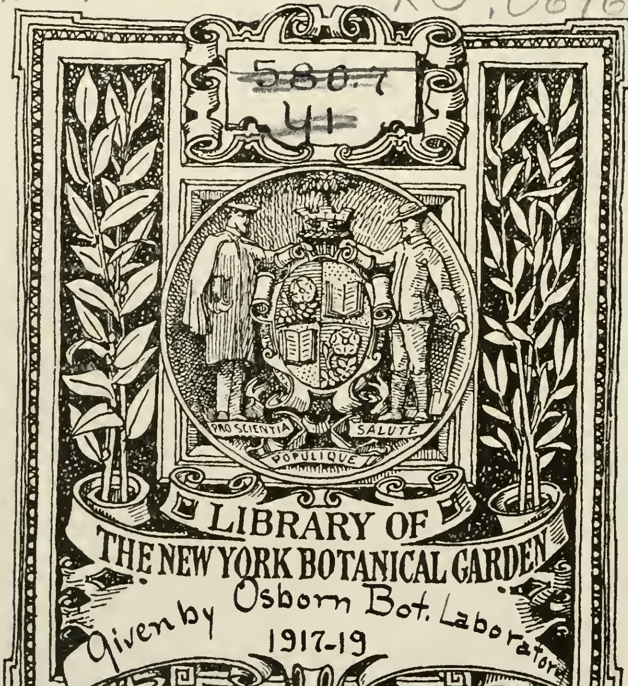
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CONTRIBUTIONS FROM
THE OSBORN BOTANICAL LABORATORY
YALE UNIVERSITY
1916

1. Hooker, H. D., Jr. Physiological observations on *Drosera rotundifolia*. Bull. Torrey Club **43:** 1:27. *f. 1-11*. February, 1916.

2. Evans, A. W. A new species of *Metzgeria* from the Galapagos Islands. Torreya **16:** 67-70. *f. 1-5*. March, 1916.

3. Evans, A. W. Additions to the hepatic flora of Quebec. Bryologist **19:** 27-30. March, 1916.

4. Evans, A. W. Notes on New England Hepaticae, – XIII. Rhodora **18:** 74-85, 103-120. *pl. 120 - f. 1-40*. April and May, 1916.

5. Nichols, G. E. The Bryophytes of Nova Scotia, with special reference to Cape Breton. Bryologist **19:** 38-47. May, 1916.

6. Nichols, G. E. The vegetation of Connecticut, – V. Plant societies along rivers and streams. Bull. Torrey Club **43:** 235-264. *f. 1-11*. May, 1916.

7. Wuist, E. D. Branched prothallia in the Polypodiaceae. Bull. Torrey Club **43:** 365-383. *f. 1-15*. August, 1916.

[From the BULLETIN OF THE TORREY BOTANICAL CLUB, 43: 1–16. 14 F 1916.]

Physiological observations on Drosera rotundifolia *

HENRY D. HOOKER, JR.

(WITH ELEVEN TEXT FIGURES)

CONTENTS

1. INTRODUCTION

The object of the work, which this paper presents, was to determine whether the bending of *Drosera* tentacles was connected with a temporary acceleration of the rate of growth or with differences of turgidity; in physiological terms, whether the bend-

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* Contribution from the Osborn Botanical Laboratory.

ing was a nutation or a variation movement. Analogy with the behavior of tendrils, which has been thoroughly investigated by Fitting, indicates that the reactions of *Drosera* are phenomena of growth, and this is substantiated by Batalin's ('77, p. 36) somewhat meager measurements. These are, in Pfeffer's words ('06, **3**: 85), "not fully satisfactory." Although the primary purpose of this paper is to settle this point, a number of observations were made during the work which pertain to other matters. These minor points are of some physiological interest and will be mentioned before proceeding to the main discussion.

2. MATERIAL

The material used was collected during the months of July and August from Beaver Swamp in the city of New Haven, Connecticut. It was found advisable to use only fresh material for experimentation.

Plants of *Drosera rotundifolia* and *D. longifolia* were found growing in *Sphagnum*. In removing them, large pieces of the substratum were taken along with the plants to prevent injury to the roots and to insure their further development in the laboratory. Slight injuries to the roots cause the secretion of the glands to stop and render the tentacles inactive, so that they fail to respond to the customary stimuli. The root-hairs are particularly remarkable, for they are not restricted to a small region above the root-tip but cover the entire length of the root. They do not die, but continue to grow and function. In this way they increase the effectiveness of the small root-system.

The plants were placed in flat dishes, made wet with distilled water and covered with bell-jars. Under these conditions the development of the plants was far from normal. The rosette arrangement of the leaves was lost, a typical stem was developed by lengthening of the internodes and every trace of red pigment disappeared. No gradations from purple to green leaves were observed. All the leaves, which unfolded in the moist atmosphere and subdued light of the culture, were green. The size of the leaves diminished and their petioles made a more acute angle with the stem, causing them to point obliquely upward instead of horizontally outward.

3. PIGMENT

The red pigment of *Drosera* occurs predominantly in the leaves and the root-cap. Young leaves frequently have the pigment restricted to the glands of the tentacles. Later it appears in the epidermal cells of the marginal pedicels. Leaves of old plants often have the entire leaf-blade pigmented and, as the leaf matures, the color spreads down the petiole and often into the stalk. In general young plants are much greener than old ones, but wide variations are found.

The red pigment of *Drosera rotundifolia* and *D. longifolia* is identical with one of the pigments which Rennie ('87, '93) extracted from rhizomes of *D. Whittakeri*. Its formula is $C_{11}H_8O_5$, and it is probably trihydroxymethylnapthoquinone, since it gives the reaction of Brissemoret and Combes ('07) characteristic of α-napthoquinones.

To obtain the pigment, place a deep red leaf on a slide, add a few drops of hot alcohol, put on a cover-glass and heat directly over boiling water. The pigment is extracted from the leaf and, on the evaporation of the alcohol, it is deposited around the edges of the cover-glass. It forms crystals which are small red disks. It is insoluble in cold water, hardly soluble in cold alcohol and glacial acetic acid, but dissolves readily in boiling water, hot alcohol and ether, and to a lesser extent in benzol and carbon disulphide. It is soluble in alkalis. When a leaf is treated with ammonia, the pigment turns dark violet or brown; on standing the color fades. A timely treatment with dilute acid precipitates the pigment and restores the red color, but this does not occur after prolonged action of the ammonia. Reduction with stannous chloride and alcoholic hydrochloric acid gives a yellow product which crystallizes in needles. This is reoxidized to the original compound, when allowed to stand in alcoholic or alkaline solution exposed to the air. These properties were found for the pigment of *D. rotundifolia*. They coincide with those given by Rennie for the compound $C_{11}H_8O_5$, and confirm the suggestion of their identity put forward by Kraemer ('10, p. 285).

Experiments were made with the green plants to determine under what circumstances the pigment reappeared. Several plants of *D. longifolia* were cultivated for a month in a moist atmosphere, without being fed with insects. They lost all traces of pigment. Six of these were fed with small flies and two days later pigment was observed in the marginal tentacles of the youngest leaves, that had just unrolled. A similar reappearance of color was observed in three other plants which caught insects. This is the opposite of the results obtained by F. Darwin ('08, p. 23) and by Büsgen ('83, p. 592), who found that plants fed with insects had much greener leaves than those which relied solely on photosynthesis for their nourishment. The contradiction may be owing to different environmental conditions, such as the chemical composition of the substrate, the intensity of the light, or the humidity of the atmosphere. The question merits further investigation.

4. HABIT

Another peculiarity observed in plants cultivated in a moist atmosphere was the peculiar habit assumed by the plant. The internodes became lengthened, and this was the case with plants exposed either to the diffuse light of the laboratory or to direct sunlight. Plants exposed to dry air were observed to retain the rosette habit under both light conditions. This shows that the rosette habit characteristic of *D. rotundifolia* is dependent upon transpiration and not upon light, as Diels ('06, p. 32) suggests. This relation represents an interesting adaptation, for as long as the plant is beneath the surface, the internodes lengthen, since transpiration is reduced to a minimum. In this way the terminal bud is brought to the surface, where rapid transpiration from the exposed leaves causes the development of a rosette.

5. PARASITES

A great many of the plants cultivated in the laboratory were destroyed by larvae accidentally brought with the material from the swamp. They were larvae of one of the cut-leaf moths or noctuids. Since the adult form has not been obtained, it has been as yet impossible to identify them. The young larvae are about a quarter of an inch long and very pale. They climb up the under side of the leaf-petioles and eat the blade from behind. In this way they avoid the tentacles which could easily catch and digest such small creatures. The larvae select the youngest leaves and destroy the plant by eating the terminal bud. Many of the fragments of partially eaten leaves fall onto the *Sphagnum* and produce new plants by regeneration. Here again is an arrangement which may be considered a reciprocal adaptation; the larvae are protected from the leaves which could consume them, and the destruction of the plant by the larvae results in vegetative reproduction. As the larvae grow older they increase greatly in size and become green. Even after they have reached a size which renders their capture by a *Drosera* leaf impossible, they continue to crawl along the under surface and eat the leaves from behind. They become exceedingly voracious and a single insect can devour a dozen flourishing plants in two days.

6. CULTIVATION

The *Drosera* plants used for experimentation were grown in uncovered dishes exposed for at least six hours a day to direct sunlight. Small flies and other insects were placed on the leaves from time to time. The best leaves were selected for reactions and were not fed. In one remarkable instance, a house-fly was placed on a small fresh leaf which was only slightly pigmented. A copious secretion resulted which enveloped and digested the fly. After five days, however, the entire leaf-blade had disappeared, being digested by its own fluid. The plant was not vigorous and the fly was too large for the leaf, but normally anti-enzymes or other adequate means must be present to prevent autolysis.

7. MECHANICS OF MOVEMENT

(*a*) NORMAL DEVELOPMENT

The blade of the undeveloped *Drosera* leaf is rolled up. As it expands the marginal tentacles are seen to be bent over the blade, the glands pointing against the leaf and the pedicels arranged like rays around the edge. As the leaf grows, these tentacles increase considerably in length, the growth being greater on the adaxial side. By this means the incurved tentacles are straightened, a process which is assisted by the simultaneous flattening of the leaf-blade. When all the tentacles are straight, the leaf is mature and able to catch insects. The full grown tentacles do not increase perceptibly in length. They remain in this condition for about two weeks, during which time their glands secrete actively. At the end of this period the tentacle begins to bend backward. In old leaves the marginal tentacles are much recurved, and in extreme cases the gland may pass through a complete revolution by the rolling up of the distal portion of the pedicel. The petiole of young leaves points up. As the leaf ages, its petiole bends down so that the mature leaf is horizontal.

The pedicels of the exterior tentacles are dorsi-ventrally flattened at the base. The abaxial side has numerous short glandular hairs distributed over its entire length. On the adaxial side they are fewer in number and are confined more or less to the base.

(*b*) EXPERIMENTAL METHOD

Fresh leaves which had not been previously touched were selected for experimentation. The entire plant was removed from the *Sphagnum* in which it grew and was placed in a large Stender dish. A piece of cork was fastened with sealing wax inside the dish and another piece attached to it by two pins. The petiole of the selected leaf was clamped horizontally between the two pieces of cork in such a way that the leaf-blade was vertical. The bottom of the dish was covered with water and the roots were wrapped in wet sphagnum. The cover of the Stender dish was replaced or discarded, as desired. A binocular microscope was used, because the greater distance from the objective to the object made it more convenient when the Stender dish was covered. An horizontal tentacle, which showed glandular hairs on both upper and lower sides and which was not obscured by its neighbors, was selected from the edge of the leaf opposite the petiole. Its pedicel was marked with China ink to facilitate identification.

Each tentacle was measured with a micrometer scale and drawn with a camera lucida before an experiment. The gland was then stimulated by placing upon it some object such as the leg of a fly. This was removed as soon as movement began. At each subsequent observation the time was recorded and the tentacle was sketched. This was continued at intervals until the pedicel was again straight. The tentacle was then measured for the second time with the micrometer scale.

The figures given in the tables are in hundredths of a millimeter. Measurements were made on the drawings, which were checked by the direct measurements. The time at the head of the first column shows when the gland was stimulated. The column to the right of the heavy line shows the first indication of unbending. The segments were marked off naturally by the presence of glandular hairs on the two flattened surfaces. They are numbered from the apex to the base. The segments on the concave side do not always correspond to those on the convex side.

TABLE I

	No. of Segment	10.00 A. M.	10.15 A. M.	10.35 A. M.	11.00 A. M.	11.20 A. M.	11.40 A. M.	12.00 M.	1.15 P. M.	2.00 P. M.	3.00 P. M.	3.30 P. M.	4.00 P. M.	4.30 P. M.	5.00 P. M.	7.35 P. M.	9.00 P. M.	9.10 P. M.
Abaxial side	1	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80	80
	2	23	23	23	23	23	25	25	25	25	25	25	25	25	25	25	25	25
	3	24	25	25	25	28	28	28	28	28	28	28	28	28	28	28	28	28
	4	29	31	31	32	34	35	35	35	35	35	35	35	35	35	34	34	34
	5	36	41	41	42	43	45	49	49	49	48	48	48	48	48	48	48	46
	6	43	51	52	53	55	57	59	59	59	59	58	57	55	55	55	55	55
	7	59	60	60	60	61	69	70	72	72	72	71	69	69	69	69	69	69
	Total..	294	311	312	315	324	339	346	348	348	347	345	342	340	340	339	339	337
Adaxial side	1	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78	78
	2	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	23	24
	3	24	25	25	25	25	25	25	25	25	25	25	25	26	26	26	27	27
	4	31	31	31	29	29	29	28	28	28	29	29	29	29	31	32	33	34
	5	40	40	40	40	40	40	40	40	41	41	41	41	41	41	43	44	46
	6	28	29	29	29	31	32	32	32	34	35	35	35	35	35	35	36	38
	7	28	28	28	28	28	28	28	28	28	29	31	32	33	34	34	35	37
	8	45	45	45	45	46	48	49	50	50	50	50	50	50	51	51	52	54
	Total..	297	299	299	297	300	303	303	304	307	310	312	313	315	319	322	328	338

(*c*) EXPERIMENTAL DATA

Measurements of the dorsal and ventral sides of a tentacle in the process of bending and unbending are given in TABLE I. The tentacle was selected from next to the outermost row on a fresh, red, young leaf which was secreting copiously. The leaf had been protected during its development and was not touched, or stimulated in any other way, prior to the experiment. Its reaction is typical of the marginal tentacles on young leaves, unless perhaps it is more than usually vigorous.

The straight tentacle measured 2.94 mm. in length. The leg of a small house-fly was laid on the gland. One minute and a half after stimulation movement was detected, whereupon the fly-leg was removed. After fifteen minutes the tentacle was well bent and the gland had moved through an angle of about fifty degrees. Marked elongation took place on the convex side near the base in Segment 6, and to a lesser extent in Segment 5. The concave side remained nearly of the same length as before. The region of bending is coincident with the region of elongation on the convex side. As the tentacle continued to bend, the area of curvature and elongation was extended upward toward the gland, including Segments 4, 3, and 2, and to a lesser extent downward so as to include a portion of Segment 7. In the ultimate stage the curved region subtended an angle of approximately 215 degrees. Both sides increased in length, but the increase of the convex side was eight times that of the concave. FIG. 1 is a series of camera lucida drawings made during the inflexion of this tentacle. In *b* the bending region is seen to be restricted at first to the lower end and to extend apically in *c* and *d*. The final

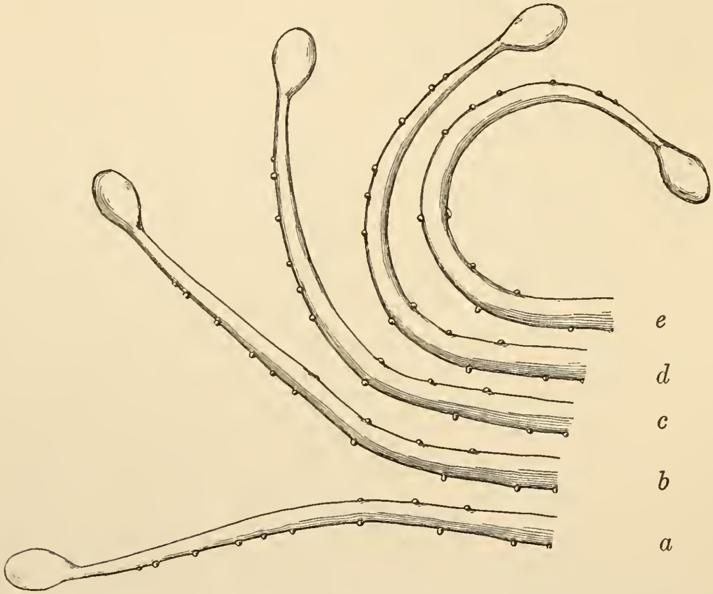

FIG. 1. Side views of a tentacle in the process of bending, × 22. *a*, before stimulation; *b*, *c* and *d*, successive stages of inflexion; *e*, the fully bent tentacle.

condition attained 3 hours and 15 minutes after stimulation is shown in *e*.

Unbending commenced immediately. TABLE I shows that this resulted from elongation of the concave side and contraction of the convex side. The region of elongation is at first near the base in Segment 7, which lies opposite the lower portion of Segment 6 on the convex side. This region gradually extends apically. The contraction on the convex side is mostly confined to the base, and it is moreover relatively slight, being only one fourth the amount of elongation on the concave side. FIG. 2 shows the result of these alterations in length. Since the reaction commences near the base, this portion is the first to straighten; as successive portions on the concave side further removed from the base elongate, the straight part of the pedicel lengthens. In unbending the tentacle is therefore curved in a different manner than during bending. In the latter case, the principal curve is near the base, in the former, nearer the apex. A comparison of

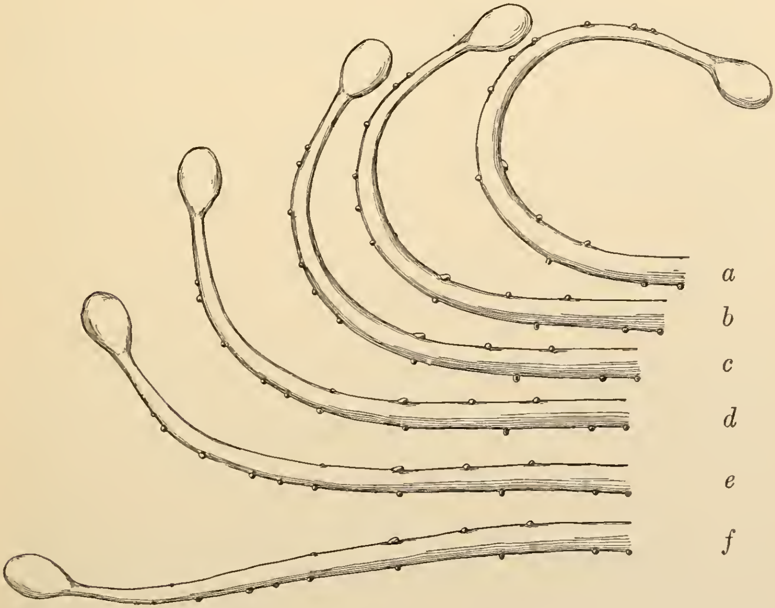

FIG. 2. Side views of the tentacle shown in FIG. 1 in the process of unbending. × 22. *a–e*, successive stage in the expansion; *f*, the tentacle at the completion of the reaction.

FIG. 1, *a* and *b*, with FIG. 2, *d* and *e*, illustrates this. The most apical part which elongated during the process of bending is the last to regain its original position. The basal portion, however, does not stop increasing its length until the entire tentacle is straight. At the end of the reaction, after 23 hours and 10 minutes, the tentacle measured 3.37 mm. It had therefore *grown* during the process of bending and unbending 0.43 mm. (See FIG. 3). A control tentacle which had not been stimulated measured before and after the experiment 2.57 mm. Another measured 2.6 mm. They had not grown a measurable amount during the interval.

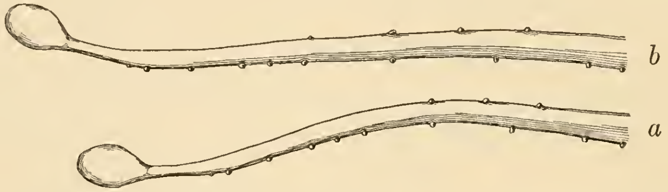

FIG. 3. Side views of the same tentacle before and after the reaction, to show the increase in length, × 22. *a* is the same as FIG. 1, *a*; *b* is the same as FIG. 2, *f*.

FIG. 4 is a graphical representation of the growth of the tentacle. The elongation of the abaxial side is shown by the

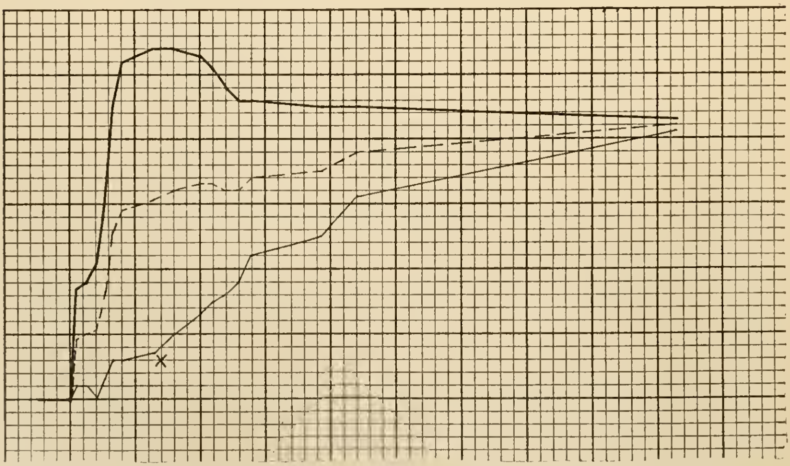

FIG. 4. A graph representing the reaction shown in FIGS. 1 and 2, drawn according to data in TABLE I. See text for explanation.

heavy line; the growth of the adaxial side is shown by the light line. The calculated growth of the median section of the tentacle is given by the broken line. The time is plotted on the abscissae; each space is thirty minutes. The changes in length are plotted on the ordinates; each space represents 0.02 mm. The reaction time is not indicated. The cross shows when the bending was completed and when unbending began. It is evident from the figure that the inflexion of the tentacle is produced by a considerable acceleration of the rate of growth on the abaxial side and in the median section. The unbending is more gradual and takes six times as long as the bending. Moreover the unbending is produced by a similar but less intense acceleration of the growth on the adaxial side and in the median section together with contraction of the abaxial side during the beginning of the process.

The reaction of another tentacle is shown in TABLE II and FIG.

TABLE II

	No. of Segment	10.16 A. M.	10.54 A. M.	11.18 A. M.	11.28 A. M.	11.31 A. M.	11.36 A. M.	12.09 P. M.	12.38 P. M.	3.58 P. M.	9.45 A. M.
Abaxial side	1	72	72	72	72	72	72	72	72	72	72
	2	118	118	118	118	118	118	119	119	119	119
	3	26	27	28	28	31	32	33	34	36	34
	4	54	54	54	58	58	58	58	59	59	58
	Total	270	271	272	276	279	280	282	284	286	283
Adaxial side	1	72	72	72	72	72	72	72	72	72	72
	2	121	121	121	121	121	121	120	120	120	121
	3	35	35	35	35	35	35	35	34	33	43
	4	38	37	37	37	36	35	35	34	34	42
	Total	266	265	265	265	264	263	262	260	259	278

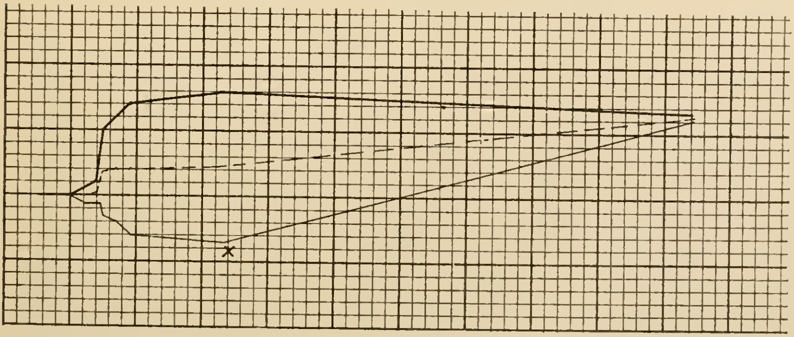

FIG. 5. A graph representing the bending and unbending of a tentacle, drawn according to data in TABLE II, and on the same scale as FIG. 4.

5. Before the experiment it measured 2.7 mm. The reaction is in all essential respects similar to the previous example, but there are important differences. The tentacle was on a mature leaf. It had not, however, been stimulated before the experiment. Bending was produced by an elongation of the convex side and the median section, accompanied by contraction of the concave side. The increase in length on the abaxial side was twice as great as the contraction of the adaxial side. The ultimate stage of bending was reached 5 hours and 45 minutes after stimulation. Unbending was caused by gradual growth on the concave side and in the median section together with slight contraction of the convex side. The original position was reached after 23 hours and 30 minutes. The tentacle then measured 2.83 mm. It had grown 0.13 mm. during the experiment.

A third example is given in TABLE III. This tentacle was in the third row from the outside, on a leaf in excellent condition. It reacted with great rapidity. Movement was detected within a minute after stimulation, and the bending was completed in twenty minutes. The table shows clearly that elongation commenced in Segment 5, the most basal portion of the abaxial side; after ten minutes Segment 4 likewise increased in length; and after three minutes more Segment 3 began to grow. The drawings in FIG. 6 show the bending, and illustrate the apical progress of the reaction. As in the previous case, the bending was produced

TABLE III

	No. of Segment	3.45 P.M.	3.52 P.M.	3.55 P.M.	3.58 P.M.	4.01 P.M.	4.05 P.M.	9.20 A.M.	4.00 P.M.	9.00 A.M.
Abaxial side	1	84	84	84	84	84	84	84	84	84
	2	57	57	58	58	58	58	58	58	58
	3	37	37	37	37	40	41	42	43	43
	4	31	31	31	34	40	43	43	43	43
	5	45	47	52	53	57	57	54	50	49
	Total...	254	256	263	266	279	283	281	278	277
Adaxial side	1	82	82	82	82	82	82	82	82	82
	2	57	57	57	57	57	57	58	59	61
	3	58	58	58	58	59	59	60	62	66
	4	46	46	42	37	37	40	42	42	42
	5	12	12	12	12	12	12	23	23	24
	Total...	255	255	251	246	247	250	265	268	275

by acceleration of the growth on the convex side and in the median section, with contraction of the concave side.

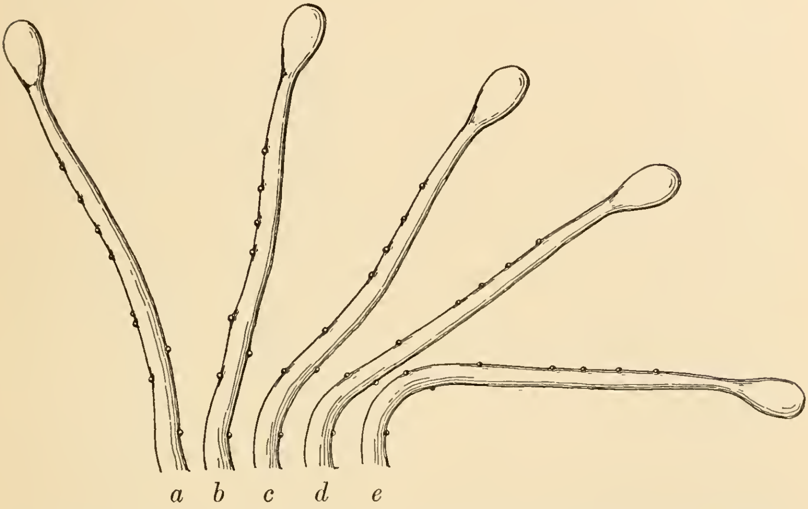

FIG. 6. Side views of a tentacle in the process of bending, × 22. *a*, the straight tentacle before stimulation; *e*, the inflected tentacle twenty minutes after stimulation.

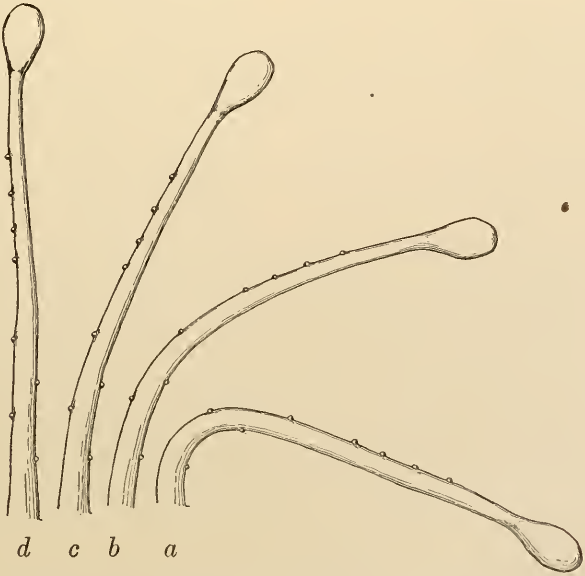

FIG. 7. Side views of the tentacle shown in FIG. 6 in the process of unbending, × 22. *a*, the fully inflected tentacle; *d*, the straight tentacle at the end of the reaction.

The unbending presents no new features. FIG. 7 shows successive stages in the process and comparison with FIG. 6 emphasizes the different configuration of the bending and unbending tentacle. The tentacle grew from 2.54 mm. to 2.77 mm., an increase of 0.23 mm.

The reaction is plotted in FIG. 8. The complete reaction took 39 hours and 15 minutes, an unusually long time. This experiment is perhaps more representative than the first in that growth was confined to the lower half of the pedicel.

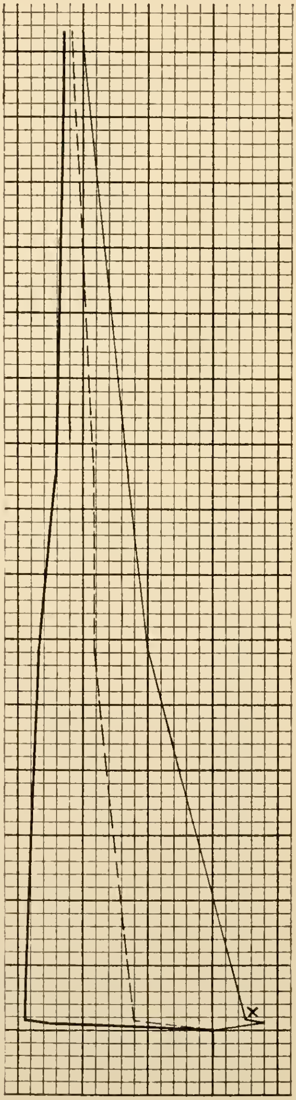

FIG. 8. A graph representing the reaction shown in FIGS. 6 and 7, drawn according to data in TABLE III, on the same scale as FIG. 4.

After a day's rest, the tentacle used in the first experiment was stimulated a second time. The leaf was still fresh and actively secreting. At the beginning of this experiment the tentacle measured 3.37 mm. The results of the reaction are shown in TABLE IV, and are represented in graphical form in FIG. 9. Movement began within two minutes. The bending was produced by elongation of the abaxial side beginning in Segment 6 and extending apically to Segments 5 and 4, and basally to a part of Segment 7. The region of elongation and curvature was shorter than in the first reaction, where it included Segments 3 and 2. The acceleration of the rate of growth was also less than during the first inflexion. The time required for the bending was increased to four hours. The time taken to regain the original position was approximately the same as before, 22 hours and 45 minutes. At the end of the reaction the tentacle measured 3.74 mm. It had increased 0.37 mm. in length. A control, that like this tentacle had made one previous inflexion, measured 2.85 mm. before and after the experiment. Another that had never reacted measured similarly 2.3 mm.

TABLE IV

	No. of Segment	10.15 A. M.	10.30 A. M.	10.45 A. M.	11.00 A. M.	*11.30 A. M.	11.45 A. M.	12.45 A. M.	2.15 P. M.	3.00 P. M.	7.00 P. M.	10.10 P. M.	9.00 A. M.
Abaxial side	1	80	80	80	80	80	80	80	80	80	80	80	80
	2	25	25	25	25	25	25	25	25	25	25	25	25
	3	28	28	28	28	28	28	28	28	28	28	28	28
	4	34	35	35	35	35	36	36	36	36	36	36	36
	5	46	46	49	53	54	55	55	57	57	57	54	53
	6	55	64	64	69	69	69	69	71	71	71	71	70
	7	69	69	69	71	73	76	76	82	82	82	82	82
	Total	337	347	350	361	364	369	369	379	379	379	376	374
Adaxial side	1	78	78	78	78	78	78	78	78	78	78	79	79
	2	24	24	24	24	24	24	24	24	24	24	25	25
	3	27	27	27	27	28	28	28	28	28	28	28	28
	4	34	35	35	35	35	35	35	35	35	35	35	36
	5	46	46	47	47	47	47	47	47	47	47	53	54
	6	55	59	59	59	59	59	59	59	59	59	60	69
	7	75	75	75	75	75	76	77	78	79	84	84	84
	Total	339	344	345	345	346	347	348	349	350	355	364	375

* Controls well bent.

This tentacle was allowed to rest over another day and it was stimulated for the third time. At this time it measured 3.74 mm.

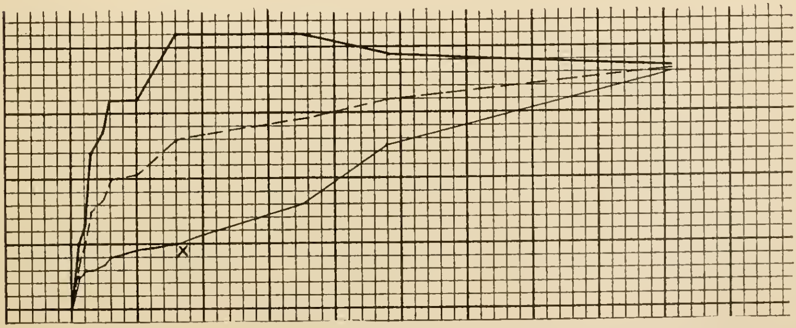

FIG. 9. A graph representing the second reaction of the tentacle shown in FIGS. 1–4; drawn according to data in TABLE IV, and on the same scale as FIG. 4.

The reaction is represented in TABLE V and FIG. 10. No movement was observed for an hour after stimulation. The region of elongation and curvature was shorter than in the second reaction.

TABLE V

	No. of Segment	12.00 M.	2.55 P. M.	7.30 P. M.	10.40 P. M.	9.15 A. M.	1.00 P. M.
Abaxial side	1	80	80	80	80	80	80
	2	89	90	92	92	92	92
	3	53	54	54	54	54	54
	4	70	79	79	79	78	77
	5	82	98	98	98	96	95
	Total	374	401	403	403	400	398
Adaxial side	1	79	79	79	79	79	79
	2	89	94	93	93	93	93
	3	54	53	54	54	54	54
	4	69	68	68	68	75	77
	5	84	84	85	85	90	93
	Total	375	378	379	379	391	396

The acceleration of growth on the convex side was less than in the previous reaction, and the tentacle was not fully bent for 7 hours and 30 minutes. It remained in this condition 2 hours and 30 minutes before unbending again. The tentacle was again straight 25 hours after stimulation. It measured 3.98 mm., an increase of 0.24 mm. After this experiment the tentacle stopped secreting, and no further reaction could be obtained.

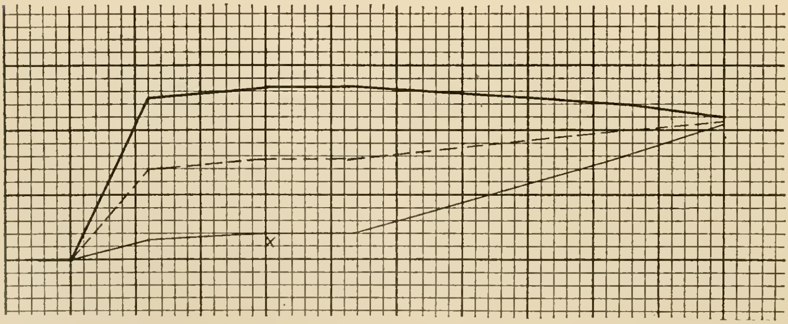

FIG. 10. A graph representing the third reaction of the same tentacle shown in FIG. 9; drawn according to data in TABLE V, and on the same scale as FIG. 4.

The results of the three successive reactions of this tentacle are summarized in TABLE VI. The increase in length for the three reactions was 0.43 mm., 0.37 mm. and 0.24 mm. The region of most intense growth moved basally. In the first reaction it was in Segments 4 and 5; in the second in Segment 5; and in the third in Segment 6. The ultimate stages of bending in the three reactions are shown in FIG. 11. In each subsequent inflexion

TABLE VI

No. of Segment	Original Length	Length after First Bending	Amt. of Growth	Relative Amt. per Mm.	Length after Second Bending	Amt. of Growth	Relative Amt.	Length after Third Bending	Amt. of Growth	Relative Amt.
1	80	80	0	0	80	0	0	80	0	0
2	47	53	6	13	53	0	0	53	0	0
3	29	34	5	17	36	2	6	39	3	8
4	36	46	10	27	53	7	15	54	1	2
5	43	55	12	28	70	15	27	77	7	10
6	59	69	10	17	82	13	19	95	13	16
Total ...	294	337	43	15	374	37	11	398	24	6

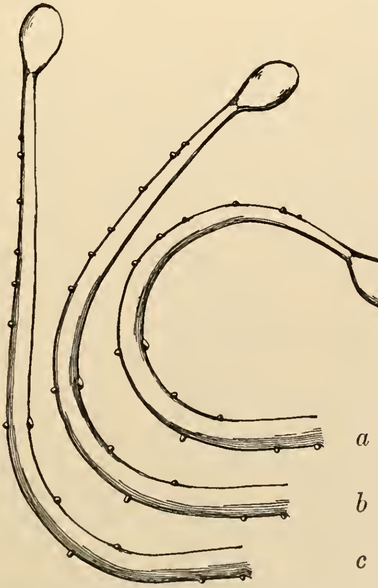

FIG. 11. The ultimate stages in three successive inflexions of the same tentacle, × 22. *a*, at the end of the first inflexion; *b*, at the end of the second inflexion; *e*, at the end of the third inflexion.

the amount of bending decreased, the gland was moved through successively smaller angles and the zone of bending was restricted to shorter and more basal portions of the tentacle.

Table VII

No. of Segment	Original Length	Length after First Reaction	Amt. of Growth	Relative Amt. per Mm.	Length after Second Reaction	Amt. of Growth	Relative Amt.	Length after Third Reaction	Amt. of Growth	Relative Amt.
1	23	23	0	0	23	0	0	23	0	0
2	40	40	0	0	40	0	0	40	0	0
3	11	11	0	0	11	0	0	11	0	0
4	22	23	1	5	23	0	0	23	0	0
5	35	34	3	9	41	3	8	41	0	0
6	20	23	3	15	25	2	8	27	2	8
7	21·	34	13	62	41	7	21	59	18	44
Total ...	172	192	20	17	204	12	6	224	20	10

Table VII shows the growth of another tentacle during three successive reactions. The respective elongations were 0.2 mm., 0.12 mm. and 0.2 mm. During the first reaction Segments 4 to 7 grew. The rate of growth was most intense in the lowest segment and decreased toward the apex. The second reaction was produced by growth in Segments 5 to 7. Segment 4 did not elongate. Here again the most intense growth was at the base. In the third reaction growth was confined to Segments 6 and 7, and was considerably more intense in the latter. Segments 4 and 5 did not increase in length. The tentacle was again stimulated but did not bend.

Table VIII

No. of Segment	Original Length	Length After First Reaction	Amt. of Growth	Relative Amt. per Mm.	Length After Second Reaction	Amt. of Growth	Relative Amt.	Length After Third Reaction.	Amt. of Growth	Relative Amt.
1	85	85	0	0	85	0	0	85	0	0
2	52	54	2	4	54	0	0	54	0	0
3	82	88	6	7	89	1	1	89	0	0
4	23	25	2	9	33	8	32	38	5	15
5	36	42	6	17	51	9	21	60	9	18
Total ...	278	294	16	6	312	18	6	326	14	15

A third example of this sort is given in Table VIII. The reaction time of the first inflexion was 1 minute, 40 seconds. Segments 2 to 5 increased in length. The rate of growth was greatest in the lowest segment and decreased apically. The second reaction was produced the day following the first. The reaction time was 1 minute, 30 seconds. Growth occurred in Segments 3 to 5. Segment 2 had stopped growing. The third reaction took place two days after the first one. More than an hour elapsed before movement was detected. Growth was confined to Segments 4 and 5. No elongation of Segments 2 and 3 took place. The third unbending of the tentacle was exceedingly slow, and the pedicel did not regain its original position until three days after stimulation. A fourth reaction could not be induced. The elongations accompanying the first, second and third inflexions were nearly constant, being 0.16 mm., 0.18 mm. and 0.14 mm., respectively.

TABLE IX

No. of Segment	Original Length	Length after First Reaction	Amt. of Growth	Relative Amt.	Length after Second Reaction	Amt. of Growth	Relative Amt.
1	80	80	0	0	80	0	0
2	19	20	1	5	20	0	0
3	20	21	1	5	21	0	0
4	16	18	2	13	18	0	0
5	37	43	6	16	44	1	2
6	32	41	9	28	43	2	5
7	34	44	10	29	49	5	11
Total....	238	267	29	12	275	8	3

TABLE IX gives the growth during two successive reactions of a tentacle. The growing region is much more restricted in the second than in the first bending. In both cases the rate of growth increases toward the base of the pedicel.

(*d*) DISCUSSION

i. *Bending*

The bending of a *Drosera* tentacle is produced by an acceleration of the rate of growth, which extends from the convex side through the middle of the tentacle. In some cases the concave side is likewise included, so that the entire cross-section of the pedicel participates. In other cases the region of accelerated growth stops at a so-called neutral line, somewhere between the middle and the concave side. Under such circumstances the concave side becomes shorter, probably as a result of compression. The acceleration is greatest on the convex surface and diminishes toward the concave. This difference in the rate of growth produces the bending when the acceleration extends all the way through the pedicel and includes the concave surface. If a neutral line is present, it presumably serves as a brace against which the elongation of the convex side acts.

The increase in the rate of growth begins in a part of the pedicel at or near its base, whence it moves toward the gland, widening its scope until one to two thirds of the pedicel is involved. The gland and the adjacent portion of the pedicel do not grow. C. Darwin ('08, p. 9) states that the distal half remains straight in all cases; but growth is not always as confined as he indicates, for in one case (TABLE VIII) 70 per cent of the tentacle grew, and in another (TABLE I) 73 per cent. If the place where the reaction begins is not the most basal portion of the pedicel, the acceleration of the rate of growth extends also a short distance in the direction of the leaf-blade (TABLE I). Those regions where the reaction commences have the highest rate of growth and are involved in the reaction for the greatest length of time: consequently they grow most, so that the amount of elongation is greatest at the base and decreases toward the apex. Ordinarily, bending is confined to one place, but in some of the long marginal tentacles the pedicel curves in two places—in the middle and again at the base (cf. C. Darwin, '08, p. 206). This is particularly characteristic of those tentacles which have the gland imbedded on the upper side of the pedicel, instead of at the apex.

The amount of bending is determined by two factors; the difference between the lengths of the convex and concave sides, and the thickness of the bending region. An increase in the former augments, in the latter diminishes the amount of bending. The longest tentacles bend most, since their growing region has the largest dimensions. The gland may be moved through a wide angle, for example 215 degrees as shown in FIG. 2. C. Darwin ('08, p. 9) describes an instance of movement through an angle of 270 degrees. The time required for bending is very variable. It may be nearly six hours (TABLE II, FIG. 5), or only twenty minutes (TABLE III, FIGS. 6, 7 and 8). C. Darwin ('08, p. 23) once saw inflexion finished in 17 minutes, 30 seconds.

In all cases of direct stimulation of the gland, the bending of *Drosera* tentacles is nastic; the inflected gland always points toward the center of the leaf. The stimulus may be contact, heat, injury or some chemical substance in solution.

