, Marin County, Mrs. Sutliffe; near Stanford University, Santa Clara County, C. F. Baker (determined

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[13] Rabenhorst's Kryptogamen-Flora 6: 340. 1908.

[14] The combination, *"Aneura major,"* was apparently first used by the writer in connection with a specimen from Alaska (see Zoe 5: 129. 1901).

[15] Student's Handb. British Hep. 55. 1912.

by Stephani and distributed in Pacific Slope Bryophytes, No. 453); Arroyo Grande, San Luis Obispo County, O. D. Allen; Libby Park, Ojai, Ventura County, Miss C. C. Haynes.

In his treatment of the genus Fossombronia, Howe (p. 80) referred all his Californian material to *F. longiseta.* In doing this he assigned to the species a wide range of variation in the surface-markings of the spores. At one extreme the spores (as shown in figs. 16, 18 and 19) were of the cristate type, the markings being in the form of narrow, subparallel ridges, sometimes anastomosing irregularly but rarely forming closed meshes. At the other extreme the spores (as shown in figs. 17 and 20) approached the echinate type, the ridges being broken up more or less completely into spines. These extremes were so different that Howe admitted the possibility of there being more than one species included in what he called *F. longiseta;* he stated, however, that he could not "draw separating lines in any satisfactory way," owing to the apparent existence of intermediate types of spores. At the same time he emphasized the fact that all his specimens "from stations north of San Francisco" had "spores of the purely cristate type."

In Stephani's monograph of Fossombronia, published the year after Howe's work, he proposed *F. hispidissima* as a new species and discussed Howe's figures of *F. longiseta.* In his opinion the differences shown were too great to fall within the limits of a single species and he recognized three species, *F. hispidissima, F. longiseta* and *F. pusilla,* as members of the Californian flora. To the first he assigned hispid spores, to the second reticulate spores, and to the third cristate spores.

The writer has examined many specimens of Fossombronia from various parts of California, but has not seen any in which the spores were reticulate. Spores of this type, moreover, are not shown in Howe's figures. Stephani's *"F. longiseta,"* therefore, must remain uncertain in the absence of the specimen upon which his description was based. However this may be, it seems advisable to recognize *F. hispidissima* as a valid species, even if the surface-markings of the spores are not invariably in the form of discrete spines.

As the writer understands the species, the spores measure 30-40µ in diameter, and the periphery of the spherical face shows about forty projections measuring 3-4μ in length. These projections sometimes represent actual slender cones tapering to sharp points. In other cases they may represent the optical sections of narrow ridges extending for a variable but short distance from the periphery toward the center of the spherical face. In exceptional cases a series of such ridges may be distinctly parallel when a spore is viewed sidewise, but this appearance is no longer to be made out when the spherical face is turned toward the observer's eye. Except for these occasional parallel ridges the thickenings of the spore wall are exceedingly irregular and consist of sharp slender cones or short and narrow ridges closely crowded together and showing no indications of closed meshes. Although ridges may be evident even in the median portion of the spherical face they are so short and so irregular that they look very different from the longer and anastomosing ridges seen in a spore of the cristate type. Howe's figs. 17 and 20 clearly represent *F. hispidissima.* Fig. 20 was drawn from a specimen collected by A. J. McClatchie at Pasadena, so that this locality also may be cited for the species. Fig. 17 was drawn from a plant which Howe thought might have represented a portion of Howe's original material of *F. longiseta.* It came from the Austin collection but no data were given regarding its collector or the part of California where it was found. The type specimen of *F. hispidissima,* collected at San Francisco by Bolander, has not been seen by the writer.

The occurrence of ridges on spores of the echinate type is by no means unusual. Even in *F. cæspitiformis* (Raddi) De Not. of southern Europe and neighboring regions, which is one of the most distinct species with spores of this character, the projections are really short ridges truncate at the tips; and these ridges, in Schiffner's var. *subcristata,*[16] have often a considerable length and give the spores an approximately cristate appearance, especially when viewed from the side. In another echinate species, the rare *F. mittenii* Tindall[17] of Devonshire, England, the projections are again in the form of short ridges with rounded, truncate or even emarginate apices. The European species which seems to come closest to *F. hispidissima* is

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[16] Verhandl. Zool.-Bot. Ges. Wien 59: 34. 1909.
[17] Jour. Bot. 36: 44. *pl. 382* B. 1898.

F. echinata Macvicar,[18] based on material from Algeria, Dalmatia and southern Italy and since reported by Casares Gil from Spain.[19] In this species the spores are described as densely hispid, the individual projections being 2-4µ long and acute or subacute at the tips. No intimation is made in the published descriptions that any of the projections are ever in the form of ridges, so that Macvicar's species must show the echinate condition in an especially typical way.

12. **Fossombronia longiseta** Aust. (p. 80)

"California", without definite locality, H. N. Bolander (distributed in Austin's Hep. Bor.-Amer. No. 118); Mill Valley, Marin County, M. A. Howe (distributed in Underwood & Cook's Hep. Amer. No. 157); same locality, Mrs. Sutliffe (a series of specimens); Mt. Tamalpais, Marin County, M. A. Howe 6; Yosemite Valley, Mariposa County, A. W. Evans; Ione, Amador County, Miss Alice Eastwood; Spencer Valley, San Diego County, L. Abrams 3800; Claremost, Los Angeles County, P. A. Munz 4727. This list is based on the specimens in the Yale Herbarium; Howe gives several additional localities for the species, but it is possible that some of his records are based on what is here called *F. hispidissima.* Outside of California the only station for *F. longiseta* known to the writer is Cherry Creek, Santa Catalina Mountains, Arizona, G. E. Nichols.[20]

The segregation of *F. hispidissima* as a species leaves a residue of California Fossombroniæ in which the spores conform to the cristate type. Unfortunately, these cristate spores vary markedly in the number of ridges that they show, this number being most conveniently estimated for comparative purposes by counting the projections at the periphery of the spherical face. In the specimens distributed by Austin in his Hepaticæ Boreali-Americanæ there are usually from 22 to 26 of these projections. Since these spore-bearing specimens were issued by Austin himself they may well be regarded as authentic representatives of *F. longiseta,* especially in the absence of an actual type specimen, to which Howe calls

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[18] Rev. Bryol **38**: 73 *f. l.* 1911.
[19] Trab. Mus. Nac. Cien. Nat. Ser. Bot. **8**: 25. 1915.
[20] See Evans, Bryologist **20**: 61. 1917.

attention. Some of the specimens collected by Mrs. Sutliffe in Mill Valley conform pretty closely to these numbers, one having spores with 24 to 27 projections, another with 21 to 24, and still another with 18 to 24. In other Californian material, however, the spores show from 16 to 20 projections; this is the case, for example, in Howe's No. 6 from Mt. Tamalpais and in Abrams' specimen from Spencer Valley. In still other material the spores have from 26 to 32 projections, as in one of Mrs. Sutliffe's Mill Valley specimens and in Miss Eastwood's specimens from Ione. These variations in the number of ridges are shown clearly in Howe's figs. 16, 18 and 19.

In Europe the two best known species with cristate spores are *F. pusilla* (L.) Dumort. and *F. wondraczeki* (Corda) Dumort. In *F. pusilla* the number of peripheral projections is given as 16 to 18 by Müller and as 16 to 24 by Macvicar. In *F. wondraczeki* the numbers are 30 to 32 and 28 to 36, respectively. There is no evidence that these species intergrade, and *F. wondraczeki* seems to be perfectly constant in eastern North America, where *F. pusilla* is apparently unrepresented. It will be noticed that the Californian specimens include forms with just as few spore-ridges as *F. pusilla,* others with as many as *F. wondraczeki,* and still others with an intermediate number. It might therefore at first appear as if three species were present, *F. pusilla, F. wondraczeki* and a species between them, for which the name *F. longiseta* could be retained. It would, however, be difficult, if not impossible, to tell where *F. longiseta* ended and the other species began, owing to the fact that the number of ridges in the intermediate type of spore tends to vary toward both extremes.

In view of these facts it seems advisable to search for differential characters in the gametophyte. It is well known that the leaves in the various species of Fossombronia are unfortunately very inconstant in size, in shape and in the character of their lobing, and that the pseudoperianths are equally inconstant in their features, so that little can be hoped for here. Differences in habit, however, seem to be more trustworthy and apparently these can be utilized in the present instance. In northern Europe, for example, *F. pusilla* and *F. wondraczeki* seem to be definitely annuals, producing their spores in the late summer and early autumn and presenting no gametophytic adaptations for carrying them through the winter. They thus stand in sharp contrast to such species as *F. angulosa* Raddi, which produce their spores in the late winter or spring and which seem to be definitely perennials. So far as observations go the Californian Fossombroniæ are all perennial and even, in some cases, produce tuberous thickenings of the stem, enabling them to withstand periods of dryness. If this perennial habit proves constant the writer suggests that the name *F. longiseta* be retained for all cristate-spored forms of the region and that a range in the number of peripheral projections from 18 to 32 be admitted. Of course, if it should be demonstrated that the perennial habit or the power to produce tubers was restricted to forms having a more limited range in the number of surface-ridges, a segregation might be indicated.

It should be mentioned in this connection that the spores with few ridges in the Californian specimens, although simulating those of *F. pusilla* in a marked degree, do not absolutely agree with them, owing to the fact that the ridges are only 2-3μ high, while those of *F. pusilla* are usually 3-5μ high and may be as much as 7μ high in the case of the var. *decipiens* Corbière. Since, however, the ridges in poorly developed plants of *F. pusilla* are often lower, this distinction must be used with caution. It should be mentioned also that Schiffner has recently described and figured, under the name *F. loitlesbergeri*,[21] a perennial species from Dalmatia with cristate spores, in which the number of marginal projections is about 25. The spores thus occupy, so far as the number of ridges is concerned, an intermediate position between those of *F. pusilla* and those of *F. wondraczeki*. Although at first sight *F. loitlesbergeri* might seem to approach *F. longiseta* very closely, its spores are considerably larger, measuring 50-60μ in diameter, and the ridges are 6-7μ high. Since the spores of *F. longiseta* are only 40-50μ in diameter and since the ridges are only 2-3μ high the two species seem to be amply distinct.

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[21] Hedwigia **48**: 195. *f. 1-14.* 1909.

13. **Fossombronia pusilla** (L.) Dumort.

Stephani's record for California[22] was based on specimens collected by Howe, no definite station being mentioned. These particular specimens have not been available for study, but the writer feels convinced that they must represent some form of *F. longiseta,* probably a form in which the number of ridges on the spores was relatively small. Spores of this character are represented in Howe's fig. 18, drawn from a Mill Valley specimen. Until it is definitely established that such spores are associated with annual gametophytes, there seems to be no conclusive reason why *F. pusilla* should be considered a member of the Californian flora. In fact, the occurrence of the species in North America is very doubtful, all the records (so far as known) being based on sterile or incorrectly determined specimens.

14. **Marsupella sullivantii** (De Not.) Evans

On rocks. Gold Lake, Plumas County, September, 1900, J. B. Leiberg 5496. New to California; widely distributed in northern countries and previously reported from Washington.

15. **Nardia crenulata** (Sm.) Lindb. (p. 94)

In the writer's opinion the true *N. crenulata* has not yet been found in the western part of North America. It is replaced in the Pacific Coast region by the closely related *N. rubra* (Gottsche) Evans,[23] a species which Howe included among the synonyms of *N. crenulata.*

16. **Nardia obovata** (Nees) Lindb. (p. 96)

The writer feels convinced that the specimens from Blue Lake, Humboldt County, upon which Howe's record was based, represent *Jungermannia sphærocarpa* Hook. or some closely related species.[24] Unfortunately the specimens are too

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[22] Mém. Herb. Boissier **16**: 25. 1900.
[23] See Bryologist **22**: 62. 1919.
[24] See Rhodora **21**: 163. 1919.

fragmentary for a positive determination, more especially since *J. sphærocarpa* is otherwise unknown from California.

17. **Jungermannia lanceolata** L.

On wet soil along a stream, Lower Salmon Lake, Sierra County, October, 1921, Mrs. Sutliffe. New to California; widely distributed in northern regions and previously known from Washington.

18. **Jungermannia pendletonii** (Pearson) comb. nov.

Aplozia pendletonii Pearson, Bryologist **23**: 50. pl. 2. 1920

This interesting species was discovered by George M. Pendleton on the western side of Mt. Shasta, at an altitude of 4000 feet. Specimens collected on May 8, 1910, were distributed by Miss Haynes in her American Hepaticæ (No. 90), under the name *Jungermannia cordifolia* Hook.; the type specimens were collected on August 4, 1917; and still other material is dated April 16, 1919. Only the 1910 and 1919 specimens have been examined by the writer.