When a tentacle reacts to a single stimulation, it begins to unbend immediately after the ultimate degree of inflexion has been reached. This is the case when the gland has been irritated by contact with some object for a limited space of time. If the source of stimulation is not removed, as for example when an insect is caught and digested, the tentacle remains inflected for a period varying from one to eleven days, according to C. Darwin ('08, pp. 11, 195). During the interval between bending and unbending the tentacle does not grow in length.

ii. *Unbending*

The unbending of the tentacle is accompanied by an increase in the rate of growth on the concave side and in the median section. The convex side always contracts so that the so-called neutral line exists somewhere between it and the middle of the tentacle. The acceleration of the rate of growth is characterized by a transverse distribution which is exactly opposite that accompanying bending. Its longitudinal distribution is however identical. The increase in the rate of growth commences opposite that basal portion of the convex side which reacted first, and extends as far apically. Growth is most rapid near the base and becomes less intense toward the gland. The contraction of the convex side is usually restricted to a short basal region.

It frequently happens that the concave grows less than the convex side, since the latter is compressed during the expansion of the tentacle. The concave side may undergo a certain amount of compression during the inflexion of the tentacle, so that the two sides grow and contract approximately equal amounts. The unbending proceeds much more slowly than the bending.

In all probability the unbending of *Drosera* tentacles is autotropic (cf. Fitting, '03, p. 612). The stimulus perceived is the inequality of conditions, pressure, tissue-tension, etc., which is produced on the opposite sides of the originally straight tentacle by its bending. The unbending is therefore of a tropic nature, since it is a reaction in response to differences existing on the opposite sides of the tentacle. The inflexion and expansion of a *Drosera* tentacle present a remarkable instance of a practically continuous reaction, produced by a single mechanism, but caused by two stimuli of different nature, so that it is partly nastic and partly tropic.

iii. *Growth and Turgidity*

Since the movement of a *Drosera* tentacle is the result of growth, it is always longer at the end of a reaction than at the beginning. The amount of elongation varies from 0.1 mm. to 0.5 mm. This suggests a simple demonstration to show that the reaction is accompanied by growth. If a single tentacle on a leaf is stimulated, it will project a noticeable distance beyond its fellows after regaining its original position. In the field, a *Drosera* leaf frequently has some tentacles longer than other ones in the same row. These inequalities are the result of growth attendant upon reaction, for all the tentacles in one row remain of equal length if not stimulated. Sometimes a small insect is caught by a single exterior tentacle, which carries it to the center of the leaf. The insect is, however, too minute to cause a sufficient impulse to be conducted from the discal to the other marginal tentacles. They do not bend, so that after the reaction is completed they are not as long as the tentacle which was inflected.

Turgidity does not play a part in the movement of the tentacles. This was proved by plasmolyzing bent tentacles in 20 per cent salt solution. The plasmolyzed tentacles remained bent.

A comparison of FIGS. 4, 5 and 8 with graphs of Fitting, which show the haptotropic reactions of tendrils of *Sicyos angulatus* (Fitting, '02, p. 378), of *Passiflora gracilis* (Fitting, '03, p. 577, *fig. 6*) and of *Pilogyne suavis* (*ibid.*, p. 578, *fig. 7*), shows that the mechanics of movement in tendrils and tentacles are the same. Similar figures are shown by Wiedersheim for photonastic reactions of leaves of *Impatiens parviflora* (Wiedersheim, '04, p. 241, *fig. 1;* p. 242, *fig. 2;* p. 244, *fig. 5*), and for thermonastic reactions of the perianth leaves of the tulip (*ibid.*, p. 250, *fig. 8*) and the crocus (*ibid.*, p. 254, *fig. 10;* p. 255, *fig. 12*). It is clear that all these reactions are produced by the same mechanism; rapid growth on the convex side and in the median section with attendant contraction or a slower rate of growth (*ibid.*, p. 255, *fig. 12*) on the concave side. *Drosera* tentacles are characterized by a contraction of the convex side during expansion; this occurred in one case of a leaf of *Impatiens parviflora* (*ibid.*, p. 242, *fig. 2*).

iv. *Conductivity*

The reaction time represents the interval necessary for the latent period and the conduction of an impulse from the gland to the region where the reaction commences. This region has been shown to be a basal portion of the pedicel, so that the impulse is conducted the entire length of the tentacle. The reaction time usually varies from one to two minutes. C. Darwin ('08, pp. 10, 191) saw movement ten seconds after stimulation. This shows that the rate of conduction can be quite high, for assuming the length of the tentacle (which Darwin does not give) to be 2 mm., the rate of conduction would be 0.2 mm. per second, which is faster than any instance given for the haptotropic reaction of tendrils (Fitting, '04, p. 424). The rate of conduction in tentacles is generally much less (cf. Pfeffer, '06, Vol. III, pp. 93, 94). It should be emphasized that in *Drosera* tentacles stimuli are perceived by cells which are fully grown, and which undergo no further development.

It has not been definitely settled through what tissue impulses are conducted in *Drosera*, but in any case an impulse, in being conducted from the gland to the base of a tentacle, must pass through cells which later react, without producing a response in them. These cells apparently respond only to a secondary impulse released in the basal cells by the impulse conducted directly from the gland. This secondary impulse is conducted in the reverse direction, from the base toward the apex.

v. *Second and Third Reactions*

A tentacle is capable of reacting several times in succession. C. Darwin ('08, pp. 11, 19) observed a leaf inflected three times over insects, and suggested the possibility of more reactions. It is probable, however, that a leaf can clasp insects a greater number of times than any individual tentacle can react, because the capture of such prey does not always necessitate the cooperation of all the tentacles. Those which remain inactive at one time, might bend on a subsequent occasion. However this may be, no tentacle has been observed to react the fourth time.

The second and third reactions of a tentacle are essentially similar to the first. After two reactions a tentacle is much less sensitive than before, as is shown by the increased reaction time. Each subsequent bending takes longer (cf. C. Darwin, '08, p. 19), but the original position is regained in approximately the same time. The amount of growth does not vary according to any definite rule. It depends rather on external conditions and is apparently uninfluenced by the age of the tentacle. If the external conditions are constant, the amount of growth remains the same. In one example (TABLE VIII) this was approximately the case, the increase in length for the first, second and third reactions being 0.16 mm., 0.18 mm. and 0.14 mm. respectively.

The region of growth is however more restricted in each subsequent reaction, and is confined to more basal portions of the tentacle. TABLE VII shows that 57 per cent of the tentacle grew in length during the first inflexion, 50 per cent during the second, and 32 per cent during the third. In another instance (TABLE VIII) the regions of growth were successively 70, 53, and 27 per cent of the length of the tentacle. In each reaction a certain portion of the tentacle becomes fully grown. A *Drosera* tentacle is therefore characterized by intercalary, basipetal growth. Because of this, the number of inflexions which a tentacle can make must necessarily be limited. It is therefore highly probable that a tentacle would bend a fourth time only under very exceptional circumstances.

Since growth is limited to more basal regions, the thickness of the reacting portion is greater at each successive inflexion. Moreover the greatest difference between the lengths of the opposite sides tends to decrease. Both of these factors cooperate in reducing the amount of bending, so that the gland is moved through successively smaller angles, as shown in Fig. 11.

vi. *Nastic reactions*

In all the experiments described, the glands of the marginal tentacles were stimulated directly, but reactions follow likewise in response to impulses received by the discal tentacles and conducted to the marginal ones. The mechanism by which these reactions are carried out is identical with that described above.

Numerous experiments were made to determine if the marginal tentacles bent toward the source of stimulation. The discal tentacles on one side of a leaf were stimulated and most of the marginal tentacles which reacted to the conducted impulse, in bending toward the center of the leaf bent likewise in the direction of the source of excitement. In a number of such cases, however, marginal tentacles were observed to bend toward the center of the leaf in a direction different from the point of excitement. One or two instances in which the tentacles bent slightly in the direction of the source of excitement and not toward the center of the leaf seemed to be purely accidental and due rather to irregularities in the contour of the leaf. Nitschke ('60, p. 240) and C. Darwin ('08, p. 198 and *fig. 10*) noticed that when a gland on one side of the disk was stimulated, "the surrounding tentacles" bent to the point of excitement and not to the center of the leaf. The statement by Darwin together with his figure has generally been understood to include the marginal tentacles. He says, however ('08, p. 200): "It is, perhaps, owing to the exterior pedicels being much flattened that they do not bend quite so accurately to the point of excitement as the more central ones." I am convinced that the peripheral tentacles seldom if ever carry out tropic movements.

vii. *Discal Tentacles*

The discal tentacles differ both anatomically and physiologically from the marginal tentacles. The latter are dorsi-ventral and nastic, the former are radial and tropic. The central tentacles do not bend in response to a direct stimulus, but only to a conducted impulse, and always toward the point of excitement. The method used for investigating the mechanics of the movement of the marginal tentacles is not adapted for studying them in the central tentacles. In all probability, however, their movements are likewise the result of differential growth on opposite sides. The angle of curvature is in any case slight. This and the small diameter of the tentacles indicate that the amount of growth is small. The bending region is confined to a very short basal portion of the pedicel.

Transitions from exterior to central tentacles occur, which exhibit intermediate conditions not only in their structure but also in their behavior. It is probable that some of these tentacles are both nastic and tropic.

8. SUMMARY

1. The red pigment which is found in the leaves and roots of *Drosera rotundifolia* is probably trihydroxymethylnapthoquinone.
2. The rosette habit is conditioned by transpiration.
3. The inflexion of *Drosera* tentacles is produced by an acceleration of the rate of growth on the convex side and in the median section. The unbending is caused by an increase in the rate of growth on the concave side and in the median section, accompanied by compression of the convex side.
4. In both cases the acceleration commences near the base and extends toward the gland. The amount of growth is greatest near the base and decreases apically.
5. A tentacle is capable of reacting three times. During each reaction an apical portion of the bending region becomes fully grown. *Drosera* tentacles have intercalary, basipetal growth.
6. The bending of the exterior tentacles is nastic; of the central tentacles, tropic. The unbending is in all cases owing to autotropism.

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A NEW SPECIES OF METZGERIA FROM THE GALAPAGOS ISLANDS*

BY ALEXANDER W. EVANS

The collection of Hepaticae made in the Galapagos Islands by Dr. Alban Stewart, while acting as botanist to the Expedition of the California Academy of Sciences, includes between fifteen and twenty species. One of the most interesting of these is the *Metzgeria* described below. It is not only a distinct addition to the genus but it apparently represents the first member of the Metzgeriaceae (Jungermanniales anacrogynae) to be reported from this group of islands.

* Contribution from the Osborn Botanical Laboratory.

Metzgeria grandiflora sp. nov.

Whitish or yellowish green, becoming brownish with age, growing in tufts: thallus spreading more or less from the substratum, apparently pendulous, dichotomous, well-developed branches mostly 1–1.5 mm. wide when explanate and 3–6 mm. long between the forks, strongly convex, the margins almost meeting ventrally; costa bounded both dorsally and ventrally by two rows of cortical cells; wings about fifteen cells wide, the cells similar throughout, with slightly thickened walls and minute, scarcely evident trigones, averaging about 45 × 35 μ; hairs scattered, restricted to the margin, sometimes truly marginal, sometimes slightly displaced to the ventral surface, occurring singly, rarely more than 60 μ long and often much shorter, straight or nearly so, thick-walled: inflorescence dioicous: female branch much longer than is usual in the genus, sometimes attaining a length of 0.8 mm.; central portion several cells thick but without a distinct costa, strongly concave dorsally; wings reniform, about 0.4 mm. wide, more or less pressed together, one cell thick; hairs marginal, scattered, usually occurring singly, rarely in pairs, similar to those of the thallus but often longer and sometimes attaining a length of 150 μ; archegonia numerous: male branch strongly curved and inflated, elliptical in outline, about 0.6 mm. long and 0.4 mm. wide, delicate in texture, without hairs; costa distinct; antheridia numerous: calyptra and sporophyte not seen [Figs. 1–5].

On bushes and trees. Chatham Island, February 23, 1906, *A. Stewart 2785, 2786;* Abingdon Island, September 19, 1906, *A. Stewart 8524.* No. 2785, a portion of which is deposited in the herbarium of Yale University, may be designated the type of the species; No. 2786 is mixed with *Frullania aculeata* Tayl. and a sterile *Plagiochila;* No. 8524 is mixed with a sterile *Frullania*, apparently referable to *F. brasiliensis* Raddi.

The female branches in *M. grandiflora* (Figs. 3, 4) are unusually large and yield some of the most distinctive characters of the species. In most members of the genus these branches are small and obcordate, the dorsal surface is plane or nearly so, the archegonia are borne in a small cluster, and the hairs are often scattered over the ventral surface. In *M. grandiflora* the dorsal surface in the median portion is so strongly concave that the wings are almost pressed together, and it is only with difficulty that they can be flattened out in one plane; the wings are reniform and rounded at each end, the archegonia are borne in a large cluster, and the hairs are restricted to the margin. The male branches likewise (FIG. 5) are considerably longer than is usual in the genus but they are typical in other respects. No gemmae were observed in the material examined.

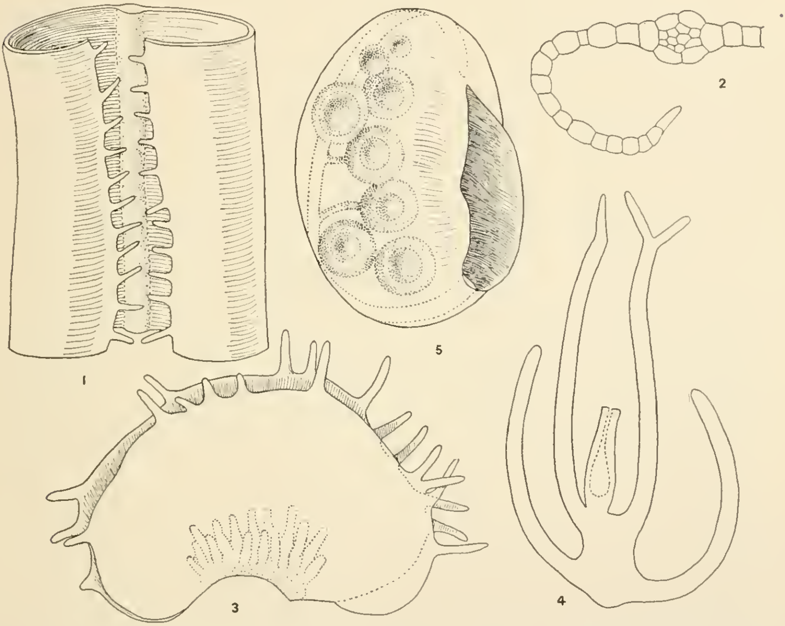

FIG. 1. METZGERIA GRANDIFLORA Evans. Portion of thallus, ventral view, × 50. FIG. 2. Cross section of costa and wing, × 60. FIG. 3. Female branch, × 50. FIG. 4. Section through thallus and female branch, the wing on the left showing one marginal hair, that on the right showing two, × 50. FIG. 5. Male branch, × 50. FIGS. 1–4 were drawn from the type specimen; FIG. 5, from No. 8524.

The characters of the thallus (FIGS. 1, 2), which should be especially emphasized, are the following: the strong convexity, the cortical cells of the costa in two rows both dorsally and ventrally, the presence of hairs along the margins of the wings, and the lack of hairs on the costa and on the surfaces of the wings. In the first volume of his Species Hepaticarum* Stephani recognizes three species of *Metzgeria* with hairs restricted to the

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* Bull. Herb. Boissier 7: 939. 1899.

margins of the wings and with a costa of the type found in *M. grandiflora*. These species are *M. comata* Steph. (of New Caledonia), *M. glaberrima* Steph. (of Chile, Patagonia, New Zealand and Australia), and *M. sinuata* Loitles. (of Peru). The first and third of these are known to the writer from description only. In *M. comata* the plants are epiphyllous, the thallus is plane, and the cells of the wings are unusually large, measuring 126 × 54 μ according to the description. In *M. glaberrima* the thallus is plane and is often naked throughout, even marginal hairs being absent; the female branch, moreover, bears surface hairs, as is usual in the genus. In *M. sinuata*, which is known only from the original material, the thallus is strongly convex as in *M. grandiflora*, but the wings are often thirty-five cells wide, the hairs are 150 μ long, and the margin is described as being deeply sinuate or, rather, interruptedly recurved, a condition which is apparently never duplicated by *M. grandiflora*. Unfortunately *M. sinuata* was described from sterile material, and there may be difficulty in recognizing it again.

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ADDITIONS TO THE HEPATIC FLORA OF QUEBEC[1]

ALEXANDER W. EVANS

In the seventh part of Professor John Macoun's Catalogue of Canadian Plants, published at Ottawa, in 1902, sixty-three species of Hepaticae are recorded from the province of Quebec. They are the following: *Riccia arvensis*, *Ricciella fluitans* (listed as *Riccia fluitans*), *Ricciocarpus natans* (listed under the variety *terrestris*), *Neesiella rupestris* (listed as *Grimaldia rupestris*), *Conocephalum conicum*, *Preissia quadrata* (listed as *Cyathophora quadrata*), *Marchantia polymorpha*, *Riccardia latifrons* (listed as *Aneura latifrons*), *R. pinguis* (listed as *A. pinguis*), *Metzgeria myriopoda*, *Pellia epiphylla*, *Blasia pusilla*, *Fossombronia foveolata*, *Jungermannia cordifolia*, *J. pumila*, *Jamesoniella autumnalis* (listed as *Jungermannia autumnalis*), *Lophozia alpestris*, *L. attenuata*, *L. barbata*, *L. incisa*, *L. inflata*, *L. longiflora* (listed as *L. ventricosa*, var. *longiflora*), *L. Muelleri*, *L. porphyroleuca* (listed as *L. ventricosa*, var. *porphyroleuca*), *L. quinquedentata*, *L. ventricosa*, *Sphenolobus exsectus* (listed as *L. exsecta*), *S. Michauxii* (listed as *L. Michauxii*), *S. politus* (listed as *L. polita*), *S. saxicola* (listed as *L. saxicola*), *S. scitulus* (listed as *L. exsecta*, var. "*scituta*"), *Plagiochila asplenioides*, *Mylia anomala*, *M. Taylori*, *Lophocolea heterophylla* (listed also as *L. Macounii*), *Chiloscyphus rivularis* (listed as *Ch. polyanthos*, var. *rivularis*), *Geocalyx graveolens*, *Cephalozia bicuspidata*, *C. catenulata*, *C. curvifolia*, *C. fluitans*, *C. media*, *Calypogeia Trichomanis* (listed as *Kantia Trichomanis*), *Bazzania trilobata*, *Lepidozia reptans*, *Blepharostoma trichophyllum*, *Temnoma setiforme* (listed as *Blepharostoma setiforme*), *Ptilidium ciliare*, *Pt. pulcherrimum*, *Trichocolea tomentella*, *Diplophyllum taxifolium* (listed as *Diplophylleia taxifolia*), *Scapania curta*, *S. glaucocephala*, *S. irrigua*, *S. nemorosa*, *S. undulata*, *Radula complanata*, *Porella platyphylla*, *Lejeunea cavifolia*, *Frullania Asagrayana*, *F. eboracensis*, *F. Selwyniana*, and *Anthoceros Macounii*. There are perhaps eight species in this list of which the writer has seen no material from Quebec.

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[1] Contribution from the Osborn Botanical Laboratory.

Only four of these, however, can be considered at all doubtful. One is *Metzgeria myriopoda*, a species with a decidedly southern range; the others are *Lophozia longiflora*, *L. Muelleri*, and *Sphenolobus scitulus*. A re-examination of Macoun's specimens of these four species is much to be desired. Since the publication of Macoun's Catalogue important collections of Quebec hepatics have been made, not only by Professor Macoun himself, but by Professor J. F. Collins, Rev. H. Dupret, Brother Victorin, and the writer. Another collection was made by Mr. J. A. Allen as long ago as 1881 but was not studied by Professor Macoun. These collections add forty-one species to those listed by Macoun. Five of the most interesting of these additions, *Clevea hyalina*, *Neesiella pilosa*, *Lophozia badensis*, *L. Hatcheri* (= *L. Baueriana*), and *Frullania Bolanderi*,[1] have already been recorded, and it is the purpose of the present paper to call attention to the others. The species are arranged according to Schiffner's system in Engler & Prantl's "Die natürlichen Pflanzenfamilien," and the only dates given are those of the earliest collections. The additions increase the total number of species known from Quebec to 104, or if the four doubtful species listed by Macoun are omitted, to 100.

1. METZGERIA FURCATA (L.) Dumort. On rocks. St. Hilaire Mountains, *Brother Victorin 30*, August, 1910; Bic, *A. W. E. 116, 125, 139, 140.*

2. PELLIA NEESIANA (Gottsche) Limpr. In bogs and on moist rocks. St. Hubert, *Brother Victorin 23*, May, 1913; Bic, *A. W. E. 146.*

3. GYMNOMITRIUM CONCINNATUM (Lightf.) Nees. On rocks. Bic, *J. F. Collins 3262*, July, 1904; *A. W. E. 173;* Table-top Mountain, *J. F. Collins 4311b.*

4. GYMNOMITRIUM CORALLIOIDES Nees. On rocks. Bic, *A. W. E. 124, 127, 174*, August, 1915.

5. MARSUPELLA SULLIVANTII (DeNot.) Evans. On moist rocks. Table-top Mountain, *J. F. Collins 4389, 4489*, August, 1906.

6. NARDIA CRENULATA (Sm.) Lindb. On sandy banks. Longueuil, *Brother Victorin 23*, July, 1910.

7. JUNGERMANNIA LANCEOLATA L. On shaded banks and rotten logs. Tadousac, *A. W. E. 16, 59*, July, 1915; Bic, *A. W. E. 137.*

8. LOPHOZIA BICRENATA (Schmid.) Dumort. On shaded earth. Salmon River, *J. Macoun 8*, July, 1905; Tadousac, *A. W. E. 13, 15.*

9. LOPHOZIA CONFERTIFOLIA Schiffn. On earth among rocks. Bic, *A. W. E. 165*, August, 1915.

10. LOPHOZIA EXCISA (Dicks.) Dumort. On shaded earth. Tadousac, *A. W. E. 14*, July, 1915.

11. LOPHOZIA FLOERKII (Web. f. & Mohr) Schiffn. On rocks. Table-top Mountain, *J. F. Collins 4387a, 4390, 4396a, 4490a*, August, 1916.

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[1] See Evans, Rhodora **16**: 63. 1914 (for *Clevea hyalina*, the record being based on specimens collected by O. D. Allen on Mt. Albert, in July, 1881); BRYOLOGIST **14**: 84. 1911 (for *Neesiella pilosa*); ibid. **13**: 34. 1910 (for *Lophozia badensis*); ibid. **18**: 72. 1915 (for *Frullania Bolanderi*); also Conklin, BRYOLOGIST **15**: 12. 1912 (for *Lophozia Hatcheri*).

12. Lophozia heterocolpa (Thed.) M. A. Howe. On shaded banks and rotten logs in calcareous regions. Bic, *A. W. E. 99, 108, 109, 149, 150*, August, 1915.

13. Lophozia Kaurini (Limpr.) Steph. On moist calcareous rocks. Between Baldé and Baie des Chaleurs, Bonaventure River, *J. F. Collins 3540, 3584*, August, 1904.

14. Lophozia Kunzeana (Hüben.) Evans. On rocks. Mt. Albert, *J. F. Collins 4055c, 4083b*, July, 1906; Rigaud, *H. Dupret 7*.

15. Lophozia longidens (Lindb.) Macoun. On rocks. Tadousac, *A. W. E. 8, 80*, July, 1915; Bic, *A. W. E. 147*.

16. Lophozia lycopodioides (Wallr.) Cogn. On shaded rocks and earth. Mt. Albert, *J. F. Collins 4143*, July 1906; Table-top Mountain, *J. F. Collins 4387c, 4547, 4552, 4576a;* Bic, *A. W. E. 158, 159*.

17. Sphenolobus exsectaeformis (Breidl.) Steph. On shaded rocks, earth, and rotten logs. Sandy Bay, *J. F. Collins 4703*, August, 1906; Tadousac, *A. W. E. 5, 42;* Bic, *A. W. E. 92, 132, 151, 154*.

18. Sphenolobus Hellerianus (Nees) Steph. On rotten logs. Trail to Table-top Mountain, *J. F Collins 4259a*, July, 1906; Bic, *A. W. E. 161*.

19. Sphenolobus minutus (Crantz) Steph. On rocks. Ste. Anne des Monts River, *J. A. Allen 3*, July, 1881; *J. F. Collins 4616;* Table-top Mountain, *J. F. Collins 4784a;* St. Columbin, *Brother Victorin 17;* Tadousac, *A. W. E. 10, 68;* Bic, *A. W. E. 128, 142*.

20. Lophocolea minor Nees. On shaded rocks and banks. Montreal, *H. Dupret 13, 41*, November, 1906; Isle d'Orleans, *A. W. E. 1;* Tadousac, *A. W. E. 41;* Bic, *A. W. E. 97, 105*.

21. Chiloscyphus fragilis (Roth) Schiffn. In pools. Oka, *H. Dupret, 19*, July, 1904; Grand River, *J. F. Collins 3665*.

22. Chiloscyphus pallescens (Ehrh.) Dumort. On rotten logs. Tadousac, *A. W. E. 18*, July, 1915.

23. Harpanthus scutatus (Web. f. & Mohr) Spruce. On rotten logs. Tadousac, *A. W. E. 26*, July, 1915.

24. Cephaloziella byssacea (Roth) Warnst. On rocks and earth. Tadousac, *A. W. E. 49, 52 56*, July, 1915; Bic, *A. W. E. 168*.

25. Cephaloziella Hampeana (Nees) Schiffn. On rocks and earth. Bic, *J. F. Collins 4857*, July, 1907; Tadousac, *A. W. E. 45*.

26. Cephaloziella myriantha (Lindb.) Schiffn. On earth. Tadousac, *A. W. E. 61*, July, 1915; Bic, *A. W. E. 110*.

27. Odontoschisma denudatum (Mart.) Dumort. On rotten logs. Montmorency River, *J. Macoun 10*, July, 1905.

28. Calypogeia Neesiana (Massal. & Carest.) K. Müll. On shaded earth. Bic, *J. F. Collins 5057*, July, 1907; Oka, *H. Dupret 42, 48*.

29. Calypogeia suecica (Arn. & Perss.) K. Müll On rotten logs. Ste. Anne des Monts River, *J. F. Collins 4622*, August, 1906.

30. Bazzania tricrenata (Wahl.) Trevis. On rocks. Mt. Albert, *J. A. Allen 27*, July, 1881; *J. F. Collins 4202;* Percé, *J. F. Collins 3728a*.

31. Scapania paludicola Kaalaas & K. Müll. In peat bogs. St. Hubert, *Brother Victorin 1, 22*, August, 1909.

32. Scapania subalpina (Nees) Dumort. On rocks. Table-top Mountain, *J. F. Collins 4487*, August, 1906.

33. Scapania umbrosa (Schrad.) Dumort. On rotten logs. Tadousac, *A. W. E. 24, July, 1915*.

34. Porella pinnata L. In running water. Montmorency River, *J. Macoun 7*, June, 1905.

35. Frullania Oakesiana Aust. On trees and rocks. Seal Cove River, Douglastown, *J. F. Collins 3797*, August, 1904; Tadousac, *A. W. E. 74, 75*.

If the four doubtful species in Macoun's Catalogue are excluded it will be seen that all the Quebec species occur also in New England, with the exception of the following three: *Sphenolobus politus*, *S. saxicola*, and *Frullania Bolanderi*. It is probable, in fact, that most of the other species now known from Maine, New Hampshire, and Vermont await discovery in Quebec. Whether the more northern types, known from Arctic America, Yukon, and Alaska, are likewise to be expected is, of course, uncertain. The occurrence of such species as *Gymnomitrium concinnatum* and *G. corallioides* at Bic, almost at the sea level, is perhaps an indication that other alpine and artic forms may reach the shores of the St. Lawrence nearer its mouth, but there is no definite evidence as yet to support this idea. According to our present information no exclusively arctic types are known from Quebec, and its hepatic flora might be described as north temperate in character.

When compared with the flora of Europe the only distinctive elements are the five species of *Frullania*, *F. Asagrayana*, *F. Bolanderi*, *F. eboracensis*, *F. Oakesiana*, and *F. Selwyniana;* and the known range of *F. Bolanderi*, as has recently been noted, stretches across North America to the Pacific Coast with an extension to the island of Saghalin in eastern Asia. Possibly the high ratio of endemic species in *Frullania* is associated with the fact that the genus is apparently tropical in origin and comparatively modern.

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NOTES ON NEW ENGLAND HEPATICAE,— XIII.[1]

ALEXANDER W. EVANS.

(Plate 120.)

IN the recent parts of Rabenhorst's Kryptogamen-Flora, Müller treats the genera *Scapania*, *Radula*, and *Porella* (or *Madotheca*). He not only gives full descriptions of the various species represented in the European flora but appends interesting remarks on geographical distribution. Many of these remarks relate to North American records, and among the species which he cites from New England the following may be particularly noted: *Scapania Oakesii* Aust. (from New Hampshire), *S. paludicola* Loeske & K. Müll. (from Connecticut), and *Radula Lindbergiana* Gottsche (from Vermont). These species do not appear in the writer's Revised List of New England Hepaticae,[2] although *S. Oakesii* is really included under *S. dentata* Dumort. and *S. paludicola* under *S. irrigua* (Nees) Dumort. The reasons for con-

[1] Contribution from the Osborn Botanical Laboratory.

[2] RHODORA **15**: 21–28. 1913.

sidering them distinct will be given below. Müller's record for *Radula Lindbergiana* was based on specimens accredited to Miss Lorenz. She suspects, however, that there must be some error about them, and the occurrence of this species in North America, where it is surely to be expected, must therefore await further confirmation. According to Müller *Scapania gracilis* (Lindb.) Kaalaas, which has been twice reported from New England, is restricted to Europe and the Atlantic Islands, the North American specimens which have been referred to this species representing a form of *S. nemorosa* (L.) Dumort.; *S. gracilis*, therefore, should no longer be included in our flora.

Müller's treatment of the genus *Porella* is of especial interest to students in America, where most of the European species are represented. In New England three species, *P. pinnata* L., *P. platyphylla* (L.) Lindb., and *P. rivularis* (Nees) Trevis., have been reported. The writer now feels convinced, however, from the study of recent descriptions and a representative collection of specimens, that the true *P. platyphylla* is much rarer than supposed, being largely replaced by the closely related *P. platyphylloidea* (Schwein.) Lindb.; and that *P. rivularis* does not occur in eastern North America at all. The specific characters of the New England species are discussed below. It may be noted in this connection that a strong tendency prevails in Europe to supplant the old generic name *Porella*, dating from 1753, by the more recent name *Madotheca*, dating from 1822. The name *Porella* has been in use on this side of the Atlantic for many years, and Howe [1] has given excellent and convincing reasons for not giving it up. It is possible, at some future International Botanical Congress, that *Madotheca* may be placed among the "nomina conservanda". Until such action is taken, however, the writer would recommend that the use of the name *Porella* be maintained although, to avoid confusion, *Porella* and *Madotheca* are used interchangeably in some of the following discussions.

As in previous papers of this series additions to local state floras and a census of the New England species will be given at the close.

1. Scapania Oakesii Aust. Bull. Torrey Club. **3**: 10. 1872. *Scapania dentata, ε. Oakesii* K. Müll. Nova Acta Acad. Caes. Leop.-Carol. Akad. **83**: 102. 1905. On rocks and banks, mostly at elevations above 600 m. Maine: Big Alder Gorge near Round Mountain

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[1] See Bull. Torrey Club **24**: 512–515. 1897; **25**: 96–103. 1898; Rev. Bryol. **25**: 76–78. 1898.

Lake, Franklin County (*A. Lorenz*). New Hampshire: White Mountains (*W. Oakes, C. F. Austin*, distributed in Hep. Bor.-Amer. *14*). Vermont: Handcock and Rochester[1] (*D. L. Dutton 633, 906*). In addition to the stations given by Austin and Howe the following station outside New England may be noted: valley of the Barrasois River, Cape Breton, Nova Scotia (*G. E. Nichols 294*).

The history of *Scapania Oakesii* gives evidence that its claims for recognition as a species are not very strong. As originally proposed by Austin it was based on four specimens, the first two from the White Mountains, New Hampshire, collected by Oakes, the third from the "Lake Superior region, Canada," collected by Macoun, and the fourth from "Observation Inlet, Columbia, Oregon," collected by Scouler. These are described as varieties α, β, γ and δ, respectively. In Hep. Bor.-Amer. *14* (1873) Austin distributed specimens from the White Mountains collected by Oakes and by himself. He compared the species with *S. undulata*, var. *purpurea* Nees, but emphasized the large spur-like teeth on the keels of the uppermost leaves as an important distinguishing character.

Nothing further was added to our knowledge of *S. Oakesii* until Howe[2] described and figured it from specimens which he found at Eureka and Kneeland Prairie Road, California. According to his account the plants from California are usually smaller than those from New Hampshire but agree closely with those from Observatory Inlet. He notes their superficial resemblance to *S. nemorosa* but considers them distinct both from this species and from *S. undulata* (L.) Dumort.

In his monograph of the genus *Scapania*, Müller,[3] in reducing *S. Oakesii* to a variety of *S. dentata* Dumort., stated that he had examined Austin's plant in two different sets of exsiccati. In one he found nothing but *S. nemorosa;* in the other a mixture of two plants, one being a green form of *S. undulata* and the other a reddish plant which he took to be the true *S. Oakesii*. He finds no important characters to separate this plant from *S. dentata*, and remarks that the carinal teeth, upon which both Austin and Howe laid emphasis, represent an uncertain character found now and then in many other species of *Scapania*. In the fourth series of the writer's Notes on New England

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[1] The Rochester specimens were cited under *S. dentata* in Rhodora **12**: 204. 1911.

[2] Mem. Torrey Club **7**: 151. *pl. 108, 109*. 1899.

[3] Nova Acta Acad. Caes. Leop.-Carol. **83**: 102, 114. 1905.

Hepaticae,[1] the example of Müller is followed, and *S. Oakesii* is included among the synonyms of *S. dentata*.

A few years later Kaalaas[2] found an ambiguous *Scapania* in Söndmöre, Norway, at an altitude of 800 m. He considered it distinct from all the known European species and identified it as *S. Oakesii*, which he knew from description only. In distinguishing his plant from *S. dentata* and *S. undulata*, he again emphasizes the carinal teeth but states that this character is associated with a series of others, both lobes, for example, being rounded as in *S. subalpina* (Nees) Dumort., while the dorsal lobe arches far across the stem and the keel is curved. Müller[3] now shares the views of Kaalaas, at least to the extent of considering *S. Oakesii* a "kleine Art," and includes it among the species of Europe, citing the Norwegian station as the only one known at the present time. For North America he cites Eureka, California, in addition to the New Hampshire localities.

The writer has examined Austin's specimens of *S. Oakesii* in two sets of his exsiccati and has found in both cases a mixture of *S. undulata* and the plant which Müller regards as Austin's type. Since the *S. undulata* has no carinal teeth while the other plant exhibits them in abundance, Müller's views are clearly correct. The plant with the carinal teeth shows further the other characteristics pointed out by Kaalaas, and the same thing is true of the specimens from Maine and Vermont which are quoted above. The carinal teeth are by no means constant, some of the leaves developing five or more while others show few or none, but leaves with teeth of this character apparently occur on every well-developed stem and form a very striking feature of the species. In reinstating *S. Oakesii* as a member of the New England flora the writer admits that its characters are less definite than might be desired; at the same time they are fully as satisfactory as the characters of such species as *S. dentata*, *S. subalpina*, and *S. undulata*, species which are universally recognized but which are nevertheless connected by transitional forms. The four varieties distinguished by Austin need further investigation.

2. Scapania paludicola Loeske & K. Müll.; K. Müller, Rabenhorst's Kryptogamen-Flora **6**^{2}: 425. *f. 125, 126*. 1915. In peat bogs. Maine: near Schoodic Lake, Piscataquis County (*A. W. E.*); Round

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[1] Rhodora **8**: 41. 1906.

[2] Kgl. Norske Vidensk. Selsk. Skr. 1910^7: 26. 1911.

[3] Rabenhorst's Kryptogamen-Flora **6**^{2}: 460. 1915.

Mountain Lake, Franklin County (*A. Lorenz*). New Hampshire: Eagle Lake, Mt. Lafayette (*C. C. Haynes, A. Lorenz & A. W. E.*). Vermont: Bloodsucker Pond, Jamaica (*F. Dobbin*); Willoughby (*A. Lorenz & A. W. E.*); Franklin and Burke (*A. Lorenz*). Connecticut: Bethany (*A. W. E.*), cited by Müller; specimens from the same locality (*F. Bement*) but incorrectly labeled "Lebanon" were distributed in Hep. Amer. *190*, as *S. irrigua;* Norfolk and New Fairfield (*G. E. Nichols*); Bailey's Pond, Voluntown (*A. W. E.*). The following stations outside New England may likewise be recorded: St. Ann's Mountain, Cape Breton, Nova Scotia (*G. E. Nichols 213*); Campobello, New Brunswick (*W. G. Farlow*); St. Hubert, Quebec (*Brother Victorin*); near Ottawa, Ontario (*J. Macoun 1*); Port Clarence, Alaska (*W. H. Brewer & W. R. Coe 673*), cited by Müller; Podunk Marsh, West Fort Ann, New York (*S. H. Burnham*); near Superior, Wisconsin (*G. H. Conklin 1009, 1258*).

In describing *S. paludicola* as a "kleine Art," Müller calls attention to the strong superficial resemblance which it bears to *S. paludosa* K. Müll. In his opinion, however, the two species are not as closely related as might be supposed; he considers that *S. paludosa* has been derived from *S. undulata,* while *S. paludicola* has been derived from *S. irrigua.* In *S. undulata* and *S. paludosa* he finds that the leaf-cells are either thin-walled throughout or develop uniformly thickened walls (in which trigones are usually absent altogether), while in *S. irrigua* and *S. paludicola,* trigones are invariably present and may be very conspicuous. Apparently *S. paludicola* is not uncommon in northern North America, having been confused with *S. irrigua.* In fact several of the stations cited above have already been reported under the older species. Müller brings out the fact that *S. paludicola* prefers calcareous bogs, without being confined to them, and this preference is apparent from its North American stations.

The occurrence of *S. paludicola* in bogs, its robust habit, its deeply divided leaves, its short and arched keel usually without alar outgrowths of any sort, its deeply cordate dorsal lobes directed toward the apex of the stem rather than obliquely outward, and the trigones in its leaf-cells will usually make its recognition an easy matter. The margins of the leaves may be sparingly and minutely toothed or subentire and both lobes are often distinctly apiculate. The short and strongly arched keel and the cordate dorsal lobe directed forward will distinguish the species at once from both *S. irrigua* and *S. undulata,* while the trigones will readily separate it from *S. paludosa.*

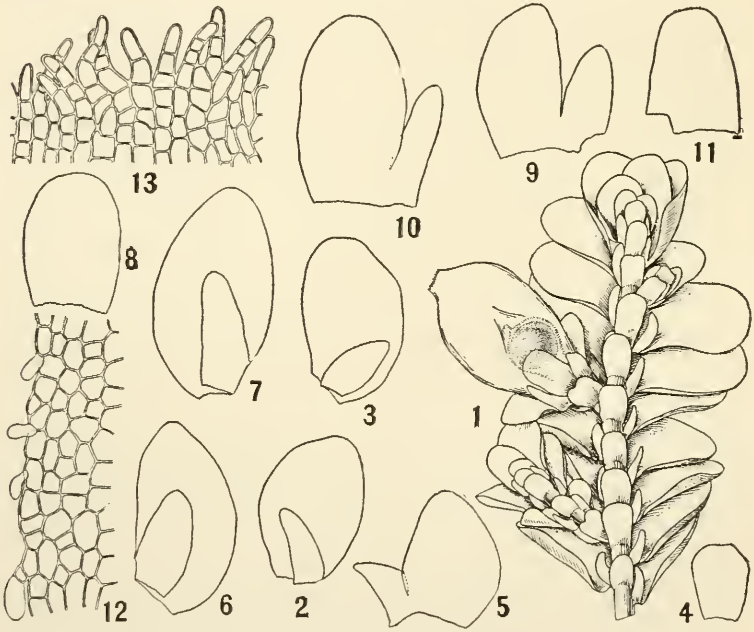
3. Porella pinnata L. Sp. Plant. 1106. 1753. *Jungermannia Porella* Dicks. Trans. Linn. Soc. **3**: 239. *pl. 20, f. 1.* 1797. *Jungermannia distans* Schwein. Spec. Fl. Am. Sept. Crypt. 9. 1821. *Madotheca Porella* Nees (in part), Naturg. der europ. Leberm. **3**: 201. 1838. *Madotheca involuta* Hampe; Lehmann & Lindenberg, Pug. Plant. **7**: 10. 1838. *Cavendishia Porella* Carruth. Seemann's Jour. Bot. **3**: 301. 1865. *Madotheca Sullivantii* Aust. Bull. Torrey Club **3**: 15. 1872. *Porella Sullivantii* Underw.; A. Gray, Man., ed. 6, 709. 1890. *Madotheca microrhyncha* Tayl.; Stephani, Species Hepat. **4**: 251. 1910. [Text figs. 1–13.]

The geographical distribution of *P. pinnata* extends, in North America, from Nova Scotia westward to Ontario and Minnesota and southward to Cuba, Florida, and Louisiana, numerous stations being known from New England. In Europe its range is restricted to the British Isles and the western coast of France, with a possible extension into Portugal. In North America the species is abundant; in Europe, exceedingly rare. It grows on stones and logs in streams as well as on the banks, and is completely submerged during a part of the year. Apparently the sporophytes reach maturity only when the plants are exposed to the air.

The species has been repeatedly described so that little need be said about its general features and great variability. There are certain details, however, which the descriptions do not bring out very clearly, and a few words about these may be in place. Attention will likewise be called to certain synonyms of the species.

The complete, or almost complete, absence of marginal teeth on the leaves, underleaves and bracts, in a genus where teeth are so frequently present, is one of the most important characteristics of *P. pinnata*. Close to the dorsal base of the lobe, to be sure, close to the inner base of the lobule and along the margins of the perichaetial bracts and bracteoles a few slime papillae (or their vestiges) can be demonstrated (Fig. 12) and these are sometimes borne on short stalks, but even here anything approaching an actual tooth in size is exceedingly rare.

The lobes of the leaves (see Fig. 1) which are ovate to oblong in form and rounded at the apex, are attached by an arched line and are commonly plane except close to the lobule, where the margin is slightly inflexed. In plants exposed to the air this portion of the margin is often more or less involute. At the dorsal base the lobe is somewhat dilated but scarcely enough to be called cordate; at the ventral base (where it meets the lobule) it is usually not dilated at all and may even be slightly decurrent, the keel being often obsolete. The small and narrow lobules, rounded or very bluntly pointed at the apex, are attached by a line which is straight or only slightly arched, and the inner edge is usually shorter than the outer, an unusual condition in the genus *Porella*. The leaf-cells average about 20 μ in the middle of the lobe and show small but distinct trigones. In the inflexed portion the marginal cells extend at right angles to the edge and form a distinct border. The underleaves (Fig. 1) are slightly if at all decurrent, the line of attachment (as in the case of the lobules) being straight or only slightly arched.



Figs. 1–13. Porella pinnata L.

1. Branch (of first order) bearing a female branch with a perianth, and also a sterile branch, ventral view, × 15. 2–4 Bracts and bracteole from a single involucre, × 35. 5. A bract from another involucre, × 35. 6–8. Bracts and bracteole from a third involucre, × 35. 9–11. Bracts and bracteole from a fourth involucre, × 35. 12. Cells from the base of a bract (lobe), showing papillae, × 200. 13. Teeth from the mouth of an immature perianth, × 200. Figs. 1–5 were drawn from a specimen collected at Columbus, Kentucky, by N. L. T. Nelson *1497;* Figs. 6–8, 12, 13 from a specimen collected at Granby, Connecticut, by G. E. Nichols; Figs. 9–11, from the type specimen of *Madotheca microrhyncha* in the Taylor herbarium.

The perichaetial bracts (Figs. 2, 3, 5–7, 9, 10) are not very fully treated in most descriptions, although Gottsche[1] has given a good account of them. They are commonly reduced to a single pair and the difference in size between the inner and outer bracts is not marked. The bracts are unequally bilobed, both lobe and lobule being ovate to oblong and usually rounded at the apex; in the case of the lobule, however, the apical portion is sometimes distinctly narrowed and the apex itself may be subacute. The bracteoles (Figs. 4, 8, 11) are oblong to obovate and usually rounded or truncate at the apex. According to Stephani[2] the lobule is lanceolate and long-attenuate, while the bracteole is suborbicular and highly coalescent on one side with a lobule. So far as the writer has been able to observe, however, the bracteole is usually quite free from the lobules, coalescence being either absent altogether or very slightly marked.