Although *J. pendletonii* is amply distinct from *J. cordifolia* the two species resemble each other very strongly, especially when well developed. Both are characterized by a tufted habit and a dark green color, often blackish when dry and sometimes tinged with a purplish, brownish, or brownish red pigmentation; both show occasional terminal branches of the Frullania type and also intercalary branches, the latter arising near the ventral bases of the leaves; and the leaves in both tend to assume a suberect position, clasping and partially concealing the stem.

When the leaves are dissected off and spread out flat certain differences at once become apparent. In *J. cordifolia* the leaves are broadest just above the base and then taper gradually but distinctly to a rounded apex. They are usually described as "heart-shaped," but the basal portion is rounded on the sides rather than cordate and is even very slightly decurrent. The leaf-cells are characterized by their thin but often pigmented walls, by the almost complete absence of trigones, and usually by the presence of delicate striolations on the cuticle. In some cases, especially toward the margins of the leaves, very minute trigones with concave sides can be demonstrated, but they are so indistinct that they are practically negligible. In *J. pendletonii* the leaves are approximately orbicular and do not show the tapering found in *J. cordifolia,* although the rounded basal portions are not dissimilar in the two species. The leaf-cells yield further distinctions. In *J. pendletonii* the median cells are mostly 40-50μ long and 25-30μ wide, while the marginal cells are 27-32μ in diameter; in *J. cordifolia* the median cells are mostly 40-45 × 20-30μ, while the marginal cells are only 20-23μ in diameter, the cells thus showing a more marked decrease in size in passing from the median portion outward. In *J. pendletonii,* moreover, it is usually possible to demonstrate distinct trigones, especially in the marginal portions of the leaves, but the striolations are very indistinct although not entirely absent.

Pearson emphasizes as a characteristic feature of his species the presence of two layers of cells in the basal portion of the leaf, the two layers not being "regularly arranged cell on cell" but crossing each other. This two-layered portion does not stretch entirely across the leaf but occupies a vaguely defined area toward the ventral side. In poorly developed leaves the area is much reduced in size and may be absent altogether. Just how distinctive this feature really is remains to be determined, since very few species of Jungermannia have been studied from this particular point of view. It is not, however, absolutely distinctive. The robust Norwegian material of *J. cordifolia,* for example, collected by E. Jörgensen at Gulen in Sördfjord and distributed in Schiffner's Hepaticæ europaeæ (No. 394), shows small basal leaf areas where the cells are in two layers; and the same thing is true of some of the more vigorous North American specimens examined by the writer. None of these, however, are comparable in distinctness with the much larger areas found in *J. pendletonii.*

The male inflorescence of *J. pendletonii* was unknown to Pearson, but he described the perichætial bracts and perianths and illustrated them in a supplementary note.[25] According

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[25] Bryologist 23: 84, 85. *f. 1-3.* 1920.

to his account the perianths are considerably shorter than the bracts, and yet he regards them as "normal-sized and perfect." They are said to be four- or five-plicate in the upper part, abruptly contracted at the mouth, and entirely free from the bracts, the latter being similar to the leaves. The writer is unable to add to this description, since the specimens at his disposal are wholly sterile, but it seems hardly probable that the perianths studied by Pearson were associated with fertilized archegonia.

The Californian species of Jungermannia are in need of further study. In September, 1866, Bolander discovered two species, *J. bolanderi* Gottsche and *J. danicola* Gottsche, on Mt. Dana, at an altitude of about 3100 meters. Neither of these species has since been collected, and our knowledge concerning them is still unsatisfactory, as Howe has pointed out (pages 99 and 101). According to his descriptions and Gottsche's figures,[26] *J. danicola* is paroicous and is evidently a member of the *J. sphærocarpa* group. *J. bolanderi,* on the contrary, may be an ally of *J. pendletonii,* and Pearson in a recent letter expressed the fear that the two species might prove synonymous. A very fragmentary specimen of *J. bolanderi* in the herbarium of the New York Botanical Garden shows that this is probably not the case. The leaves do not show a two-layered area; neither do they clasp the stem, but spread obliquely, as Gottsche's figures show. Howe's description of the perianth in an immature condition is much like Pearson's account of that organ in *J. pendletonii,* but fully developed perianths might perhaps yield distinctive characters.

19. **Jungermannia riparia** Tayl.

In the rocky bed of a stream, near Willoughby Mine, Sierra County, October, 1921, Mrs. Sutliffe; near Shasta Retreat, Siskiyou County, September 1, 1922. Miss Eastwood. New to California; widely distributed in Europe but previously known in North America from British Columbia and Washington only.

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[26] Published by Underwood, Bot. Gaz. 13: *pl. 3, 5.* 1888.

20. **Lophozia baueriana** Schiffn.

Reported from California by Conklin,[27] the record being based on a specimen collected at Sisson by George M. Pendleton. By most writers *L. baueriana* is now regarded as a synonym of *L. hatcheri* (Evans) Steph.

21. **Lophozia exisa** (Dicks.) Dumort.

Lake Lagunitas, Marin County, March, 1922, Mrs. M. L. Campbell 2, in part. New to California; widely distributed in northern regions and previously known from Washington.

22. **Lophozia hornschuchiana** (Nees) Schiffn.

On moist earth, decayed wood and rocks, Lower Salmon Lake and vicinity, October, 1921, Mrs. Sutliffe (nine specimens). New to California; widely distributed in northern regions and previously known from Oregon and northward.

23. **Lophozia ovata** (Dicks.) M. A. Howe (page 111)

Most recent writers refer this species to the genus Diplophyllum, where it appears under the name *D. ovatum* (Dicks.) Steph.[28]

24. **Chiloscyphus polyanthos** (L.) Corda (p. 118)

If Schiffner's recent segregations[29] are accepted the occurrence of the true *C. polyanthos* in California must be regarded as doubtful. The genus is represented in the state, however, by the three species cited below. Some of the specimens enumerated are listed by Howe under the typical form of the species and others under *C. polyanthos rivularis* (Schrad.) Nees (p. 119). Several of Howe's specimens have not been seen by the writer.

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[27] Bryologist 15: 11. 1912.

[28] See Miss Haynes, Bryologist 21: 89. 1918.

[29] See Beih. Bot. Centralbl. 29^2: 74-116-*pl. 1, 2.* 1912.

25. **Chiloscyphus fragilis** (Roth) Schiffn.

Without definite locality, H. N. Bolander; Yosemite Valley, C. M. Cooke.[30]

26. **Chiloscyphus pallescens** (Ehrh.) Dumort.

On wet logs, Big Valley Mountains, Modoc County, M. S. Baker and F. P. Nutting.