The mouth of the perianth is described as slightly crenulate, or minutely crenulate, or dentate. These expressions, however, do not depict the condition of the mouth accurately and were probably based on old and disintegrated specimens. In uninjured perianths (see Fig. 1) the mouth is shortly and closely ciliolate, the cilia varying from one to four cells in length (Fig. 13). The spores and elaters are well described by Howe.[3]

Of the synonyms cited above *Madotheca Sullivantii* and *M. microrhyncha* require a few words of explanation. *M. Sullivantii* was based on specimens collected by W. S. Sullivant in the "Alleghany Mountains" and distributed by Austin in his Hep. Bor.-Amer. *94*. It was first included among the synonyms of *P. pinnata* by Howe, but neither Stephani nor Müller follows his example. Stephani gives it among the synonyms of *M. Thuja*, while Müller[4] considers it a valid species. The specimens in Austin's distribution show, in the writer's opinion, that Howe was undoubtedly correct in considering the species synonymous with *P. pinnata*. They represent a small and slender form with perianths, and evidently grew in a more or less exposed position. The habit of the plants, which Müller emphasizes in maintaining the validity of the species, is not a constant feature and is not supported by characters drawn from the leaves and floral organs.

The habitat of *M. microrhyncha* is given by Stephani as "Ohio."

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[1] Gottsche & Rabenhorst, Hep. Eur. *639* (accompanying text).

[2] Species Hepat. **4**: 252. 1910.

[3] Bull. Torrey Club **24**: 517. 1897.

[4] Rabenhorst's Kryptogamen Flora **6**^{2}: 571. 1915.

Through the kindness of Professor Farlow it has been possible to examine a portion of the type material from the Taylor herbarium. On the original packet the following words are written: "*Jungermannia microrhyncha* Tayl. Mss. (*Madotheca*). Ohio: Sir W. J. Hooker. 1843." Apparently Taylor had little faith in his species, for he never published it formally, but it is cited (as a manuscript species) among the synonyms of *Madotheca Porella* in the Synopsis Hepaticarum. Stephani was the first to give it adequate publication. Among the characters which he emphasizes are the following: the small, slightly projecting and minutely crenulate mouth of the perianth; the ovate-oblong lobes of the perichaetial bracts, rounded at the apex; and the small triangular lobules, discrete almost to the base. In *M. Porella* he gives, as more or less contrasting characters: the small, shortly rostrate, and minutely crenulate mouth of the perianth; the oblong and obtuse lobes of the perichaetial bracts; and the lanceolate lobules, discrete to about the middle. These differences, even if they were constant and accurately described, are so slight that they would have but doubtful specific value. As a matter of fact the type specimens, when compared with *P. pinnata*, do not show the differences which Stephani brings out. The two plants are essentially alike in all important respects, and there seems to be no reason for considering *M. microrhyncha* a distinct species. The same conclusion was reached by Underwood, who examined Taylor's type many years ago and placed it under *P. pinnata*.

Müller objects to the use of the specific name "*pinnata*" for the present species and gives two reasons. First, because he considers it disadvantageous to use so old a name for a plant which has been so much confused even in recent times; and, second, because Linnaeus could hardly have understood this plant under his *Porella pinnata* on account of its great rarity in Europe. These reasons are not very convincing. In the first place, writers who have used the specific name "*pinnata*" (such as Lindberg, Howe, Underwood, and Pearson) have used it in a very definite sense and have based their use of the name on the specimen in the Dillenian herbarium, which represents the type of the *Porella pinnata* of Linnaeus; and, in the second place, Linnaeus cites the species from Pennsylvania only, the date of its discovery in Europe being much later.

4. Porella platyphylla (L.) Lindb. Acta Soc. Sci. Fenn. **9**: 339. 1869. *Jungermannia platyphylla* L. Sp. Plant. 1134. 1753. *Antoiria vulgaris* Raddi, Mem. Soc. Sci. Modena **18**: 19. *pl. 2, f. 1.* 1818.

Cavendishia platyphylla S. F. Gray, Nat. Arr. British Pl. **1**: 690. 1821. *Madotheca platyphylla* Dumort. Comm. Bot. 111. 1822. *Porella Notarisii* Trevis. Rend. Ist. Lomb. II. **7**: 785. 1874. *Bellincinia platyphylla* O. Kuntze, Rev. Gen. Plant. 833. 1891. [Plate 120.]

On rocks and trees. Maine: Dover (*J. F. Collins 1685*); Vassalboro (*E. B. Chamberlain 966*). Vermont: Stowe (*E. G. Britton*); Willoughby (*E. Faxon; A. Lorenz & A. W. E.*); Jamaica (*F. Dobbin*). Connecticut: New Haven (*D. C. Eaton*); Brookfield, Sherman, and New Milford (*A. W. E.*); West Hartford (*A. Lorenz*). The following specimens from stations outside New England may likewise be recorded: Bic, Quebec (*A. W. E.*); Syracuse, New York (*L. M. Underwood & O. F. Cook*, distributed in Hep. Amer. *29*); Dresden Station, Adirondack Mountains, New York (*C. H. Peck 60*); Narrowsville, Pennsylvania (*T. P. James*); near Yellow Springs, Ohio (*W. S. Sullivant*, distributed in Hep. Bor.-Amer. *91b*, as *Madotheca rivularis*); near Big Bay, Lake Superior region, Wisconsin (*L. S. Cheney 5705*); Vermilion Lake, Minnesota (*Arthur, Bailey & Holway 114a*); Vasa, Minnesota (*N. L. T. Nelson 5, 945 1/2*); Fall Lake, Minnesota (*J. M. Holzinger*), male plants, doubtful; Iowa City, Iowa (*B. Shimek*). In Europe the species is exceedingly abundant.

Although *Porella* (or *Madotheca*) *platyphylla* has long been recognized as one of the commonest and most widely distributed of the Hepaticae, questions have arisen from time to time regarding the limitations of the species. By many writers it has been understood in a broad sense, with characters varying within wide limits, the variations, however, being thoroughly unstable and due to environmental conditions. By other writers it has been understood in a narrower sense, and one or more closely related species, forming with *P. platyphylla* a well-defined aggregate, have been distinguished. The difficulties involved were well stated by Nees von Esenbeck.[1] In discussing certain Mexican specimens of *Madotheca platyphylloidea*, the species most frequently segregated from *M. platyphylla*, he remarked that they were really intermediate between his earlier conceptions of these two species. And he stated further that two conclusions were possible: either, that *M. platyphylloidea* and *M. platyphylla* formed a single series of forms (that is, a single species), the extremes being connected by the Mexican specimens; or, that *M. platyphylloidea* should be made to include the forms which he had

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[1] Naturg. der europ. Leberm. **4**: 497. 1838.

previously referred to *M. platyphylla β major*, thus ascribing to the two species ranges of variability different from those at first assigned. As to which conclusion was correct he made no attempt to decide. In spite of this uncertainty both species were recognized as valid in the Synopsis Hepaticarum, published a few years later by Nees von Esenbeck, in collaboration with Gottsche and Lindenberg.

Lindberg, in his revision of the Scandinavian species of *Porella*, published in 1869,[1] expressed the opinion that Nees von Esenbeck's "*M. platyphylloidea*" was a mixed species. He considered that part of it belonged to the var. *major* of *P. platyphylla*, and that the other part (which he thought might be synonymous with the original *Jungermannia platyphylloidea*) was a synonym of *P. Thuja* (Dicks.) Lindb. A few years later [2] he added the interesting observation that he had examined many North American specimens labeled *P. platyphylla* but that they were all referable to *P. Thuja*, and he commented on the rarity and restricted range of this latter species in Europe. Soon afterwards he published the combination *Porella platyphylloides* (Schwein.) Lindb.[3] and the same name reappears in his last general synopsis of the Scandinavian bryophytes.[4] Apparently he used this name as a substitute for *P. Thuja*, although this conclusion could hardly be deduced with certainty from his published writings. If he did make this substitution, it is difficult to understand why he preferred Schweinitz's specific name to the older name of Dickson, and it is to be regretted that he did not explain his use of the name *P. platyphylloides* more fully. In any case, however, it is clear that he considered Schweinitz's species distinct from *P. platyphylla*.

Among American writers the tendency has been to define *P. platyphylla* in a broad sense. This is the course pursued by Howe [5] in his treatment of the North American species of *Porella*, published in 1897. He admits that the species is very variable and that the common form in America corresponds with the *Jungermannia platyphylloidea* of Schweinitz better than with the common European form. He maintains, however, that the European form does occur in America and that there are so many transitional conditions that any attempt at segregation would be ill-advised.

A few years later an important paper on certain European species

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[1] Acta Soc. Sci. Fenn. **9**: 329–345. 1869.
[2] Ibid. **10**: 493. 1875.
[3] Hepat. Utveckl. 20. 1877.
[4] Musc. Scand. 3. 1879.
[5] Bull. Torrey Club **24**: 521. 1897.

of *Madotheca* was published by Schiffner.[1] He not only recognized *M. platyphylloidea* as valid but segregated two other species from *M. platyphylla*, describing them as new under the names *M. Baueri* and *M. Jackii*. He pointed out further that Lindberg was in error when he confused *M. platyphylloidea* with *M. Thuja*, and he emphasized the fact that the true *M. Thuja* was a species of western and southern Europe, allied to *M. laevigata* (Schrad.) Dumort. rather than to *M. platyphylla*. Basing his opinion on the material at his disposal he stated that the true *M. platyphylla* was totally lacking in America, being everywhere replaced by *M. platyphylloidea*. The latter species he did not report from Europe at all, although he pointed out that *M. Jackii* was an exceedingly close ally. In his descriptions he laid especial stress on specific characters drawn from the sporophyte and particularly from the elaters. Some of these characters had been noted by previous writers but had not been employed to any great extent in separating species, and Schiffner deserves credit for recognizing their value.

In his monograph of the genus *Madotheca*, published in 1910,[2] Stephani accepts *M. Baueri* and *M. Jackii* as valid but does not follow Schiffner in his treatment of *M. platyphylloidea*. This species he includes among the synonyms of *M. Thuja*, as Lindberg had done forty-one years before. Both *M. Thuja* and *M. platyphylla* are quoted from Europe and North America. Although the sporophytes are described in the case of *M. Baueri* and *M. Jackii*, nothing is said about them in the descriptions of *M. Thuja* and *M. platyphylla*, so that Stephani apparently regards their features as of secondary importance.

Müller,[3] in his treatment of *M. platyphylla* and its allies, follows Schiffner in most respects but reduces *M. Jackii* to synonymy under *M. platyphylloidea* and thus gives the latter species a much wider geographical distribution than Schiffner had assigned to it. He quotes the true *M. platyphylla* from North America, Africa, and Asia, as well as from Europe, but restricts the range of *M. Baueri* to Europe. In his opinion *M. Baueri* is a "kleine Art," because he finds transitional conditions between the gametophyte of this species and that of *M. platyphylla*, but he apparently finds little difficulty in separating *M. platyphylloidea* from *M. platyphylla*.

(*To be continued.*)

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[1] Lotos **48**: 346–350. 1900.

[2] Species Hepaticarum **4**: 241–315. 1910.

[3] Rabenhorst's Kryptogamen-Flora **6**^{2}: 573–584. *f. 161, 164–166*. 1915.

NOTES ON NEW ENGLAND HEPATICAE,—XIII.

Alexander W. Evans.

(*Continued from page 85.*)

In *P. platyphylla*, according to Müller and other recent writers who define the species in a narrow sense, the secondary stems are more or less regularly bipinnate or even tripinnate, thus giving the shoot-system a fern-like appearance; the lobes of the leaves are closely imbricated and ovate when spread out flat, the base being cordate, the apex rounded, and the margin entire or nearly so; the lobules are much smaller than the lobes, about half again as wide as the stem, ovate, gradually narrowed toward the blunt apex, scarcely or not at all decurrent at the base, recurved along the outer side, and entire along the margin; the leaf-cells average 25 μ in diameter in the middle of the lobe, the cell-walls are thin and the trigones small and triangular; the underleaves are two or three times as broad as the stem and about twice as wide as the lobules, their outline is rotund-quadrate, and they are broadly long-decurrent on both sides, the decurrent portion being sometimes sparingly toothed, while the rest of the margin is narrowly revolute and entire; the perichaetial bracts, which are reduced to a single pair, are smaller than the leaves, and subequally bifid one-half to two-thirds, the lobe being blunt, the lobule pointed, and the margin entire throughout; the perichaetial bracteole is broadly oval, entire, and reflexed in the upper part; the perianth is shortly pyriform, bluntly three-keeled in the lower part and dorsi-ventrally compressed in the upper part, the mouth being two-lipped and bearing scattered teeth; the capsule is deeply divided into four valves, which are often unequal and further subdivided; the wall of the capsule is two or three cells thick, the cells of the outer wall having small triangular trigones; the spores measure 45–55 μ in diameter, and the elaters measure 8 μ in diameter and have two spirals extending to their very ends. In the var. *subsquarrosa* Schiffn., which Müller admits has been the cause of confusion, the lobes of the leaves are broadly ovate, the lobules are broader than in the type but are still narrower than the underleaves, and the cell-walls average about 30 μ in diameter in the middle of the lobe.

A study of numerous specimens, both European and North American, in which the elaters were bispiral throughout, showed that some of the gametophytic characters relied upon by Müller were subject to variation, although his characterization of the species was essentially correct. In considering these variations the lobes, the lobules, the underleaves, the bracts and bracteoles, and the mouth of the perianth will be taken up in order. The leaves and underleaves discussed are in all cases those of the stem itself.

Although the lobes are normally ovate as described (see Figs. 1, 2, 4, 5) they are sometimes as broad as long and may be practically orbicular in outline (Figs. 3, 6). The cordate condition of the base, moreover, is not always as clear as might be desired. At the junction with the short keel, to be sure, the base is distinctly dilated into a cordate expansion, which may be either plane, or slightly crispate or revolute, but this expansion is by no means as constant on the other side of the lobe. In the case of the lobes shown in Figs. 4 and 5 the basal dilations are distinct enough, and similar dilations are shown in Figs. 1 and 2; but in Figs. 3 and 6 the lobe gradually narrows toward the base and is actually short-decurrent. It should be noted in this connection that the line of attachment of the lobe is strongly arched, so that the extent of the decurrent portion is not easy to define. The margin of the lobe is not quite so uniformly entire as Müller's description implies, and the portion of the margin which extends from the dorsal base to the apex is frequently more or less dentate. The teeth, which in some cases at least mark the position of slime papillae, are exceedingly irregular in size, in number and in distribution, and they are usually little more than blunt and vaguely defined projections (Figs. 1, 2, 5). Sometimes, however, they are sharper, and it is not unusual to find one or two sharp and minute teeth close to the base (Figs. 1, 2). Aside from these basal teeth, a larger and very variable tooth about midway between the base and the apex is fairly frequent. The presence of teeth on the lobe is briefly alluded to by Warnstorf.[1]

In the case of the lobule the line of attachment is even more sharply arched than in the case of the lobe and makes the degree of decurrence even more difficult to define clearly. Perhaps the most accurate method would be to consider the lobule decurrent only when the inner edge extends farther backward than the outer edge, and this is apparently what is implied in Müller's description. His account of the

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[1] Kryptogamenflora der Mark Brandenburg **1**: 270. 1902.

form and relative width of the lobule could hardly be improved upon, but here again the margin is not invariably entire as he maintains. A very few minute and irregular teeth may be present along the inner edge (especially when this is slightly decurrent) and also close to the junction with the lobe, where the lobule is more or less dilated.

Müller's description of the leaf-cells and underleaves portrays very accurately the conditions which are present in the material studied by the writer. On account of the strongly arched line of attachment of the underleaves the decurrent portion is vaguely delimited from the portion which is not decurrent, but in any case the decurrence is strongly marked.

His account of the perichaetial leaves, however, deserves a little amplification. The two bracts are usually unequal in size, the one (see Fig. 7) which is turned toward the apex of the axis bearing the female branch (that is, the outer bract) being the smaller of the two. Although the lobe and lobule are frequently of about the same size, it is more usual for the lobe to be distinctly larger than the lobule (see Figs. 7, 8), and the apices of both lobe and lobule vary from acute to obtuse or even rounded. Marginal teeth are sometimes absent but this is by no means invariably the case. In some of the bracts examined both lobe and lobule bore a number of scattered irregular teeth, some of which were little more than projecting cells while others were larger and more lobe-like. In connection with some of the teeth vestiges of slime papillae could be discerned. Similar teeth are sometimes present on the perichaetial bracteole (Fig. 9).

In European specimens of *P. platyphylla* the mouth of the perianth with its scattered teeth (Fig. 10) presents a very distinctive appearance. Each lip usually bears from fifteen to twenty teeth, and the teeth themselves vary from single projecting cells to cilia four or five cells long and one cell wide throughout or to triangular teeth as long as such cilia but three or four cells wide at the base. The teeth are exceedingly fragile, and their peculiarities cannot always be made out from old and weathered perianths. Fortunately the perianth starts to develop even when no archegonia are fertilized and, since the mouth is the first part to mature, the undeveloped perianths dissected out from unfertilized inflorescences will usually show the marginal teeth clearly.

In the North American specimens which the writer would refer to *P. platyphylla* the teeth show a tendency to be more crowded than in the European specimens, a condition which Figs. 11–14 clearly bring out. Some of the teeth, moreover, are large and compound and show a development of secondary teeth. Teeth of this character are represented in Fig. 11, which shows one of the sinuses between the lips of the perianth, and also in Fig. 14, which unfortunately is taken from a specimen without mature capsules. Sometimes a few surface cells close to the mouth project slightly, as shown in Fig. 13.

The sporophytic characters of *P. platyphylla* are well described by Müller. It might perhaps be added that the two spirals in the elaters are continuous at the extreme ends and form loops. This interesting feature is brought out by Schiffner and is very evident in both European and North American material. The writer is inclined to follow Schiffner and Müller in restricting the name *P. platyphylla* to plants in which the elaters are bispiral. The difficulties in determining material without capsules will be discussed under *P. platyphylloidea.*

The third species of *Porella* which has been reported from New England is *P. rivularis* (Nees) Trevis., the full description of which by Howe[1] may be consulted. This species has been more or less confused with both *P. pinnata* and *P. platyphylla.* Although the name *P. rivularis* has been in widespread use for a considerable period, Müller[2] has recently shown that the oldest synonym for the species is *Jungermannia Cordaeana* Hüben.[3] and therefore describes it under the old name *Madotheca Cordaeana* (Hüben.) Dumort.[4] In order to avoid the publication of a new combination, Dumortier's name will be employed in the present paper. *M. Cordaeana* is especially at home on stones and rocks along mountain brooks. In such localities it is more or less subject to inundation, but in dry seasons may be exposed to the air for considerable periods. In very shady places it sometimes grows on trees close to the base. Müller comments on the variability of the species, due to environmental conditions, and notes its occurrence in North America, northern Africa, and western Asia, as well as in Europe. In the writer's opinion, however, the records not only from New England but from other parts of eastern North America are based on incorrect determinations, as will be shown below.

In general appearance *M. Cordaeana* resembles *P. pinnata* very

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[1] Bull. Torrey Club **24**: 519. 1897.

[2] Rabenhorst's Kryptogamen-Flora **6**^{2}: 585. 1915.

[3] Hepat. Germ. 291. 1834.

[4] Recueil d'obs. sur les Jung. 11. 1835.

strongly although its relationships with *P. platyphylla* are perhaps closer. The stems are pinnate or sparingly bipinnate, and the shoot-system on account of the regularity of the branching may assume a fern-like form. This, however, is always less marked than in typical specimens of *P. platyphylla,* and in some cases, especially in drier situations, the branching may be very irregular.

The lobes, lobules, and underleaves differ from those of *P. pinnata* in being usually more or less dentate. The dentation, in fact, although not to be compared with that of the European *P. laevigata* (Schrad.) Lindb. in its typical forms, is commonly more marked than in *P. platyphylla* and its immediate allies, and often helps in determining sterile specimens of *M. Cordaeana.* Taking up the lobes (of the stem-leaves) more in detail they are found to be ovate and rounded at the apex, much as in *P. platyphylla.* In some cases they are not attached to the lobule at all, no keel being present. In other cases an extremely short keel can be demonstrated. Whether a keel is developed or not the lobe is usually distinctly dilated at the carinal base (as it may be called) and may therefore be described as cordate; at the dorsal base the cordate condition is much less frequent, the lobe in most cases gradually narrowing into a short decurrent portion. The teeth of the lobe are much like those of *P. platyphylla* but tend to be sharper, more distinct and more numerous.

The lobules afford some of the most distinctive characters of the species. They are usually much smaller than in *P. platyphylla* and are ovate to lanceolate in form, the apex varying from obtusely pointed to acute. On branch-leaves the apices may even be acuminate. The margins of the lobules are often irregularly revolute in places, the whole lobule being thus variously contorted or crispate. The line of attachment is sharply arched and the inner edge is usually twice or three times as long as the outer, so that the decurrence is very evident. Sometimes, when no keel is present, the outer edge extends farther backward than the lobe in the form of a narrow wing, but this is never so long as the inner edge. Marginal teeth or cilia are restricted for the most part to the decurrent portions. They are exceedingly variable in number, in form, and in size, but are usually more in evidence than in the lobules of *P. platyphylla.*

The leaf-cells average about 30 μ in the middle of the lobe and are therefore a trifle larger than in typical forms of *P. platyphylla* and considerably larger than in *P. pinnata.* They have thin walls and small but distinct trigones. The underleaves are even more decurrent than in *P. platyphylla* and the decurrent portions tend to be more strongly toothed. In other respects the underleaves are much the same in the two species, although in *M. Cordaeana* they are distinctly narrower, being only a little wider than the stem.

The female branches, which bear a single pair of bracts, sometimes arise directly from the stem and sometimes from a primary branch. In most cases, especially when the branch springs directly from the stem the contrast in size between the bracts is very marked, the inner bract being much larger than the outer. In the outer bract the lobule is narrower than the lobe but almost equals it in length; in the inner bract the lobe tends to be longer and broader than the lobule, although it is always distinctly smaller than the lobes of ordinary leaves. With respect to the apices of the lobes and lobules there is much variety. The lobe of the inner bract, however, is usually rounded at the apex, while the lobe of the outer bract and the lobules of both bracts are usually more or less sharply pointed. The bracteole is much the same as in related species. Both bracts and bracteole are variously toothed, the teeth varying from slightly projecting cells to cilia or broader teeth two to four cells long. The teeth are irregularly scattered but tend to be closer together in the basal regions, where they sometimes show vestiges of hyaline papillae.

The perianth is especially remarkable on account of the character of its mouth. In the other North American species of *Porella* the mouth is variously ciliate; in *M. Cordaeana* it is subentire or vaguely crenulate from projecting cells. Sometimes a slight lobing or indistinctly sinuate appearance is present, but even then the mouth is very different from what is found in other species. The sporophytic characters are much as in *P. platyphylla*, the elaters being bispiral throughout their entire length.

In separating *M. Cordaeana* from *P. platyphylla* the subentire mouth of the perianth, the large inner perichaetial bract, and the small and long-decurrent lobules yield the most helpful characters. The mouth of the perianth will likewise distinguish it from *P. pinnata*, although there is now little danger of confusing these two species even when sterile, on account of the blunt, entire, and transversely attached lobules and underleaves in *P. pinnata*.

Although *M. Cordaeana* is not uncommon from the Rocky Mountains westward very few stations from the eastern part of North

America have been reported. In New England there is one record for Connecticut [1] and one for Vermont.[2] The Connecticut record was based on poorly developed male specimens collected in 1856 by D. C. Eaton in the town of Cheshire; the Vermont record, on a few fragmentary specimens, apparently quite sterile, which were found in 1910 by F. Dobbin in the town of Jamaica. These specimens do not agree with the European and western American material of *M. Cordaeana.* The Connecticut specimens are hardly determinable but clearly belong to the *P. platyphylla*-group. The Vermont specimens agree closely with the plants from Willoughby, which are listed above under *P. platyphylla,* and are therefore included under the same species.

Only two other reports from the region east of the Mississippi are known to the writer. One was based on specimens collected by W. S. Sullivant near Yellow Springs, Ohio [3]; the other on specimens collected by T. P. James at Narrowsville, Bucks County, Pennsylvania.[4] These specimens show rather broad lobules with a short decurrence and very immature perianths, in which the teeth at the mouth are scattered. It seems safe to refer them to *P. platyphylla,* as is done above. Two records made by the writer, one from Stair Portage, Minnesota (*MacMillan, Lyon & Brand 42*),[5] and the other from near Estabrook, Platte Canyon, Colorado (*J. M. Holzinger*),[6] seem to be equally open to criticism. The specimens in both cases should be referred to the *P. platyphylla*-group and probably represent a poorly developed form of *P. platyphylla* itself; unfortunately it is not possible to reach a positive conclusion.

According to the statements just made the occurrence of *M. Cordaeana* in eastern North America seems to be improbable. There are other European species, however, which are restricted, in North America, to the Pacific Coast region, so that the distribution of *M. Cordaeana* in this respect is by no means unique.

5. Porella platyphylloidea (Schwein.) Lindb. Hepat. Utveckl. 20. 1877 (as *Porella platyphylloides*). *Jungermannia platyphylloidea*

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[1] See Howe, Bull Torrey Club **24**: 520. 1897.

[2] Rhodora **14**: 18. 1912.

[3] Distributed by Austin in Hep. Bor.-Amer. *91b.* 1873. The habitat is given on the label as follows: "On shaded rocks, near Yellow Springs, Ohio, *Sullivant;* also in California, *Bolander.*" In the writer's set the specimens are unlike any form of *Porella* known from California and doubtless represent Sullivant's plants.

[4] See Porter, Cat. Bry. and Pterid. Pennsylvania 8. 1904.

[5] Minnesota Bot. Stud. **3**: 144 1903.

[6] Bryologist **18**: 47 1915

Schwein. Spec. Fl. Am. Sept. Crypt. 9. 1821. *Madotheca platyphylloidea* Dumort. Recueil d'Obs. sur les Jung. 11. 1835. *Madotheca Jackii* Schiffn. Lotos **48**: 348. 1900. *Porella Jackii* C. Jensen, Danmarks Mosser **1**: 240. 1915. [Text figs. 14–40].

On rocks and trunks of trees. Maine: Auburn (*E. D. Merrill 8*); Mt. Desert Island (*E. L. Rand*); vicinity of Schoodic Lake, Piscataquis County (*A. W. E.*); Bristol and Madison (*E. B. Chamberlain 1344, 1503*); Hebron (*J. A. Allen*); Southwest Harbor (*S. A. Linsey*); Pleasant Ridge Township, Somerset County (*E. B. Chamberlain 3287*); Farmington (*J. F. Collins 1173*); near Prospect Harbor (*A. R. Northrop*). New Hampshire: Crawford Notch (*E. Faxon*); Jackson and Franconia Notch (*A. W. E.*); Madison (*H. H. Bartlett 1250, 1251*); White Mountains ("*E. T. 7*"). Vermont: Willoughby (*A. Lorenz*); Leffert's Mills, Chittenden County (*C. M. Cooke, Jr.*); Bolton (*A. W. E.*); Newfane (*M. A. Howe*, distributed in Amer. Hep. *87*, as *M. platyphylla*). Massachusetts: Dedham and Brookline (*E. Faxon*); West Newbury (*C. C. Haynes*); Woods Hole (*A. W. E.*); Brewster (*F. S. Collins*). Rhode Island: Providence and North Kingston (*J. F. Collins 599, 798*); Chepacket (*G. W. Burlingame 207*). Connecticut: Hamden (1858), New Haven, Danbury, Bethany and East Haven (*D. C. Eaton*); Kent, Ledyard, Hamden, Orange, West Hartford, Meriden and Salisbury (*A. W. E.*); Plainfield (*J. L. Sheldon*); Stafford, Portland, North Haven, Bolton and Vernon (*G. E. Nichols*); Southington ((*E. B. Chamberlain 1437*); Redding (*C. C. Haynes*); Killingworth (*F. W. Hall*); Canterbury (*S. B. Hadley*); Portland and Glastonbury (*F. Wilson*); East Lyme (*C. B. Graves*); Durham (*A. Lorenz*). To give a further idea of the distribution of the species in North America the following stations outside of New England may be given. Nova Scotia: near Indian Brook and in the valley of the Barrasois, Cape Breton (*G. E. Nichols 42, 65, 1545*); Kentville (*H. B. Bailey*); Big Intervale and Baddeck, Cape Breton (*J. Macoun 55, 58*); near Pictou (*Howe & Lang 584*); near Yarmouth (*J. Macoun 24*); Sandy Cove (*J. D. Lowe 22*). Ontario: Ottawa (*J. Macoun*, distributed in Can. Hep. 9, as *P. platyphylla*); Algonquin Park (*J. Macoun 135*); Owen Sound (*Mrs. Roy*). New York: Chittenago and Clarkson (*D. C. Eaton*, 1855); Yonkers (*E. C. Howe*); Murray Island, Jefferson County (*Robinson & Maxon 106*); Mt. Colburn (*E. G. Britton 24*), somewhat doubtful; Undercliff (*C. C. Haynes 330*); Onteora (*A. M. Vail 3*); Bear's Head, Sand Lake (*S. H.*

Burnham 2). Pennsylvania: Erie (*L. G. Olmstead*, 1843); Glen Riddle and Moylan, Delaware County (*A. F. K. Krout*), doubtful; near Conewago, mouth of the Tucquan, near Safe Harbor and near Penryn (*J. K. Small 21, 23, 7, 20, 11*); Sayre (*W. C. Barbour 8*). Ohio: Colombus (*W. S. Sullivant*, 1842); Fairfield County (*E. C. Miller*). Kentucky: Berea (*N. L. T. Nelson 33*). Maryland and District of Columbia: near Washington (*J. M. Holzinger*); High Island (*F. H. Knowlton*). Virginia: Hungry Hollow (Smyth County), McMillan's Cave (near Marion), Brushy Mountain and Holston River (*J. K. Small 44, 71, 85*); Marion, Dickey's Creek, Pine Mountain, White Top summit, and Holston River (*E. G. Britton & A. M. Vail 81–84, 110–115, 33, 128, 58*). West Virginia: Morgantown and Beaver Spring (*C. F. Millspaugh 1291, 1292, 1530*); Cheat Bridge (*J. L. Sheldon 2519*). North Carolina: Salem (*Schweinitz*, type of *Jungermannia platyphylloidea*); Hendersonville (*A. M. Smith*); Blowing Rock, Aunt Sallie Ridge and Grandfather Mountain (*J. K. Small 40, 41, 35, 36*). Georgia: Athens (*R. M. Harper 59a*); Stone Mountain (*J. K. Small 95, 98, 109*); near Thompson, McDuffie County (*H. H. Bartlett 917*). Florida: West Florida (*A. W. Chapman*). Indiana: near Greencastle (*L. M. Underwood*). Wisconsin: Gordon, Douglas County (*C. H. Conklin 157*); near Mason, Lake Superior region (*L. S. Cheney 5166*). Minnesota: Knife River and Albert, St. Louis County (*G. H. Conklin 841, 922*); Old Iron Trail (*J. M. Holzinger*). Missouri: St. Louis (*T. Drummond*); Horine, Cliff Cave, Creve Coeur Lake and Chadwick (*N. L. T. Nelson 770½, 820, CC, 1616, 15*); Silver Mines, Iron County (*C. Russell 4*). New Mexico: Mogollon Mountains, Socorso County (*E. O. Wooton*); Eagle Creek, Lincoln County (*E. O. Wooton*), doubtful; West Fork of the Gila River (*O. B. Metcalfe 490*). A number of these stations have already been recorded under the name *P. platyphylla*, and the specimens from Jackson, New Hampshire, have been figured under this name by the writer.[1] The specimens distributed by Austin (Hep. Bor.-Amer. *89, 90*, as *Madotheca platyphylla* and *M. platyphylla* var.) should also be referred to *P. platyphylloidea;* they were probably collected in New Jersey although this fact is not stated on the labels. The writer has seen no specimens from Mexico. In Europe Müller gives the species a continental distribution, citing specimens from Germany, Austria and northern Italy only.

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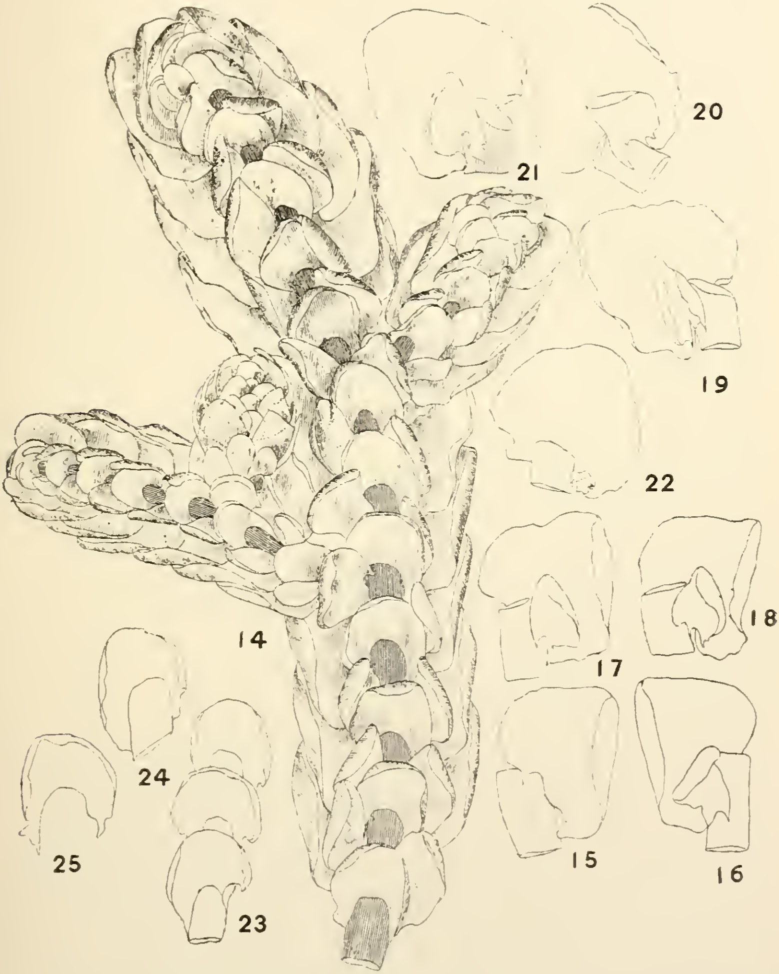
[1] Plant World **2**: *pl. 5*. 1899.

In the account just given of *P. platyphylla* the history of *P. platyphylloidea* is likewise briefly treated. When Schiffner proposed *M. Jackii* as a new species he stated that it differed from *M. platyphylloidea* in its simply pinnate shoots and slightly larger cells, the North American species being described as closely bipinnate. Müller considers these differences of but slight importance and was, moreover, unable to confirm them in his study of authentic specimens of the two species in question. He therefore reduced *M. Jackii* to synonymy and the writer, from a study of European specimens cited by Müller, sees every reason for following his example.

In *P. platyphylloidea*, according to Müller's accounts, the plants are somewhat more robust than in *M. platyphylla*, and the secondary stems are usually only once-pinnate with branches of variable length, the shoot-system thus acquiring an irregular contour; the lobes of the leaves are closely imbricated and suborbicular (usually as broad as long or even broader), the base being crispate and auriculate, the apex broadly revolute, and the margin practically entire; the lobules are about twice as wide as the stem, broadly ovate, broadly rounded at the apex, shortly or not at all decurrent, and slightly revolute along the margin; the leaf-cells average 25 μ in diameter in the middle of the lobe, and the development of the trigones varies according to the environment; the underleaves are of about the same width as the lobules, their outline is suborbicular, and they are shortly decurrent on both sides, the decurrent portions sometimes bearing a few small and scattered teeth, while the rest of the margin is entire and sometimes revolute; the perichaetial bracts, which are reduced to a single pair as in *P. platyphylla*, are smaller than the leaves, the lobe is elongated-ovate and entire, and the lobule is only one-third as large as the lobe, ovate in form, rounded at the apex, and entire, or indistinctly dentate; the perichaetial bracteole in broadly oval, entire or sparingly toothed in the basal region; the perianth is ovate in outline, narrowed toward the two-lipped mouth and shortly dentate or (in Schiffner's words) densely ciliated with cilia one to five cells long. The capsules split as in *P. platyphylla* and the spores average about 46 μ (according to Schiffner); the elaters are mostly 9–10 μ in diameter and usually show a single spiral band throughout their length; in some cases two spiral bands are present in the middle of the elater but only one extends to each end.

Since *P. platyphylloidea* is the commonest species of *Porella* in eastern North America the writer has had abundant material for study. The North American specimens have been carefully compared with European material. A few slight deviations from the



Figs. 14–25. Porella platyphylloidea (Schwein) Lindb.
14. Branch bearing a male inflorescence and two sterile branches, ventral view. 15. A leaf. dorsal view. 16–21. Leaves, ventral view. 22. A leaf at the base of a branch. 23–25. Underleaves. All magnified about 14 times. The figures are a reproduction of those by Gottsche, distributed with Gottsche and Rabenhorst's Hepaticae europaeae *372*. They were drawn from an authentic North American specimen of *Jungermannia platyphylloidea* Schwein. in the Lindenberg herbarium.

published accounts of the species have been noted and these will be considered in order. The differences between *P. platyphylloidea* and *P. platyphylla* will then be discussed.

Although the lobes (of the stem-leaves) are usually orbicular and are sometimes even broader than long, as shown in Figs. 16–21, 26–29, it is not unusual for some of the leaves to be longer than broad and thus to approach in form the typical leaves of *P. platyphylla*, a condition shown in Fig. 30. At the junction with the keel the cordate expansion is strongly developed and tends to be conspicuously crispate or irregularly folded. On the other side of the lobe, however, although a cordate expansion may be present, as shown in Fig. 30, it is much more usual for the lobe to narrow gradually and show a short decurrence, as shown in Figs. 15, 26–29. Marginal teeth are often present, just as they are in *P. platyphylla*, and tend if anything to be more pronounced, but they are essentially the same in character.

In typical material of *P. platyphylloidea* the lobules are about as wide as the underleaves and have broad rounded apices and narrowly revolute margins. Unfortunately this typical condition is not always realized, a fact clearly brought out by Gottsche's figures of the species, which were drawn from an authentic American specimen in the Lindenberg herbarium. These figures were issued with No. 372 of Gottsche and Rabenhorst's Hepaticae europaeae, and are here reproduced as Figs. 14–25. It will be noted that many of the lobules shown are narrower than the underleaves, that some of them are narrowed toward the apex, and that the outer side only is recurved. The objection might perhaps be brought forward that Gottsche's figure was drawn from a male individual, and that a plant often produced androecia before it had reached the full luxuriance of which it was capable.[1] The writer, however, has observed female plants, bearing mature sporophytes with unispiral elaters, in which the lobules were fully as narrow as those in Gottsche's figures and essentially like them in other respects. Among plants of this character the Virginia specimens collected by J. K. Small at the Falls of Holston River (No. 85) might be especially mentioned, although similar specimens have been found in other localities. It is clear, therefore, that the characters drawn from the form and relative size of the lobule must be interpreted with discretion. The remarks made under *P. platyphylla* with regard to the degree of decurrence and the occasional presence of teeth near

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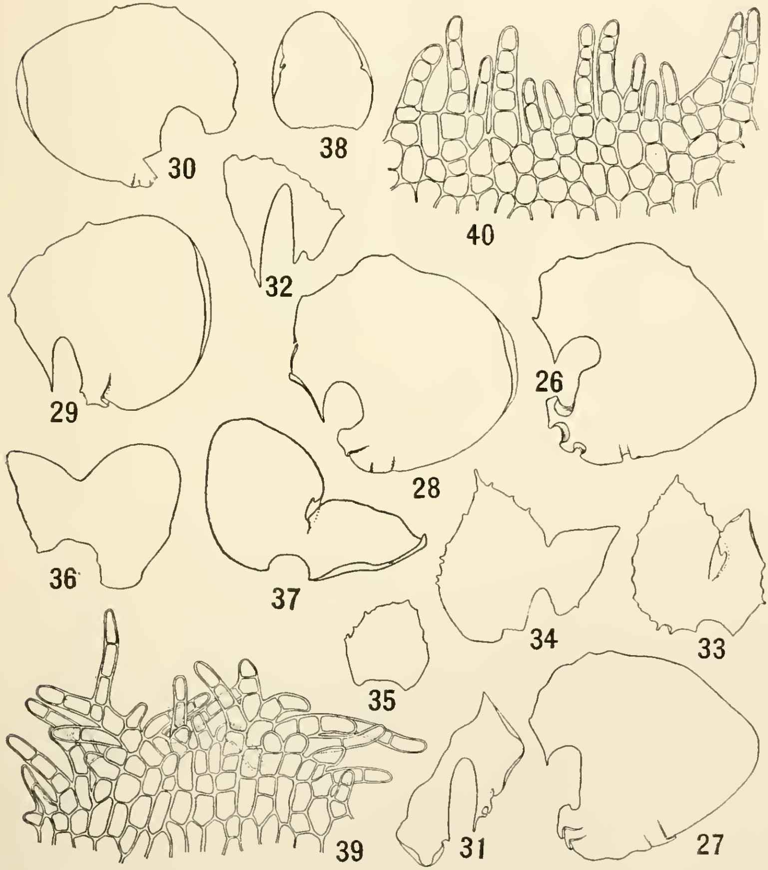
[1] Compare Goebel, Organographie, 2d ed. 142. 1913.

the base of the lobule would apply equally well to *P. platyphylloidea,* although the tendency to bear teeth is rather more pronounced in the latter species.

The writer can add nothing of importance to the published descrip-



Figs. 26–40. Porella platyphylloidea (Schwein.) Lindb.
26–30. Lobes of stem leaves, × 15. 31, 32. Lines of attachment of lobules, 31 showing keel on left hand side, and 32, on right hand side, × 35. 33–35. Bracts and bracteole from a single involucre, × 25. 36–38. Bracts and bracteole from another involucre, × 25. 39, 40. Teeth from mouths of perianths, × 200. Figs 26, 27, 31, 33–35, 39 were drawn from a specimen collected on Mt. Carmel, Hamden, Connecticut, by the writer; Figs. 28–30, 32, from a specimen of *Madotheca Jackii* Schiffn., collected at Salem in Baden, Germany, by J. B. Jack and distributed by Gottsche & Rabenhorst, Hep. eur. *140;* Figs. 36–38, from another specimen collected at Salem in Baden, Germany, by J. B. Jack; Fig. 40, from a specimen collected at Madison, New Hampshire, by H. H. Bartlett, *1250.*

tions of the leaf-cells and the underleaves (see Figs. 14, 23–25). In the case of the female inflorescence, however, a few remarks may be in place. Although the perichaetial bracts are almost invariably reduced to a single pair, a second pair is occasionally developed. When this is the case the pair next to the perianth is essentially the same as when a single pair is present. Müller implies that there is a much greater discrepancy in size between the lobe and lobule than in *P. platyphylla,* but this idea is not borne out by the writer's observations. As a matter of fact the bracts (Figs. 33, 34, 36, 37) are much the same as in *P. platyphylla* and are subject to the same variations in the character of the apex and the degree of the marginal dentation; sometimes, indeed, the apex is tipped with an apiculum (Figs. 33, 34). In the case of the bracteole teeth are occasionally present in the upper part as well as in the basal region (Figs. 35, 38).

The mouth of the perianth is more contracted in *P. platyphylloidea* than in *P. platyphylla* and is densely ciliate. The cilia are usually one cell wide and vary from one to five or more cells in length (as Schiffner states); sometimes compound cilia are present with secondary cilia along their sides, but simple unbranched cilia are the rule. The cilia are sometimes straight as in Fig. 40 but it is much more usual for them to be variously contorted as in Fig. 39. Projecting cells in the neighborhood of the mouth are sometimes present as in the North American specimens of *P. platyphylla* (see Fig. 39).

In studying a large series of capsules of *P. platyphylloidea* the elaters have shown for the most part a single spiral throughout their length. Elaters with two spirals in the middle portion have, nevertheless, been repeatedly observed, and in some capsules a rather high percentage of the elaters have been of this type. In no case, however, has an elater with two spirals throughout its entire length been noted, so that in the elaters at least the differences between *P. platyphylla* and *P. platyphylloidea* are definite and constant. In distinguishing the two species the most trustworthy differences are, in fact, those drawn from the elaters. Boulay [1] comments on the difficulty of using sporophytic characters in the genus at all on account of the habitual sterility of material, but this difficulty does not detract in any way from the importance of such characters.

In the absence of mature capsules the mouth of the perianth, even when undeveloped perianths are the only ones available, should be

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[1] Musc. de la France **2**: 18. 1904.

examined. This can best be done by dissecting off the upper part of the perianth, splitting it, and spreading it out flat, and care must be taken in making sure that the teeth or cilia at the mouth are still intact. The study of old and disintegrated perianths has led to many errors. The teeth or cilia yield characters which can be employed with safety. In *P. platyphylla* they are scattered; in *P. platyphylloidea*, densely crowded. It has already been noted that in North American specimens of *P. platyphylla* the teeth are more numerous than in the European material; they are never so numerous, however, as in *P. platyphylloidea* and do not present the appearance of being everywhere close together.

If neither capsules nor perianths are present the much less satisfactory characters drawn from the habit of the plants and from the leaves are still available. If the specimens to be determined are robust, if the stems are irregularly pinnate, if the lobes of the stem-leaves are as broad as long and distinctly crispate at the base, and if the lobules are about as wide as the underleaves and rounded at the broad apex, there can be little question that the plants should be referred to *P. platyphylloidea*. If, on the other hand, the specimens are of a medium size, if the stems are regularly bipinnate, if the lobes of the stem-leaves are longer than broad and scarcely or not at all crispate at the base, and if the lobules are distinctly narrower than the underleaves and show a tapering toward the apex, a determination as *P. platyphylla* is indicated. Unfortunately there are cases where the vegetative characters by themselves can hardly lead to a positive decision. This is true not only of poorly developed specimens but also of well-developed specimens in which the distinctive characters just given are differently grouped; where, for example, an irregularly pinnate stem is associated with narrow lobules or with lobes which are distinctly longer than broad. Male specimens seem to be especially troublesome in this respect and sometimes fail to show the characters of the species clearly when female plants growing with them are typically developed. In the writer's opinion Schiffner's var. *subsquarrosa* [1] of *P. platyphylla*, based on European material, includes forms which cannot be determined positively by means of the vegetative characters alone; and very similar American specimens are listed above under *P. platyphylloidea* on the basis of perianths and capsules.

It is evident from the remarks just made that *P. platyphylloidea*,

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[1] Lotos **48**: 346. 1900.

even if recognized as a valid species, must be regarded as a "kleine Art" in the *P. platyphylla*-group. According to our present knowledge the range of the true *P. platyphylla* is northern rather than southern in North America, but it must be admitted that our knowledge is still incomplete. Perhaps when more is known about the geographical distribution of these two species it may be possible to utilize this knowledge in the determination of doubtful specimens.

Schiffner's *Madotheca Baueri* has as yet been reported from Europe only. The writer has not had access to Schiffner's types but has examined a series of authentic specimens including those in Jack, Leiner & Stizenberger's Kryptogamen Badens *164*, and in Rabenhorst's Hepaticae europaeae *52*, both of which are referred by Müller to *M. Baueri*. No. 164 was collected by F. Himmelseher near Salem in Baden and No. 52 by A. Röse near Schnepfental in Thuringia. The specimens studied agree closely with the published descriptions but indicate that the validity of *M. Baueri* is fully as doubtful as that of *M. platyphylloidea*. The characters emphasized by Schiffner are the following: the large size and irregular branching; the broadly elliptical to almost orbicular lobes; the distant, small, almost plane underleaves, broadly rounded at the apex; the large leaf-cells, averaging about 36 μ near the apex of the lobe; the narrow mouth of the perianth with crowded cilia; and the elaters with one spiral, except in the median portion where two are present. Müller describes the cells in the middle of the lobe as 30–35 μ in diameter, and adds that one or two blunt teeth are borne on the margin of the lobe, that the lobule is long decurrent and often toothed in the decurrent portion, that the perichaetial bracts are shortly and bluntly denticulate throughout, and that the crowded cilia at the mouth of the perianth are three or four cells long. Aside from the features mentioned *M. Baueri* is described as being much like *P. platyphylla*.

The material studied by the writer brings out the fact that many of the differential characters relied upon are subject to great variation. This is particularly true of those drawn from the form and dentation of the leaves. The large leaf-cells afford a character which deserves more weight. The difference in size, when these cells are compared with those of *P. platyphylla* and *P. platyphylloidea*, is usually pronounced, although Müller brings out the fact that in the variety *subsquarrosa* of *M. platyphylla* the cells approach those of *M. Baueri*. In the mouth of the perianth the resemblance to *P. platyphylloidea* is particularly striking, and, according to the description, the characters drawn from the elaters would indicate a relationship with this species rather than with *P. platyphylla*. Unfortunately the structure of the elaters is not quite so uniform as Schiffner implies. In the single mature capsule examined by the writer (taken from Kryptogamen Badens *164*), some of the elaters agree closely with Schiffner's description; in others, however, the unispiral portions at the ends are very short, and a few elaters are bispiral throughout, the two spirals forming a loop just as in *P. platyphylla*. In its elaters, therefore, *M. Baueri* is intermediate between *P. platyphylloidea* and *P. platyphylla*.

The additions to local state floras, not already mentioned on the preceding pages, are as follows:—

For Maine. *Cephalozia macrostachya*, Round Mountain Lake and vicinity, Franklin County (*A. Lorenz*).

For New Hampshire. *Calypogeia sphagnicola,* Mt. Monadnock (*A. Lorenz*).

For Massachusetts. *Riccia Lescuriana,* Northampton (*A. Lorenz*). *Riccia sorocarpa,* Deerfield (*A. Lorenz*). *Lophozia alpestris* and *Sphenolobus Hellerianus,* Sheffield (*A. Lorenz*). *Lophozia attenuata* and *Sphenolobus minutus,* Mt. Everett, town of Mt. Washington (*A. Lorenz*).

As already noted the New England records for *Scapania gracilis* and *Porella rivularis* and the Vermont record for *Scapania dentata* should be erased. The New Hampshire, Massachusetts and Rhode Island records for *Porella platyphylla,* which were marked in the Revised List with the sign "+," should now be marked with the sign " −." The Massachusetts record for *Grimaldia fragrans,* however, which was marked in the Revised List with the sign " −," may now be marked with the sign "+," the necessary specimens having been collected by A. Lorenz.

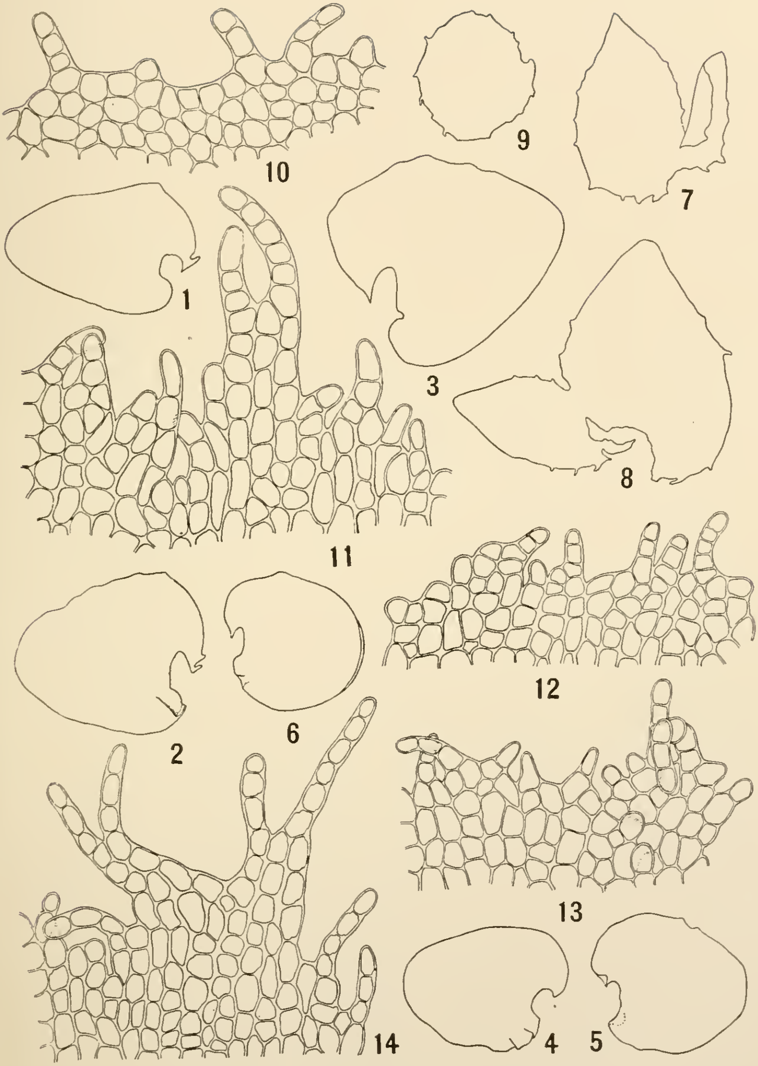
The census of New England Hepaticae now stands as follows: Total number of species recorded, 185; number recorded from Maine, 131, for New Hampshire, 138; for Vermont, 120; for Massachusetts, 110; for Connecticut, 141; common to all six states, 59.

SHEFFIELD SCIENTIFIC SCHOOL, YALE UNIVERSITY.

Explanation of Plate.

Porella platyphylla (L.) Lindb.

1–6. Lobes of stem-leaves, × 15. 7–9. Bracts and bracteole from a single involucre, × 25. 10–14. Teeth from mouths of perianths, × 200. Figs. 1, 2, 7–10 were drawn from a specimen collected near Florence, Italy, by E. Levier, and determined by Schiffner as the typical form of *Madotheca platyphylla;* Fig. 3, from a specimen collected at Fiesole, near Florence, Italy, by E. Levier, and determined by Schiffner as *M. platyphylla* var. *subsquarrosa;* Figs. 4–6, 11, from a specimen collected at Bic, Quebec, by the writer *98;* Fig. 12, from a specimen collected at New Haven, Connecticut, by D. C. Eaton; Fig. 13, from a specimen collected at Vasa, Minnesota, by N. L. T. Nelson *945½;* Fig. 14, from a specimen collected at New Milford, Connecticut, by the writer.



Porella platyphylla (L.) Lindb.

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[Reprint from THE BRYOLOGIST, Vol. XIX, No. 3, May, 1916.]

THE BRYOPHYTES OF NOVA SCOTIA, WITH SPECIAL REFERENCE TO CAPE BRETON[1]

GEORGE E. NICHOLS

Cape Breton, projecting so far out into the Atlantic that the distance to the west coast of Ireland is less by a thousand miles than from New York, has sometimes been referred to as "the long wharf of Canada." Politically it is a part of the province of Nova Scotia, but geographically it is separated from the mainland by the Gut of Canso, a narrow strait about a mile in breadth. Although it has been visited by several botanists in recent years, very few additions appear to have been made to the list of bryophytes recorded from this region in Macoun's catalogue.[2] During a short trip to Cape Breton in 1909 the writer collected a number of liverworts and mosses not before recorded from there, and this number has been considerably augmented on two subsequent trips, in 1914 and 1915, when about four months were spent in botanical investigations. The primary object of the present paper is to present a list of the various species collected in Cape Breton by the writer. Incidentally it has seemed worth while to summarize briefly all previous records, so far as known to the writer, concerning Cape Breton bryophytes, and to include some account of the brypohytes of other parts of Nova Scotia. For the sake of convenience the term Nova Scotia will be used to embrace only parts of the province outside of Cape Breton. In order to economize space the following system of symbols has been adopted. An asterisk (*) placed after a species indicates, "collected in Cape Breton by the writer also"; a dagger (†), "recorded from Nova Scotia in Macoun's catalogue"; a double dagger (‡), "represented from Nova Scotia by a specimen either in the herbarium of Yale University or in the herbarium of New York Botanical Garden, but not recorded by Macoun"; a question mark [?], "some doubt as to identity of specimens on which record was based."

For assistance in the determination of various species, indebtedness is acknowledged to the following bryologists: Mrs. Elizabeth G. Britton, Professor Alexander W. Evans, Mr. Robert S. Williams, Professor A. LeRoy Andrews, Dr. Abel J. Grout, Dr. George N. Best, Dr. Carl Warnstorf, Dr. Ingebrigt S. Hagen and Dr. Leopold Loeske.

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Catalogue of Canadian Plants: Part 6. Montreal, 1892; Part 7. Ottawa, 1902.

1. Species Recorded from Cape Breton by Macoun

Below is a list of the bryophytes recorded from Cape Breton in Macoun's catalogue. Liverworts: *Conocephalum conicum**‡, *Preissia quadrata**† (as *Cyathophora*), *Marchantia polymorpha**†, *Riccardia latifrons**‡, (as *Aneura*), *Pellia epiphylla**†, *Blasia pusilla**‡, *Marsupella emarginata**†, *M. Sullivantii**† (as *M. sphacelata*), *Nardia crenulata**†, *Jungermannia cordifolia**, *J. lanceolata*, *Jamesoniella autumnalis**†, (as *Jungermannia*), *Lophozia attenuata**†, *L. barbata**‡, *L. incisa**†, *L. inflata**†, *L. longidens**, *L. quinquedentata**, *L. ventricosa**, *Sphenolobus minutus** (as *Lophozia*), *Plagiochila asplenioides**†, *Mylia Taylori**†, *Lophocolea heterophylla**‡, *Chiloscyphus rivularis**‡ (as *C. polyanthos*), *Harpanthus scutatus**†, *Geocalyx graveolens**†, *Cephalozia bicuspidata**†, *C. catenulata**†, *C. curvifolia**†, *C. media**†, *Odontoschisma denudatum*†, *O. Sphagni*, *Calypogeia Trichomanis**‡ (as *Kantia*), *Bazzania tricrenata**† (as *B. triangularis*), *B. trilobata**†, *Lepidozia reptans**†, *Blepharostoma trichophyllum**†, *Ptilidium ciliare**‡, *Diplophyllum albicans**† (as *Diplophylleia*), *D. taxifolium**† (as *Diplophylleia*), *Scapania nemorosa**† (also as *S. gracilis*), *S. undulata**†, *Radula complanata**‡, *Porella platyphylla**†, *Lejeunea patens**, *Frullania Asagrayana**†, *F. eboracensis**†, *F. Oakesiana**, *F. Tamarisci**‡. Mosses: *Sphnagnum imbricatum**, *S. Pylaesii**, *Andreaea petrophila**†, *Trematodon ambiguus**†, *Swartzia montana** (as *Distichium capillaceum*), *Trichodon tenuifolius* [?] (as *T. cylindricus*), *Ceratodon purpureus**†, *Ditrichum flexicaule*, *D. heteromallum* (as *D. homomallum*), *D. lineare** (as *D. vaginans*), *Blindia acuta**, *Dicranella heteromalla**†, *D. pusilla** (as *D. cerviculata*), *D. squarrosa**, *Oncophorus Wahlenbergii**†, *Dicranum Bergeri**†, *D. flagellare**, *D. fulvum*† (also listed as *D. viride**), *D. fuscescens**† (listed also as *D. congestum*, *D. crispulum*, and *D. sulcatum*), *D. longifolium**, *D. majus**, *D. rugosum**‡ (as *D. undulatum*), *D. scoparium**† (also listed as *D. canadense*), *D. spurium**† (†also as *D. brachycaulon*), *Dicranodontium denudatum* [?] (as *D. longirostre*), *Dichodontium pellucidum**, *Leucobryum glaucum**† (as *L. vulgare*), *Fissidens adiantoides**†, *F. cristatus* (as *F. decipiens*), *F. osmundioides**†, *Gymnostomum calcareum*†, *Gyroweisia pusilla* [?] (as *Gymnostomum*), *Leptodontium excelsus* (as *Amphoridium Sullivantii*), *Tortella tortuosa** (as *Barbula*), *Didymodon rubellus**†, *Barbula unguiculata*†, *Encalypta contorta* (as *E. streptocarpa*), *Grimmia apocarpa**†, *G. gracilis*, *Racomitrium aciculare**†, *R. canescens**, *R. fasciculare**, *R. hypnoides**† (also as *R. lanuginosum*), *R. microcarpum*†, *Anoectangium lapponicum**† (as *Amphoridium*), *A. Mougeotii* (as *Amphoridium*), *Orthotrichum affine**, *O. fastigiatum*, *O. obtusifolium*†, *O. rupestre*, *Ulota Drummondii*, *U. intermedia*, *U. Ludwigii**†, *U. maritima*, *U. phyllantha*†, *U. ulophylla**† (as *U. crispa*), *Tayloria tenuis*†, *Tetraplodon australis*, *Splachnum ampullaceum*†, *Funaria hygrometrica**†, *Leptobryum pyriforme**†, *Pohlia cruda**† (as *Webera*), *Bryum acutiusculum*, *B. pallens*, *B. pallescens**, *B. ventricosum** (as *B. pseudotriquetrum*), *Mnium affine*†, *M. ciliare**, *M. Drummondii*†, *M. hornum**†, *M. hymenophylloides*†, *M. punctatum**†, *M. stellare*, *Aulacomnium palustre**†, *Plagiopus Oederi**† (as *Bartramia*), *Bartramia crispa*, *Philonotis fontana**†, *Hedwigia albicans**† (as *H. ciliata*), *Fontinalis dalecarlica**†, *F. gigantea**†, *F. Delamarei**, *F. seriata*, *Neckera complanata*†, *N. pennata**†, *Homalia Jamesii*†, *Pylaisia polyantha, P. polyantha pseudo-platygyrium* (as *P. pseudo-platygyrium*), *P. Schimperi*† (as *P. intricata*), *Pterygynandrum decipiens, Myurella gracilis**† (as *M. Careyana*). *Anomodon attenuatus**†, *A. viticulosus, Thuidium Philiberti, Amblystegium fluviatile, A. varium*† (as *A. porphyrhizon*), *Drepanocladus Sendtneri* (as *Hypnum*), *Hypnum* (*Drepanocladus*) *pseudolycopodioides, Hypnum* (*Drepanocladus*) *Moseri, Calliergon cordifolium**† (as *Hypnum*), *C. stramineum** (as *Hypnum*), *Acrocladium cuspidatum** (as *Hypnum*), *Hygrohypnum eugyrium**† (as *Hypnum*), *H. ochraceum**† (as *Hypnum*), *Hypnum* (*Chrysohypnum*) *sinuolatum, Hylocomium brevirostre**†, *H. umbratum**†, *Rhytidiadelphus loreus**† (as *Hylocomium*), *R. squarrosus**† (as *Hylocomium*), *Stereodon canariensis* (as *Hypnum Waghornei*), *S. fertilis** (as *Hypnum*), *S. imponens**† (as *Hypnum*), *Hypnum* (*Stereodon*) *molluscoides, Plagiothecium aciculari-pungens*†, *P. denticulatum**†, *P. striatellum**† (as *P. Muhlenbeckii*), *Sematophyllum delicatulum* (as *Raphidostegium laxepatulum* (also as *R. Roellii* and *R. Whitei*). *Brachythecium digastrum, B. glaciale* (as *Eurynchium*), *B. plumosum**†, *B. populeum**†, *B. reflexum**, *B. rivulare**, *B. salebrosum**†, *Oxyrrhynchium rusciforme**† (as *Eurynchium*), *Webera sessilis**† (as *Diphyscium foliosum*), *Georgia geniculata**, *G. pellucida**†, *Catharinaea Haussknechtii* [?] (as *Atrichum*), *C. Selwyni* [?] (as *Atrichum*), *Polytrichum alpinum**‡ (as *Pogonatum*), *Polytrichum ohioense**, *Pogonatum tenue**† (as *P. brevicaule*), *P. urnigerum**†.

2. SPECIES SINCE RECORDED FROM CAPE BRETON

The following bryophytes have been recorded from Cape Breton since the publication of Macoun's catalogue: *Metzgeria furcata***,[1] *Nardia scalaris**,[2] *Cephalozia Francisci***,[3] *C. leucantha***,[3] *Hygrobiella laxifolia***,[3] *Sphagnum palustre**,[4] *Gymnostomum rupestre**,[4] *Philonotis americana***‡,[5] *Anacamptodon splachnoides***,[6] *Stereodon curvifolius**[4] (as *Hypnum*) and *Polytrichum commune**.[4] Cape Breton records for double starred (**) species are based on the writer's specimens.

3. SPECIES NEW TO CAPE BRETON

The writer's explorations have been confined to the northernmost portion of Cape Breton. With the exception of Cape Dauphin (in Cape Breton County), all stations cited for specimens collected by the writer are situated in that part of Victoria County lying north of North River. This area is one of varied topography and geological diversity. The interior is mountainous and in places the mountains form massive promontories along the coast. Elsewhere the shore is bordered by a narrow strip of flatter land averaging less than a mile

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[1] A. W. Evans, Rhodora **11**: 186. 1909.

[2] A. W. Evans, Rhodora **14**: 12. 1912.

[3] A. W. Evans, BRYOLOGIST **18**: 83. 1915.

[4] C. B. Robinson, Bull. Pictou Acad. Sci. Asso. **1**: 32. 1907.

[5] G. Dismier, Bull. Soc. Bot. France **57**: 22. 1910.

[6] G. E. Nichols. Rhodora **13**: 46. 1911.

in width but locally extending inland for several miles. Along the coast are occasional outcrops of dolomite, and extensive beds of gypsum occur in many localities. With these exceptions the rocks are predominantly potassic. For the most part the calcareous rocks are dry or otherwise unfavorable for the growth of bryophytes, so that comparatively few strictly calciphilous species have been found. The general vegetational features of this region are to be discussed in a forthcoming paper. Suffice it to state here that, except on the mountains where there are extensive heath-like "barrens," the country is forested with a mixture of coniferous and deciduous types. Some of the localities mentioned in the subtended list require brief definition. "Barrasois" includes the area within a radius of five miles of the mouth of Indian Brook. A large proportion of the specimens so designated came from the valley of the Barrasois River. Similarly, "Ingonish" includes the area within a radius of five miles north and west of South Bay, Ingonish; and "Aspy Bay" embraces the area within a radius of five miles of Dingwall, on Aspy Bay. "Barrasois barrens" refers to a large barren about eight miles northwest of the mouth of Indian Brook—locally known as Scotchman's Barren. "Ingonish barrens" include a series of barrens from eight to twelve miles west (approximately) of South Bay, Ingonish. "Ingonish mountains" include the mountains between these barrens and the settlement at South Bay. "Aspy Bay barrens" refer to barrens about seven miles west-southwest of Dingwall. "Aspy Bay mountains" are in the vicinity of these barrens. The numbers cited under the various species refer to specimens preserved in the herbarium of Yale University. Specimens numbered *091–09180* were collected in 1909, *1–1050* in 1914, and *1101–1750* in 1915. Liverworts collected in 1909 (and so cited) were not numbered. The list of species new to Cape Breton is as follows:

Liverworts

1. Riccardia multifida (L.) S. F. Gray.‡ Barrasois *1334b*, *1446*, *1449b*.

2. Riccardia pinguis (L.) S. F. Gray. Barrasois *1203*, *1204*.

3. Riccardia sinuata (Dicks.) Trevis. Barrasois *199;* Ingonish barrens *789*, *840*, *1665*.

4. Pallavicinia Lyellii (Hook.) S. F. Gray. Barrasois *1169;* Ingonish mountains *796*, *1657;* Ingonish barrens *1637*, *1660;* Aspy Bay *968*.

5. Pellia Fabroniana Raddi. Ingonish *722*.

6. Pellia Neesiana (Gottsche) Limpr.‡ Barrasois *1205*, *1245;* Ingonish *704*.

7. Fossombronia foveolata Lindb. Aspy Bay *975*.

8. Marsupella aquatica (Lindenb.) Schiffn. Barrasois *1500*.

9. Marsupella ustulata (Hüben.) Spruce. Barrasois barrens *509*.

10. Nardia obovata (Nees) Carringt. Barrasois *1269*, *1445*, *1478;* Ingonish mountains *1725*.

11. Lophozia alpestris (Schleich.) Evans. Barrasois 1909, *1371*.

12. Lophozia badensis (Gottsche) Schiffn. Ingonish *715*.

13. Lophozia Binsteadii (Kaalaas) Evans. Barrasois *1431b*.

14. Lophozia Kaurini (Limpr.) Steph. Ingonish mountains *1722;* Aspy Bay *961*, *965*.

15. Lophozia porphyroleuca (Nees) Schiffn.‡ Barrasois 1909, *300*, *322*, *1292*, *1358*.

16. Sphenolobus exsectus (Schmid.) Steph. Barrasois 1909; collected also at Half Way Brook by *Macoun* (1898, in herb. A. W. Evans).

17. Sphenolobus Hellerianus (Nees) Steph.‡ Barrasois 1909.

18. Sphenolobus Michauxii (Web.) Steph.† (listed by Macoun under *Lophozia*). Barrasois 1909, *263*, *299*, *1549*.

19. Mylia anomala (Hook.) S. F. Gray.‡ Barrasois *1170*, *1198;* Barrasois barrens *461*, *463*, *467*, *469*, *470;* Ingonish barrens *1638*.

20. Chiloscyphus fragilis (Roth) Schiffn. Barrasois *1487;* Ingonish *1726*.

21. Chiloscyphus pallescens (Ehrh.) Dumort.‡ Barrasois 1909, *507*, *1395;* Ingonish *721;* Ingonish mountains *791;* Aspy Bay mountains *1010*.

22. Cephalozia fluitans (Nees) Spruce. Barrasois *1195*, *201;* Barrasois barrens 460; Ingonish barrens *1684;* Aspy Bay barrens *999*.

23. Cephalozia Loitlesbergeri Schiffn. Barrasois *1243b*. New to North America.

24. Cephalozia pleniceps (Aust.) Lindb.‡ Ingonish barrens *1653b*.

25. Cephaloziella byssacea (Roth) Warnst. Barrasois 1909, *1378*.

26. Odontoschisma Macounii (Aust.) Underw. Barrasois *1431a*.

27. Calypogeia fissa (L.) Raddi. Barrasois *1482*.

28. Calypogeia Neesiana (Massal. & Carest.) K. Müll. Barrasois *89*, *1449a*.

29. Calypogeia suecica (Arn. & Perss.) K. Müll. Ingonish *711*.

30. Lepidozia setacea (Web.) Mitt. Barrasois *1211;* Barrasois barrens *472*.

31. Ptilidium pulcherrimum (Web.) Hampe.‡ Barrasois 1909; also Big Intervale (*Macoun*, as *P. ciliare*), North Sydney (*Howe & Lang*).

32. Trichocolea tomentella (Ehrh.) Dumort.‡ Barrasois 1909, *639;* Aspy Bay mountains *1015*.

33. Scapania dentata Dumort. Barrasois *1397*, *1409*, *1444*.

34. Scapania Oakesii Aust. Barrasois *294*.

35. Scapania paludicola Loeske & K. Müll. Barrasois *213*.

36. Scapania subalpina (Nees) Dumort. Barrasois 1909, *1370*, *1405*.

37. Scapania umbrosa (Schrad.) Dumort. Barrasois 1909, *634;* Ingonish barrens *833 b*.

38. Lejeunea cavifolia (Ehrh.) Lindb.‡ Barrasois 1909, *273*, *640*, *1136*, *1273*, *1319*, *1346*, *1349*, *1354*, *1472*. Mount Smoky *739*.

39. Anthoceros punctatus L.† Barrasois 1909.

Mosses

40. Sphagnum capillaceum (Weiss) Schrank.† *S. acutifolium* Ehrh. Barrasois *200*, *1234;* Ingonish barrens *834*. The Cape Breton specimens belong to

var. *tenellum* (Schimp.) A. L. Andrews, which is also recorded by Macoun from Nova Scotia (as *S. tenellum rubellum*).

41. Sphagnum cuspidatum Ehrh. Barrasois barrens *511*; Ingonish barrens *1676;* Aspy Bay barrens *1000*.

Var. Torreyi (Sull.) Braithw. Barrasois *1227*, *1164b;* Ingonish barrens *835*, *836*.

42. Sphagnum fuscum (Schimp.) H. Klinggr. Barrasois *1194*, *1235;* Barrasois barrens *465*, *478*, *481;* Ingonish barrens *808*, *838*, *1677;* Mount Franey *1703*.

43. Sphagnum Girgensohnii Russ. Barrasois *0925*, *1210;* Ingonish barrens *1674;* Mount Franey *1701*.

44. Sphagnum magellanicum Brid. Barrasois *1165*, *1196;* Barrasois barrens *476;* Aspy Bay barrens *999*.

45. Sphagnum papillosum Lindb.† Barrasois *206*, *1166*, *1197;* Barrasois barrens *477;* Ingonish barrens *807*, *1668*, *1669*, *1672*, *1675*.

46. Sphagnum plumulosum Röll var. flavicomans (Card.) A. L. Andrews. Barrasois barrens *480*.

47. Sphagnum pulchrum (Lindb.) Warnst. Barrasois *203;* Ingonish barrens *837*, *1671*, *1673*.

48. Sphagnum quinquefarium (Lindb.) Warnst. Barrasois *0918*, *1498*, *1499*.

49. Sphagnum recurvum Beauv.† (the Nova Scotia plants are referred to var. *amblyphyllum*). Barrasois *0920*, *1233*.

50. Sphagnum robustum (Russ.) Röll. Barrasois *0919*.

51. Sphagnum squarrosum Crome. Barrasois *0923*, *0926*.

52. Sphagnum subsecundum Nees.† *S. rufescens* Limpr. Barrasois *207*, *1433;* Mount Franey *1702*.

53. Sphagnum tenellum Pers. Ingonish barrens *1670*, *1678*.

54. Sphagnum tenerum Sull. & Lesq. Barrasois *1167;* Barrasois barrens *482;* Ingonish barrens *1667*.

55. Sphagnum teres (Schimp.) Aongstr. Barrasois *1164*.

56. Ditrichum pusillum (Hedw.) Timm.† *D. tortile* (Schrad.) Lindb. Barrasois *09157*, *627*.

57. Dicranella varia (Hedw.) Schimp.† Barrasois *09154*.

58. Oncophorus polycarpus (Hedw.) Brid. Barrasois *1461*, *1462*.

59. Dicranum Bonjeanii DeNot.† *D. subpalustre* C. Müll. & Kindb. Barrasois *190*, *191;* Indian Brook barrens *459;* Ingonish barrens *1650*.

60. Dicranum condensatum Hedw.† Ingonish barrens *818*.

61. Dicranum Drummondii C. Müll. Barrasois *196*, *1344*.

62. Dicranum montanum Hedw.† Barrasois *09156*, *197*.

63. Dicranum Muhlenbeckii Br. & Sch. Ingonish barrens *811*.

64. Weisia viridula (L.) Hedw. Barrasois *09159*.

65. Hymenostylium curvirostre (Ehrh.) Lindb. Cape Dauphin 595.

66. Encalypta ciliata (Hedw.) Hoffm. Barrasois *1470*.

67. Grimmia conferta Funck.† Barrasois *0979*.

68. Racomitrium sudeticum (Funck) Br. & Sch.† Ingonish barrens *1663b*.

69. Ulota americana (Beauv.) Limpr.† Barrasois *1345*, *1574*, *1577*.

70. Tetraplodon angustatus (Sw.) Br. & Sch. Ingonish barrens *827*, *1632*, *1640*, *1680*.

71. Tetraplodon bryoides (Zoeg.) Lindb. Barrasois barrens *493;* Ingonish barrens *824*, *1679*, *1681*.

72. Pohlia nutans (Schreb.) Lindb.† Barrasois *09131*, *09139*, *1347;* Mount Franey *1705*.

73. Bryum bimum Schreb.† Aspy Bay *1044*.

74. Bryum capillare L.† Barrasois *09136* (var. *flaccidum* Br. & Sch.); Aspy Bay *1026*.

75. Bryum cyclophyllum Br. & Sch. Barrasois *1304*.

76. Bryum Duvalii Voit.† Barrasois *389*.

77. Mnium cinclidioides Hüben. Barrasois *1172*; Ingonish *717*.

78. Mnium cuspidatum (L.) Leyss.† Barrasois *0954*, *1389;* Ingonish *708*.

79. Mnium marginatum (Dicks.) Beauv. Barrasois *638*.

80. Mnium medium Br. & Sch. Barrasois *0956;* Ingonish *705*.

81. Mnium orthorrhynchum Br. & Sch.† Ingonish *710*.

82. Mnium spinulosum Br. & Sch.† Barrasois *0958; 1294*, *1337*.

83. Aulacomnium androgynum (L.) Schwaegr.† Barrasois *0937*, *1237* *1350*.

84. Bartramia pomiformis (L.) Hedw.† Barrasois *0992*, *1348;* Mount Franey *1706*.

85. Philonotis marchica (Willd.) Brid. Aspy Bay mountains *1004*.

86. Fontinalis antipyretica L.† Barrasois *1207;* Ingonish *682*, *723*.

87. Fontinalis biformis Sull. Barrasois *214*.

88. Fontinalis Cardoti Ren. Barrasois *1481*.

89. Fontinalis flaccida Ren. & Card. Mount Smoky *728b*.

90. Fontinalis Lescurii Sull. Ingonish *700*.

91. Fontinalis novae-angliae Sull.† Barrasois *416*.

92. Fontinalis Sullivantii Lindb. Aspy Bay mountains *1012*.

93. Dichelyma capillaceum (L.) Schimp. Barrasois *1171*.

94. Leucodon sciuroides (L.) Schwaegr. Barrasois *0994*, *1332;* Ingonish *917*.

95. Pylaisia intricata (Hedw.) Ren. & Card. (*P. velutina* Schimp.). Barrasois *1484*, *1537*.

96. Ptergynandrum filiforme (Timm) Hedw. Barrasois *394*, *631*, *1291*, *1375*, *1402*, *1403*.

97. Heterocladium squarrosulum (Voit) Lindb. Barrasois *0950*, *0964*, *0965*, *1105*, *1400*, *1460*, *1540*, Mount Smoky *735*; Ingonish *707;* Aspy Bay *1048*.

98. Myurella julacea (Vill.) Br. & Sch. Cape Dauphin *599*.

99. Anomodon rostratus (Hedw.) Schimp.† Ingonish *706*.

100. Leskeella nervosa (Schwaegr.) Loeske. Barrasois *0966*, *385*.

101. Thuidium abietinum (L.) Br. & Sch.† Barrasois *0963*.

102. Thuidium delicatulum (L.) Br. & Sch.† Barrasois *0962, 93, 315, 1396.*

103. Thuidium recognitum (Hedw.) Lindb.† Barrasois *0961.*

104. Elodium Blandowii (Web. f. & Mohr) Broth.† *Thuidium Blandowii* Br. & Sch. Aspy Bay *972.*

105. Amblystegium riparium (L.) Br. & Sch. Ingonish *683, 884.*

106. Amblystegium vacillans Sull. Ingonish *888.*

107. Amblystegiella confervoides (Brid.) Loeske. Cape Dauphin *594.*

108. Amblystegiella Sprucei (Bruch) Loeske. Ingonish *1714.*

109. Amblystegiella subtilis (Hedw.) Loeske. Barrasois *091.*

110. Hygroamblystegium filicinum (L.) Loeske.† *Hypnum filicinum* L. Aspy Bay *969.*

111. Drepanocladus aduncus (L.) Warnst.† *Hypnum uncinatum* Hedw. Barrasois *099, 0928, 1134, 1146; 09122* (var. *plumosus* [Schimp.] Warnst.); *09126* (var. *gracilescens* [Br. & Sch.] Warnst.); *09127* (var. *gracillimus* [Berg.] Warnst.); *1200* (var. *alpinus* [Ren.] Warnst.); Ingonish *712.*

112. Drepanocladus exannulatus (Gümb.) Warnst.† *Hypnum exannulatum* Gümb. Barrasois *88, 201, 215;* Ingonish mountains *795, 798a, 996.*

113. Drepanocladus fluitans (L.) Warnst.† *Hypnum fluitans* L. Barrasois *0913, 503, 570, 1231, 1232.* Ingonish *883.*

114. Drepanocladus purpurascens (Schimp.) Loeske. Ingonish mountains *1659.*

115. Drepanocladus revolvens (Sw.) Warnst. Ingonish mountains *794, 798b.*

116. Drepanocladus scorpioides (L.) Warnst. Ingonish mountains *792, 803;* Aspy Bay *963;* Aspy Bay barrens *1013.*

117. Drepanocladus serratus (Milde) Warnst. Barrasois *0911, 0912.*

118. Drepanocladus submersus (Schimp.) Warnst. Ingonish barrens *822.*

119. Hygrohypnum alpestre (Sw.) Broth. Barrasois *1496.*

120. Hygrohypnum dilatatum (Wils.) Loeske. Barrasois *09162, 09163;* Cape Dauphin *601.*

121. Hygrohypnum palustre (Huds.) Loeske. Barrasois *1133.*

122. Hygrohypnum Smithii (Sw.) Broth. (*Hypnum arcticum* Sommerf.). Barrasois *1448.*

123. Chrysohypnum chrysophyllum (Brid.) Loeske.† *Hypnum chrysophyllum* Brid. Barrasois *09175;* Aspy Bay *973.*

124. Chrysohypnum hispidulum (Brid.) G. Roth.† *Hypnum hispidulum* Brid. Barrasois *09108.*

125. Chrysohypnum polygamum (Br. & Sch.) Loeske. Barrasois *540.*

126. Chrysohypnum stellatum (Schreb.) Loeske. Barrasois *672;* Ingonish mountains *797;* Aspy Bay *1045.*

127. Rhytidiadelphus triquetrus (L.) Warnst.† *Hylocomium triquetrum* Br. & Sch. Barrasois *0951, 94, 1202, 1485.*

128. Hylocomium splendens (Hedw.) Br. & Sch.† Barrasois *0987a.*

129. Hypnum Schreberi Willd.† Barrasois *0989a, 0989b, 0989c.*

130. Ptilium Crista-Castrensis (L.) DeNot.† *Hypnum Crista-Castrensis* L. Barrasois *09118, 09177.*

131. Stereodon callichrous Brid.† *Hypnum callichroum* Brid. Ingonish mountains *1664.*

132. Stereodon cupressiformis (L.) Lindb.† *Hypnum cupressiformis* L. Barrasois *097, 09125, 1332, 1473.*

133. Stereodon Lindbergii (Mitt.) Warnst. Barrasois *0910, 0929, 199;* Ingonish mountains *870b,* Aspy Bay *962.*

134. Stereodon pallescens (Hedw.) Lindb. Barrasois *09113a, 09113b 09114.*

135. Stereodon pratensis (Koch) Warnst. Barrasois *0930;* Ingonish *13.*

136. Stereodon reptilis (Michx.) Mitt.† *Hypnum reptilis* Michx. Barrasois *09117, 09176, 09178, 09179, 312, 630.*

137. Heterophyllon Haldanianum (Grev.) Kindb.† *Hypnum Haldanianum* Grev. Barrasois *09107, 1391, 1429.*

138. Isopterygium elegans (Hook.) Lindb.† *Plagiothecium elegans* Schimp. Barrasois *1339.*

139. Isopterygium Muellerianum (Schimp.) Lindb. Barrasois *09172, 1308.*

140. Isopterygium pulchellum (Dicks.) Jaeg. Barrasois *1336.*

141. Isopterygium turfaceum (Lindb.) Lindb.† *Plagiothecium turfaceum* Lindb. Barrasois *09170, 1290, 1314;* Ingonish *1716.*

142. Plagiothecium sylvaticum (Huds.) Br. & Sch. Barrasois *09167.*

143. Sematophyllum recurvans (Michx.) E. G. Britton. Barrasois *09180, 09181, 265, 1311.*

144. Sematophyllum tenuirostris (Br. & Sch.) E. G. Britton. Barrasois *266.*

145. Camptothecium nitens (Schreb.) Schimp. Barrasois *1208.*

146. Brachythecium albicans (Neck.) Br. & Sch. Barrasois *1486.*

147. Brachythecium flexicaule Ren. & Card. Barrasois *1542.*

148. Brachythecium novae-angliae (Sull. & Lesq.) Jaeg. & Sauerb. Barrasois *09100.*

149. Brachythecium Rutabulum (L.) Br. & Sch.† Barrasois *09104.*

150. Brachythecium Starkei (Brid.) Br. & Sch. Barrasois *0999.*

151. Oxyrrhynchium praelongum (Hedw.) Warnst. Barrasois *09173.*

152. Oxyrrhynchium rusciforme (Neck.) Warnst. var. *complanatum* H. Schultze. Barrasois *1539, 1560.*

153. Eurynchium strigosum (Hoffm.) Br. & Sch.† Barrasois *09102.*

154. Climacium dendroides (L.) Web. f. & Mohr. Barrasois *0990, 1297, 1541.*

155. Buxbaumia indusiata Brid. Barrasois *1.*

156. Catharinaea angustata Brid. Barrasois *0948;* Aspy Bay *1022.*

157. Catharinaea undulata (L.) Web. f. & Mohr.† *Atrichum undulatum* Beauv. Barrasois *0947;* Aspy Bay *1023.*

158. Polytrichum commune L.† Barrasois *0938, 131, 502, 514, 568;* Aspy Bay mountains *1001.*

159. Polytrichum gracile Dicks. Aspy Bay barrens *1002* (var. *anomalum* Milde).

160. Polytrichum juniperinum Willd.† Barrasois *0939, 188.*

161. Polytrichum strictum Banks.† Barrasois *0944, 0945.*

4. Additional Species Recorded from Nova Scotia

The following list includes species which have been reported from Nova Scotia but have not been collected in Cape Breton. Except where otherwise indicated the records are to be found in Macoun's catalogue. Liverworts: *Riccardia palmata, Nardia Geoscyphus* (DeNot.) Lindb.‡, *Jamesoniella heterostipa* Evans‡, *Lophozia lycopodioides, Cephalozia connivens* (Dicks.) Lindb.‡, *Cephaloziella divaricata* [?] (as *Cephalozia*), *C. elachista* (Jack) Schiffn.‡, *Scapania apiculata* Spruce‡, *S. Bolanderi* [?], *S. irrigua* (Nees) Dumort.‡, *Microlejeunea ulicina* (Tayl.) Evans‡. Mosses: *Sphagnum imbricatum affine, S. tabulare* (as *S. molle*), *Andreaea alpestris, Dicranum consobrinum* [?], *Fissidens minutulus, Tortula mucronifolia* (as *Barbula*), *Racomitrium affine, R. Nevii, R. robustifolium, Orthotrichum speciosum, O. strangulatum, Ulota crispula, Pohlia annotina* (as *Webera*), *P. proligera*‡, *P. pseudo-carneum* (as *Webera*), *P. pulchella* (as *Webera Lescuriana*), *P. sphagnicola* (as *Webera*), *Mniobryum albicans* (as *Webera*), *M. carneum* (as *Webera*), *Bryum argenteum, B. caespiticium, B. erythrophyllum, B. inclinatum, B. intermedium, B. Knowltoni, B. Raui, B. torquescens, Mnium pseudo-lycopodioides, Cinclidium stygium, C. subrotundum, Meesia trichodes* (as *M. uliginosa*), *Leucodon brachypus, Homalia Macounii, Amblystegium orthocladon, Ctenidium molluscum* (as *Hypnum*), *Rhytidiadelphus calvescens* (as *Hylocomium*), *Stereodon canadensis* (as *Hypnum*), *S. fastigiatus* (as *Hypnum*), *S. Jamesii* (Sull.) Broth.‡, *Isopterygium deplanatum* (as *Rhynchostegium*), *Plagiothecium Roeseanum* (as *P. Sullivantiae*), *Polytrichum piliferum.*[1]

5. Summary

In the present paper, 349 bryophytes are recorded as having been collected in Cape Breton.[2] Of this number, 93 species are liverworts, 256 are mosses. Of the total number, 170 species (51 liverworts, 119 mosses) have been recorded from Nova Scotia also, while 179 species (41 liverworts, 138 mosses) are accredited only to Cape Breton. On the other hand, 50 of the species listed from Nova Scotia (9 liverworts, 41 mosses) have yet to be recorded from Cape Breton. Considering the province of Nova Scotia as a whole, its bryophyte flora, as summed up in the present paper, includes 399 species: 102 liverworts and 297 mosses.

Sheffield Scientific School of Yale University.

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[1] Common in Cape Breton also, but no specimens preserved.