27. **Chiloscyphus rivularis** (Schrad.) Loeske.

Without definite locality, H. N. Bolander; Humboldt County, Miss K. Inglis; near Lake Lagunitas, Marin County, Mrs. Sutliffe; Sacramento River, near Sisson, Siskiyou County, M. A. Howe (specimens from this locality were distributed in Underwood & Cook's Hep. Amer., No. 170, as *C. polyanthos rivularis);* McCloud River country, Siskiyou County and near Shasta Retreat, Siskiyou County, Miss Eastwood; near Salmon, Horse and Packer Lakes, Sierra County, Mrs. Sutliffe (six specimens); Horse Corral Meadows and vicinity, Tulare County, F. J. Coulter (five specimens).

28. **Cephalozia affinis** Lindb.

Reported from California by the writer,[31] the record being based on specimens collected by G. M. Pendleton at Sisson, Siskiyou County.

29. **Cephalozia divaricata** (Sm.) Dumort. (p. 127)

During recent years *"C. divaricata"* and its allies have been intensively studied, especially by the European hepaticologists Schiffner and Douin. As a result of his investigations Douin reached the conclusion that this group of plants was not only generically distinct from Cephalozia but that it represented a distinct and well-marked family, to which he gave the name Cephaloziellaceæ. He distinguishes six genera, only two of which, Cephaloziella and Prionolobus, are recognized members of the California flora. His latest paper dealing with the

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[30] See Evans, Rhodora 14: 218. 1912.
[31] Bryologist 17: 89, 1914.

group was published in 1920[32] and has been of great help to the writer in determining the Californian material. Howe's "*Cephalozia divaricata*" is listed below (at least in part) under the name *Cephaloziella byssacea,* while his var. *scabra* (p. 129) is regarded as a synonym of *C. papillosa.* Two other species are reported for the first time from the state, and a fifth species, *C. palulifolia,* although unknown to the writer, is briefly alluded to.

30. **Cephaloziella byssacea** (Roth) Warnst.

Without definite localities, H. N. Bolander (several specimens); "Mission Hills," H. N. Bolander; Yosemite Valley, A. W. Evans.

31. **Cephaloziella hampeana** (Nees) Schiffn.

On banks, Wheeler's Sulphur Springs, Ventura County, February, 1921, Miss C. C. Haynes 2041. New to California, but widely distributed in Europe and in most parts of North America.

32. **Cephaloziella limprichtii** Warnst.

On earth, Mill Valley, Marin County, February, 1922, Mrs. M. L. Campbell 3. New to California; widely distributed in northern regions but heretofore known from very few North American localities. The synonymy of the species is greatly confused.

33. **Cephaloziella papillosa** (Douin) Schiffn.

Cazadero, Sonoma County, M. A. Howe; Mill Valley and Lake Lagunitas, Marin County, M. A. Howe; Muir Woods (Redwood Canyon), Marin County, Mrs. M. L. Campbell. Howe's specimens were determined by Douin.

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[32] Mém. Soc. Bot. France 29: 1-90. *f. 1-9.* 1920.

34. **Cephaloziella patulifolia** (Steph.) Douin, Mém. Soc. Bot. France 29: 70. 1920
Cephalozia patulifolia Steph. Bull. Herb. Boissier II. 8: 509

This species was based on a specimen collected in California by Bolander, no more definite locality being mentioned in the published descriptions. Through the kindness of Mr. Maxon the writer has had the privilege of studying Bolander's Cephaloziellæ in the U. S. National Herbarium but has found nothing that agrees with Stephani's or Douin's account. According to the latter writer *C. patulifolia* agrees with *C. papillosa* in having rough leaves and underleaves but differs in its autoicous inflorescence. Stephani quotes Howe's var. *scabra* as a possible synonym of *C. patulifolia* but Douin cites it definitely under *C. papillosa.*

35. **Cephalozia Turneri** (Hook.) Lindb. (p. 129)

This species is a representative of the genus Prionolobus and may be known as *P. turneri* (Hook.) Schiffn.

36. **Scapania heterophylla** M. A. Howe (p. 155)

This interesting Scapania is still known only from the type locality, Sisson, Siskiyou County, where it was collected on submerged stones in a mountain stream by Howe in 1894. Since its description by Howe it has been studied by Müller,[33] by Stephani[34] and by Warnstorf.[35] Müller admitted its validity but recognized its close relationship to *S. undulata* (L.) Dumort. Stephani regarded it as "ganz deformiert" and suggested that it might perhaps be referable to some other species of the genus, without attempting to settle the matter definitely. Warnstorf went still further and reduced it to varietal rank under *S. undulata,* its name thus becoming *S. undulata* var. *heterophylla* (M. A. Howe) Warnst. In his opinion the uninjured leaves at the tips of the stems and branches are quite indistinguishable from those of *S. undulata,* and for this

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[33] Nova Acta Kais. Leop.-Carol. Akad. Naturf. 83: 137. 1905.
[34] Sp. Hepat. 4: 138. 1910.
[35] Hedwigia 63: 111. 1921.

reason he considers the reduction justifiable. He makes no mention, however, of the unlobed leaves, which Howe describes as interpolated among the more normal bilobed leaves. Until the significance of these is more fully understood, it seems wisest to keep *S. heterophylla* distinct from *S. undulata*.

37. **Scapania perlaxa** Warnst. Hedwigia 63: 70. 1921

The type specimen of this species is preserved in the Botanical Museum at Berlin-Dahlem and was collected by Bolander on wet granite rocks in the Yosemite Valley. The writer has as yet been unable to examine this specimen and has seen no material of Bolander's that agrees with Warnstorf's description, although all the Californian Scapaniæ in the U. S. National Herbarium have been available for study. According to its author, *S. perlaxa* bears a resemblance to *S. geniculata* Massal., a species which Arnell[36] considers a synonym of *S. helvetica* Gottsche and scarcely distinct from the widely distributed *S. irrigua* (Nees) Dumort. The distinctive features emphasized by Warnstorf are the rounded and entire leaf-lobes, the hydrophytic habit, the distant leaves, and the long flagelliform branches. The implied absence of trigones in the leaf-cells might seem to indicate an approach to *S. undulata,* but further studies are clearly necessary before the relationships of the species are adequately established.

38. **Scapania subalpina** (Nees) Dumort.

First recorded from California by Müller,[37] the following two stations being cited: Yosemite Valley, bank of the Merced River, H. N. Bolander, and Sierras, June, 1864, W. H. Brewer. It is now possible to report the species from three additional localities, namely: "wet bank of stream flowing out of Deer Lake, Sierra County, 6950 ft. alt.," Mrs. Sutliffe; Horse Corral Hill and East Fork of Clover Creek, Tulare County, F. J. Coulter.