[2] The figures here given do not include species queried [?] in the preceding lists. For various reasons it seems not unlikely that a few others of the mosses listed by Macoun should also be excluded.

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[From the BULLETIN OF THE TORREY BOTANICAL CLUB, 43: 235-238. 18 Je 1916.]

The vegetation of Connecticut

V. Plant societies along rivers and streams*

GEORGE E. NICHOLS

(WITH ELEVEN TEXT FIGURES)

In the present series of papers on the vegetation of Connecticut, the principle of succession has been adopted as the most satisfactory basis for classifying plant associations. This scheme of classification, it may here again be remarked, treats vegetation both from a genetic and a dynamic standpoint. It recognizes the fact that plant societies, or associations, as they exist today, are the product not alone of contemporaneous conditions, but of past conditions as well. It also emphasizes the fact that the plant associations of today are not necessarily permanent, but are liable to change through the influence of various factors.

In the third and fourth papers of the series,† attention was directed to the plant associations of uplands and of lowlands. There the changes in vegetation, and therefore the succession of plant associations, are influenced primarily by plant and animal agencies—in other words, by biotic factors. There remain to be considered, then, successions which are associated not only with biotic factors but with topographic factors as well. Succession of this sort has been termed TOPOGRAPHIC SUCCESSION. Topographic succession is seen principally along rivers and streams and along the coast. The present paper deals with plant societies along rivers and streams. Some of these societies might almost equally well have been treated along with the societies of uplands and of lowlands; yet, on the whole, so marked may be the impress of a stream on the vegetation at its margin, and so closely linked may be the development of the one with that of the other that the two cannot well be treated separately.

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* Contribution from the Osborn Botanical Laboratory.

† Torreya 14: 167-194. 1914; Bull. Torrey Club 42: 169-217. 1915.

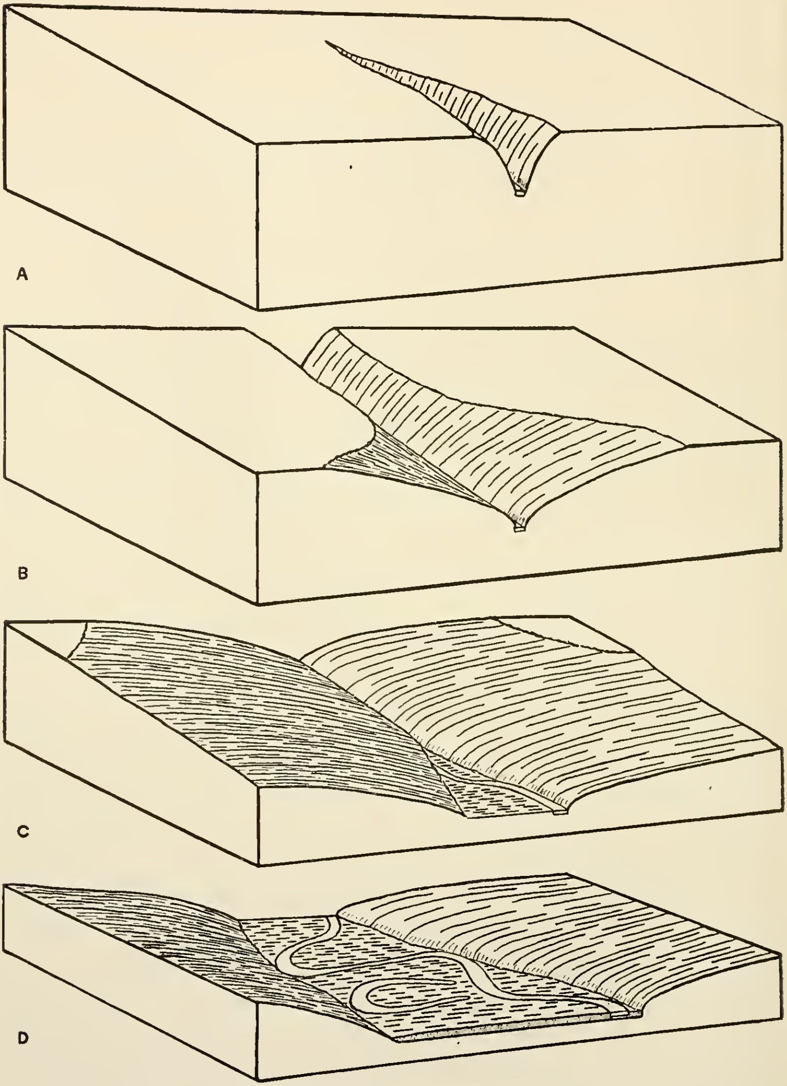

Fig. 1. Diagrams showing various stages in the development of a river.

The Life History of a River

Various stages in the life history of a river are graphically represented in Fig. 1. In a young stream the current is swift and wears away the floor and sides of its channel. Vertical erosion, however, is greater than lateral, so that the stream may gradually intrench itself in a narrow ravine or canyon. At this stage of stream development vegetation is largely confined to the flanks of the ravine. During the course of time, as the channel is cut deeper and deeper, downward erosion proceeds more and more slowly, ultimately ceasing altogether, while lateral erosion becomes correspondingly more pronounced; so that, as the stream approaches maturity, it comes to occupy a broad valley which it has carved out for itself. Vegetation covers both the bordering bluffs and the floor of the valley. As the level of the stream approaches the level of the water at its mouth, the current becomes sluggish and aggradation largely succeeds degradation. An old age river meanders about in broad, sweeping curves on the flood plain which it has built up out of sediment derived from younger parts of its system. A very distinctive type of vegetation is developed on flood plains.

Of course, the rate at which the topographic changes outlined in the preceding paragraph are effected varies widely according to the nature of the rock formations concerned. The scouring out of a ravine in clay or gravel, for example, may proceed with comparative rapidity, but the erosion of a ravine in rock is extremely slow. Ravines in glacial till and outwash have been developed since the retreat of the glaciers, and may even now be observed in the process of active formation. In most rock ravines, on the other hand, the topographic changes since the ice age have been practically negligible. The bearing of these facts on the nature of the vegetation will be referred to in later paragraphs (pp. 245, 249).

ROCK RAVINES

Occurrence and General Features.—Throughout the region under discussion the rock ravine is the common type. It abounds in the highland districts, and in the Central Lowland is frequent along the trap ranges and elsewhere. Owing mainly to the nature of the rocks concerned, canyons with overhanging or perpendicular walls are absent. The predominant type of rock ravine (FIG. 2) is somewhat V-shaped in cross section, often narrow and precipitous below but broadening out above. Toward the bottom the vegetation may be restricted to such forms as can cling to the rock face or maintain a foothold in crevices, but higher up the sides are usually forested.

There are, of course, all sorts and sizes of ravines. In the remarks on the nature of ravine vegetation which follow, the writer has in mind a number of unusually good examples, such as Sage's Ravine and the Wolf Den in Salisbury, the Glen along Spruce Brook at Beacon Falls, Wintergreen Falls ravine in

FIG. 2. Precipitous rocky slopes along stream in Sage's Ravine, Salisbury. The cliffs in the foreground are covered with mosses and liverworts.

Hamden, Woodbridge Glen in Woodbridge, Roaring Brook ravine in Cheshire, Devil's Gulch in Branford, and Ninevah Falls ravine in Killingworth. Most of these are ravines of considerable depth and have a good-sized brook at the bottom. To shallower, less well-developed ravines the remarks naturally may not be equally applicable.

The Bryophytic Flora of Rock Ravines.—Perhaps the most striking feature of the vegetation near the bottom of a ravine (Fig. 2) is the rich display of mosses and liverworts. In the stream itself, attached to rocks but always submerged, grow various aquatic forms, such as *Fontinalis*. Other more or less hydrophytic species cover the low-lying, wet and frequently submerged rocks along the margin and in the bed of the stream, mantle the spray-dashed rocks at the foot of waterfalls, and form extensive mats even in rapids and similar precarious situations. The following more or less hydrophytic species may be looked for in such places:

Chiloscyphus rivularis
Scapania undulata
Porella pinnata
Fontinalis dalecarlica
Fontinalis gigantea
Fontinalis Lescurii
Oxyrrhynchium rusciforme
Amblystegium fluviatile
Amblystegium irriguum
Hygrohypnum dilatatum
Hygrohypnum eugyrium
Hygrohypnum ochraceum

Growing on periodically inundated rock surfaces, either in the bed of the stream or along its sides, are such forms as *Fissidens incurvus*, *Grimmia apocarpa*, *Racomitrium aciculare*, and *Brachythecium plumosum*. Along with these, but usually on springy banks or on continuously moist rock surfaces, where they may or may not be submerged during flood time, may occur:

Conocephalum conicum
Pellia epiphylla
Plagiochila asplenioides
Lophocolea bidentata
Jubula pennsylvanica
Anthoceros laevis
Fissidens adiantoides
Mnium hornum
Mnium punctatum
Philonotis fontana
Thuidium delicatulum
Brachythecium rivulare
Climacium americanum
Catharinaea undulata

Higher up on the slopes, numerous species thrive in the crevices or plaster the faces of overhanging cliffs and precipitous rocks. The following are fairly characteristic of wet or moist cliffs:

Marsupella emarginata
Plagiochila asplenioides
Scapania nemorosa
Radula complanata
Lejeunea cavifolia
Hymenostylium curvirostre
Didymodon rubellus
Anoectangium Mougeotii
Plagiopus Oederi
Plagiothecium denticulatum
Hylocomium brevirostre
Thamnium alleghaniense

Inhabiting the drier cliffs, either in crevices or on the rock face, are such forms as:

Metzgeria conjugata
Cephaloziella Hampeana
Porella platyphylloidea
Leucolejeunea clypeata
Frullania Asagrayana
Rhabdoweisia denticulata
Grimmia conferta
Ulota americana
Bartramia pomiformis
Hedwigia albicans
Neckera pennata
Haplohymenium triste
Anomodon attenuatus
Anomodon rostratus

The Influence of the Chemical Nature of Rocks on the Distribution of Bryophytes.—In earlier papers of this series* brief reference has been made to the influence of the chemical composition of the substratum on vegetation. In glaciated regions like Connecticut, where most soils are transported and residual soils are rare, this influence is nowhere seen to better advantage than in ravines and similar localities where there are exposures of bare rock. In Connecticut, the problem as to the effect of the chemical nature of the substratum on vegetation concerns chiefly calcareous versus potassic rocks. The granites, gneisses, schists and sandstones, which comprise the bed rock over much of this state, are for the most part rich in potassium, which is one of the principal constituents of orthoclase feldspar and of mica (muscovite and biotite). Calcium also, as one of the components of plagioclase feldspar, hornblende, and certain other minerals, is present in some of these rocks, and in the sedimentary formations—the sandstones and shales—small amounts of calcium carbonate may be included in the cementing material. But, except locally, the amount of lime in these rocks, in so far as it affects vegetation, appears relatively insignificant. The important lime-bearing formations of Connecticut are trap and marble. The former contains potassium in small amount, one or two per cent.; the latter con-

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* See Torreya 13: 109, 110. 1913; 14: 185. 1914.

tains none. Trap outcrops (diabase and basalt) occur chiefly in the Central Lowland. The marble (sometimes referred to as a limestone or dolomite) forms extensive deposits in the western part of the state, particularly in the upper Housatonic Valley.

Owing to their frequently intimate association with rock surfaces, no group of plants, with the possible exception of the lichens, is better qualified to demonstrate the influence of the chemical composition of the substratum on vegetation than the bryophytes. To be sure, many mosses and liverworts apparently flourish indiscriminately on any sort of rock substratum, provided only that requisite conditions of moisture and shade are present. But a large number of species undoubtedly "prefer" either calcareous or potassic rocks, and some are confined to such substrata. A list is given below of local species which favor calcareous rocks. Nearly all of these are commonest in the marble areas of western Connecticut, and several of them have been collected only there. Some, however, occur also along the trap ranges, while a few are known from other scattered localities.

Grimaldia fragrans
Preissia quadrata
Pellia Fabroniana
Lophozia badensis
Lophocolea minor
Cololejeunea Biddlecomiae
Frullania riparia
Saelania glaucescens
Fissidens cristatus
Cratoneuron filicinum
Hymenostylium curvirostre
Tortella tortuosa
Encalypta contorta
Mnium orthorrhynchum
Plagiopus Oederi
Myurella julacea
Amblystegiella confervoides
Amblystegium noterophilum

The species cited in the next list are reputedly calciphobous (i.e. "lime-avoiding"), and are for the most part restricted to potassic rocks.

Marsupella emarginata
Sphenolobus exsectus
Scapania nemorosa
Scapania undulata
Radula obconica
Andreaea petrophila
Andreaea Rothii
Rhabdoweisia denticulata
Dicranum fulvum
Glyphomitrium incurvum
Racomitrium aciculare
Ulota americana
Pterigynandrum filiforme
Brachythecium plumosum
Sematophyllum carolinianum
Hygrohypnum dilatatum
Hygrohypnum eugyrium

The Mesophytism of the Flora in Rock Ravines.—A rock ravine, more than any other sort of habitat, affords environmental conditions congenial to pronounced mesophytic plants. Seepage water is usually abundant along the sides, there is protection from sun and wind, and the humidity of the air, as compared with the surrounding upland, is high. Certain mosses and liverworts are practically confined to such habitats. In a more arid region than Connecticut the same observation might be made with regard to many of the higher plants, but while it is a familiar fact that in this region as elsewhere the flora of rock ravines includes many of the most extreme shade- and moisture-loving ferns and flowering plants, most of the species present are equally representative of other habitats. Species intolerant of shade are largely excluded. The majority of the forms cited in earlier papers as typical of the climax forest of this region are to be found here, and not a few of the common plants of rock ravines thrive elsewhere in wooded swamps. The following list includes a number of ferns and herbaceous flowering plants which may be considered characteristic of rock ravines, though by no means peculiar to them.

Polypodium vulgare
Phegopteris polypodioides
Asplenium Trichomanes
Asplenium acrostichoides
Aspidium spinulosum
Cystopteris bulbifera
Cystopteris fragilis
Lycopodium lucidulum
Arisaema triphyllum
Smilacina racemosa
Streptopus roseus
Trillium erectum
Laportea canadensis
Pilea pumila
Solidago latifolia
Asarum canadense
Actaea rubra
Caulophyllum thalictroides
Chrysosplenium americanum
Impatiens pallida
Viola cucullata
Viola blanda
Viola rotundifolia
Circaea alpina
Aralia racemosa
Sanicula gregaria
Hydrocotyle americana
Cryptotaenia canadensis
Collinsonia canadensis

The Ravine Forest.—The intense mesophytism of a rock ravine is further accentuated by the nature of the ravine forest (FIG. 3). As a rule the hemlock and yellow birch are prominent, and more often than not they predominate. Along with them commonly occur the sugar maple and others of the trees elsewhere cited as characteristic of the climax forest in this region. The woody undergrowth usually includes *Hamamelis virginiana*, *Kalmia latifolia*, and *Viburnum acerifolium*, while forms such as *Carpinus caroliniana*, *Alnus rugosa* and *Benzoin aestivale*, which one ordinarily associates with swamps, frequently grow along the stream at the bottom. On the whole, ravine forests almost invariably are more mesophytic, and approximate more closely the climax

FIG. 3. Primeval forest in Sage's Ravine. Hemlock and yellow birch the common trees.

formation of this region than do the forests on the adjoining uplands. In a large measure this fact of course is due to the exceptionally favorable conditions of environment under which they have been developed. But there are other contributory causes which, while they have nothing to do with the development of these forests, may at least be partly responsible for their perpetuation. Thus, on account of their comparative topographic isolation, ravine forests may be largely immune from the fires which frequently devastate the surrounding uplands, while by reason of the difficulty in removing the timber they offer little temptation to the lumberman.

The Boreal Aspect of the Vegetation in Rock Ravines.—A few locally rare Canadian plants, such as *Lophozia alpestris*, *Lophozia attenuata*, *Gymnostomum rupestre*, *Polytrichum alpinum*, *Lycopodium Selago*, *Streptopus amplexifolius*, and *Viola Selkirkii* have been collected only in rock ravines. From an ecological standpoint, however, it is the mass-effect of the vegetation rather than the occurrence of isolated species which is significant. Many of the bryophytes, which have already been referred to as being largely restricted to rock ravines in Connecticut, are much more generally distributed farther north. But even if these rock-face and crevice forms are ignored, the stamp of the north on the vegetation here is unmistakable. The predominant trees of ravine forests are usually species of northward range. The bryophytic flora of these forests—the mossy carpet of *Bazzania trilobata*, *Hylocomium splendens*, *Ptilium Crista-castrensis* and *Hypnum Schreberi* which frequently covers the forest floor—likewise is strongly suggestive of the north. In Sage's Ravine, and doubtless elsewhere, masses of *Sphagnum* grow high up on the slopes—a common phenomenon in the Maritime Provinces of eastern Canada. Moreover, in Connecticut, many vascular plants characteristic of the north woods, while by no means confined to this sort of habitat, attain their optimum development in rock ravines. As representative of this latter group of species may be cited:

Phegopteris polypodioides
Taxus canadensis
Streptopus roseus
Actaea rubra
Oxalis acetosella
Acer pennsylvanicum
Acer spicatum
Viola rotundifolia
Lonicera canadensis
Aster acuminatus

On the whole, the display of Canadian plants in rock ravines is noticeably richer than in any other sort of habitat, with the exception of bogs. Various explanations for this fact may be suggested. In the first place, the atmospheric conditions here are congenial to northern plants. As compared with less protected habitats, the air is more humid, while, especially in summer, the temperature is uniformly lower and less subject to extremes. Moreover, the length of the growing season is presumably shorter than in more open situations. In a Connecticut rock ravine there may thus be reproduced in miniature a type of climate similar to that which in the Canadian Zone prevails over vast areas. In the second place, geological factors are of undoubted significance. As has already been remarked, most rock ravines have remained practically unaltered since glacial times; they represent very ancient plant habitats. It seems probable, therefore, that boreal plants which today are confined to rock ravines may formerly have been much more widely distributed, and that they have been able to persist in their present habitats because of the unusually favorable environmental conditions there afforded. In the same way it is conceivable that the present boreal aspect of the vegetation in rock ravines may be reminiscent of a one-time much more universal aspect of vegetation in this region.

RAVINES IN UNCONSOLIDATED ROCKS

The unconsolidated stony materials which form so considerable a portion of the superficial crust of the earth are not commonly designated as rocks. "Yet no line of separation can be drawn between such solid rocks as those into which the sands and muds of distant geological ages have been transformed and the semi-consolidated deposits of more recent times, or the sediments now accumulating."* In the present paper, the term UNCONSOLIDATED ROCK embraces any uncompacted rock formation, such as sand, gravel, and clay. For the sake of convenience, the word ROCK itself, written without a qualifying adjective, is used in its popular sense to include only consolidated rock formations.

Distribution, Character, and Vegetation of Ravines in Unconsolidated Rocks.—In Connecticut, ravines of this description are by

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* Barrell, J. & Loughlin, G. F., Conn. State Geol. and Nat. History Survey, Bull. 13: 17. 1910.

no means uncommon. They are developed along streams throughout the Central Lowland, while in the Highlands they may occur wherever there are deposits of glacial drift. More often than not they are relatively small and correspondingly unimpressive; but in some cases, particularly in the northern half of the Central Lowland, they may assume considerable size and importance.

One of the best examples which the writer has examined of a ravine in unconsolidated rock is located in the town of Windsor. It has been scoured out to a depth of perhaps thirty feet from a coarse, sandy substratum through the activity of a small brook which flows into the Farmington River from the north. The slopes of the ravine, forested with hemlock, yellow birch, sugar maple, beech, white ash and tulip, contrast sharply with the surrounding upland which is largely overgrown with white pine, oaks, and chestnut. The undergrowth includes many of the herbaceous and shrubby species which have been listed as characteristic of rock ravines. But along with these grow *Lycopodium obscurum*, *Oakesia sessilifolia*, *Corylus americana*, *Geranium maculatum*, *Chimaphila umbellata*, *Pyrola rotundifolia*, and *Erigeron pulchellus* —all plants of relatively dry, open woods. As might be anticipated, the bryophytic flora is poorly represented. The rock-face and crevice mosses and liverworts, which constitute such a striking feature of the vegetation in rock ravines, are absent. Along the wet, sandy banks of the stream are a few species, such as *Pellia epiphylla*, *Conocephalum conicum*, *Mnium hornum*, and *Catharinaea undulata;* but aside from these about the only bryophytes present are a few forms which grow on rotten wood or humus, such as *Mnium cuspidatum*, *Stereodon cupressiformis* and *Georgia pellucida.*

Ravines in unconsolidated rock compare neither in scenic nor botanic interest with rock ravines. To be sure, all gradations are found between extremely shallow and scarcely perceptible depressions, which ordinarily would hardly be classed as ravines, and ravines of considerable depth, with fairly steep sides, like the one at Windsor. As a result of the diversity in environments which it is obvious may thus be afforded by different ravines, all stages of transition may be found between the vegetation of swamps and uplands on the one hand and that of typical ravines on the other. On the average, however, ravines in unconsolidated rock are smaller in size and are relatively broader and shallower than rock ravines. In consequence, the atmospheric conditions are seldom as favorable as those of rock ravines, and the vegetation rarely equals that of rock ravines in the high degree of mesophytism attained. Soil moisture, as a rule, would seem to be more important here in its effect on vegetation than atmospheric humidity. The boreal tone which characterizes the vegetation of rock ravines is likewise lacking. This would naturally be expected, not only on account of the less congenial environmental relations but also because of the comparative recency with which ravines in glacial deposits have been developed.

Spring Brooks.—As Cowles* has remarked, "springs and spring brooks may be classed with ravine streams, but differ from them in the relative absence of erosion phenomena." They might equally well, if not better, be classed with spring swamps,† with which they are usually associated. Spring brooks are common throughout Connecticut. Perhaps their most familiar floristic feature is the fringe of alders (*Alnus rugosa, Alnus incana*) which almost invariably lines their banks. Aside from these, the brookside flora may include any of the species elsewhere cited as characteristic of spring swamps.

The Succession of Vegetation during the Development of Ravines in Unconsolidated Rocks.—In his treatment of the plant societies of the Chicago region, Cowles‡ has described the development of clay ravines and the concomitant sequence of plant associations. The following observations are quoted from this work: "Wherever there is an elevated stretch of land adjoining a body of water, such as a lake bluff, one is apt to find excellent examples of the beginning of a ravine. *Fig. 1* [reproduced in this paper as FIG. 4] shows an embryonic ravine of a type which may frequently be seen along the clay bluffs. . . . A ravine of this type is essentially a desert, so far as plant life is concerned. The exposure to wind and to alternations of temperature and moisture is excessive. The lack of vegetation, however, is due chiefly to the instability of the soil; this instability is particularly great in the case of clay bluffs, where the seepage of water causes extensive landslide action.

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* The physiographic ecology of Chicago and vicinity. Bot. Gaz. 31: 98. 1901.

† See Bull. Torrey Club 42: 192, 193. 1915.

‡ *Op cit.*, pp. 86–88.

No plants can yet get a foothold in such a place, unless it be a few species that may be able to make their appearance between periods of landslide action; among these plants annuals particularly predominate. The perennials that may be found in such places are almost entirely plants which have slid down the bank. Ravines of a similar type may be seen in many places inland, and wherever found the poverty of vegetation on the slopes is the most striking character.

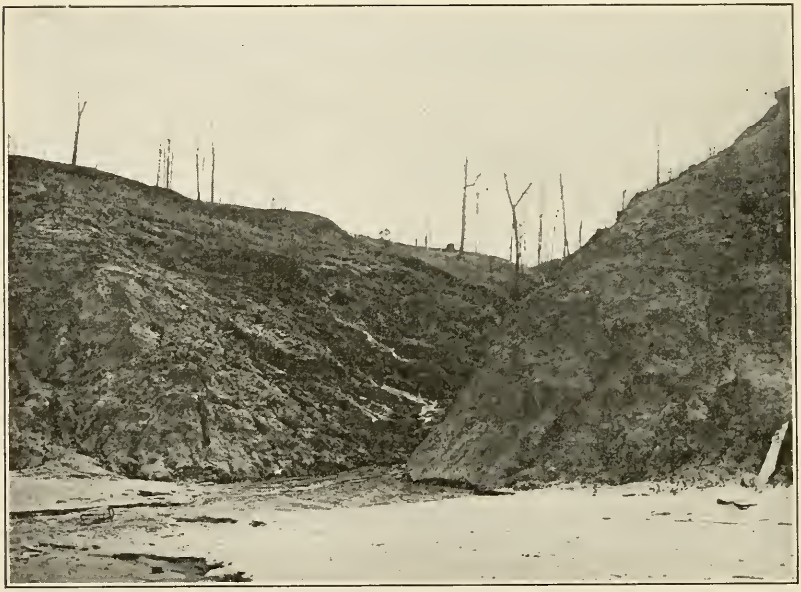

FIG. 4. An embryonic ravine in a clay bluff along the western shore of Lake Michigan. Vegetation entirely absent on the unstable clay slopes, except for shrubs and grasses which have slid down from the top. (After Cowles, Physiographic ecology of Chicago and vicinity; photograph furnished by H. C. Cowles.)

"As the ravine extends itself inland the conditions outlined above may be always seen about its head, but toward the mouth of the ravine the slopes are less precipitous. Torrents cut down the bed of the ravine until a depth is reached approaching the water level at its mouth. From this time on the slopes become reduced and the ravine widens more than it deepens, by reason of lateral cutting, landslide action, and side gullies. After a time a sufficient stability is reached to permit a considerable growth of vegetation.

If the erosion is slight enough to allow a vegetation carpet to develop, a high degree of luxuriance may be attained. In fact, ravine conditions are usually extremely favorable for plants, after the initial stages have passed. In a comparatively few years the vegetation leaps, as it were, by bounds through the herbaceous and shrubby stages into a mesophytic forest, ... Nothing shows as well as this the brief period necessary for a vegetation cycle in a favored situation as compared with an erosion cycle."

In Connecticut, clay ravines are much less frequent than are those in rock. They exist on a small scale in many parts of the Central Lowland, especially along the Connecticut River from Glastonbury to Windsor Locks, but elsewhere they are rare. Nowhere in this state are the successive changes in vegetation which accompany the development of a clay ravine so clearly shown as in the area described by Cowles, an area which the writer has visited on several occasions. So far as it has been possible to compare, however, the observations recorded in the Chicago region seem quite applicable to conditions in Connecticut.

PRE-EROSION TOPOGRAPHY AND ITS BEARING ON THE PHENOMENA OF SUCCESSION IN ROCK RAVINES

"From the standpoint of dynamic plant geography our land areas are divided into two well-marked categories: on the one hand is the erosion topography which is characteristic of the eroding and depositing phases of present streams and shores, and on the other hand is the preërosion topography which is characteristic of those areas that have not as yet been invaded by erosive forces."* To this latter category, speaking from the standpoint of the succession of plant associations, belong rock ravines. For while it is conceivable that, just as in the case of clay ravines, the topographic changes which accompany the development of rock ravines might react on the vegetation, yet such changes are brought about with such extreme slowness that their effect on plant life may be regarded as practically negligible. Whatever changes in the nature of ravine vegetation may have taken place in the past have probably been associated not only with topographic changes but with climatic changes as well; and the same will very likely

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* Cowles, H. C. Bot. Gaz. 51: 172, 173. 1911.

hold true in the future. From a standpoint of present-day plant geography, therefore, the climax vegetation of rock ravines may be looked upon as practically permanent.

Although the fact cannot be overlooked that ordinarily the plant societies of rock ravines are associated with a definite phase of stream development, it should also be recognized that while very commonly the formation of a ravine has been due to the activity of streams which are still operative, this is by no means always the case. There are many rock ravines whose formation cannot be accounted for by contemporaneous factors at all. Often, as in the Devil's Gulch, the streams now present in such ravines can have played little part in their formation. Many streams have been superposed, so to speak, on the topography. They have found rather than made their channels. Not infrequently, as in the Wolf Den, ravines have been developed in other ways than by stream erosion. It is largely due to the prevalence of this preërosion type of topography, which has been moulded by physiographic forces of the geologic past, that rock ravines are so much more highly developed in the Highlands than in the Lowland.

RIVER AND STREAM BLUFFS

The later phases in river activity may be observed along most of the larger streams throughout the state. As the result of lateral cutting, the ravine once present has been replaced by a broad valley. As a ravine widens out, the exposure to wind, sun, and changes of temperature increases, and the moisture content of the slopes is appreciably modified. The effect of these environmental changes on vegetation can be seen by comparing the flora of a river valley with that of a ravine. In a general way, the vegetation of stream valleys can be treated under two heads: BLUFFS and FLOOD PLAINS. The term Bluff, as used here, includes not only the relatively steep slopes which frequently demarcate the valley from the upland, but also the gentler slopes which commonly occupy most of the intervening valley floor. In other words, it embraces all parts of the valley which, in contrast to flood plains, have been formed by erosion rather than by deposition.

The Vegetation of Bluffs in Unconsolidated Rocks.—In the

Chicago region,* the increased exposure which follows the widening out of a clay ravine may have a disastrous effect on the ravine flora.

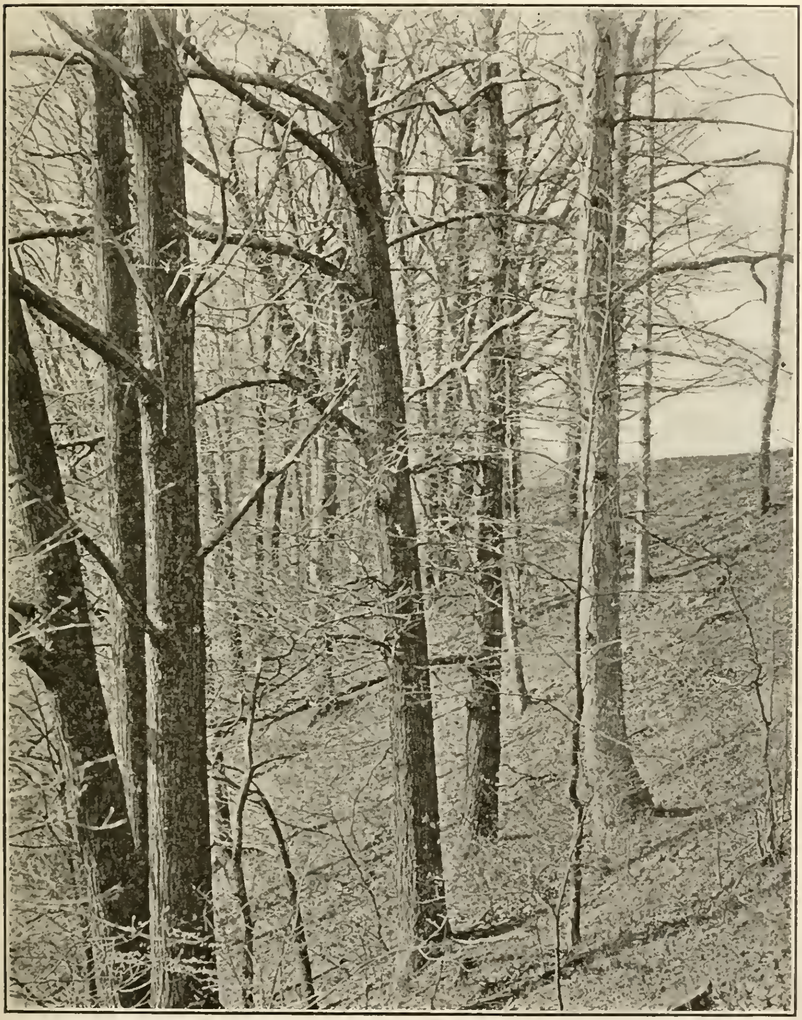

FIG. 5. Forest of chestnut, white oak, red oak, etc., along a sandy bluff bordering West River, New Haven. Elsewhere along the bluff, hemlock, beech and basswood are more or less abundant.

"The rich mesophytic herbs, including the liverworts and mosses, dry up and die, . . . and a xerophytic undergrowth comes in. . . .

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* See Cowles, H. C., 1901, *op. cit.*, pp. 90–93.

After a few years have passed, xerophytic shrubs appear, . . . and it is not long until xerophytic or semi-xerophytic thickets prevail in place of the former mesophytic undershrubs. The last of the mesophytes to die are trees, because they are longer-lived than herbs and shrubs, and also because their roots reach down to the moisture"; but eventually these too give way to relatively xerophytic species. In Connecticut, the changes are not so radical; in fact, a bluff forest may be scarcely less mesophytic than a ravine forest. This is not surprising when it is considered that the climax formation in this region (that is, the most mesophytic type of vegetation which is capable of development on uplands) is very nearly as mesophytic as the climax association (termed by Cowles a "temporary climax") of ravines. In the Chicago region, on the other hand, the contrast between the mesophytic ravine forests and the xero-mesophytic climax forests on uplands is very pronounced.

The most striking difference between a bluff forest (FIG. 5) and a ravine forest is seen in the greater abundance of relatively intolerant trees. The undergrowth also, while it may contain any of the characteristic ravine species, includes many forms which ordinarily do not thrive under the shadier ravine conditions. On bluffs in unconsolidated rock, especially on clay and till, the soil moisture relations usually favor the continuance of a mesophytic flora. Near the mouth of the Windsor ravine, to select a concrete example, along the bluffs which border the Farmington Valley, common trees are *Juglans cinerea*, *Tilia americana*, *Betula alba papyrifera*, *Ulmus americana*, *Platanus occidentalis*, *Carya cordiformis*, *Quercus rubra*, *Ostrya virginiana*, and *Carpinus caroliniana*. Along with these occur the trees of the ravine forest—the sugar maple, white ash, tulip and yellow birch, and to a less extent the hemlock.

The undergrowth of moist valley forests is particularly rich in spring-flowering species. Among the herbaceous plants characteristic of such habitats may be mentioned the following:

Aspidium noveboracense
Asplenium Filix-femina
Adiantum pedatum
Osmunda Claytoniana
Botrychium virginianum
Oakesia sessilifolia
Allium tricoccum
Erythronium americanum

Asarum canadense
Claytonia virginica
Thalictrum dioicum
Anemonella thalictroides
Smilacina racemosa
Polygonatum biflorum
Medeola virginiana
Trillium erectum
Hepatica triloba
Anemone quinquefolia
Caulophyllum thalictroides
Sanguinaria canadensis
Dicentra cucullaria
Dentaria diphylla
Dentaria laciniata
Viola pubescens

The Vegetation of Rock Bluffs.—In comparing rock bluffs with rock ravines, one striking dissimilarity concerns the bryophytic flora. Species inhabiting the rock-face or the crevices, together with certain of the forest-floor species, may be well represented, but most of the others are absent. Under favorable circumstances a rock bluff may support a highly mesophytic vegetation; much apparently depends on exposure and on ground-water relations. Along the Connecticut River, south of Middletown, the north-facing bluffs are (or were) well forested; most of the vascular plants already cited as characteristic of rock ravines grow luxuriantly; *Acer pennsylvanicum* is common, attaining a height of more than thirty feet; and the mesophytic ravine mosses are well represented. The vegetation on the south-facing bluffs across the river, however, especially as regards the herbaceous flora, is much less mesophytic. In general, north- or east-facing bluffs are more mesophytic than those which face south or west. As might be expected, the highest degree of mesophytism prevails toward the bottom of a bluff; toward the top the vegetation is more xerophytic. In some cases, where the water supply is insufficient, mesophytes may be virtually lacking and xerophytes predominate from top to bottom. On the whole, the vegetation of the rock bluffs which border stream valleys throughout the state resembles that which has been described elsewhere* as characteristic of talus slopes.

FLOOD PLAINS

The topographic changes which take place during the building up of a flood-plain are accompanied by a fairly definite succession of plant associations. In the earlier stages of flood plain develop-

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* See Torreya 14: 181–184. 1914.

ment, the surface of the ground is so low that it is covered with water at all seasons of the year. Here the vegetation consists of aquatic or semi-aquatic plants. As the surface is built up higher, it reaches a level where it is exposed to the air during summer, the period of low water, and here aquatic plants are replaced by terrestrial herbs. As the constructive process continues, the surface is built up to a height where it is out of water much of the year, and finally it may attain an elevation where it is out of reach of all but the highest floods. On these older flood plains grow shrubs and trees.

Flood Plain Associations along the Connecticut River.—Flood plains are formed to some extent along every sizable stream. In Connecticut, as might be expected, they are developed on the largest scale along the Connecticut River. Here, on the higher flood plains from Middletown northward, the rich alluvial soil furnishes the most fertile farm-lands in the state. As the result of agriculture, much of the primitive vegetation has been obliterated,* but it may still be seen to advantage on various flood plain islands (FIG. 6) and elsewhere. On an island at Windsor, in particular, the natural vegetation has never been disturbed. Whether or not it is true, as old residents maintain, that this island —now about three-quarters of a mile long, perhaps a hundred yards wide, and rising to a height of more than a dozen feet above low water level—has been developed entirely within the last thirty years, it is certain that it is growing rapidly at the present time, having increased several hundred feet in length at the lower end since it first came under the writer's observation in 1910. The following notes on the vegetation of the Connecticut River flood plains are based partly on the study of this island, partly on studies made at Middletown, Haddam and other points along the river.

As compared with a lake-swamp succession, free-floating aquatics, for obvious reasons, are rarely represented in a flood

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* Many of the grassy meadows along the Connecticut date back to pre-colonial days. It is recorded that when the first settlers arrived these areas were open and under cultivation by the Indians, who were accustomed to burn them over annually. But from the fact that today trees occur along the sloughs and scattered through the grassland, wherever they are permitted to grow, it would seem probable that these meadows were formerly forested, and that, if left to themselves, they would soon revert to their original condition.

plain succession. The pond-lilies also are usually absent. Commonly the first forms to appear are submersed species, such as the pondweeds (*Potamogeton* sp.), *Vallisneria spiralis* and *Elodea canadensis*, which may grow in water four or even more feet in depth. In shallow water various aquatics with aerial foliage are ordinarily conspicuous. Of these, the following species are perhaps the most noteworthy:*

Fig. 6. Flood plain island in the Connecticut River, at Haddam. The plant in the foreground is the wild rice (*Zizania palustris*).

Equisetum fluviatile
Typha latifolia
Sagittaria latifolia
Zizania palustris
Scirpus americanus
Scirpus validus
Peltandra virginica
Orontium aquaticum
Pontederia cordata
Polygonum Muhlenbergii

While the number of species present at this early stage of flood plain development is relatively small, any lack of variety is more than counterbalanced by the luxuriance with which these

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* From this and the two following lists have purposely been omitted a number of species which, while peculiar to the Connecticut River flood plains, seem too rare or too local to be of importance in the present connection. The majority of such species, so far as known, have already been mentioned elsewhere (Torreya 13: 106. 1913).

few forms often grow. Fringing zones of pickerel weed and the like are quite as characteristic of flood plains as of lake shores, while marshy swamps, predominated by wild rice (FIG. 7) and other grass-like plants, are a prominent feature of many low flood plains, particularly toward the mouth of the river. Here, within the sphere of tidal influence, the ground occupied by these plants may be submerged at high tide and bare at low tide.

FIG. 7. Wild rice along banks of the Quinnipiac River, North Haven. Some idea of the height of this grass is suggested by the bow of the canoe in the foreground.

The second phase of flood plain development may well be designated the Strand Stage (FIG. 8). The surface of the ground is exposed for a longer or shorter period during summer, but is covered with water during winter. Certain algae, such as *Vaucheria* and *Botrydium*, are common here, as are also ephemeral bryophytes, such as *Riccia*, *Ephemerum*, and *Physcomitrium immersum*. The predominant vascular plants are either annuals or herbaceous perennials (or biennials)—forms which are able to develop between successive periods of submergence. On the lower, muddier parts of the strand, species with more or less pronounced amphibious proclivities may be well represented: such, for example, as *Echinochloa Walteri*, *Eleocharis aciculare*, *Penthorum sedoides*, and *Ludvigia palustris*. A list of other species characteristic of the strand stage is here given.

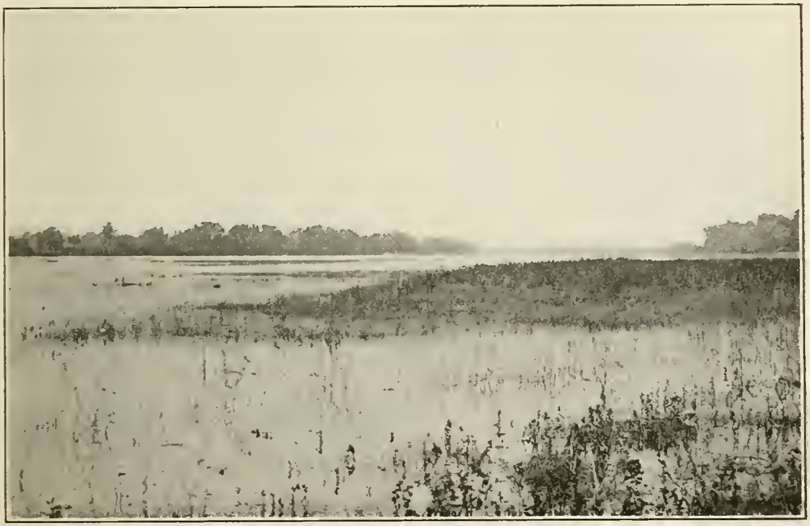

FIG. 8. A typical, low, flood plain strand along the Connecticut River, at East Windsor. Vegetation mostly herbaceous, but seedlings of willow and cottonwood abundant.

Equisetum arvense
Panicum agrostoides
Leersia virginica
Cyperus strigosus
Juncus effusus
Rumex crispus
Polygonum pennsylvanicum
Radicula palustris
Gnaphalium uliginosum
Ambrosia trifida
Xanthium echinatum
Bidens vulgatum

Woody plants are seldom wholly absent from the strand stage of a flood plain; commonly, seedlings of willow and cottonwood are abundant. Indeed, certain species of willow, such as *Salix cordata* and *Salix longifolia*, occur here which are usually lacking on older flood plains. But woody plants are rarely well developed; for even if they are able to withstand submergence in winter, trees and shrubs of any size are liable to be badly battered or else uprooted and carried away by the ice when it breaks up in spring. As soon, however, as the surface has been built up to such a height that it is beyond the reach of the winter ice, trees become the controlling element of the vegetation and ultimately a luxuriant forest may be developed. The boundary between the wooded part of a flood plain and the strand area is often marked by a distinct shelf or step—the result of ice-shove in winter.

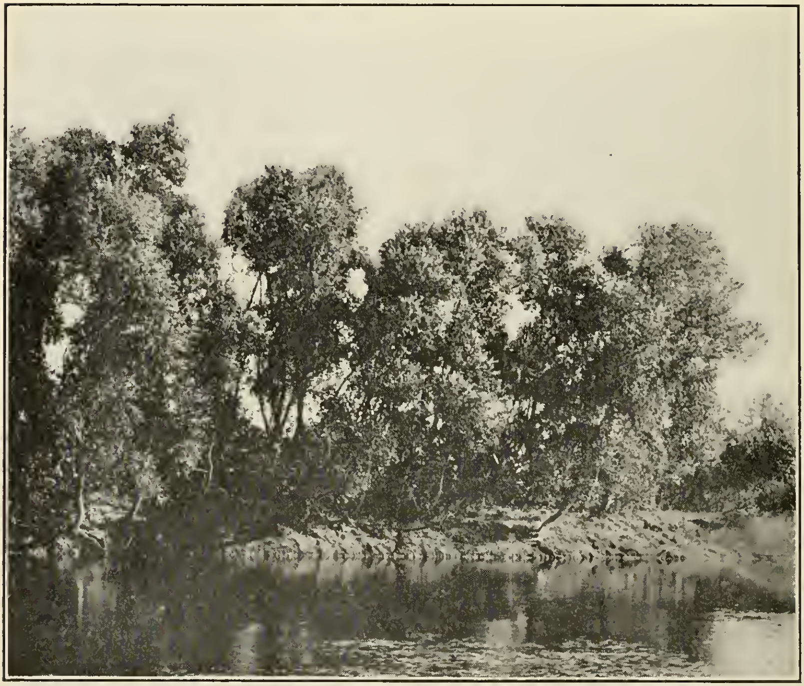

FIG. 9. Nearly pure growth of willow (*Salix nigra*) near southern extremity of flood plain island in Connecticut River, Windsor.