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[36] Schwedish. Art. Diplophyllum u. Martinellia 37. 1922.
[37] Nova Acta Kais. Leop.-Carol. Akad. Naturf. 83: 69. 1905.

39. **Porella rivularis** (Nees) Trevis.

The correct name for this species seems to be *P. cordæana* (Hüben.) Evans.[38]

The additions and subtractions recorded in the preceding notes represent a net addition of 16 species to the flora of California since the date of Howe's work. The total number of species now known from the state is thus increased to 101.

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[38] See Bryologist 22: 72. 1919.

Reprinted for private circulation from
THE BOTANICAL GAZETTE, Vol. LXXVI, No. 4, December 1923

REACTION OF PROTOPLASM TO SALTS AND ANTAGONISTIC ACTION OF SALTS AND ALCOHOL[1]

WILLIAM SEIFRIZ

Introduction

Some recent experiments by the writer on the reaction of the leaf cells of *Elodea* to certain reagents, revealed a striking difference in the toxic effects of the two bivalent cations, strontium and calcium, and a similarity in the effects of the monovalent cation sodium and the bivalent cation calcium. The changes in osmotic pressure and in protoplasmic streaming were qualitatively the same in the case of Na and Ca, but the exact opposite in the case of the two bivalent ions, Ca and Sr. Further, the change in osmotic pressure occasioned by Sr gave every indication of being due to an increase in permeability. These facts all stand in opposition to the widely accepted hypothesis that protoplasm reacts similarly to all monovalent cations on the one hand, and to all bivalent cations on the other hand, the former increasing, the latter decreasing permeability.

The experimental work on which this article is based was done in the laboratories of the Botanical Institute of the University of Geneva, Switzerland, where the writer enjoyed the privileges of a guest through the courtesy of the Director of the Institute, Professor R. CHODAT, to whom the writer's thanks are due for many kindnesses.

Method and material

The plasmolytic method of determining changes in osmotic pressure of the cell contents was followed. This method is not suitable for accurate quantitative measurements, but does give results which are often in harmony with those obtained by other methods, notably in regard to the order of absorption of different salts. A decided advantage of the plasmolytic method is the fact that the cells studied are under direct observation, so that any abnormal conditions, such as changes in surface tension, viscosity,

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[1] Contribution from the Osborn Botanical Laboratory.

etc., which have an important bearing on permeability changes, can be detected.

The electrical conductivity method, while making quantitative measurements possible, is subject to criticism because of the impossibility of knowing whether the changes in resistance are actually due to corresponding changes in permeability. There exists the possibility that a change in conductivity may well result from a diffusion of substance from the salt solution into the tissue, bringing about changes in cell content of electrolytes without any change in permeability. That this may be true is indicated by the rapidity with which salts enter a cell in sufficient quantity to produce an immediate change in the relative positions of the cell inclusions. The writer has repeatedly observed a sudden aggregation of chloroplasts, before plasmolysis takes place, when a dilute solution of KNO_3 is added to an *Elodea* leaf. This immediate change in the position of the chloroplasts on the addition of a salt can only mean that there has been a very rapid entrance of the electrolyte into the cell, with no increase in permeability sufficiently great to permit a noticeable exosmosis of water. The whole problem of permeability presents so many difficulties that at present we can only present the data obtained from every possible method of attack. To restrict ourselves to any one theory or any single method of investigation is likely to lead to faulty conceptions.

Leaves of *Elodea* served as material. All observations were made on the superficial cells of the upper surface of the leaf. The reagents used were potassium nitrate (KNO_3), potassium chloride (KCl), sodium chloride($NaCl$), calcium chloride ($CaCl_2$), barium chloride ($BaCl_2$), copper hydroxide ($Cu(OH)_2$), and ethyl alcohol (C_2H_6O). Spring water was used, the same in which the *Elodea* plants were kept growing in the laboratory, and which in Geneva is very pure.

I. Reaction of protoplasm to some monovalent and bivalent cations

Experimental data

Potassium nitrate was used as the plasmolyzing salt. The critical plasmolytic values were determined by ascertaining the concentration of salt which would plasmolyze 50 per cent of the cells of a leaf in one-half hour. Owing to the rapidity with which the salt enters a normal protoplast, as is evident from the immediate aggregation of the chloroplasts, it was deemed best to shorten the time of application of the plasmolyzing salt as much as possible. The concentration of potassium nitrate which is isosmotic with the contents of the average normal epidermal cell of an *Elodea* leaf, that is, the critical plasmolytic concentration, is 0.3 M. Unless otherwise stated, this value is used for comparison. Since, however, the critical plasmolytic concentration of untreated cells varies considerably (it may be as low as 0.2 M and as high as 0.5 M KNO_3), it is highly important that the critical plasmolytic concentration of control leaves be determined in every experiment, and that these control leaves come from the same general region of the same shoot of *Elodea*.

Isosmotic concentrations of salts were used for treating the *Elodea* leaves in the case of potassium nitrate, sodium chloride, and calcium chloride. Lower concentrations of strontium chloride and barium chloride were ultimately employed, owing to the greater toxicity of these two salts. The following concentrations of solutions were used: KNO_3, 0.128 M, being the maximum concentration of this salt which will not plasmolyze a normal cell, no matter how long the time of treatment; NaCl, 0.128 M; $CaCl_2$, 0.128 M; $SrCl_2$, 0.064 M; and $BaCl_2$, 0.064 M.

CHANGES IN OSMOTIC VALUE OF CELL.—Brief treatment, up to eighteen hours, in potassium nitrate, sodium chloride, and calcium chloride produces no change in the osmotic value of the cell which can consistently be determined by changes in the critical concentration of the plasmolyzing salt. Longer treatment in all three salts results in a gradual increase in osmotic pressure of the cell. This increase is much more pronounced in the case of the two monovalent ions, potassium and sodium, than it is in the case of the bivalent ion calcium. Two days in either potassium nitrate or sodium chloride will usually result in a critical plasmolytic concentration of 0.4 M or 0.5 M, as compared with a normal of 0.3 M. In calcium chloride prolonged treatment seldom results in a critical plasmolytic concentration of more than 0.4 M, and sometimes there is no increase at all. Three days in potassium or sodium will result in an extraordinarily high critical plasmolytic concentration, which will reach 0.5 M for a few cells, 0.6 M for the majority, and over 1.0 M KNO_3 for some of the cells. The critical plasmolytic concentration of calcium treated cells never exceeds 0.5 M.