One of the first trees to establish itself on the flood plain is the black willow (*Salix nigra*). The willow is essentially a pioneer. Young flood plain forests (FIG. 9) may be composed almost wholly of this tree, while a zone of willow almost invariably fringes the shoreward margin of older forests. Closely following the willow, in fact often appearing simultaneously with it, are other trees, such as the sycamore (*Platanus occidentalis*) and the cottonwood (*Populus deltoides*), particularly the latter. As the surface of the ground continues to be built up higher, the soil becomes relatively drier and better aerated, so that conditions rapidly become less hydrophytic and more mesophytic. Under the changing conditions of soil and light, the willow gradually assumes a position of less and less importance, while the cottonwood comes to occupy a more and more prominent place in the rising forest (FIG. 10).

FIG. 10. Cottonwood forest with luxuriant herbaceous undergrowth (*Laportea*, etc.) on flood plain island at Windsor.

For while, like the willow, the cottonwood is relatively intolerant of shade, it grows more rapidly and to a much larger size, so that it tends to overtop and shade out the willow. Meanwhile other trees make their appearance. In addition to the species already enumerated, common trees on the Connecticut River flood plains are the elm (*Ulmus americana*), silver maple (*Acer saccharinum*), basswood (*Tilia americana*), white ash (*Fraxinus americana*) and red ash (*Fraxinus pennsylvanica*). Without exception, all of these last-named trees are more tolerant of shade than their predecessors. Springing up in the light shade which the cottonwood and willow produce, these more tolerant species become increasingly abundant until ultimately they dominate the forest. And while today the cottonwood and willow are perhaps the most conspicuous trees of the Connecticut River flood plains, there is little doubt that the forests which originally clothed the higher flood plains were made up largely of elm, silver maple, basswood, and ash.

A striking feature of the vegetation in flood plain forests is the wealth of lianas. Woody forms, such as *Rhus Toxicodendron*, *Vitis vulpina*, and *Psedera quinquefolia*, ascend the trunks of trees and hang in graceful festoons from the branches. A few herbaceous lianas also, notably *Sicyos angulatus* and *Echinocystis lobata*, clamber the trees, while numerous less vigorous species, *e.g.* *Polygonum scandens*, *Amphicarpa monoica*, *Convolvulus sepium*, *Solanum Dulcamara*, and *Clematis virginiana*, twine about or cling to any available support. The parasitic *Cuscuta obtusiflora* is a common form on the Windsor flood plain. Shrubs are usually few and scattered, about the only forms ordinarily present being *Cornus Amomum* and *Sambucus canadensis*.

The herbaceous undergrowth in such a forest is rank and luxuriant; some idea of its character is conveyed by FIG. 10. Tall, broad-, thin-leaved mesophytic plants predominate. The giant ragweed (*Ambrosia trifida*) commonly reaches a height of from ten to twelve feet, and the ostrich fern (*Onoclea Struthiopteris*), largest of the native ferns, a height of more than six feet. The nettles (*Laportea canadensis* and species of *Urtica*), growing more than waist-high, are uncomfortably abundant. Other characteristic herbaceous species worthy of mention are the following:

Asplenium Filix-femina
Onoclea sensibilis
Leersia virginica
Muhlenbergia mexicana
Cinna arundinacea
Bromus altissimus
Elymus canadensis
Pilea pumila
Boehmeria cylindrica
Thalictrum polygamum
Impatiens biflora
Viola cucullata
Circaea lutetiana
Verbena hastata
Eupatorium purpureum
Eupatorium urticaefolium
Solidago serotina
Aster paniculatus
Helenium autumnale

Flood Plain Associations along Other Streams.—The conditions described in the preceding paragraphs are found not only along the Connecticut, but also along the Housatonic and to a considerable extent along others of the larger rivers. But even along these rivers, there is a more or less noticeable variation in the aspect of flood plain associations, while along the smaller streams the departure from the described conditions may be very pronounced. On gravelly or stony flood plains, such as occur along swift streams, the pioneer forms of vegetation may be scraggly willows, alders

FIG. 11. Cat-tail (*Typha latifolia*) marsh along Muddy River, North Haven. In the background is a flood plain forest of elm, pin oak, etc.

and red-osier dogwood, along with which may grow a few herbaceous plants. Along many of the smaller streams throughout the state, during the building up of a flood plain, a sequence of plant associations is commonly encountered which is essentially similar to what has been described in an earlier paper* as characteristic of lakes and swamps. With the exception of the free-floating forms, any of the aquatic plants there mentioned may occur here. Of the species with aerial photosynthetic organs, the cat-tail (*Typha latifolia*) is especially conspicuous along many slow streams, frequently monopolizing wet, swampy tracts to the exclusion of practically everything else (FIG. 11). Marshes and meadows are quite as frequently developed along streams as along lake margins, and in general the aspect of the vegetation is similar in either case.† *Phalaris arundinacea* and *Leersia oryzoides*, however, might be mentioned as being more common in alluvial swamps than in other habitats. All of the shrubs and trees listed as characteristic of lake swamps are likewise found on flood plains along streams. Typical flood plain forests are best developed in areas which are subject to inundation only in spring. Here the soil relations are essentially those of a periodic swamp. Prominent trees in these forests along most streams are *Quercus bicolor* and *Quercus palustris*, species which are at least very infrequent in similar situations along the Connecticut. Except along the larger rivers, on the other hand, the cottonwood is practically absent and the silver maple is scarce. In addition to the two oaks already mentioned, the following trees are commonly represented in flood plain forests.

Carya cordifolia
Carpinus caroliniana
Ulmus americana
Liriodendron tulipifera
Acer rubrum
Tilia americana
Nyssa sylvatica
Platanus occidentalis

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* Bull. Torrey Club 42: 176–194. 1915.

† Regarding the vegetation of Connecticut meadows in general it should be remarked here that while in the case of many wet meadows there seems to be no doubt that the present vegetation represents the original type, this is probably not true of all present-day meadow-lands. There is reason to believe that most of the less wet areas now occupied by meadow associations were formerly forested, and that their present vegetation has been developed only as a result of human interference with the original conditions. See footnote on p. 254.

Fraxinus americana	*Fraxinus pennsylvanica*
Fraxinus nigra	

The Temporary Nature of Flood Plain Forests.—It has been shown in the preceding pages that during the development of a flood plain the vegetation becomes less hydrophytic and more mesophytic, culminating in the formation of a mesophytic forest. Such a forest is to be regarded as the climax association of flood plains. But it can easily be seen that, owing to the activity of the river, this forest may be relatively short lived; in other words, it may represent only a temporary climax. For as the river meanders about on its flood plain in serpentine curves, it is constantly wearing away its banks on the outer, concave side of each bend, while at the same time deposition is usually taking place on the opposite, convex shores. In this way "a river may swing quite across its flood plain, destroying all that it has built, including the mesophytic forest."* Changes of this sort take place with appreciable speed and may be observed along almost any depositing stream.

Ox-bow Ponds.—In this connection should also be mentioned the crescent-shaped curves, or ox-bows, which are a characteristic feature of old-age streams. Frequently the meandering river shifts its course, abandoning a loop-like channel for a more direct route. The loop then becomes an ox-bow pond (FIG. 1, D), and as such its vegetation can best be treated with that of ponds and swamps.†

The Subsequent History of Flood Plains.—One other phase of river activity may be briefly sketched. It has already been shown that while deposition is the main feature of old-age streams, erosion is not wholly absent. In the course of time, for various causes, downward cutting may be renewed, the flood plains become terraces, and new flood plains may ultimately be formed at lower levels. The resultant topography is well illustrated along the Connecticut and others of the larger streams. The low flood plains of today are comparatively recent in origin. The more ancient flood plains are represented by sandy terraces, of which

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* Cowles, H. C., 1901, *op. cit.*, p. 107.

† See Bull. Torrey Club 42: 171. 1915. *Fig. 1* of this paper pictures a typical ox-bow pond.

there may be one or more. These have attained their present condition through the downcutting of the rivers into the deep fill of glacial drift and outwash.* The effect of the changed topographic relations on these former flood plains as habitats for plants is readily comprehended. With the lowering of the river they must gradually have become more and more xerophytic and thus less and less tenable for the flood plain mesophytes. The actual effect of these changes on vegetation can only be conjectured. For, just as has been pointed out in the case of rock ravines, the period of time involved has been so great that oscillations in climate as well as changes in topography must presumably be taken into account. At the present day the vegetation of river and stream terraces is perhaps best treated with that of uplands, since the river has long since ceased to act as a dynamic factor in its development.

ACKNOWLEDGMENTS

For suggestions in connection with the preparation of this paper, the writer is greatly indebted to Professor Joseph Barrell, of the Geological Faculty, and Professor A. W. Evans, of the Botanical Faculty of Yale University, and to Mr. C. A. Weatherby, of East Hartford.

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* In this connection, see Rice, W. N., & Gregory, H. E., Manual of the Geology of Connecticut. Conn. State Geol. and Nat. Hist. Surv. Bull. 6: 35, 36. 1906.

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[From the BULLETIN OF THE TORREY BOTANICAL CLUB, 43: 365-383. 14 Aug 1916.]

Branched prothallia in the Polypodiaceae*

ELIZABETH D. WUIST

(WITH FIFTEEN TEXT FIGURES)

INTRODUCTION

Branching in the early stages of the gametophytes of the Polypodiaceae has received little attention in the literature. Branching in older prothallia by means of adventitious outgrowths arising from any part of the prothallium has been described for various genera by Wiegand ('49), Hofmeister ('51), Kny ('70), Goebel ('77), De Bary ('78), Bauke ('78), Dodel-Port ('80), Klebs ('93), Heim ('96), Lagerburg ('06), Pace ('10), Heilbronn ('10), Fischer ('11), Schlumberger ('11), Wuist ('13), Pickett ('14), and Black ('15). Few cases have been cited where branching took place at an early period in the development of the gametophyte, except in the case of *Vittaria* which has been described and figured by Britton and Taylor ('02). As it is characteristic of the prothallia of that genus to branch extensively, resembling in this respect the gametophytes of the Hymenophyllaceae, no examples will be cited. Among the other genera of the Polypodiaceae the following cases of branching, while the prothallia were still in the filamentous stage, have been noted. Beck ('80) described branched prothallia of *Scolopendrium vulgare* Sm., while Klebs ('93) by means of weak light obtained, in *Polypodium aureum* L., branched prothallia with adventitious outgrowths. Atkinson ('94) observed "in *Adiantum cuneatum* . . . some curious forms of starved prothallia," and added: "In one case, first noted by a student, the protonemal thread forked a short distance from the spore, and the branches extended at right angles to the primary thread like the arms of the letter T, each arm bearing a prothallium. In another case observed the young prothallium produced nearly colourless protonemal threads from marginal cells. Each of these threads bore a prothallium, and in turn produced marginal threads

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* Contribution from the Osborn Botanical Laboratory.

bearing other prothallia." Lagerburg ('06) figured a slightly branched filamentous male gametophyte of *Pteridium aquilinum* (L.) Kuhn. Pace ('10) described branched filamentous prothallia of an unknown genus, and Black ('15) observed extensive branching among the filamentous prothallia of *Onoclea sensibilis* L. which had grown in a submerged condition in cultures of distilled water.

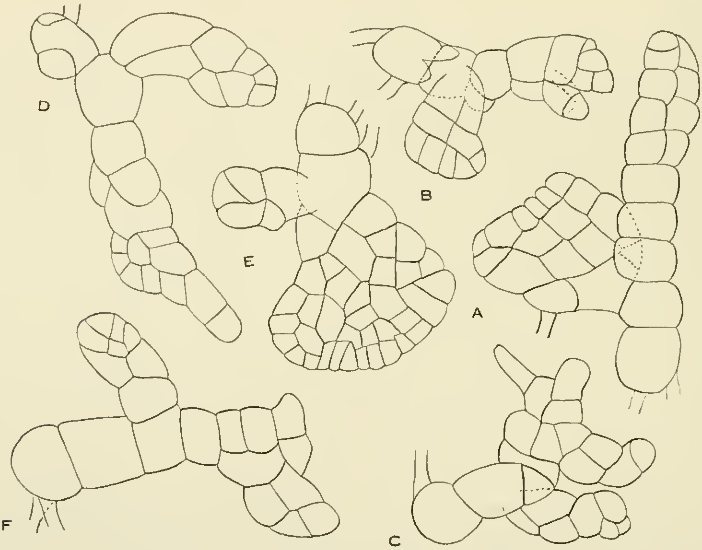

FIG. 1. Branched prothallia of *Onoclea sensibilis* L., × 125.

MATERIAL

The branched prothallia described in this paper occurred in cultures which had been made for the study of the comparative length of the filamentous stage in various genera of the Polypodiaceae. The genera which showed a tendency to branch were the following: *Adiantum*, *Asplenium*, *Camptosorus*, *Onoclea*, *Phegopteris*, *Polypodium*, *Pteridium*, *Scolopendrium*, *Woodsia* and *Woodwardia*. The spores of these various genera were obtained from several sources. Those of *Adiantum* were secured from the greenhouse of the botanical department, Cornell University, and those of *Phegopteris* came from a lawn in Ithaca, New York. The spores of *Camptosorus* and *Scolopendrium* were collected in eastern New York by Mr. Ten Eyck Burr; while those of *Asplenium*, *Onoclea*, *Pteridium* and *Woodsia* were obtained from the wild botanical gardens of Minneapolis, Minnesota, through the courtesy of Miss Eloise Butler. The spores of *Woodwardia* were collected near Ann Arbor, Michigan.

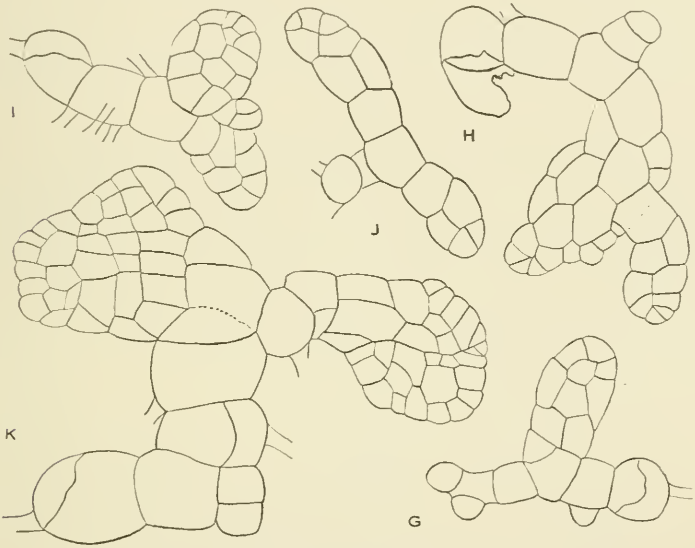

FIG. 2. Branched prothallia of *Onoclea sensibilis* L., × 125.

Cultures of these genera were made by sowing the spores on distilled water and on soil. A series of cultures of *Camptosorus*, *Phegopteris*, *Pteridium*, *Onoclea*, *Scolopendrium*, and *Woodwardia* were made by sowing the spores on Knop's and Prantl's full solutions and on certain modifications of these solutions.

The formulas used in making up Knop's and Prantl's ('81) nutrient solutions are as follows:

Knop's Solution	
$MgSO_4$	0.25 g.
$Ca(NO_3)_2$	1.00 g.
K_2HPO_4	0.25 g.
KCl	0.12 g.
$FeCl_3$	trace

Prantl's Solution	
K_2SO_4	0.7 g.
$NaCl$	0.23 g.
$CaSO_4$	0.7 g.
$MgSO_4$	0.5 g.
Na_3PO_4	0.5 g.
NH_4NO_3 solution, 0.064 per cent.	20 c.c.

The modifications employed were the following:

Knop's Solution	Prantl's Solution
(*a*) $Ca(NO_3)_2$ omitted	(*a*) NH_4NO_3 omitted
	(*b*) NaCl and Na_3PO_4 omitted
	(*c*) NaCl omitted
	(*d*) Na_3PO_4 omitted
	(*e*) $CaSO_4$ omitted

After the spores were sown, the cultures were placed before an east window where the conditions of light and temperature were approximately the same for all.

DESCRIPTION OF THE BRANCHED PROTHALLIA

In all the cases observed, the germination of the spores, the manner and the rate of growth in the branching prothallia did not differ from that of the unbranched prothallia. Neither were the branched prothallia limited to one kind of culture, but were found in all three kinds. In some of the genera they appeared simultaneously in the three kinds of cultures.

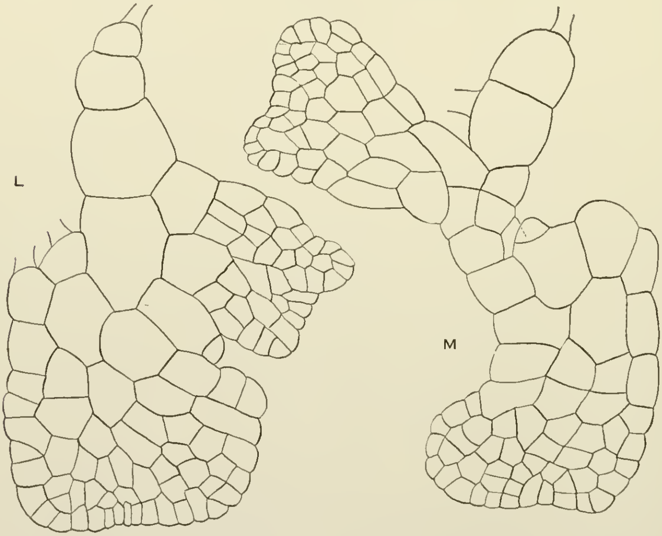

FIG. 3. Branched prothallia of *Onoclea sensibilis* L., × 75.

Onoclea sensibilis L.—The prothallia of this species both on the distilled water and the soil cultures showed a decided tendency to branch. Likewise, the branches showed a great diversity of origin and form, and the beginnings of apical cells or more advanced apical growth was present in all of them. The branched prothallia shown in FIGS. 1, A–F; 2, G–J; 4, N–Q; and 5, R–T, developed on the distilled water cultures, while those in FIGS. 2, K; 3, L, M; and 5, U, developed close to the inner pot wall on the soil cultures. FIG. 1, A, D, shows branched prothallia whose branches originated in the second cell of the filament. In these prothallia the branches tended to form immediately a plate of cells, while the cells of the filaments continued to divide transversely until three and five cells were formed before they developed an expanded region. In FIG. 1, B, C, while the first branches developed from the second cell of the filament, later branches were given off by the expanded portions of the prothallia. FIG. 1, D, shows not only the development of a branch from the second cell of the filament but also

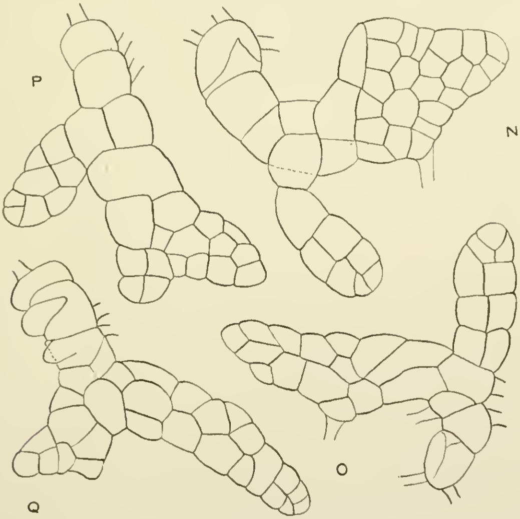

FIG. 4. Branched prothallia of *Onoclea sensibilis* L., × 125.

the tendency of the prothallium to revert to a filamentous stage after a small plate of cells has been formed, if the nutrition is not sufficient to meet its needs. In FIGS. 1, F; and 2, G, H, it seems characteristic for the first branch to originate in the third cell of the filament. However, other branches developed from the more expanded portion of the prothallia. FIG. 2, I, J, shows pronounced cases of dichotomous branching which occurred where the filament usually gave rise to the expanded portion of the prothallium. In both of these cases the branches originated in the third cell of the filament. In FIG. 2, J, the group of cells at the apex between the branches indicate that there will be a continuation of the main growth of the prothallium. In FIGS. 2, K, and 3, L, M, dichotomous branching developed at a slightly later stage after the first divisions of the expanded portion of the prothallia had been formed. FIG. 4, N–Q, show single lateral branches which appear to have originated at about the same period in the development of the prothallia as the dichotomous branches shown in FIGS. 2, K, and 3, L, M. FIG. 5, R, S, shows branches developed from the expanded portions of the prothallia. In FIG. 5, R, the branch formed a plate of cells while in FIG. 5, S, it tended to assume a filamentous character. FIG. 5, T, shows another case of dichotomous branching but at a later stage in the development of the prothallium. Here it occurred at the apex of the expanded region of the young prothallium. FIG. 5, U, is unique in that the branch appears to have originated in the first, second and third cells of the filament.

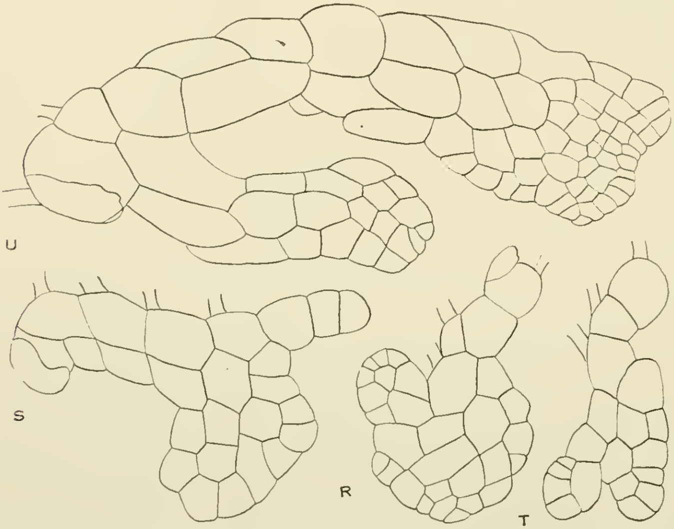

FIG. 5. Branched prothallia of *Onoclea sensibilis* L. R–T, × 125; U, × 75.

Adiantum bellum Moore.—Branched prothallia in the various species of *Adiantum* studied occurred only on the distilled water cultures. In FIG. 6, A, is shown the only case of branching which was observed *in A. bellum.* Here the filamentous branch originated in the first cell of the filament.

Adiantum Capillus-Veneris L.—Examples of branching among the prothallia of this species were frequently observed. In all cases the branching was monopodial and in the majority of cases, as shown in FIG. 6, B–G, the branches developed from the second cell of the filament. FIG. 6, C–E, shows the manner of development of the branch and likewise the continued growth of the main filament. In FIG. 6, F, no filament had been developed; the second cell divided to form the beginnings of the expanded portion of the prothallium. From this expanded region the branch was given off.

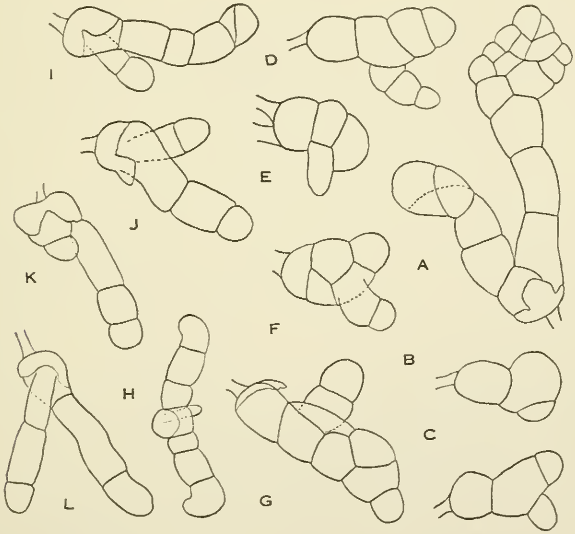

FIG. 6. A. Branched prothallium of *Adiantum bellum* Moore, × 175. B–G. Branched prothallia of *A. Capillus-Veneris* L., × 125. H. Branched prothallium of *A. cardiochloena* Kunze, × 125. I–L. Branched prothallia of *A. cuneatum* Langsd. & Fisch., × 125.

Adiantum cardiochloena Kunze.—FIG. 6, H. Here the branch developed from the cell which was cut off by the formation of a vertical wall in the second cell of the filament.

Adiantum cuneatum Langsd. & Fisch.—FIG. 6, I–L. Branching in this species occurred at an early stage in the development of the prothallia. The branches originated in the first cell of the filament and the growth in all cases was very rapid. In FIG. 6, L, is shown a prothallium with a branch as long as the main filament.

Adiantum trapeziforme L.—FIG. 7, A–G, represents branched prothallia of this species. Here branching was both dichotomous and monopodial. In FIG. 7, E, is shown an unusual case of dichotomous branching where both branches tended to grow in the same direction.

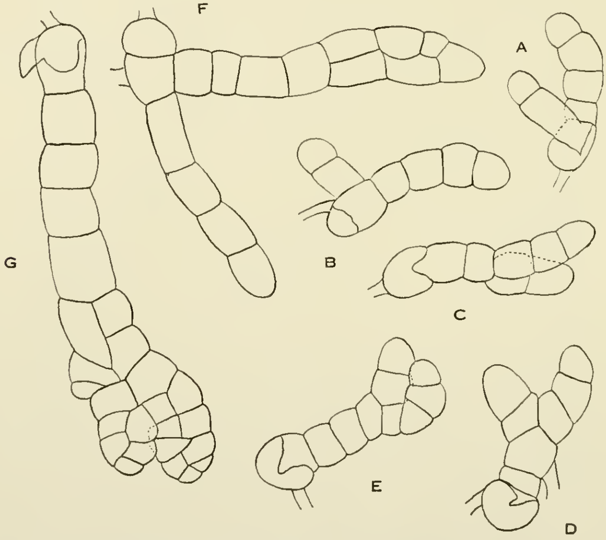

FIG. 7. Branched prothallia of *A. trapeziforme* L., × 125.

Camptosorus rhizophyllus (L.) Link.—FIG. 8, A–D, shows branched prothallia of this species which developed on the distilled water cultures, while FIG. 8, E, shows a prothallium which developed on the inner surface of the pot wall of the soil cultures. FIG. 8, A–D, shows the beginnings of branching in very young prothallia. Branching in two of the cases was dichotomous and in the other two cases monopodial. A few days after the spores were sown on the distilled water, germination took place in the normal manner. In FIG. 8, A, the first prothallial cell instead of dividing by a transverse wall to form a filament of two cells, cut off by two oblique longitudinal walls, a branch cell on either side. FIG. 8, B, C, shows similar cases, however in FIG. 8, B, the second instead of the first prothallial gave rise to the branches. In FIG. 8, C, both the second and third cell each gave rise to a branch while the third cell of the filament continued the growth of the prothallium. In FIG. 8, D, the branch cell which developed from the first prothallial cell divided immediately to form the beginning of a plate of cells. The branched prothallium shown in FIG. 8, E, is in a much more

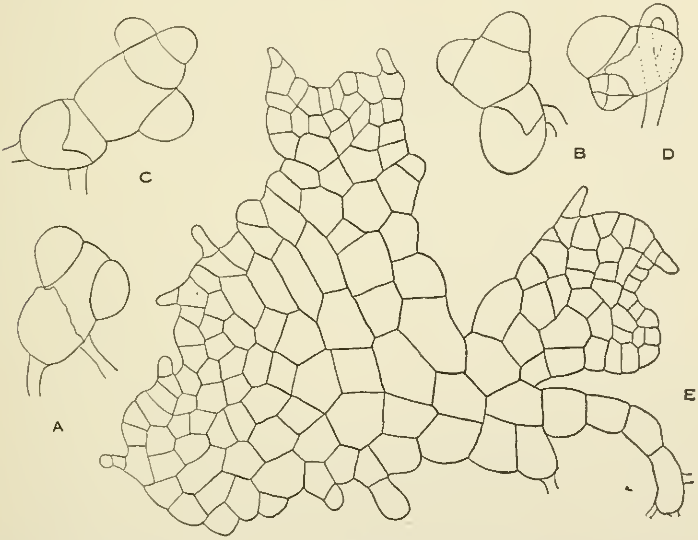

FIG. 8. Branched prothallia of *Camptosorus rhizophyllus* L. A–D, × 125; E, × 75.

advanced stage of development. Here a filament of four cells was formed, then a plate of cells developed. From this plate, early in its development, a lateral branch was cut off which in turn formed an expanded prothallium. The original plate of cells continued its growth into a broad prothallium which showed a decided tendency to branch at its apex.

Asplenium Filix-femina (L.) Bernh.—The branched prothallia of *A. Filix-femina* were observed on both the soil and distilled water cultures. FIG. 9, A, B, developed on the distilled water cultures and FIG. 9, C, on the inner surface of the pot wall where the light conditions were good and the prothallium was not crowded by other prothallia. FIG. 9, A, shows a young branched prothallium of about twenty cells, which had formed a filament of three cells in the usual manner before the expanded portion of the prothallium developed. The second cell of this filament gave rise to a filamentous branch of three cells; the terminal one of which divided by two oblique longitudinal walls to form the beginnings of an apical cell. From the first cell of the branch was cut off laterally a cell which would later develop into another branch. The expanded portion of the prothallium also gave rise to a short filamentous branch of two cells.

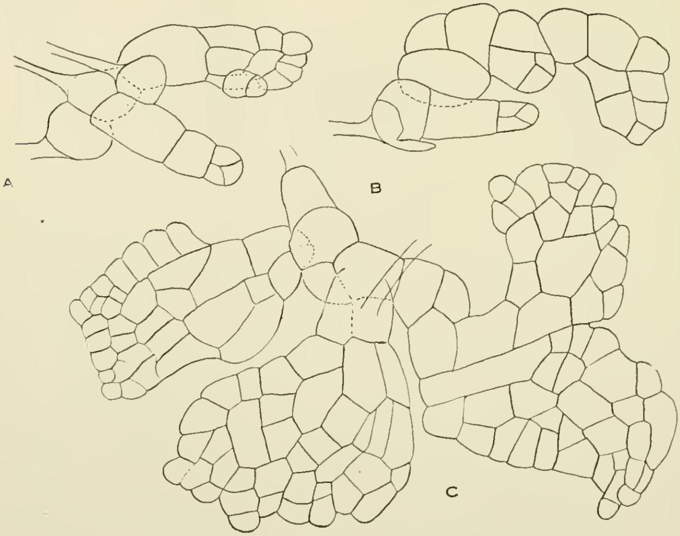

FIG. 9. Branched prothallia of *Asplenium Filix-femina* (L.) Bernh., × 75.

In FIG. 9, B, a short filament of three cells was first formed by transverse divisions, then the third cell divided in such a manner as to form the beginnings of an apical cell. In the meantime a cell was cut off laterally from the first cell of the filament. By transverse and longitudinal divisions this branch developed becoming two cells in width and forming at the apex the beginnings of an apical cell. An extreme case of branching is shown in FIG. 9, C. A filament of three cells formed in the usual manner. From the second cell there was cut off laterally a cell which developed immediately by longitudinal and transverse divisions into an expanded branch with a definite growing region at the apex. The third cell of the original filament divided by a longitudinal division into two cells, a larger and a smaller one. From the larger of these two cells a branch developed which formed another expanded prothallium whose growing point was not definitely marked. In the meantime the growth of the primary prothallium had continued and an expanded part was formed showing a decided tendency to branch dichotomously at the apex.

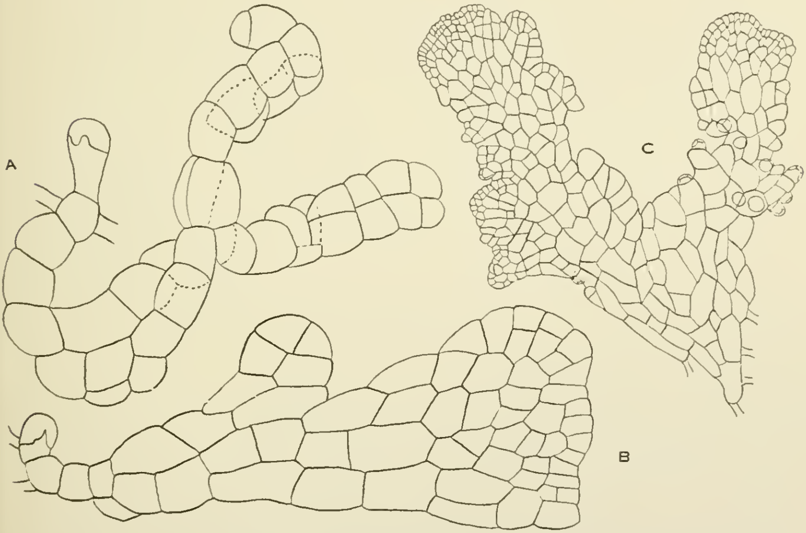

FIG. 10. A, B. Branched prothallia of *Asplenium bulbiferum* Forst., × 75. C. Branched prothallium of *Asplenium platyneuron* (L.) Oakes, × 75.

Asplenium platyneuron (L.) Oakes.—FIG. 10, C, shows a prothallium of this species which developed in a crowded region on a soil culture. In this case branching occurred at a later period in the development of the prothallia. No filament was formed in the early development of the prothallium, but the second cell by division gave rise immediately to the beginnings of an expanded cell plate which during development branched dichotomously. Each branch in turn formed a distinct growing region at its apex.

Asplenium bulbiferum Forst.—The two examples of branched prothallia which are shown in FIG. 10, A, B, developed on the distilled water culture. In both cases the branches originated after the expanded portion of the prothallia had been formed. In FIG. 10, A, the branching was dichotomous. This example is especially interesting as showing the tendency of the prothallium to revert to a filamentous condition at the time of the formation of the filamentous branch. In FIG. 10, B, branching was monopodial and the branch tended to form immediately a plate of cells.

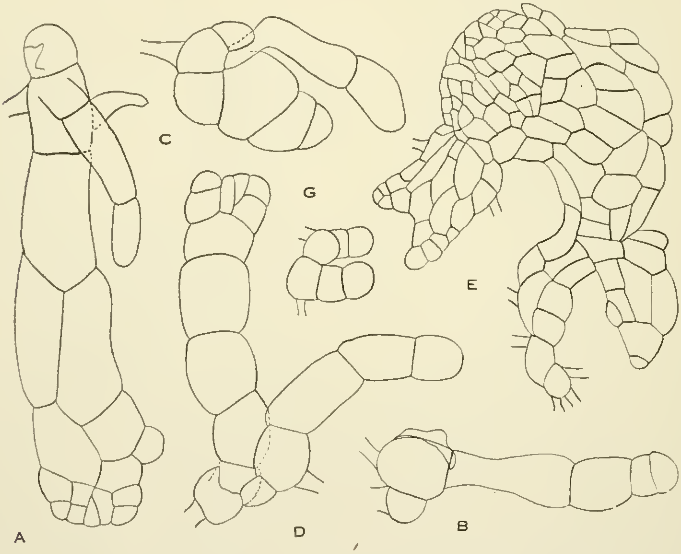

FIG. 11. A–E. Branched prothallia of *Phegopteris polypodioides* Fée, × 125. G. Branched prothallium of *Polypodium aureum* L., × 125.

Phegopteris polypodioides Fée.—The branched prothallium which is shown in FIG. 11, A, occurred in an uncrowded region of the soil culture while those shown in FIGS. 11, B–E, and 12, F, developed in modified Prantl's solutions. FIG. 11, B–D, was found in the Prantl's solution with K_2SO_4 omitted, while FIGS. 11, E, and 12, E, occurred in Prantl's solution from which $CaSO_4$ had been omitted. In all cases observed the branching was monopodial. In FIG. 11, A, the branch was filamentous in form and originated in the second cell of the filament. FIG. 11, B, shows the origin of the branch from the first cell of the filament and FIG. 11, D, shows the further development of this branch into a filament of five cells. In FIG. 11, C, is shown an interesting example of branching. Here the first prothallial cell instead of dividing by a transverse wall into two cells, divided by means of a longitudinal wall, thus forming two cells side by side. One of these cells by growth and transverse division continued the growth of the filament while the other gave rise to two branches. One formed a filament of two cells, the first of which was extremely long. In FIGS. 11, E, and 12, the branches were not formed until the expanded portion of the prothallia had begun to develop. In FIG. 12, the expanded portion later showed a decided tendency to branch monopodially at its apex.

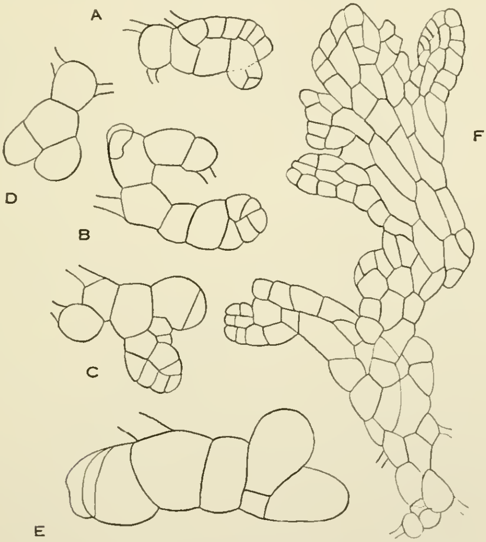

FIG. 12. A–E. Branched prothallia of *Woodsia obtusa* (Spreng.) Torr., × 125. F. Branched prothallium of *Phegopteris polypodioides* Fée, × 75.

Polypodium aureum L.—Only one case of branching was observed in this species and it developed on the distilled water culture. As shown in FIG. 11, G, the branch originated in the first prothallial cell. The rate of growth was the same for both the main filament and the branch.

Woodsia obtusa (Spreng.) Torr.—All the cases of branched prothallia of *Woodsia obtusa* were observed on distilled water cultures; in two cases branching was dichotomous while in the other three cases it was monopodial. FIG. 12, B, shows the branch originated from the first cell of the filament. In FIG. 12, A, the branch originated from the slightly developed cell plate. FIG. 12, C, D, shows different stages in the development of the dichotomous branches. FIG. 12, E, was an interesting case of branching. Here the wall which cuts off the branch from the main filament did not form at the usual place, but formed almost in the center of the filament cell which gave rise to the branch.

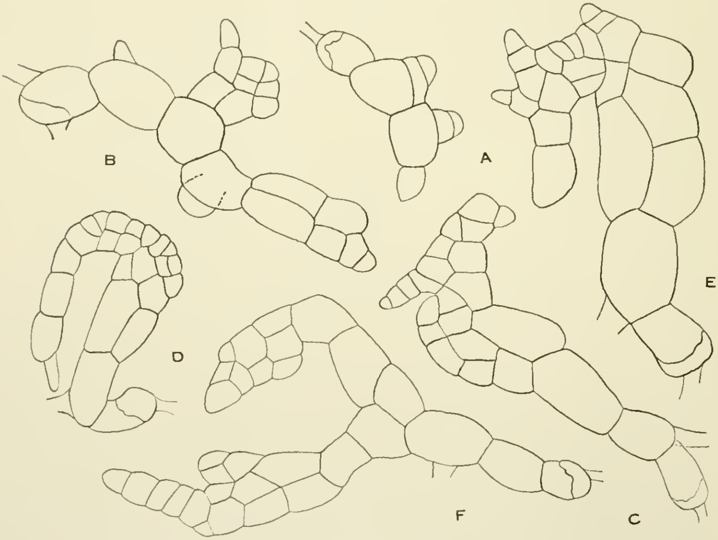

FIG. 13. Branched prothallia of *Scolopendrium vulgare* Sm., × 125.

Scolopendrium vulgare Sm.—All cases of branching in this genus were observed on Prantl's solution with $CaSO_4$ omitted. FIG. 13, A–E, shows typical examples of the types of branching found in these cultures. FIG. 13, A, is interesting as showing the tendency of both the second and third cells of the filament to form monopodial branches with very short cells. In FIG. 13, B, the branch which originated from the third cell of the filament formed immediately a plate of cells which in turn showed a tendency to branch at one side of the apex. FIG. 13, C, shows the origin of a branch from the apex of the expanded portion of the prothallium, while FIG. 13, D, E, shows further development of such a branch. These branches formed a small plate of cells, two rows in width, then tended to revert to a filamentous condition, at the same time growing downward, thus giving the appearance of two young prothallia attached by their apexes. FIG. 13, F, shows the only case of dichotomous branching which was observed. One of the branches reverted from a plate of cells to a filament four cells in length.

Woodwardia virginica (L.) Sm.—The branched prothallia of *Woodwardia virginica* varied in size and shape and showed a decided tendency to branch dichotomously. Those shown in FIG. 14, A–D, and 15, E, F, developed on the inner surface of the pot wall of the soil culture. They were not crowded by other prothallia and were well lighted. FIG. 15, G, developed on Prantl's nutrient solution with $CaSO_4$ omitted. In FIG. 14, A, B, branching took place from the first and second cells of the filament. In FIG. 14, C, D, and 15, G, branching took place after the plate of

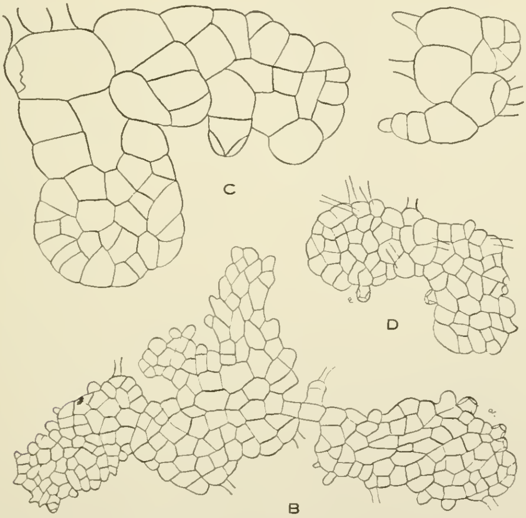

FIG. 14. Branched prothallia of *Woodwardia virginica* (L.) Sm. A, D, × 125; B, C, × 75.

cells had begun to develop, while in FIG. 15, E, F, branching occurred much later in the development of the prothallia.

Pteridium aquilinum (L.) Kuhn.—The only example of branching observed in this species was on Prantl's full solution (FIG. 15, H). Here the branch developed from the second cell of the filament and seemed to show a more vigorous growth than the main filament. The branch formed a short filament of two cells, then developed the beginnings of an expanded region while the main filament developed three cells of irregular length before cutting off the beginnings of an apical cell. This slowness in growth and the irregularity of length of the cells of the filament would seem to indicate a poorly nourished condition of the main filament.

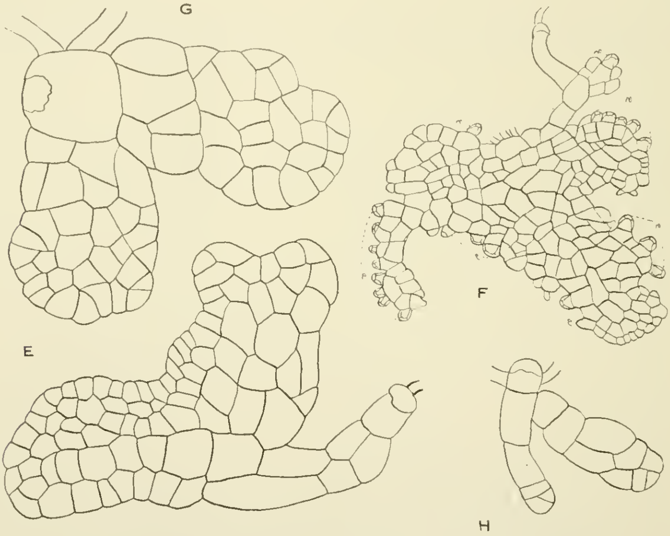

FIG. 15. E–G. Branched prothallia of *Woodwardia virginica* (L.) Sm., × 75; *a*, antheridia. H. Branched prothallium of *Pteridium aquilinum* (L.) Kuhn, × 125.

DISCUSSION

A comparison of the previously described branched prothallia with those found by other writers would seem to indicate that whatever factor, or set of factors, working separately or together, may have been the determining ones, the development of branches was associated with conditions of the environment. In Klebs's experiment weak light seemed to have been the cause of branching. Light may be the determining factor in branching where the prothallia are crowded and therefore shaded by other prothallia, but it can not be considered the determining factor in all the cases described in this paper, for the majority of these branched prothallia occurred in uncrowded regions of the cultures under good light conditions. However, all the branched prothallia except one developed on cultures of distilled water or nutrient solutions, from which some chemical element had been omitted; while all but two of the branched prothallia on the soil cultures were found on the inner surface of the pot wall. This is especially interesting as indicating that other factors than light entered into the problem. Atkinson designates the branched prothallia of *Adiantum* as "starved prothallia," which would seem to indicate that they had developed under poor nutritive conditions. Miss Black suggested the possibility of a lack of oxygen as the determining factor in the production of the branched prothallia in her cultures. This explanation would not hold good for the present cases, as all three cultures, distilled water, soil, and nutrient solution, were covered with loosely fitting glass plates and, since the prothallia were not submerged in the nutrient solution or distilled water they received a sufficient supply of oxygen.