According to work on the permeability of protoplasm by the electrical conductivity method, one would expect the two bivalent elements strontium and barium to produce an effect on protoplasm similar to that produced by the bivalent element calcium, if, as is stated by OSTERHOUT (**6**), all bivalent cations (Ca, Ba, Sr, etc.) decrease permeability to a marked degree. Results obtained with the bivalent ions strontium and barium, however, are contrary to those of calcium. After twenty-four hours' treatment in 0.064 M $SrCl_2$, there is a slight reduction in critical concentration of salt. After forty-eight hours this reduction becomes pronounced, being then 0.2 M as compared with a normal of 0.3 M KNO_3.

Critical concentration values expressed in figures do not impress one with the change in osmotic value of the cell so forcibly as does a visual demonstration. If leaves treated for about two days (forty hours) in a 0.064 M $SrCl_2$ solution are plasmolyzed, together with untreated leaves, with 0.3 M KNO_3, and examined in half an hour, numerous cells will be slightly plasmolyzed in the control leaves, while in the strontium-treated leaves nearly every cell will be prominently plasmolyzed. Although these results were obtained in the great majority of cases, it is not always true that the decrease in osmotic value of strontium-treated leaves is so evident. Cells of different leaves, and especially of different lots of *Elodea* collected at different times and in different localities, vary greatly in their reaction to strontium.

The most startling reduction in critical plasmolytic concentration was observed in the case of barium chloride. A critical concentration value of plasmolyzing salt of 0.11 M was obtained with barium-treated cells, a value far below the average normal and considerably below the minimum value of 0.18 M ever found for a control leaf.

More highly toxic to protoplasm than any of the ions so far considered is copper. The copper ion was used in the form of "oligodynamic" water. The term "oligodynamic" is NÄGELI'S (2), and refers to water which has a very slight trace of copper. The slight trace of copper in water distilled in a copper still, or water in which copper coins have remained for a day or two, causes a very pronounced reduction in osmotic value of *Elodea* cells which are allowed to remain in the oligodynamic water over night. If an untreated leaf and a leaf which has been in the copper water for eighteen hours are plasmolyzed with 0.35 M KNO_3, within less than a minute all of the cells of the treated leaf (with the exception of the few which have been killed) will be slightly plasmolyzed, while none in the control leaf is plasmolyzed.

STIMULATION TO PROTOPLASMIC STREAMING.—Little streaming is to be observed in cells treated for a short time in potassium nitrate, sodium chloride, or calcium chloride. After prolonged treatment in these salts no streaming at all is seen. In strontium chloride, barium chloride, and oligodynamic water the stimulation to streaming is very great. Eighteen hours in a 0.064 M $SrCl_2$ solution is sufficient to arouse many cells to active streaming in a leaf reasonably sensitive to strontium. Two days will cause a great abundance of streaming, much of which is abnormal. In a leaf which had been in 0.128 M $SrCl_2$ for seventy-two hours (many cells succumb to so high a percentage of strontium for so long a period of treatment), the individual paths of flow in some cells were so numerous and so indefinite in their direction that all the chloroplasts seemed to wander about aimlessly. A very pronounced increase in the thickness of the protoplasmic layer, equaling five times that of the normal cell, resulted from treatment in strontium. The increase in thickness of the protoplasmic layer is probably the result of increased permeability of the protoplast as a whole to water and a resulting excessive imbibition. It is interesting to note that this highly swollen protoplast, undoubtedly in the gel state, continues very active streaming. Copper also has a very pronounced stimulating effect on protoplasmic streaming, even more so than strontium and barium.[2]

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[2] A full discussion of the stimulation to streaming caused by strontium, barium, copper, alcohol, and saponin is given in a recently published article (7).

DISCUSSION

If the cations potassium, sodium, calcium, strontium, barium, and copper are grouped on a basis of their effect upon the osmotic pressure of the cell sap and streaming of protoplasm, then potassium, sodium, and calcium fall into one class, and strontium, barium, and copper into another. Treatment of *Elodea* cells in potassium nitrate, sodium chloride, and calcium chloride results in an increase in osmotic value of the cell, as evidenced by the increase in critical concentration of the plasmolyzing salt. In contrast with the effect of the bivalent cation calcium on protoplasm is that of the bivalent cations strontium, barium, and copper.[3] As a result of treatment in the salts of these three elements, there is a surprisingly great decrease in osmotic value of the cells. Further, the bivalent cation calcium has no effect on protoplasmic streaming after short treatment, and puts an end to all streaming after long treatment, while strontium, barium, and copper cause a pronounced stimulation to streaming until death results from the high toxicity of these three elements.

There is every reason to regard the reduction in osmotic pressure of the cell, from treatment in strontium, as the result of increased permeability. Through a more porous membrane (using membrane in an abstract sense, since it is probable that the permeability of the protoplast as a whole is affected) an exosmosis of dissolved substances would take place which would lower the osmotic value of the cell. There is the possibility, of course, that the toxic substance might enter the cell and break down larger indiffusible molecules into smaller diffusible ones, and thus cause exosmosis without any change in permeability. The writer considered this possibility in the case of the reduction of osmotic pressure by senegin (a saponin), and was able to show by testing the resistance of the cells to alcohol, and on the basis of other observations as well, that decreased osmotic value of the cell in this case meant increased permeability (8).

The increase in osmotic pressure of the cell due to treatment in potassium, sodium, and calcium cannot so readily be interpreted in terms of permeability. That there has not been an increase in

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[3] Copper in oligodynamic water probably exists as the hydroxide $Cu(OH)_2$, and is, as such, bivalent.

permeability is evident; otherwise exosmosis of the cell contents and a consequent decrease in osmotic value would have resulted. On the other hand, there is no reason to assume that increased osmotic pressure has been due to a decrease in permeability. The permeability might well remain unchanged, and the change in osmotic value be due to the toxic influence of the entering salt.

While the reaction of protoplasm to the bivalent cation calcium, in these plasmolytic experiments, cannot be interpreted in terms of permeability, it is quite clear that the bivalent cations strontium and barium cause a pronounced increase in permeability of the *Elodea* protoplast. This fact is in opposition to the statement of OSTERHOUT (6) that "all the bivalent kations" are able to decrease permeability "to a marked degree." This may be true of calcium, but, on the basis of these experiments, is not true of strontium and barium. It is possible that the difference in the results obtained with strontium by OSTERHOUT and the writer is due to the method of experimentation. It is also possible that the difference is due to the kind of material experimented upon. OSTERHOUT worked on marine plants (*Laminaria*). My experiments were done with a fresh water plant. The marked difference in salt content of sea water and river water would undoubtedly have a telling effect on the reaction which an aquatic growing in one or the other water would manifest as a result of treatment in salt solutions. FITTING (1), whose data stand in partial support of the writer's results, worked with the land plant *Tradescantia* (*Rhoeo*). He found that "salts for which the plasma has shown itself to be permeable, may, in concentrations approaching the critical plasmolytic concentration, diminish if not ultimately practically put an end to the permeability of the plasma membrane, long before the isosmotic value is reached, and whether the cells are plasmolyzed or not." FITTING worked primarily with KNO_3, but is of the opinion that other monovalent salts behave similarly.

Regardless of our interpretation of the experimental results in terms of permeability changes, one fact remains clear, that the reaction of protoplasm to the bivalent ion calcium is markedly different from the reaction of the living substance to the bivalent ions strontium and barium. It is quite evident, therefore, that while strontium, barium, and calcium possess certain physicochemical properties in common, and consequently can be grouped together chemically, they cannot be placed in the same biological class. This deduction can be stated in another way, that a plant shows the same discrimination in its reaction to ions as it does in its nutrition requirements.

Summary

1. Potassium, sodium, and calcium increase the osmotic value of the leaf cell of *Elodea*. The same three ions cause no stimulation to streaming after short treatment, and ultimately put a stop to all streaming.

2. Strontium, barium, and copper decrease the osmotic value of the *Elodea* leaf cell, owing to exosmosis due to an increase in permeability. These three ions cause a pronounced stimulation to protoplasmic streaming.

3. The results obtained by this plasmolytic method of experimentation indicate that elements which are of the same chemical class are not therefore necessarily of the same physiological class, as determined by their effect on protoplasm.

At the time that these experimental data were obtained, I fully appreciated that they were opposed to the widely accepted belief that monovalent cations such as Na produce an effect on permeability, coagulation, and like phenomena, which is opposite to that caused by bivalent cations such as Ca; and that two bivalent cations such as Ca and Sr each produce the same effect on protoplasm. The data were there, however, and no other interpretation was possible than that Na and Ca have an effect on protoplasm which is qualitatively the same, although differing quantitatively, while the effects of Ca and Sr are of opposite kinds. It was impossible to escape the conclusion that there is selective "permeability" in living cells, and that the valency hypothesis of the diffusion of ions through the protoplasmic "membrane" does not hold strictly.[4]

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[4] After the manuscript of this article had been submitted for publication, an article appeared by LOEB (Jour. Gen. Physiol. 5:231–254. 1922) stating that "NaCl acts similarly to $CaCl_2$ and $LiCl_3$ on the rate of diffusion of acid into the egg of *Fundulus*." As Loeb states, it is thus necessary to regard the earlier experiments as incomplete, and to modify the valency hypothesis as applied to permeability. Certain

II. Antagonistic effect of salts on toxicity of alcohol

Experiments by LOEB and OSTERHOUT have shown that salts, such as sodium chloride and calcium chloride, which are toxic to protoplasm when alone, are not toxic when in combination. These two salts when in solution together represent a typical case of what is known as salt antagonism. According to the experimental work of OSTERHOUT, sodium chloride produces an increase in permeability, while calcium chloride produces a decrease. Consequently, when the two salts are together in proper proportion, that is, in a physiologically balanced solution, the normal diosmotic properties of protoplasm are not disturbed.

In some experiments on the reaction of protoplasm to alcohol (8), the writer found that ethyl alcohol in low concentrations is highly toxic to the protoplasm of the cells of the *Elodea* leaf, and that the osmotic value of these cells is greatly lowered by treatment in dilute ethyl alcohol, due to increased permeability and consequent exosmosis of cell contents. If sodium also increases permeability, as OSTERHOUT states, then one would rather expect it to add to the toxic effect of alcohol. Interpreted in terms of effect on osmotic value, as determined in these experiments, one would, on the contrary, expect sodium, which was found to raise osmotic pressure, to oppose the toxic effect of alcohol, since alcohol lowers the osmotic value of the cell. This latter assumption proved to be true. On the other hand, calcium, if it decreases permeability, should oppose the dispersing effect of alcohol. On the basis of effect on osmotic pressure, one would also expect antagonism between calcium and alcohol, but to a much less extent than in the case of sodium. In reality, calcium in solution with ethyl alcohol has no apparent effect whatever on the toxicity of alcohol.

European investigators have objected from the outset to the theory that "all the bivalent cations" are able to decrease permeability, while all monovalent cations (except H) increase permeability. The objections have been based in part on their own experiments and in part on lack of confidence in the electrical conductivity method of determining permeability changes. It is impossible to tell conclusively that the changes in conductivity observed by this method are actually due to changes in permeability. The selective permeability hypothesis of the early investigators apparently has come into its own again. The valency hypothesis, while receiving substantial support in many instances both in the non-living and the living world (for example, in "antagonism"), cannot be regarded as a theory of universal applicability.

In the majority of cases sodium chloride excellently prevented alcohol from exercising its toxic influence on protoplasm. To cite one convincing experiment, of twenty-five leaves placed in 10 per cent alcohol, and another twenty-five put in a solution of 10 per cent alcohol plus 0.128 M NaCl, and allowed to remain in these solutions for one hour the average number of cells killed in the alcohol was 86 per cent (maximum 98, minimum 75 per cent), while the average number killed in alcohol plus sodium chloride was 1 per cent (maximum 10 per cent in only one leaf, the next highest being 3 per cent, minimum 0 per cent). While these results were obtained in the greater number of instances, sodium chloride did not always so perfectly inhibit the toxic influence of alcohol. Occasionally the number of cells killed in a solution of alcohol and sodium chloride almost, although never quite, equaled the average number killed by alcohol alone. These experiments were repeated with calcium chloride instead of sodium chloride added to the alcohol. In not a single case was the number of cells killed in 10 per cent alcohol plus 0.128 M $CaCl_2$ much less than in alcohol alone, and frequently more.