As branching was not observed in the nutrient solution cultures, where all the chemical elements necessary for growth were present in sufficient quantities to meet the needs of the prothallia; as few cases of branching were observed among the prothallia of the soil cultures, in positions which appeared favorable for nutrition, it would seem as if there was an intimate connection between nutrition and branching, that poor nutritive conditions accelerated the stimulus of branching, and that good nutritive conditions weakened the stimulus. However, it is impossible to say just what factor of nutrition was the determining one; for even by cultivating prothallia on nutrient solutions whose chemical formula are known, we do not know the physiological effect from the chemical reactions due to the presence or absence of various chemical elements.

SUMMARY

1. Branched prothallia occurred in cultures of *Adiantum bellum*, *A. Capillus-Veneris*, *A. cardiochlaena*, *A. cuneatum*, *A. trapeziforme*, *Asplenium bulbiferum*, *A. Filix-femina*, *A. platyneuron*, *Camptosorus rhizophyllis*, *Onoclea sensibilis*, *Phegopteris polypodioides*, *Pteridium aquilinum*, *Scolopendrium vulgare*, *Woodsia obtusa*, and *Woodwardia virginica*.

2. Branched prothallia were not confined to one type of culture medium, but developed on distilled water, on soil and on nutrient solutions.

3. Branches were not developed at any definite period in the life history of the prothallia, but were formed: (*a*) by any cell of the filament; (*b*) by divisions of the last cell of the filament; (*c*) from the margin and apex of the expanded portion of the prothallium.

4. Branching was both dichotomous and monopodial.

5. A definite relation seemed to exist between branching and nutrition.

In conclusion I wish to express my thanks to Professor Alexander W. Evans of Yale University and to Dr. C. H. Kauffman of the University of Michigan, to both of whom I am indebted for valuable suggestions in the preparation of this paper.

YALE UNIVERSITY

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YALE UNIVERSITY
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NOTES ON NORTH AMERICAN HEPATICAE. VII*

ALEXANDER W. EVANS

(WITH PLATE II)

Of the ten species noted in the present paper five represent additions to the flora of North America, north of Mexico. Four of these additions, including a species of *Cololejeunea* proposed as new, were found in Florida; the fifth was found in Wisconsin and British Columbia. Two other species which are included have recently been reported as American by other writers. Of the three remaining species one is introduced for nomenclatorial reasons and the other two to record extensions of range.

1. PLAGIOCHASMA INTERMEDIUM Lindenb. & Gottsche. *Aitonia japonica* Steph. Bull. Herb. Boissier **5**: 54. 1897. *Plagiochasma japonicum* Massal. Mem. Accad. Verona **73**: 47. 1897.

In the writer's recent revision of the North American species of *Plagiochasma*,[1] specimens from Japan are listed under *P. intermedium*, and the identity of *P. japonicum* with the North American species is claimed. Through an unfortunate oversight, however, the Asiatic species was not formally listed among the synonyms of *P. intermedium*. It is not possible to record any additional stations for the species at the present time.

2. PLAGIOCHASMA WRIGHTII Sulliv.

Collected in March, 1915, in the Arbuckle Mountains, near Davis, Oklahoma, on dry travertine formations, by W. H. Emig (No. 1030). A noteworthy extension of range. Formerly known from one station in Texas, one in Arizona, and four in Mexico.[2]

3. BUCEGIA ROMANICA Radian, Bull. Herb. Inst. Bot. Bucarest 3-4. 1903.

The discovery of this remarkable liverwort by A. H. Brinkman was announced by Miss Haynes[3] over a year ago. His specimens were collected in the following localities, altitudes 7200-8800 feet: Willock Mountain and Mt. Bosworth, near Stephen, Alberta, July, 1913 (Nos. 792 and 822); Long Lake, south of Pharaoh, Alberta, August, 1915 (No. 983); Cathedral Mountain, Hector, British Columbia, July, 1913 (Nos. 810, 811 and 812). They are unfortunately

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* Contribution from the Osborn Botanical Laboratory.

[1] Bull. Torrey Club **42**: 259-308. f. *1-8*. 1915.

[2] See Evans, *l. c.* 295. 1915.

[3] BRYOLOGIST **18**: 93, 94. *f. 1*. 1915.

sterile, but the structure of the thallus, which is figured by Miss Haynes, is so distinctive that there can be little doubt about the correctness of the determination. The genus *Bucegia* is monotypic. The type material was collected by its author, Simeon St. Radian, in the Bucegi Mountains of Rumania, in 1899. Specimens from the same mountains, collected by K. Loitlesberger in 1897, are likewise noted in the original account. The genus is accepted without question by K. Müller,[1] who adds a number of interesting details and figures the structural features of the thallus. He was unable, however, to cite any additional localities. In the following year Schiffner[2] recorded *B. romanica* from five stations in the Tatra Mountains of Austria, as well as from the two Rumanian localities. He likewise gave an exhaustive account of the plant and brought out in his figures the morphological characteristics of the male and female receptacles. A few years later he[3] reported additional stations in the Tatra Mountains and stated that he knew the plant from ten stations in all in that portion of Austria. Apparently no other European localities are known, and the report of the species from British Columbia and Alberta is therefore of unusual interest.

The genus *Bucegia* is a representative of the higher Marchantiaceae, the so-called Compositae of Leitgeb. It agrees with *Marchantia* and *Preissia* in having compound or dolioform epidermal pores in the vegetative thallus. The inner opening of the pore approximates the cruciate condition found in *Preissia* and certain species of *Marchantia* (for example, *M. paleacea* Bertol.)[3] In other words the cells bounding the opening approach one another very closely and leave a narrow four-rayed space, which may be partially or wholly closed by an increase in the turgidity of the cells. Although the pores are essentially the same as in *Marchantia* and *Preissia* the air-chambers and photosynthetic tissue are very different. Instead of being in a single layer the air-chambers are often in two or more layers; while the photosynthetic tissue, instead of being in the form of upright rows of cells, is represented by the walls a single cell thick separating the air-chambers from one another. The type of air-chambers found in *Bucegia* does not recur in any of the other Compositae but is found in *Reboulia*, *Asterella* and other genera belonging to the group Operculatae of Leitgeb. Here, however, it is always associated with simple epidermal pores.

The compact tissue below the air-chambers shows none of the sclerotic cells which form so distinct a feature in *Preissia* and in many of the species of *Marchantia*. It even lacks oil-bodies and is composed of thin-walled parenchyma throughout. The ventral scales are in two rows, differing in this respect from *Marchantia* but agreeing with *Preissia* and the other Compositae. The scales have the usual semicircular or broadly lunulate form and each one bears a single lanceolate appendage. Both rhizoid-initials and cells containing oil-bodies are absent.

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[1] Rabenhorst's Kryptogamen-Flora **6**: 295–298. *f. 180, 181.* 1907.

[2] Beih. Bot. Centralbl. **23²**: 273–290. *f. 1–24.* 1908.

[3] Magyar Bot. Lapok **10**: 280. 1911.

[4] For a description of the morphological features of *Marchantia*, see Evans, Trans. Conn. Acad. **21**: 208–228. 1917.

For full accounts of the receptacles reference may be made to the published descriptions and especially to the work of Schiffner. It is sufficient to state here that the male receptacle is stalked as in *Preissia* and *Marchantia*, that the disc of the female receptacle is bluntly lobed, that the groups of archegonia (each enclosed by a membranous involucre) lie beneath the lobes, and that each sporophyte is enclosed within a pseudoperianth. Here again *Bucegia* resembles *Preissia* closely and also agrees with such species of *Marchantia* as the Asiatic *M. geminata* R. Bl. & N. and its allies. The photosynthetic tissue of both receptacles is, however, essentially the same as in the vegetative thallus and therefore differs markedly from the branched rows of cells found in both *Preissia* and *Marchantia*.

4. FOSSOMBRONIA LAMELLATA Steph. Hedwigia **33**: 9. 1894. *F. tuberifera* Goebel, Organographie der Pflanzen 292. *f. 190, 191.* 1898. [FIGS. 1–4.]

Collected in December, 1915, May, 1916, and January, 1917, at Sanford, Florida, by S. Rapp (No. 80). New to North America. The species is characterized by the possession of numerous tubers, some of which are highly differentiated while others are more rudimentary. The material collected in 1917 shows mature capsules.

Apparently Ruge, in 1893, was the first to describe tubers in the genus *Fossombronia*.[1] His material, which he does not attempt to name, was collected by Goebel at Tovar, Venezuela. He states that the stem of a tuberiferous plant turns downward instead of upward and becomes swollen at the apex, the enlarged portion, or tuber, being filled with stored food, some of which is in the form of starch. One of his figures shows the change in the direction of growth, but no sign of a tuber, although the leaves exhibit a characteristic reduction in size.

The following year Stephani described *F. lamellata* from Argentine specimens in the Otto Kuntze herbarium, collected by R. Hauthal at Buenos Aires, no other material being cited. He makes no mention of tubers but gives an account of the vegetative structure and capsules and doubtfully assigns a monoicous inflorescence to the species.

A few years afterwards, in 1898, Goebel published his *F. tuberifera*, giving a general account of the plant and two interesting figures in which the characteristic tubers are brought out. One figure (*f. 190*) shows a short plant with archegonia, which has grown out from the tip of an old tuber; the stem, without branching, turns abruptly downward and swells distinctly at the apex into a new spherical tuber. The other figure (*f. 191*) shows a plant which bears a sporophyte, while the apex of the stem is beginning to show the characteristic modification into a tuber. Goebel's material of *F. tuberifera* came from Peldegue, Chile, and he doubtfully assigned to the same species the *Fossombronia* from Venezuela which Ruge had already discussed.

In 1900 Stephani[2] published a new description of his *F. lamellata* and cited *F. tuberifera* definitely as a synonym. In addition to Hauthal's specimens he

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[1] Flora **77**: 305, 306. *pl. 4, f. 6; text f. 14.* 1893.

[1] Mém. Herb. Boissier **16**: 30. 1900.

listed Goebel's Venezuelar material but made no mention of the Chilean type of *F. tuberifera*. This time he described the tuberous and leafless apices of the stem and stated definitely that the inflorescence was dioicous.

It will be seen that *F. lamellata*, according to the published records, has a wide distribution in South America, being known from Argentina and probably from Venezuela and Chile as well. Mr. Rapp's specimens seem to be constantly dioicous, and the spores agree closely with Stephani's description. It seems safe, therefore, to refer the plants to *F. lamellata*, and the discovery of this species in Florida marks an interesting extension of range to the northward. The spores measure 36–44μ in diameter and the spherical surface is covered over with a fine reticulum, the meshes measuring 8–9μ across. In most cases the reticulum is regular, but sometimes the low ridges of which it is formed leave an occasional mesh incomplete. The elaters are about 8μ wide and show two distinct spirals. It will be seen from this description that the spores and elaters are much like those of the more northern *F. foveolata* Lindb. This species differs, however, in its annual habit, lack of tubers and monoicous inflorescence. In *F. salina* Lindb., a common Florida species, the spores are likewise reticulated, but the meshes are coarser and are often incompletely formed. This species is likewise monoicous and lacks tubers, although it agrees with *F. lamellata* in being perennial.

One of the largest of the Florida specimens is shown in FIG. 1. After bearing a series of leaves and a small cluster of archegonia, one of the branches abruptly turned downward, ceased forming leaves, and became swollen into a spherical tuber densely covered with rhizoids. The other branch, only the base of which is shown, behaved similarly. In addition to these terminal tubers the plant bore a number of smaller oval or clavate tubers on the tips of leafless and short adventitious branches arising from the ventral surface. These tubers lacked rhizoids completely although some of them showed indications of very rudimentary leaves.

A much simpler condition is shown in FIG. 2. In this case a tuber gave rise to a leafy shoot from the apex, and this shoot, without branching, developed a new apical tuber. The leaves produced were all irregular and rudimentary, there were no sexual organs, and the new tuber was destitute of rhizoids; on its surface it bore a series of projecting cells or groups of cells, but these were irregularly arranged and could hardly be interpreted as leaves. The plant here figured behaved in much the same way as the one shown in Goebel's *f. 190*, except that the latter developed archegonia and much larger leaves.

Conditions approximating those shown by Ruge are represented in FIGS. 3 and 4, although a change in the direction of growth is scarcely or not at all apparent. The plants here figured showed a gradual decrease in the size of the leaves, accompanied by a marked irregularity in their form, while the apices of the stem were leafless or nearly so without being tuberous. In FIG. 3 a single antheridium with a small subtending scale is shown.

In some of Mr. Rapp's specimens the tuberiferous shoots are much more elongated than any of those figured, but the more important variations have been shown. Most of the rhizoids, as is usual in *Fossombronia*, are deep vinous purple. They are represented in Fig. 2 and on the terminal tuber in Fig. 1. The small tubers in Fig. 1 were practically free from rhizoids, and the same thing was true of the two shoots shown in Figs. 3 and 4 and of the long leafless portion of the shoot in Fig. 1. In the leafy portion of this shoot, however, rhizoids were present in abundance, although omitted from the drawing.

In connection with *F. lamellata* it should be remembered that tubers have been described in the case of the Californian *F. longiseta* Aust. In his description of this species Howe,[1] in 1899, stated that the stems were "commonly somewhat tuberously thickened at the apex and perennial through the resumption of apical growth on termination of the dry season." Humphrey,[2] several years later, treated the matter at greater length and figured "an example of tubercular thickening of stem," which bears a striking resemblance to some of the small tubers shown in Fig. 1. He found that fungal hyphae were present in the tubers and thought at first that the fungus might bear a causative relation to them. He afterwards found, however, that plants which were kept moist produced no tubers, although fungi were still present, and he decided that the tubers were adaptive and largely dependent upon external factors for their development.[3] *F. longiseta* seems to be amply distinct from *F. lamellata:* the spores are strikingly different, and the tubers seem to be less abundant and less highly differentiated.

5. **Jungermannia Schiffneri** (Loitles.) comb. nov. *Aplozia Schiffneri* Loitles. Verhandl. der k.k. zool.-botan. Gesellsch. in Wien **55**: 482. 1905.

Collected in April, 1915, at Manitou Falls, Black River, Douglas County, Wisconsin, by G. H. Conklin (No. 1255); also in July, 1913, at Hector and Stephen, British Columbia, by A. H. Brinkman (Nos. 806, 823). New to North America.

The type material of this interesting species was found by C. Loitlesberger in the vicinity of Görz, Austria. Its occurrence in Switzerland and Tirol was soon reported by Schiffner,[4] who described a number of structural details not brought out in the original account and added a series of figures. It has since been recorded and figured from Scotland by Macvicar.[5] The illustrated description of Müller[6] may likewise be consulted.

The section or subgenus *Luridae*, to which *J. Schiffneri* belongs, is characterized by a dark green color, often masked by a brownish or purplish pigmentation; by ovate to cordate leaves; by thin-walled leaf-cells, with or without trigones; and by an ovate to clavate perianth, plicate at the mouth but not contracted into a beak. Four other species of this section are known from both Europe and North America, namely: *J. cordifolia* Hook., *J. riparia* Tayl., *J. atrovirens* Schleich., and *J. pumila* With. The first three of these are dioicous and thus

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[1] Mem. Torrey Club **7**: 80. 1899.

[2] Ann. Bot. **20**: 86. *text f. 3.* 1906.

[3] Proc. Washington Acad. **10**: 6. 1908.

[4] Hedwigia **48**: 184–187. *f. 1–13.* 1909.

[5] Student's Handb. Brit. Hep. 147. 1912.

[6] Rabenhorst's Kryptogamen-Flora **6**: 570. *f. 285.* 1909.

differ from *J. Schiffneri* and *J. pumila*, both of which are characterized by a paroicous inflorescence.

If the dioicous species are left out of consideration and the two paroicous species compared, it will be found that the latter are very closely related. The size, habit, and color are much the same in both, and there are no essential differences in the shape of the leaves, in the size of the leaf-cells, in the walls of the cells, or in the perichaetial and perigonial bracts. The perianths and the valves of the capsule, however, yield important differences. In *J. Schiffneri* the perianth contracts abruptly in the upper part, the broadest part being above the middle; in *J. pumila* the perianth is gradually contracted toward the mouth, the broadest part being usually at or below the middle. In *J. Schiffneri* the cells in the outer layer of the valves have the thickenings in their radial walls arranged in such a way that every alternate wall is nearly or quite free from thickenings; in *J. pumila* the thickenings are present in equal abundance in all the walls. The walls of the inner layer, moreover, are about half as large in *J. Schiffneri* as in *J. pumila* and the spores are considerably smaller (about 15μ and 21μ, respectively). These differences are clearly brought out in the published descriptions.

A third paroicous species of the *Luridae* was recently described by Schiffner under the name *Aplozia rivularis* Schiffn.[1] He had already called attention to the plant under the name *A. pumila* var. *rivularis* Schiffn.,[2] and it is described under this name by Müller.[3] The species is now known from Bohemia, the Harz Mountains and Saxony, specimens from the last region having been distributed by Schiffner in his Hep. Europ. Exsic. No. 402. Since *A. rivularis* is probably to be expected in North America a few words about its characteristics are perhaps in place. It agrees closely with *J. pumila* but is much larger and has larger leaf-cells (40 x 20μ in the middle of the leaf, instead of 25 x 18μ). It differs also in its large cylindrical or clavate perianths, in the narrower cells of the inner layer of its capsular valves, and in its slightly smaller spores (about 16μ in diameter). *A. rivularis*, as its name implies, grows on stones in streams.

6. Cephalozia Loitlesbergeri Schiffn. Oesterr. Bot. Zeitschr. **62:** 9. 1912; K. Müller, Rabenhorst's Kryptogamen-Flora **6**^{2}**:** 45. *f. 12.* 1912.

Collected in 1915, at Barrasois, Cape Breton, Nova Scotia, by G. E. Nichols (No. 1243 b); already reported by its collector.[4] The type material of this distinct species was found near the Ladachsee in the vicinity of Gmunden, Austria, by C. Loitlesberger. Müller was able to add several new stations from Baden, Styria and Switzerland, and Schiffner soon afterwards reported the plant from Bavaria[5] and Sweden.[6] For the British Isles Macvicar[7] doubtfully recorded the species from Lancashire, the specimens which he cites having poorly developed

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[1] Lotos **59:** 2. 1911.

[2] *l. c.* **48:** [5]. 1900.

[3] Rabenhorst's Kryptogamen-Flora **6:** 568. 1909.

[4] Bryologist **19:** 42. 1916.

[5] Oesterr. Bot. Zeitschr. **62:** 162. 1912.

[6] Ibid. **63:** 455. 1913.

[7] Student's Handb. Brit. Hepat. 454. 1912.

perianths and bracts. Ingham,[1] however, lists it without question from West Lancashire and from South Aberdeen. Specimens from the original locality and from Koppelsberg in Pomerania have been distributed by Schiffner in his Hep. Europ. Exsic., Nos. 543 and 544.

The group of *Cephaloziae* in which the leaves have more or less connivent lobes includes a number of closely related species. Of this group *C. catenulata* (Hüben) Dum., *C. connivens* (Dicks.) Lindb., *C. media* Lindb., and *C. pleniceps* (Aust.) Lindb. have long been known in both Europe and North America, while *C. affinis* Lindb., *C. compacta* Warnst., *C. Loitlesbergeri* Schiffn., and *C. macrostachya* Kaalaas have been published during the past few years. These recent segregates were based on European material, but *C. affinis*[2] and *C. macrostachya*[3] have since been definitely reported from North America. Now that *C. Loitlesbergeri* has been added to our flora, the discovery of *C. compacta* would not be surprising.

The essential characters of *C. Loitlesbergeri* may be briefly described as follows: the color is pale or yellowish green; the lobes of the leaves are long, entire, and usually connivent and acuminate, each being tipped by a row of from two to four cells; the leaf-cells have firm walls without trigones and average about 30μ in diameter; the inflorescence is autoicous; the innermost perichaetial bracts are deeply divided into four or more, sub-parallel and long-acuminate lobes separated by narrow sinuses; the mouth of the perianth is long-ciliate. Although the lobes of the bracts are sometimes subequal in size, the two median lobes are often longer and broader than the others, so that the lobes might be described as bifid with accessory lobes.

It will at once be seen that the essential characters of *C. Loitlesbergeri* are shared by other members of the group to which it belongs, although they occur in different combinations. In *C. connivens*, for example, the inflorescence is autoicous, the lobes of the bracts are numerous and long-pointed, and the perianth is ciliate at the mouth; in *C. affinis* the inflorescence is autoicous, and the mouth of the perianth is ciliate; in both *C. macrostachya* and *C. catenulata* the perianth is long-ciliate; and in *C. pleniceps* the inflorescence is autoicous. In *C. connivens*, however, the cells are much larger than in *C. Loitlesbergeri*, averaging 50μ or more in diameter; in *C. affinis* the lobes of the bracts are broader and blunter, and the cilia at the mouth of the perianth are shorter; in *C. macrostachya* the inflorescence is dioicous and the bracts are distinctly bifid with shorter lobes; in *C. catenulata* the inflorescence is dioicous, and the shortly bifid bracts are coarsely dentate; in *C. pleniceps* the lobes of the bracts, although sometimes more than two, are broader and acute, rather than acuminate, while the mouth of the perianth is crenulate. In *C. media*, which often grows with *C. Loitlesbergeri*, the inflorescence is dioicous, the bracts are distinctly bifid (although sometimes with supplementary teeth), and the mouth of the perianth is crenulate.

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[1] Census Cat. Brit. Hepat. 26. 1913.

[2] See Evans, BRYOLOGIST **17:** 89. 1914.

[3] See Schiffner, Hedwigia **54:** 322. 1914; also Evans, Rhodora **17:** 114. 1915.

As Schiffner has pointed out, however, the closest ally of *C. Loitlesbergeri* is *C. compacta.* In this species the inflorescence is autoicous and the mouth of the perianth long-ciliate, while the size and color of the plant and the size of the leaf-cells are much the same as in *C. Loitlesbergeri.* In *C. compacta*, nevertheless, the lobes of the leaves are acute rather than acuminate, the bracts are distinctly bifid, their divisions are shortly acute instead of being long-acuminate, and the cilia at the mouth of the perianth are shorter.

7. Radula flaccida Lindenb. & Gottsche; G. L. & N. Syn. Hep. 726. 1847.

Collected in March, 1915, on leaves of *Trichomanes sphenoides* Kunze, on Hattie Bauer Hammock, Dade County, Florida, by J. K. Small and C. A. Mosier. New to the United States but widely distributed in tropical North and South America.

In its constantly epiphyllous habit *R. flaccida* is almost unique among the American species of *Radula.* It lies closely appressed to the leaves upon which it grows, its lobes are rounded, its lobules are more or less sharp-pointed and its long, funnel-form perianth narrows very gradually toward the base. The most distinctive organs of the species, however, are its discoid gemmae, which are characterized by their large size and complex structure. Since the development, mature structure, and germination of these gemmae have been fully described and figured by Miss Williston, it will be sufficient here to refer to her paper.[1] Similar gemmae had been described a few weeks earlier in the African *R. epiphylla* Mitt. by Goebel.[2]

8. **Cololejeunea subcristata** sp. nov.

Collected in March, 1915, on leaves of *Tectaria minima* Underw., on Hattie Bauer Hammock, Dade County, Florida, by J. K. Small and C. A. Mosier (No. 5327); also on leaves of *Trichomanes Krausii* Hook. & Grev., on Nixon-Lewis Hammock, Dade County, by the same collectors (No. 6008). No. 5327 may be designated the type.

Plants delicate, pale green, often becoming bleached with age, scattered or growing in small thin patches: stems prostrate, about 0.05 mm. in diameter, irregularly and sometimes rather abundantly branched, the branches widely spreading, essentially like the stem but usually with somewhat smaller leaves: leaves loosely imbricated, obliquely to widely spreading, plane or nearly so, the lobe ovate, often arching partially across the axis dorsally, when well developed 0.4–0.45 mm. long and 0.25–0.3 mm. wide, but often considerably smaller, abruptly narrowed to a broad, acute to rounded apex, margin varying from subentire to vaguely and irregularly crenulate from projecting cells; lobule usually well developed, strongly inflated with an arched keel, ovate, about 0.15 mm. long and 0.09 mm. wide, free margin involute as far as the apical tooth, the latter usually consisting of two cells in a row, the hyaline papilla at the base of the tooth on the inner surface, proximal tooth indistinct, consisting of a rounded

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[1] Bull. Torrey Club **39**: 329–336. *f. 1–20.* 1912.

[2] Flora **104**: 156. 1912.

projecting cell separated from the apical tooth by a single cell, sinus shallow and only one or two cells long; cells of lobe averaging about 14μ along the margin and 24 x 22μ in the middle and at the base, slightly convex, trigones small but distinct, sometimes coalescent, triangular, with straight or rounded sides, intermediate thickenings occasionally present, oval; stylus reduced to a hyaline papilla: inflorescence autoicous: ♀ inflorescence borne on a more or less abbreviated branch, innovating on one side, the innovation more or less elongated, usually sterile but sometimes with a second ♀ flower; bracts obliquely spreading, complicate, vaguely crenulate along the keel but not winged, the lobe ovate to obovate, 0.45–0.5 mm. long, 0.25–0.3 mm. wide, rounded to acute, margin as in the leaves, lobule ovate, 0.2–0.3 mm. long, 0.12–0.2 mm. wide, the broad apex varying from acute to rounded, often shortly indented, margin irregularly crenulate; perianth obovoid, about 0.75 mm. long and 0.45 mm. wide, rounded to truncate at the apex with a short but distinct beak, sharply five-keeled, the keels extending below the middle, vaguely and irregularly cristate, the crests sometime double, usually interrupted, rarely more than one cell wide, irregularly crenulate or denticulate from projecting cells, surface of perianth otherwise smooth: ♂ inflorescence (so far as known) terminal on a more or less elongated branch, not proliferating; bracts in three to five pairs, imbricated, similar to the leaves but with smaller lobes and larger lobules, apparently monandrous: capsule about 0.15 mm. in diameter: gemmae broadly orbicular, about 0.04 x 0.035 mm. composed of sixteen cells, each apical quadrant cutting off two segments, margin subentire, organs of attachment not present. [Figs. 5–14.]

The genus *Cololejeunea* is now represented in Florida by six distinct species, while the related genera *Leptocolea* and *Aphanolejeunea* are represented by one species apiece. Since all three genera include species which are exceedingly minute and inconspicuous, it would not be surprising if these numbers were substantially increased in the future. In *C. subcristata* the characteristic features are the following: the ovate leaf-lobes, longer than broad, with the apex varying from acute to rounded; the inflated lobules, with rudimentary proximal teeth; the leaf-cells with distinct trigones but without surface-papillae of any sort; and the five-keeled perianth with rudimentary crests on the keels. The crests are very variable and sometimes scarcely distinguishable; when well developed they are sometimes doubled and may show a width of two cells. This increased width, however, is usually localized and may involve a single cell only, in which case a larger tooth than the ordinary marginal crenulations is present. The gemmae belong to the simplest type known in the genus and are comparable with those found in *C. myriocarpa* (Nees & Mont.) Evans, *C. tuberculata* Evans and the various species of *Aphanolejeunea*.[1] In their lack of marginal projections and organs of attachment they come especially close to the gemmae of *C. myriocarpa*, where, however, the marginal crenulations are much more pronounced.

Among the Florida species of *Cololejeunea*, *C. subcristata* is perhaps most closely related to *C. minutissima* (Sm.) Schiffn, and *C. setiloba* Evans,[2] but in

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[1] See Evans, Bull. Torrey Club **38**: 281. 1911; also Bryologist **18**: 68. 1915.

[2] Bryologist **16**: 51. 1913.

both of these species the leaf-cells are somewhat smaller, averaging about 18μ in the middle of the lobe, the walls show no local thickenings whatever, and the gemmae are larger and more complex. *C. minutissima* is further distinguished by its convex, more distant, smaller and relatively broader leaf-lobes, by its larger lobules, and by the distinctly and regularly crenulate margins of its leaves and bracts. In *C. setiloba* the remarkable lobules ,each a long and slender tooth, afford excellent differential characters. The other Florida species would hardly be confused with *C. subcristata*. *C. Biddlecomiae* (Aust.) Evans and *C. tuberculata* are both distinguished by their roughened leaves and perianths, while *C. diaphana* Evans is a much more delicate species with narrower and more pointed leaves, the elongated cells of which are almost or quite destitute of trigones.

9. LEPTOLEJEUNEA ELLIPTICA (Lehm. & Lindenb.) Schiffn.

Collected in January, 1916, on the leaves of various plants, on Royal Palm Hammock, Dade County, Florida, by J. K. Small & R. L. Lowe (Nos. 7024, 7036, 7041, 7042); also in February, 1916, at the same locality, by J. K. Small (Nos. 7045–7047, 7050–7058, 7060–7062); also in January, 1916, on Long Key Hammock, by J. K. Small (No. 7063). Genus and species new to the United States. In some of the packets listed the species is abundantly represented, in others traces only are present. Although it is not possible to give a complete list of the plants upon which the *Leptolejeunea* was found, the following partial list may be of interest: *Anacheilium cochleatum* (L.) Hoffmgg. (No. 7045), *Auliza nocturna* (L.) Small (No. 7046), *Calyptranthes Zuzygium* (L.) Sw. (No. 7060), *Chrysobalanus Icaco* L. (Nos. 7041, 7055), *Encyclia tampensis* (Lindb.) Small (No. 7050), *Guettarda scabra* Vent. (No. 7054), *Hippocratea volubilis* L. (No. 7036), *Icacorea paniculata* (Nutt.) Sudw. (No. 7062), *Ilex Krugiana* Loesener (No. 7025), *Laurocerasus myrtifolia* (L.) Britton (No. 7051), *Ocotea Catesbyana* (Michx.) Sarg. (No. 7056), *Psychotria undata* Jacq. (No. 7057), *Schoepfia chrysophylloides* (A. Rich.) Planch. (No. 7058), *Simaruba glauca* DC. (No. 7061), *Spathiger rigida* (Jacq.) Small (No. 7047), *Zamia pumila* L. (No. 7053).

The discovery of this widely distributed tropical species in Florida is of noteworthy. Although almost always epiphyllous in habit, the plants sometimes grow on bark. The blunt leaf-lobes with ocelli in a median row, the distant underleaves with setaceous divisions, the five-keeled perianth with the smooth keels projecting upward as acute or truncate horns, and the specialized caducous branches will serve to characterize the species. For a full description, with figures, reference may be made to an earlier paper of the writer.[1]

10. LEUCOLEJEUNEA CLYPEATA (Schwein.) Evans.

Collected in April, 1915, at Monticello, Florida, by E. Nelson (No. 1). The species is widely distributed in the eastern United States, but this is apparently the first record for Florida. It represents the fourth species of *Leucolejeunea* and the thirty-eighth member of the Lejeuneae to be definitely reported from

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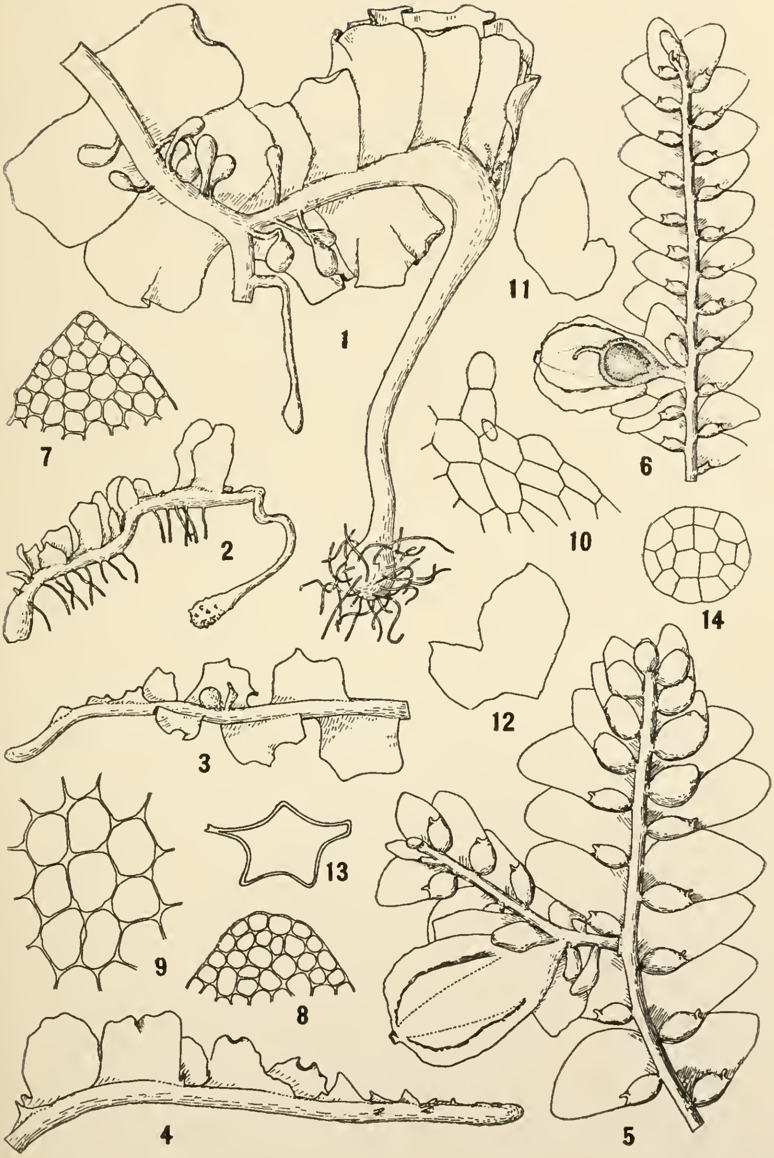
[1] Bull. Torrey Club **29:** 499. *pl. 23, f. 1–7.* 1902.



Fossombronia lamellata Steph. Figs. 1–4.
Cololejeunea subcristata Evans. Figs. 5–14.

the state. In the writer's revision of the Lejeuneae of the United States and Canada,[1] published in 1902, only seventeen Lejeuneae were known from Florida and only twenty-one from the whole United States.

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EXPLANATION OF PLATE II

FOSSOMBRONIA LAMELLATA Steph.

FIG. 1. Part of a robust female plant with a large terminal tuber and numerous small tubers, × 8.

FIG. 2. Small unbranched sterile plant with a terminal tuber, × 14.

FIG. 3. Tip of a male plant with rudimentary leaves, × 14.

FIG. 4. Tip of a sterile plant with rudimentary leaves, × 14.

The figures were all drawn from the specimens collected by Mr. Rapp.

COLOLEJEUNEA SUBCRISTATA Evans

FIG. 5. Part of a plant with a perianth and a male inflorescence, ventral view, × 40.

FIG. 6. Branch with a perianth, ventral view, × 32.

FIGS. 7, 8. Apices of lobes, × 200.

FIG. 9. Cells from the middle of a lobe, × 240.

FIG. 10. Apex of a lobule, × 240.

FIGS. 11, 12. Bracts from a single inflorescence, × 40.

FIG. 13. Transverse section of a perianth at about the middle, × 40.

FIG. 14. Gemma, × 240.

The figures were all drawn from the type specimen.

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[1] Mem. Torrey Club **8:** 113–183. *pl. 16–22.* 1902.

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TRANSACTIONS OF THE
CONNECTICUT ACADEMY OF ARTS AND SCIENCES
INCORPORATED A. D. 1799

VOLUME 21, PAGES 201-313 MARCH, 1917

The American Species
of
Marchantia

BY

ALEXANDER W. EVANS

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I. INTRODUCTION

The genus *Marchantia* is almost world-wide in its distribution and includes some of the largest and most conspicuous of the Hepaticae. According to the current rules of nomenclature the genus was not definitely established until 1753, when Linnaeus published it in the first edition of his Species Plantarum, but the use of the name *Marchantia* dates from the year 1713. Linnaeus recognized seven species, only the first two of which, *M. polymorpha* and *M. chenopoda,* are now retained in the genus. The type species, *M. polymorpha,* he cites from Europe only, and gives Martinique as the habitat of *M. chenopoda.* At the present time *M. polymorpha* is known to be almost cosmopolitan, while the range of *M. chenopoda,* although apparently restricted to tropical America, is likewise very extended.

For a long time *M. polymorpha* was the only species recognized in Europe. In 1817, however, a second species, *M. paleacea,* was described by Bertolini[1] from material collected in Italy. This species had been distinguished and figured by Micheli[2] nearly a century earlier but had not been accepted by Linnaeus. It is now known to have a wide distribution in tropical and subtropical regions, its range extending far beyond the confines of Europe. Other European species which have been proposed from time to time, such as *M. macrocephala* Corda and *M. Sykorae* Corda, have never received wide acceptance and undoubtedly represent mere forms of *M. polymorpha.*

The history of the genus in America, when the entire continent is considered, is very much involved. This is due partly to the full representation of the genus and partly to the confusion which has arisen in the interpretation of certain species. Before the publication of Gottsche, Lindenberg and Nees von Esenbeck's Synopsis Hepaticarum, in 1847, the following species of *Marchantia* had been recorded from North and South America: *M. papillata* Raddi (1823) from Brazil, *M. platycnemos* Schwaegr. (1827) from Brazil, *M. Swartzii* Lehm. & Lindenb. (1832) from Jamaica, *M. squamosa* Raddi (1832) from Brazil,

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[1] Opus. Sci. Bologna 1 : 242. 1817.

[2] Nova Plant. Gen. 2. *pl. 1, f. 4.* Florence, 1729.

M. cartilaginea Lehm. & Lindenb. (1832) from St. Vincent, *M. brasiliensis* Lehm. & Lindenb. (1832) from Brazil, *M. Berteroana* Lehm. & Lindenb. (1834) from Juan Fernandez, *M. domingensis* Lehm. & Lindenb. (1834) from Santo Domingo, *M. tholophora* Bisch. (1835) from Mexico, *M. inflexa* Mont. & Nees (1838) from Martinique, *M. plicata* Nees & Mont. (1838) from Bolivia, *M. quinqueloba* Nees (1838) from the West Indies,[3] *M. peruviana* (Nees & Mont.) Nees (1839, as *Grimaldia peruviana*) from Bolivia. In the Synopsis Hepaticarum these species are all recognized with the exception of *M. Swartzii,* which is made a synonym of *M. chenopoda,* and *M. platycnemos,* which is made a synonym of *M. papillata.* Two other species, *M. pusilla* Nees & Mont. from Chile and *M. lamellosa* Hampe & Gottsche from Venezuela, are described as new; a third species, *M. linearis* Lehm. & Lindenb. (1832), originally described from Nepal, is quoted from several of the Lesser Antilles; while both *M. polymorpha* and *M. chenopoda* are cited from numerous American localities. The Synopsis, therefore, recognizes sixteen species in all from North and South America.

During the period from 1847 to 1899 comparatively little was added to our knowledge of the genus in America. The following species, however, were described as new: *M. flabellata* Hampe (1847) from Venezuela, *M. Notarisii* Lehm. (1857) from Chile, *M. Dillenii* Lindb. (1883) from Jamaica, *M. subandina* Spruce (1885) from Peru, *M. Bescherellei* Steph. (1888) from Brazil, and *M. oregonensis* Steph. (1891) from Oregon. Two of the most noteworthy papers on *Marchantia* appearing during this time were by Schiffner. In the first he brought out the fact that *M. brasiliensis* and *M. cartilaginea* were synonyms of *M. chenopoda*[4]; in the second he showed that *M. tabularis* Nees, a South African species, was a synonym of the older *M. Berteroana.*[5] Another reduction to synonymy was suggested by Howe,[6] who showed that *M. oregonensis* was based on very uncertain characters and that it could not be well separated from *M. polymorpha.*

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[3] No station is cited for this species in the original publication; the Synopsis, however, gives, "in India occidentali."

[4] Nova Acta Acad. Leop.-Carol. 60: 287, 288. 1893.

[5] Oesterr. Bot. Zeitschr. 46: 41-44, 100-103. 1896.

[6] Mem. Torrey Club 7: 62. 1899.

In 1899 Stephani[7] published his monograph on *Marchantia* in the first volume of his Species Hepaticarum. He describes eighteen species in all from America, six of which are confined to North America and eight to South America. Of these eighteen species *M. Elliottii* of Dominica and *M. caracensis* of Venezuela and Mexico are described as new, while *M. cephaloscypha* Steph. (1883), originally described from New Zealand, is quoted from Chile and Patagonia. He accepts Schiffner's reduction of *M. cartilaginea* to synonymy but maintains both *M. brasiliensis* and *M. oregonensis* as valid. Under *M. tabularis* he cites *M. Berteroana* as a synonym (on the authority of Schiffner) but gives no American localities. Under *M. domingensis* he gives *M. inflexa* as a synonym and states further that the American stations for *M. linearis* (as given in the Synopsis) belong to *M. domingensis* instead. He includes *M. Dillenii* among the synonyms of *M. chenopoda* and considers that *M. peruviana* and *M. Notarisii* are very close to this species and may be merely forms of it. Two species recognized by the Synopsis, *M. quinqueloba* and *M. pusilla,* he gives up altogether, because they were based on fragmentary specimens, and he makes no mention whatever of *M. flabellata.*

If *M. Berteroana* is reinstated as an American species and if *M. flabellata* is added, Stephani's total of eighteen species would still be maintained, even if *M. brasiliensis* and *M. oregonensis* are considered synonyms. It will be seen that this total is scarcely different from the total of sixteen species given in the Synopsis Hepaticarum. The writer hopes to show, however, that these numbers are much too high and that further reductions to synonymy are necessary. In his opinion there are only nine species based on characters which seem trustworthy, and it is possible that two of these will not be considered distinct when they become more fully known. There remain five species which are doubtful, either because the published descriptions are incomplete or because the original material is immature or fragmentary. Two of these, as noted above, are discarded altogether by Stephani, and it is probable that the other three deserve the same fate. The doubtful species, however, will be alluded to briefly at the close of the paper.

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[7] Bull. Herb. Boissier 7: 383-407, 518-533. 1899.

II. MORPHOLOGICAL NOTES ON THE GENUS

No other liverwort has been so much discussed and described as *Marchantia polymorpha.* According to Lindberg[1] it attracted the attention of naturalists at a very early date and was known to both Aristotle and Theophrastus. Within more recent times it has repeatedly been the subject of morphological researches and has served in numerous text books as a typical representative of the thallose Hepaticae. Over eighty years ago Mirbel[2] published the first extensive account of its morphology. He brought out the essential features of the thallus and of its various tissues and gave a clear description of the receptacles and the gemmae. Of the later works dealing with the morphology of the species those by Leitgeb,[3] Kny,[4] Ikeno,[5] and Durand[6] may be particularly mentioned. The first two deal with the plant in a general way, very much as Mirbel's memoir did, although they include many original observations. The last two are much more specialized and deal with the cytology and development of the reproductive organs. Although *M. polymorpha* itself has been treated so exhaustively the other species of the genus have been but little studied by morphologists. In one of his earlier papers Schiffner[7] published a series of interesting observations on the Javan *M. geminata* R. Bl. & N.; but aside from this,

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[1] Hepat. Utveckling 15. Helsingfors, 1877.

[2] Recherches anatomiques et physiologiques sur le *Marchantia polymorpha.* Mus. Hist. Nat. Nouv. Ann. **1**: 92-130. *pl. 5-7.* 1832. For a reprint of this paper, with a few slight alterations, and a Complément des observations sur le *Marchantia polymorpha,* see Mém. Acad. Sci. **13**: 337-436. *pl. 1-8.* 1835. For a translation into German by Von Flotow, see Nees von Esenbeck, Naturg. Europ. Leberm. **4**:445-494. Breslau, 1838.

[3] Unters. über Leberm. **6**: 114-123. *pl. 9.* Graz, 1881.

[4] Bau und Entwickelung von *Marchantia polymorpha* L. Bot. Wandtafeln 364-401. *pl. 84-90.* Berlin, 1890.

[5] Beiträge zur Kenntnis der pflanzlichen Spermatogenese: Die Spermatogenese von *Marchantia polymorpha.* Beih. Bot. Centralbl. **15**: 65-88. *pl. 3 + f. 1.* 1903.

[6] The development of the sexual organs and sporogonium of *Marchantia polymorpha.* Bull. Torrey Club **35**: 321-335. *pl. 21-25.* 1908.