The experimentation was carried further on the assumption that since calcium and sodium antagonize each other, then calcium and sodium both added to alcohol should antagonize each other and leave the alcohol free to exercise its full toxic effect on protoplasm. This assumption proved to be wrong. Leaves were placed in a solution of 10 per cent (2 M) C_2H_6O+0.128 M NaCl+0.128 M $CaCl_2$, and other leaves in 10 per cent alcohol, for one-half hour. The average number of cells killed in 10 per cent alcohol was 64 per cent. In the solution of alcohol plus the two salts, not a single cell succumbed, and this result was obtained in every instance of the many times that the experiment was performed. Sodium alone with alcohol varied considerably in its inhibitory powers. Sodium and calcium together successfully exercised their combined antagonistic effect on the toxicity of alcohol in every case. Potassium in the form of KNO_3 was substituted for sodium, and found to be as good an antagonizer as the latter; sometimes, like sodium, inhibiting the toxic effect of alcohol almost perfectly, and at other times showing little or no inhibitory influence.

The concentrations of sodium chloride and calcium chloride used with alcohol were the 0.128 M ones employed in the earlier experiments. While these concentrations of the two salts always prevented the death of all cells, yet all the cells were not always normal in appearance. With the idea that some other proportion might prove to be a more perfectly balanced solution, the quantity of calcium chloride was gradually reduced, keeping the amount of sodium chloride constant; and in another series the amount of sodium chloride was reduced, while the concentration of calcium chloride was kept constant. Two other solutions were prepared, in which the amounts of sodium chloride and calcium chloride in one solution were reduced to half, and in the other doubled. Of all these various combinations, only one proved to be less toxic than the original proportion. Doubling the amount of sodium chloride and calcium chloride (that is, 0.256 M $NaCl+0.256$ M $CaCl_2$) gave a combination of salts which more perfectly antagonized the alcohol, since not only were there no cells killed (when the percentage of cells killed in alcohol alone was 95 per cent), but all the cells were more normal in appearance, with only one apparent slight abnormality, namely an unusually high viscosity as evidenced by the irregular shape maintained by many of the plasmolyzed protoplasts.

Discussion

Three prominent facts stand out as a result of the foregoing experiments: first, calcium chloride never opposes the ill effect of ethyl alcohol on protoplasm; second, sodium chloride usually does act as an antagonizer, sometimes completely (so far as preventing death goes), but sometimes with very slight effect; and third, a combination of sodium chloride and calcium chloride acts unfailingly as an almost perfect inhibitor of the toxic influence of 10 per cent alcohol.

The effect of sodium on the toxicity of alcohol is in harmony, in part, with the other results obtained by the plasmolytic method. It was found (9) that alcohol lowers the critical plasmolytic concentration, and therefore decreases osmotic pressure (due to increase in permeability). It was further found that sodium chloride raises the critical concentration, at times to exceedingly high values, and therefore increases osmotic pressure. A combination of these two substances should, and usually does, leave the protoplasm in a relatively undisturbed condition.

Calcium was found to be much less pronounced in its effect on the osmotic value of the protoplast than was sodium. One would expect, however, some effect from calcium as an inhibitor of the toxicity of alcohol. The fact that it does not antagonize alcohol while sodium does corresponds with the difference in valency of the two elements. It will be advisable to test the inhibitory effect of many other monovalent and bivalent ions on ethyl alcohol before arriving at any definite conclusions.

Similar cases of antagonism have been studied by other workers. TRAUBE (9) found that hemolysis of red blood corpuscles by NaCl was suppressed by isomyl alcohol. ZEHL (10) found that the sulphates of Co, Cu, Ni, and Al depress the poisonous action of isobutyl alcohol and an isomyl alcohol on the germinating power of fungus spores, but increase the toxicity of antipyrin, chloral hydrate, and chloroform. NOTHMANN-ZUCKERKANDL (3) found that NaCl causes no change in the toxic effect of ethyl alcohol (on *Echeveria* species), and materially increases the effect of propyl alcohol. $CaCl_2$ added to the toxic effect of propyl alcohol even more so than did NaCl.

Only a vast number of experiments will determine in what way the various salts and alcohols antagonize each other. The fact that NOTHMANN-ZUCKERKANDL found that NaCl has no influence on the toxicity of ethyl alcohol, while the writer found that it usually well inhibits the toxic effect of ethyl alcohol, is less disturbing than the fact that in my series of experiments, on one and the same plant, NaCl sometimes almost perfectly antagonizes alcohol, and sometimes exhibits little or no inhibitory action.

The word "antagonism" has been used in reference to the effect exercised by sodium chloride, and sodium chloride plus calcium chloride, on the toxicity of alcohol. The antagonism between sodium chloride and alcohol may not be such as that between sodium chloride and calcium chloride. The latter two salts are electrolytes, while alcohol is not. Antagonism between substances in physiologically balanced solutions is not yet fully understood. The antagonistic action of salts was first thought to be "largely or entirely due to the fact that they hinder or prevent one another from entering the protoplasm" (4). This assumption was thought to be incompatible with the normal diosmotic functioning of the protoplast, and the theory of antagonism was changed. It is now believed that "salts antagonize each other because they produce opposite effects on the protoplasm" (5). While it is still possible that the original theory of antagonism is the correct one, namely, that the two substances in solution mutually hinder one another at the surface (or in the surface layer) of the protoplast, without totally preventing each other from entering in small quantities, yet between alcohol and sodium one is inclined to regard the antagonism as due to opposite effects of the alcohol and the salt on the protoplasm.

The variability in the behavior of sodium as an inhibitor of the toxicity of alcohol can only be explained on the assumption that it is due to a variability in the physiological state of the cells. The great variability in the resistance of cells to alcohol, where, for example, actively streaming cells are found next to dead ones, justifies such an assumption.

The behavior of sodium plus calcium in alcohol is equally puzzling. Calcium alone never inhibits the poisonous effect of alcohol, while sodium alone usually does, although it sometimes is as ineffective as calcium. Yet the two ions together always serve as almost perfect inhibitors of the toxicity of alcohol. It is possible that the sodium ion, which when alone usually prevents alcohol from causing death, is always able to exercise this inhibitory influence in the presence of the calcium ion. This suggestion is, in principle, supported by a very interesting hypothesis made to me by Professor CHODAT. It was suggested that, by virtue of Gibb's law, the Na and the Ca ions occupy different regions in the cell, whence the additive protective effect of the two when in solution together. If the monovalent ion is more in the periphery and the bivalent ion more toward the center, this would explain why the Ca ion when alone is unable to exercise any inhibitory influence.

Summary

1. Sodium chloride usually prevents ethyl alcohol from exercising its toxic influence on *Elodea* leaf cells.

2. Calcium chloride never antagonizes ethyl alcohol.

3. Sodium chloride and calcium chloride in combination always prevent ethyl alcohol from causing death in the *Elodea* cell.

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