[7] Ueber exotische Hepaticae. Anhang I. Morphologische Bemerkungen über *Marchantia.* Nova Acta Acad. Leop.-Carol. **60**: 279-284. *pl. 19.* 1893.

records of morphological importance are mostly in the form of scattered notes, and these are often to be found in taxonomic treatises.

In the present paper the morphology of *Marchantia* will be treated largely from the standpoint of the taxonomist. In other words the parts of the plant which yield the most distinct and constant specific characters will be primarily considered. These parts include the epidermis and the epidermal pores, the compact ventral tissue, the ventral scales, the rhizoids, the receptacles, and the cupules. The photosynthetic layer, the sexual organs, and the sporophyte, although yielding important generic characters, are less helpful when the individual species are considered. For the sake of completeness, however, a brief account of the sporophyte will be included.

The flat thallus of *Marchantia* is of the usual prostrate dorsiventral type and branches repeatedly by forking. It varies considerably in size and in thickness in certain species, so that measurements of its various dimensions have to be employed with caution. At the same time some of the species are distinctly larger than others. The growth of the thallus is normally unlimited until the sexual branches or receptacles (see Fig. 9, A, B) are produced. These represent the erect prolongations of prostrate branches and are limited in growth. The inflorescence is dioicous throughout the genus. Vegetative reproduction is carried on by means of discoid gemmae, which may be formed on either male or female individuals and which apparently do not interfere with the growth of the plant.

The thallus shows clearly the usual differentiation into an epidermis, a photosynthetic layer and a compact ventral tissue bearing scales and rhizoids. The photosynthetic tissue consists of a single layer of large air-chambers separated from one another by continuous plates of cells. Each air-chamber is connected with the outside by a single pore in the epidermal roof. From the floor of the chamber arise numerous short rows of green cells, subspherical in form and freely exposed to the air of the chamber. The rows, which are simple or branched, are mostly from two to five cells long and the uppermost cells, except in the vicinity of the pore, are usually attached to the epidermis. The air-chambers vary greatly in size, not only in different species but often in different parts of an individual thallus.

1. Epidermis and Epidermal Pores

The ordinary epidermal cells are fairly uniform throughout the genus and it is doubtful if they offer any very trustworthy differential characters. Their size often varies markedly on an individual thallus and may be directly affected by differences in external conditions. Although the cells are usually colorless or pale they sometimes produce chloroplasts in abundance. In the majority of cases they are arranged in a single layer, but in certain species at least, such as *M. chenopoda* (Fig. 19, E) and *M. paleacea* (Fig. 8, D), the epidermis may be two cells thick in parts of its extent. The walls may vary considerably in thickness, but they are rarely very firm and are destitute of distinct trigones.

Cells containing oil-bodies, cells containing slime, and minute surface papillae are sometimes found in the epidermis. The cells containing the oil-bodies are usually distinctly smaller than the neighboring cells and are easily distinguished by their granular contents, which nearly or quite fill the cell cavities. In *M. chenopoda* these cells are not infrequent and do not seem to be restricted to any definite part of the thallus; in *M. polymorpha* they occur near the margin and seem to be absent elsewhere; while in certain other species there are apparently no cells of this character in the epidermis.

Epidermal cells containing slime are, according to our present knowledge, restricted to *M. chenopoda.* The slime-cells are scattered about in the epidermis and always occur in regions where the epidermis is two cells thick, being situated in the inner layer (Fig. 19, L). They are much larger than the surrounding epidermal cells and strongly compress those of the outer layer. When a piece of the epidermis is examined from above the slime cells are seen to be covered over by these compressed cells. Apparently Voigt[8] was the first to observe the slime-cells, although he failed to recognize their true character. The much larger slime-canals in *Conocephalum conicum* (L.) Dumort. were soon afterwards described by Goebel,[9] and Leitgeb[10] pointed out that the slime-cells of *M. chenopoda* were of the same

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[8] Bot. Zeit. **37**: 733. 1879.

[9] Arb. Bot. Inst. Würzburg **2**: 531. 1880.

[10] Unters. über Leberm. **6**: 16. 1881.

nature. He showed that they occurred not only *under* the epidermis, as he expressed it, but also in the compact ventral tissue and in the partitions between the air-chambers, and he emphasized the fact that they were especially abundant in the female receptacles. The distribution of the slime-cells in *Marchantia* was a little later discussed at length by Prescher.[11] He found no trace of them in *M. Berteroana, M. papillata, M. emarginata* R. Bl. & N., or *M. linearis;* he found them restricted to the compact tissue of certain definite regions in *M. polymorpha* and *M. paleacea;* and it was only in *M. chenopoda* (including *M. cartilaginea*) that he found them in the epidermis.

Surface papillae have been figured very accurately by Kny[12] in the case of *M. polymorpha.* They are minute appendages of the epidermis, which are cut off by walls and rounded or bluntly pointed at their free ends (FIG. 2, J, L, O, P). Sometimes a papilla is situated over a single cell and sometimes over the partition between two cells, showing in the latter case that an epidermal cell had divided after the papilla had been formed. Papillae of this type seem to be rare on vegetative branches and confined to certain species. So far they have been reported in two East Indian species, *M. emarginata* and *M. Treubii* Schiffn.,[13] but they seem to be absent from all the American species except *M. polymorpha.* In this last species, as shown by Schiffner,[14] the median portion of the thallus is always free from papillae, while the marginal regions sometimes show them clearly. The distribution is very different, however, in *M. Treubii,* where the papillae are most abundant in the median portion and gradually decrease toward the margins. Whether papillae of this character form a constant feature of any of the species where they have been found is perhaps doubtful. In one specimen of *M. emarginata,* for example, in the writer's collection (Schiffner, Iter Indicum *37*), the plants seem to have developed no papillae, and they are frequently absent from the vegetative branches in *M. polymorpha.* When they occur on receptacles or cupules, as in this same species, they seem to be more constant.

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[11] Die Schleimorgane der Marchantieen. Sitzungsb. Kais. Acad. Wissen. Wien, Math.-naturw. Cl. 86^1: 132-158. *pl. 1, 2.* 1882.

[12] Bot. Wandtafeln *pl. 84, f. 2, 3.* 1890.

[13] See Schiffner, Fl. de Buitenzorg 4: 32, 35. Leiden, 1900.

[14] Lotos 49: 93. 1901.

The complex epidermal pores of *Marchantia* are of much interest. They are of the dolioform or barrel-shaped type, that is, the opening of the pore is surrounded by two series of cells arranged in concentric rows, one series projecting more or less above the surface of the thallus, the other projecting into an air-chamber. Although pores of this type are found on the sexual branches of most of the Marchantiaceae, the only genera where they occur on the vegetative branches are *Marchantia, Preissia,* and *Bucegia.* Even in *Marchantia,* as shown by Kamerling,[15] immature shoots sometimes produce pores of the simple type found in most of the other members of the group.

The first attempt to utilize the structural features of the pores for taxonomic purposes seems to have been made by Voigt.[16] He studied eight species of the genus, and showed that the number of pores in a given area, the number of rows of cells surrounding a pore, and the number of cells in a row were fairly constant for each species. Stephani also has drawn specific characters from the pores, but certain of his distinctions, as will be shown below, are subject to variation and must be used with caution.

In the case of *M. polymorpha* the pores have been repeatedly figured, although the published illustrations are not all of the same degree of excellence. Among recent figures those by Voigt, Kny, and Müller[17] bring out most of the essential points. According to Voigt, whose account of the pores is unusually full, the opening is surrounded by five circular rows of cells, three belonging to the upper and two to the lower series, but both Kny and Müller state that the upper series is normally composed of only two rows making four rows in all, a statement which agrees with the writer's observations (see Fig. 2, A, B). Under some conditions the number of rows may be reduced to three or even to two. In the upper series each row is composed (in most cases at least) of four cells (Fig. 2, A, B), and immediately surrounding the pore a circular membranous ridge is present, probably representing, as in the simple pores of *Targionia,*[18] a collapsed series of cells. This ridge is shown by Voigt (*f. 1*),

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[15] Flora 84 (Ergänzungsb.): 57. 1897.

[16] Bot. Zeit. 37: 741. 1879.

[17] Rabenhorst's Kryptogamen-Flora 6: *f. 187.* Leipzig, 1907.

[18] See Deutsch, Bot. Gaz. 53: 494. *f. 9.* 1912.

but is not brought out in the figures of Kny and Müller. It is sometimes very narrow and absolutely colorless and can then be demonstrated only with difficulty. In the lower series each row is likewise composed in most cases of four cells, those bounding the inner opening being distinctly differentiated. Their usual appearance is clearly shown by Kny (*pl. 84, f. 2*), each cell being in the form of a narrow, curved, four-sided figure with a rounded median projection extending toward the center of the pore. All the cell-walls immediately bounding the pore are shown covered over with a granular deposit of some resinous substance, which hinders or prevents the entrance of water through the pore. Kny comments on the fact that the pores vary greatly in size and that the projections from the cells bounding the inner opening sometimes meet. In his opinion these projections probably make still more difficult the entrance of water through the pore. This view is upheld by Ruge,[19] who finds the pores almost completely closed by the projections in a submerged form of *M. polymorpha.* In FIG. 2, D-I, some of the variations shown by the cells bounding the inner opening are brought out. In FIG. 2, E, the projections are only slightly developed, although the upper cell on the left approaches the condition portrayed by Kny; in FIG. 2, D, F, I, the projections are well developed but not sharply defined from the rest of the cell; in FIG. 2, G, H, the projections are both well developed and sharply defined. These last figures, drawn from a plant growing in a very wet locality, support the statements of Ruge and agree with the figures published by Müller. The cells drawn, however, seem to be nearly or quite destitute of the resinous deposit so conspicuously shown in the remaining figures and in Müller's figures also.

Although the inner openings of the pores in *M. polymorpha* are subject to so much variation, Stephani insists that important specific characters in the genus *Marchantia* are yielded by the inner openings. He recognizes four types[20] and states that they are not connected by transitional conditions. In the first type the four cells bounding the opening are narrow and not materially changed in shape by increased turgidity, the opening itself exhibiting a quadrate form. In the second type the four bounding

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[19] Flora 77: 294. *f. 11.* 1893.

[20] Bull. Herb. Boissier 7: 385. *f. a-d.* 1899.

cells bulge into the opening in the form of rounded projections, the opening itself showing an outline with four strongly concave sides and four sharp angles; by increasing the turgidity this opening can be almost completely closed. In the third type (which is essentially the same as the pores of *Preissia*) the four cells likewise bulge into the opening but the bulging portions are more sharply defined and the opening appears in the form of a four-sided figure with very concave sides but with rounded dilations at the angles; this opening, which Stephani describes as cruciate, can be completely closed by an increase of turgidity. In the fourth type the opening is very large and bounded by many cells (fifteen in Stephani's figure), each cell bulging into the opening in the form of a longer or shorter cylindrical projection, the opening itself thus acquiring a very irregular outline. To the first type Stephani assigns (among others) *M. polymorpha, M. plicata* and *M. domingensis;* to the second type, *M. disjuncta;* and to the third type, *M. cephaloscypha* and *M. paleacea.* The only representative of the fourth type is *M. macropora* Mitt. of New Zealand.

Schiffner,[21] however, had already called attention to the danger of placing too much confidence in the peculiarities of the cells bounding the inner openings. According to his account these cells in most species of *Marchantia* bulge more or less into the opening, the form of which may vary accordingly, and his statements would support the view that there was no sharp distinction between the first and second types of Stephani. Even in *M. Berteroana,* which Stephani would assign to his third type, Schiffner finds only an insignificant modification of the usual condition. He adds that the number of bounding cells in this species, although usually four, may vary from three to six on an individual thallus, and that the walls of the cells commonly lack the resinous deposit found in *M. polymorpha.* Goebel[22] is likewise inclined to recognize a single type of pore in *Marchantia* with respect to the inner opening, and he sees no essential difference between Stephani's fourth type and the others. He expresses no positive opinion on this last point, however, because he had no material of *M. macropora* at his disposal. He considers that the pores are plastic structures, subject to modifica-

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[21] Nova Acta Acad. Leop.-Carol. 60: 286. *pl. 19, f. 8. 20.* 1893.

[22] Flora 96: 193. 1906.

tion through external conditions, and he emphasizes the fact that the pores of xerophilous forms can often be more or less completely closed by an increased turgidity of the bounding cells.

It is clear from the observations of Schiffner and Goebel that the pores in *Marchantia* (excepting perhaps in *M. macropora*) conform to one general type and that the distinctions relied upon by Stephani are less constant than he supposed. This is especially well seen in *M. polymorpha,* where the inner opening shows all gradations from a quadrate to a cruciate form and thus exemplifies all three of the conditions upon which the first three of Stephani's types were based. *M. polymorpha,* however, is an exceedingly plastic species and it is doubtful if any of the other members of the genus exhibit the same wide range of variation in the inner opening. Schiffner's figures of *M. geminata,* for example, although illustrating conditions connecting the first and second of Stephani's types, show no approach to the third; while in *M. paleacea,* according to the information at hand, the inner opening is always cruciate and thus does not deviate from the third type. For purposes of taxonomy, therefore, the writer would still consider it expedient to recognize two types of pore among the American species, the distinctions between the types breaking down in the case of *M. polymorpha.* In the first type (which includes Stephani's first and second types) the inner opening is bounded by three to six cells, the usual number being four, and shows all gradations between a polygon, commonly four-sided, with slightly convex sides and one with strongly concave sides and sharp angles. In the second type (which is the same as Stephani's third type) the inner opening is distinctly cruciate with four rays dilated at the apex or, in the rare cases where the number of bounding cells is less or greater than four, with fewer or more rays. Stephani's fourth type, which does not occur in America so far as known, need not be further considered.

As an example of the first type of pore *M. chenopoda* may be selected. In this the opening, as pointed out by Voigt, is surrounded by about seven rows of cells, shown clearly in cross-section (FIG. 19, C-G), four of the rows usually belonging to the upper and three to the lower series. The walls bounding the opening are either smooth or with a resinous deposit. In the upper series (FIG. 19, A, B) the innermost row is usually composed of four narrow cells and the second row of the same number, but the third row commonly shows twice as many and the fourth row a much larger number. The ridge immediately around the opening is clearly marked. In the lower series (Fig. 19, H-K) the innermost row lies almost directly beneath the second row, so that only the first and third rows show clearly from below. The first and second rows are usually composed of four cells each, the walls bounding the pore being more or less strongly convex. The third row usually contains more cells than the first and sometimes twice as many, but it rarely contains as many as the fourth row of the upper series, where the cells are essentially like the ordinary epidermal cells. Of course the numbers just given are subject to variation, the number of cells bounding the outer and inner openings being often more than four.

As an example of the second type of pore *M. paleacea* may be selected, and the illustrations given in the present paper (Fig. 8, A-H) may be compared with the one published by Müller.[23] The descriptions given by Voigt may likewise be consulted. The cells bounding the pore are usually in six rows, three belonging to each series, and the rows are commonly composed of four cells apiece. The cell-walls bounding the pore are smooth throughout. In the upper series the ridge around the opening is distinct and the cells are very narrow, standing in sharp contrast to the neighboring epidermal cells. In the lower series the cells bounding the inner opening are much broader than the others and project so strongly that they often touch in the center and almost occlude the cruciate opening. Sometimes one or more cells of the second row project also (Fig. 8, D), but the cells of both the second and third rows are usually narrow, resembling in this respect the cells in the upper series.

According to the account given by Kamerling,[24] the size of the inner opening in a pore of the first type is not decreased to any great extent by an increase of the turgidity of the surrounding cells, while in a pore of the second type the decrease is very marked. In his opinion the cells surrounding the inner opening act independently of the cells in the other rings. As a definite example of a species with pores that can be closed he quotes *M. nitida* Lehm. & Lindenb., a species which is to be regarded as a synonym of *M. paleacea*.

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[23] Rabenhorst's Kryptogamen-Flora 6: *f. 188.* 1907.

[24] Flora 84 (Ergänzungsb.): 46. 1897.

2. COMPACT VENTRAL TISSUE

The ventral tissue in *Marchantia* gradually thins out from the thickened median portion until it is frequently only two or three cells thick along the margins of the thallus. It consists primarily or even wholly of parenchyma and its chief function apparently is to act as a storage-tissue for water and organic food. In some parts of the thallus it is usually possible to demonstrate the presence of elongated pits in the cell-walls, and a purplish pigmentation of the walls is often apparent. Cells containing oil-bodies are usually conspicuous among the other parenchyma cells (FIG. 20, A) and seem to be present in all the species. In herbarium material, however, it is not always easy to demonstrate them. Cells containing mycorrhiza are likewise very frequent. In *M. chenopoda,* as noted by Leitgeb and Prescher, the ventral tissue and the partition walls between the air-chambers contain scattered slime-cells similar to those found in the epidermis. Slime-cells of this character occur also in the compact tissue of *M. paleacea, M. breviloba* sp. nov. and the East Indian *M. emarginata,* but have not yet been detected in other species except in connection with the reproductive organs. According to Cavers[25] the slime-cells and slime-canals of *Conocephalum conicum* fail to develop when the plants are cultivated under water, and it is therefore possible that slime-cells may not always be present in the species of *Marchantia* just listed. In fact Prescher reported that they were absent from *M. emarginata,* and specimens of *M. paleacea* and of *M. chenopoda* might be cited where they are very infrequent or perhaps not present at all.

The only cells found in the ventral layer which are not parenchymatous in their nature are the more or less elongated sclerotic cells with yellow or brown walls, which occur in certain species. Cells of this character were first demonstrated by Goebel[26] in the case of *Preissia quadrata* (Scop.) Nees, and the same author has called attention to their occurrence in the New Zealand *M. foliacea* Mitt.[27] In this species, according to his account, the sclerotic cells are variable in length and are usually scattered singly among the parenchyma cells. Occasionally two

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[25] Ann. Bot. **18**: 93. 1904.

[26] Arb. Bot. Inst. Würzburg **2**: 533. 1882.

[27] Flora **96**: 194. *f. 143.* 1906.

cells will occur end to end and sometimes even longer groups or strands are formed, perhaps corresponding with Stephani's "strands of sclerenchyma." The walls of the cells are thick and pigmented, showing that their functions are primarily mechanical, but Goebel finds that the cavities sometimes contain starch-grains. Sclerotic cells occur in several American species, such as *M. paleacea, M. chenopoda* (FIG. 20, A, B) and *M. domingensis,* and agree closely with Goebel's description. Whether they are always produced by the species where they have been detected is perhaps a question. Cavers[28] calls attention to the fact that *Preissia quadrata,* when grown indoors in a moist atmosphere, fails to develop thick-walled cells, and in all probability the formation of the similar cells in *Marchantia* is influenced by environmental conditions. In any case, however, the presence of sclerotic cells is associated with certain definite species.

3. VENTRAL SCALES

The ventral scales in *Marchantia* exhibit considerable diversity, not only when different species are compared but also when an individual species is considered. This is due to the fact that each species produces at least two distinct kinds of scales, only one of which bears appendages. In the other genera of the Marchantiaceae the scales with appendages are the only kind produced.

Taylor[29] was apparently the first to observe that the scales in *M. polymorpha* were not all alike. He distinguished three different kinds, and these are described at length by Leitgeb,[30] who designates them as median, laminar and marginal scales, respectively. The median scales are attached by a long line, which begins near the axis of the thallus, then extends almost longitudinally and finally curves gently outward, reaching perhaps half way to the margin. The scales are at first very narrow but become abruptly dilated in the outer part; here on each scale the characteristic appendage is attached, strongly contracted at its junction with the scale and then abruptly dilated into an orbicular expansion, rounded to apiculate at the apex (FIG. 1).

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[28] Contrib. to the Biol. of the Hepat. 28. Leeds and London, 1904.

[29] Trans. Linn. Soc. 17:377. 1835.

[30] Unters. über Leberm. 6: 114. 1881.

The laminar scales are more numerous than the median scales and form a series about midway between the median scales and the margin. They are attached by a much shorter line and broaden out at once into lunulate or ovate structures, rounded at the apex and destitute of appendages. The marginal scales are still more numerous and attached by even shorter lines, but they resemble the laminar scales in lacking appendages and in most other respects. They are situated near the margin and some of them extend beyond. The arrangement of the scales is shown clearly in a figure by Goebel,[31] who brings out the fact that the laminar scales are arranged in an irregular row and that the marginal scales are still more irregular in their arrangement, although a linear series is approximated.

The account of the scales just given is somewhat at variance with the description and figures of Müller.[32] According to this author the innermost scales are long and very narrow; they are attached almost longitudinally throughout their entire length and are destitute of appendages. These are said to be borne instead on the scales of the next outer row, which agree in all respects with the median scales as described by Leitgeb. The third type of scale recognized by Müller includes both the laminar and marginal scales of Leitgeb. An interpretation of the scales, closely agreeing with Müller's, has recently been published by Massalongo.[33] The present writer, however, has been unable to demonstrate the narrow innermost scales without appendages. According to his observations the statements of Leitgeb are essentially correct.

The scales in *M. polymorpha,* as well as in the other species, are delicate in texture and are sometimes more or less pigmented; in most cases, however, the pigmentation is of short duration and the scales become bleached and transparent. The cells tend to be wavy and irregular, especially toward the margin (Figs. 7, A; 20, C). The cell-walls are thin, although trigones may sometimes be demonstrated on the marginal scales. Scattered about among the other cells are cells containing oil-bodies (Fig. 20, D) and rhizoid initials, the latter giving rise to tuberculate rhizoids (Fig. 20, E). In the appendages rhizoid initials are absent, but cells containing oil-bodies can often be distinguished (Figs. 1, 3, etc.).

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[31] Organographie der Pflanzen *f. 158.* Jena, 1898.

[32] Rabenhorst's Kryptogamen-Flora 6:17. *f. 12.* 1905.

[33] Atti R. Ist. Veneto 75:696. *pl. 4, f. 12-15.* 1916.

According to Leitgeb the scales in certain species, such as *M. domingensis* and *M. nitida,* are all of the median type while in *M. chenopoda* the laminar scales are less numerous than the median scales and the marginal scales are absent altogether. In Goebel's figure of *M. chenopoda*[34] a single laminar scale is shown among sixteen median scales and the implication is made that the number of laminar scales is very small. The writer has examined numerous specimens of *M. paleacea* (which includes *M. nitida*), of *M. chenopoda* and of other species and finds laminar scales always present (see Fig. 6, H-O). They differ from the laminar scales in *M. polymorpha,* however, in being situated much closer to the median scales. On account of their shorter lines of attachment they extend only a small part of the distance toward the median line. The laminar scales usually alternate with the median scales but occasionally there may be two laminar scales between two successive median scales. Under these circumstances one of the laminar scales is often reduced in size.

The species just noted will give some idea of the differences in arrangement which the ventral scales may show. These differences can often be utilized in separating species, but the best differential characters yielded by the scales are those drawn from the appendages. These are, with very rare exceptions, borne singly and, as has been shown, are confined to the median scales. Although the appendages vary, within wide limits in certain species, they nevertheless present striking and distinctive features. In comparing them the form, the character of the margin and apex, the size of the cells, and the presence or absence of cells containing oil-bodies should be taken into consideration. With respect to size the cells may be approximately the same throughout the entire extent of an appendage (see Fig. 16, F, G). It is much more usual, however, for the median cells to be much larger than the marginal cells and the gradation from one to the other may be either gradual (see Fig. 7) or very abrupt (see Fig. 5, A-D). The texture of the scales, aside from the appendages, is much the same throughout the genus. The scales and their appendages will be again considered in connection with the various species discussed below.

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[34] *L. c. f. 157.*

4. RHIZOIDS

The rhizoids in the genus *Marchantia,* as in practically all of the Marchantiales, are of two types, the smooth and the tuberculate. In the smooth type the walls are thin or uniformly thickened; in the tuberculate type numerous local thickenings of the wall extend into the lumen of the rhizoid in the form of cylindrical or bluntly conical projections. In some of the tuberculate rhizoids the projections are discrete and irregular in their distribution; in others they are more or less coalescent and show a spiral arrangement. Kamerling[35] has shown that these spiral tuberculate rhizoids are abundant in *M. polymorpha* and Schiffner[36] has examined this and other species of the genus with reference to these peculiar structures. He confirms Kamerling's statements about their occurrence in *M. polymorpha* and finds, so far as American species are concerned, that they are equally abundant and typical in *M. chenopoda;* that they still occur, although in less typical form, in *M. domingensis* and its allies; and they are wanting altogether in *M. paleacea.*

Most of the rhizoids in *Marchantia* run in parallel bundles under the scales and converge to form a single large median bundle. There are, however, numerous rhizoids in the thickened median portion which spread at right angles to the surface, and Schiffner has made a number of interesting observations on these. In forms of *M. polymorpha* where a definite dorsal band lacks air-chambers, the rhizoids in question are smooth; in forms where the air-chambers extend across the median region, the rhizoids are tuberculate. In *M. plicata* the spreading rhizoids are smooth; in *M. chenopoda,* smooth; in *M. Berteroana,* tuberculate; in *M. paleacea,* smooth or with scattered tubercles. These differences may sometimes be of help in distinguishing species.

5. RECEPTACLES

The receptacles in *Marchantia* are strikingly different from the vegetative branches and attain a higher degree of complexity than in any other genus of the group. Two distinct portions may be distinguished, the erect stalk and the horizontal disc (or recep-

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[35] Flora **84** (Ergänzungsb.): 31. *pl. 1, 2, f. 7.* 1897.

[36] Ann. Jard. Bot. Buitenzorg **2** (Suppl. 3): 489, 490. 1909.

tacle proper), which bears the sexual organs. In some cases the disc shows clearly that it has but one plane of symmetry. In other cases it presents the appearance of being radial; but even here, as recently emphasized by Goebel,[37] there is actually but a single plane of symmetry, a fact made clearly evident when the structure and development of the receptacle are considered. The stalk, likewise, looks superficially as if it were radial, but here again a single plane of symmetry is present, and the stalk maintains its dorsiventrality (or zygomorphy) in spite of its erect position.

It has already been noted that the receptacles represent prolongations of prostrate branches. These branches may be more or less elongated, but they are often very short, a receptacle being developed almost immediately after a dichotomy has taken place. A receptacle, as shown so clearly by Leitgeb,[38] is a branch-system, the growing point of the original prostrate branch undergoing one or more divisions. A study of the stalk shows that the first division usually takes place very early in the development of the receptacle. If a cross-section is examined (Figs. 5, K; 8, 5; etc.) the dorsiventrality of the stalk becomes at once apparent, and the side which represents the ventral portion usually shows two deep longitudinal furrows, enclosed by scales and containing tuberculate rhizoids, the dorsal side being destitute of such furrows. In very rare cases a single furrow is present near the base of the stalk (Fig. 20, I). The presence of two furrows is evidence that the growing point has already divided once, even if the stalk itself remains undivided. Usually no further divisions take place until the disc begins to develop, but in some cases the stalk shows three or four rhizoid furrows, indicating that one or two secondary divisions have occurred. This is seen clearly in *M. breviloba* and *M. domingensis* (Figs. 9, I-K; 12, A, D). In the first the stalks of both male and female receptacles show four furrows apiece; in the second the stalk of the male receptacle which is figured shows three furrows, the stalk of the female receptacle showing four. The occurrence of more than two furrows has apparently been rarely observed in *Marchantia* and allied

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[37] Organographie der Pflanzen, 2d ed. 686. 1915.

[38] See Unters. über Leberm. **6**: 20-37. 1881.

genera. Spruce[39] mentions the occasional presence of three furrows in the stalk of the female receptacle in *Marchantia,* without citing definite species; Leitgeb,[40] in a single instance, found four furrows in the stalk of the female receptacle in *Preissia quadrata;* Stephani[41] states that the stalk of the male receptacle in the African *M. Wilmsii* Steph. has four furrows but doubts the constancy of this condition; and Schiffner[42] notes that the stalk of the female receptacle in *Bucegia romanica* Radian sometimes shows four furrows. These seem to be the only references to more than two furrows in the literature, but in all probability a higher number than two would occasionally be found in most species of *Marchantia* if enough stalks were examined. In *M. breviloba* four furrows seem to be the rule in the female receptacle, although it would hardly be safe to state that four were always present.

In the case of *M. polymorpha* it was noted long ago by Mirbel that the dorsal side of the stalk of the female receptacle showed a distinct strip of photosynthetic tissue with air-chambers, epidermal pores and short green filaments. This strip seems to be of constant occurrence throughout the genus. It commences close to the base of the stalk and extends nearly to the disc. In most cases the strip is continuous (Figs. 5, K; 8, J; 9, K; etc.) but sometimes, as in *M. chenopoda,* it may be separated into two strips by a median groove (Fig. 20, G-I). In the stalk of the male receptacle photosynthetic tissue is usually absent, the dorsal portion being composed of compact parenchyma. In certain species, however, such as *M. domingensis,* the photosynthetic tissue is about as well developed in the male (Fig. 12, A) as in the female receptacle. In *M. breviloba* the lower part (Fig. 9, I) of the stalk develops photosynthetic tissue while the upper part (Fig. 9, J) lacks it completely.

In the disc of the male receptacle the dichotomous branching usually continues and a distinct division into rays becomes apparent. Although the number of rays is subject to variation, certain numbers seem to be normal or typical for certain species. In *M. polymorpha,* for example, there are usually eight rays

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[39] Trans. Bot. Soc. Edinburgh **15**: 558. 1885.

[40] Unters. über Leberm. **6**: 31. 1881.

[41] Hedwigia **31**: 196. 1892.

[42] Beih. Bot. Centralbl. **23**^{2}: 282. *f. 16.* 1908.

present and in *M. chenopoda,* four, although deviations from these numbers are of frequent occurrence. Goebel[43] considers that the number of rays developed is dependent on nutritive conditions. In an unnamed species from the Fiji Islands, related to *M. geminata,* he notes a reduction in the number of rays to two, showing that only one dichotomy has taken place, and he compares this extreme condition with the two-rayed female receptacles found in *Exormotheca* and *Aitchisoniella.*

The rays are in one plane and vary greatly in length. They are sometimes much shorter than the undivided portion of the receptacle, appearing in the form of rounded marginal scallops separated by shallow but acute sinuses. This condition is seen clearly in *M. polymorpha* and its allies. It is much more usual, however, for the rays to be longer than the undivided portion, the whole receptacle thereby acquiring a palmate appearance. This type of receptacle is found in such species as *M. chenopoda* and *M. domingensis* and is commonly associated with a smaller number of rays than the first type. In some cases at the tip of a ray a slight depression marking the position of a growing point can be discerned, even in an old receptacle, but often all traces of the growing points disappear. The stalk is not attached to the disc marginally but peltately, although often excentrically. The peltate attachment is due to intercalary growth taking place in the region where the dorsal surface of the stalk and the dorsal surface of the disc would naturally be continuous. In this way a thin plate of tissue is formed between the two external rays of the disc, which would theoretically be distinct to their junction with the stalk. The presence of this plate, similar in all essential respects to the tissue forming the sinuses, intensifies the radial appearance which the receptacles of certain species show.

In its structure the disc shows many of the features which are found in the vegetative thallus. It is distinctly dorsiventral and the differentiation into epidermis, photosynthetic tissue and compact ventral tissue is clearly marked. On the ventral surface of the rays scales with appendages and scales without appendages can be distinguished in two or more series, and the appendages are much like those of the ordinary scales except that they are smaller and sometimes less constricted at the base. Rhizoid

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[43] Organographie der Pflanzen, 2d ed. 699. *f. 669 II.* 1915.

initials are present among the cells of the scales, the appendages alone being free from them.

The antheridia arise in acropetal succession, the oldest being formed near the center of the disc. In many species each ray develops two distinct rows of antheridia, but in certain species, such as *M. polymorpha*, the antheridia are more irregular in their arrangement and each ray shows more than two indistinct rows. The antheridia are borne singly in deep depressions with small circular openings. The depressions extend down into the compact ventral tissue, and are surrounded by the characteristic air-spaces with their branched rows of photosynthetic cells and dolioform epidermal pores.

The stalk of the female receptacle develops more slowly than that of the male receptacle and persists in an active condition until the sporophytes are mature. In the disc the division into rays takes place just as in the male receptacle and the number of rays present is subject to similar variations. The archegonia form groups and arise in acropetal succession, beginning when the disc is very young; but, on account of the strong intercalary growth in the median region of the dorsal portion, the archegonia are arched over and displaced until they seem to be situated on the ventral surface of the disc. In this way the oldest archegonia come to lie nearest the periphery of the disc and the youngest nearest the stalk. Each group of archegonia contains a variable number, arranged in two or three more or less definite radial rows, and is derived from one of the growing regions of the disc.

In the East Indian *M. geminata* and its allies the groups of archegonia are clearly situated underneath the rays of the receptacle. These rays, therefore, are obviously homologous with the rays of the male receptacles throughout the genus. This condition, however, is very exceptional. In most species of the genus, including all the American representatives, the groups of archegonia alternate with the rays of the receptacle and are situated in the sinuses between them. This is caused by the rapid intercalary growth of the regions between the growing points, the so-called "middle lobes"; the rays, accordingly, are formed by the middle lobes and are not homologous with the rays of the male receptacle but rather with the sinuses. These relationships are discussed at length by Leitgeb,[44] who notes also the fact that the two external rays are to be compared with the "side lobes" in an ordinary dichotomy. In *M. polymorpha,* where nine rays are commonly present, seven would represent middle lobes and two, side lobes. Between the two side lobes there is of course no group of archegonia, so that there are eight groups for the entire receptacle, showing that three dichotomies have taken place.

The rays of the female receptacles vary in length, very much as in the case of the male receptacles. There is, however, no correspondence between the two. In *M. polymorpha,* for example, the rays of the female receptacle are long, and those of the male receptacle are short, while in *M. chenopoda* the conditions are reversed. The rays of the female receptacle differ also in form, being flat in some species and cylindrical in others. When they are flat they are often retuse or shortly bilobed at the apex, and Goebel points out that a deepening of the apical sinuses would lead to the condition found in *M. geminata,* where sinuses instead of rays are present between the groups of archegonia. In young receptacles the rays are strongly curved downward, but they gradually straighten out if fertilization has taken place and assume a horizontal position.

On account of the strong intercalary growth which displaces the archegonia to the lower surface of the disc, the portion of the receptacle which is morphologically ventral is less extensive than at first appears. The lower surface between the groups of archegonia is ventral in character and the same thing is of course true of the lower surface of the rays, especially when these represent the middle lobes of the branch-system. Even here, however, when the rays become cylindrical through intercalary dorsal growth, the ventral surface is much less extensive than the dorsal. In *M. geminata* the ventral surface of the rays is situated on both sides of the groups of archegonia. The ventral surface is characterized by the presence of tuberculate rhizoids and slender scales, the latter being sometimes branched and strikingly different from the ventral scales of the vegetative thallus. The dorsal portion (except where the archegonia are situated) develops a complex system of air-chambers of the usual type.

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[44] Unters. über Leberm. 6: 34. 1881.

Each group of archegonia is enclosed by an involucre, which consists of a pair of membranous structures often toothed or laciniated on the margin (Figs. 2, M; 4, F, G; 8, K; etc.). Each archegonium is further protected by a campanulate pseudoperianth contracted at the mouth to a small opening. It begins its development soon after the archegonium is formed but does not reach full maturity unless fertilization has taken place. The pseudoperianth is very delicate and becomes irregularly torn when the stalk of the sporophyte elongates.

6. SPOROPHYTE

The sporophyte, as in all the Marchantiaceae, shows the usual differentiation into foot, stalk and capsule. The foot is flattened and forms a low ridge enclosing the base of the stalk. The latter is at first very short, but it elongates sufficiently at maturity to push the capsule through the calyptra and beyond the mouth of the pseudoperianth. The capsule constitutes the principal part of the sporophyte. It is nearly spherical in form and is bounded on the outside by a wall composed of a single layer of cells. These cells throughout the genus have brownish ring-like thickenings in their walls, although the rings are often incomplete. The entire cavity of the capsule is filled with spores and elaters. The spores are much smaller than in most genera of the Marchantiaceae, especially in *M. polymorpha* and its allies. In some cases a distinct border is present where the spherical face meets the three plane faces, and under these circumstances low and irregular surface lamellae are usually developed. In other cases the spores are destitute of distinct markings and become completely rounded off after the tetrads break up. The elaters are long and slender and of the usual type, showing two distinct spiral bands. At maturity the wall of the capsule splits from the apex to about the middle into an indefinite number of lobes, some of which may become further subdivided. There are apparently no very definite lines of dehiscence, the edges of the splits being irregular and jagged from projecting cells which formerly interlocked. Except for the spores, which differ in size and in the peculiarities of their walls, the sporophyte yields very few differential characters.

7. CUPULES

The characteristic gemmae of *Marchantia* have been repeatedly described. They consist of flat discoid structures, each bearing two opposite marginal growing points in shallow indentations. They are attached to the thallus by a short stalk, which joins the margin of the gemma midway between the growing points, the gemma in consequence being vertical in position. The gemmae occur in clusters on the upper surface of the thallus and are surrounded by a circular membranous outgrowth, forming a cup or cupule. Although the gemmae are very uniform throughout the genus, the cupules yield a few differences which sometimes assist in the determination of species. Two principal types occur: in the one, the margin of the cupule is simply dentate to ciliate, the teeth being sometimes scattered and sometimes close together; in the other type the margin bears a series of triangular pointed lobes, the edges of which are dentate to ciliate. As an example of the first type *M. domingensis* (FIG. 12, K) may be cited, while *M. polymorpha* (FIG. 2, N) shows the second type clearly.

III. DESCRIPTION OF SPECIES

Nees von Esenbeck[1] divided the genus *Marchantia* into the two sections *Astromarchantia* and *Chlamidium.* The first included species in which the female peduncle was "central"; the second, which was first proposed by Corda as a genus, included species in which the female receptacle was "excentric." In the first section he placed *M. polymorpha,* in the second *M. paleacea.* These two sections are retained in the Synopsis Hepaticarum, except that the first is renamed *Stellatae;* they are likewise retained by Dumortier,[2] who coined the name *Marchantiotypus* for the first section. Schiffner[3] follows the example of the Synopsis, emphasizing the radial symmetry of the female receptacle in the *Stellatae;* while Stephani bases his two groups, "a" and "b," which he does not designate by formal names, upon differences in the symmetry of the female receptacle, the first group including species with "symmetrical" receptacles and the second, species with "unsymmetrical" receptacles. It is interesting to note that he includes *M. paleacea* in his first group, although his predecessors had placed it definitely in the section *Chlamidium.*

The fact has already been brought out that the female receptacles throughout the genus are always symmetrical with respect to one plane of symmetry but never with respect to more than one. Stephani's distinction, therefore, falls to the ground, and the distinction in the position of the stalk, emphasized by Nees von Esenbeck, is not much more trustworthy. In certain species, where the two basal rays are sometimes distinctly shorter than the others and sometimes about as long, it breaks down altogether; in the first case the stalk would be "excentric," in the second "central." At the same time the sections *Astromarchantia* and *Chlamidium* represent natural groups of species and can still be maintained if different characters are used to distinguish them. In *Astromarchantia,* for example, there are no sclerotic cells in the thallus, and the rays of the female receptacle are terete, at least in the outer part; in *Chlamidium,* sclerotic cells

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[1] Naturg. Europ. Leberm. 4: 60. 1838.

[2] Bull. Soc. Bot. Belgique 13: 150. 1874.

[3] Engler & Prantl, Nat. Pflanzenfam 1^3: 37. 1893.

are normally present in the thallus, and the rays of the female receptacle are flat or convex. In both these sections the involucres (and clusters of archegonia) alternate with the rays. A third group, typified by *M. geminata,* in which the involucres are situated beneath the rays, also seems worthy of sectional rank, but since this group is not represented in America (at any rate according to our present knowledge), it need not be further considered here.

In the preparation of this paper the writer has had the privilege of examining the large collection of *Marchantiae* in the herbarium of the New York Botanical Garden (N. Y.),[4] which includes the Mitten and Underwood herbaria. This has been supplemented by the specimens in the Cryptogamic Herbarium of Harvard University (H.), which includes the Taylor and Sullivant herbaria, and by the material in the United States National Herbarium (U. S.), the private herbarium of Miss C. C. Haynes (C. C. H.), and the herbaria at Yale University (Y.), the last including the Eaton herbarium and the writer's private herbarium. Several specimens from the Montagne (M.) and Boissier (B.) herbaria, including a number of types, have likewise been available for study, through the courtesy of MM. Paul Hariot and G. Beauverd, respectively. The writer would extend his sincere thanks to all who have aided him in his work.

Key to the species

Thallus destitute of sclerotic cells: stalk of male receptacle destitute of air-chambers, with two rhizoid-furrows; rays short and broad: stalk of female receptacle with a single band of air-chambers and two rhizoid-furrows; rays mostly nine or more, terete, at least in outer part; involucre with dentate or ciliate lobes: cupules with dentate lobes, bearing papillae on outside.
Section I. ASTROMARCHANTIA.

- Epidermal pores usually surrounded by four rows of cells, never distinctly cruciate: marginal scales present; appendages of median scales irregularly crenulate or denticulate.
  - Rays of female receptacle bearing papillae; basal sinus scarcely or not at all wider than the others.
1. *M. polymorpha.*
  - Rays of female receptacle destitute of papillae; basal sinus usually distinctly wider than the others.
2. *M. plicata.*

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[4] The letters in parentheses are abbreviations used below in the citation of specimens.

Epidermal pores usually surrounded by six rows of cells, distinctly cruciate; marginal scales not present; appendages of median scales minutely and regularly crenulate or denticulate; rays of female receptacle destitute of papillae; basal sinus scarcely or not at all wider than the others.

3. *M. Berteroana.*

Thallus with sclerotic cells: epidermal pores usually surrounded by five to seven rows of cells: marginal scales not present: rays of female receptacle mostly five to nine, rarely more, flat to convex on upper surface, never terete, destitute of papillae; basal sinus usually distinctly wider than the others: cupules destitute of papillae.

Section II. CHLAMIDIUM.

Stalk of female receptacle with a single band of air-chambers.

Epidermal pores cruciate: appendages of scales entire or slightly toothed: stalk of male receptacle destitute of air-chambers, with two rhizoid-furrows; rays short and broad: stalk of female receptacle with two rhizoid-furrows; rays long and narrow; involucre with ciliate lobes: cupules with dentate lobes.

4. *M. paleacea.*

Epidermal pores not cruciate: stalk of male receptacle with a single band of air-chambers and two to four rhizoid-furrows; rays long and narrow (at maturity): stalk of female receptacle with two to four rhizoid-furrows; involucre vaguely or not at all lobed, entire to ciliate: cupules not lobed, dentate to ciliate.

Appendages of ventral scales sparingly crenulate or denticulate: rays of female receptacle short and broad, mostly eleven; involucre ciliate.

5. *M. breviloba.*

Appendages of ventral scales usually closely denticulate or ciliolate: rays of female receptacle long and usually narrow.

Epidermal pores mostly 90-130 x 70-80μ: rays of female receptacle slightly or not at all dilated at the apex, rarely emarginate; involucre crenulate to ciliate.

6. *M. domingensis.*

Epidermal pores mostly 50-70 x 40-45μ: rays of female receptacle distinctly dilated at the apex, usually emarginate; involucre entire to crenulate.

7. *M. papillata.*

Stalk of female receptacle with two bands of air-chambers and two rhizoid-furrows; rays normally five, short and rounded, not dilated; involucre dentate to ciliate or laciniate: stalk of male receptacle with two rhizoid-furrows: epidermal pores not cruciate: appendages of ventral scales entire to sparingly dentate: cupules not lobed, dentate to ciliate.

Thallus thin and very delicate.

8. *M. Bescherellei.*

Thallus usually thick and firm.

9. *M. chenopoda.*

SECTION I. **Astromarchantia**

1. MARCHANTIA POLYMORPHA L.

Marchantia polymorpha L. Sp. Plant. 1603. 1753.

Marchantia stellata Scop. Fl. Carn. 24 ed. 353. 1772.

Marchantia umbellata Scop. *l. c.* 354. 1772.

Marchantia coarctata Corda; Opiz, Beitr. zur Naturg. 647. 1828 (*nomen nudum*).

Marchantia elliptica Corda, *l. c.* 647. 1828 (*nomen nudum*).

Marchantia Kablichiana Corda, *l. c.* 647. 1828 (*nomen nudum*).

Marchantia macrocephala Corda, *l. c.* 647. 1828. (*nomen nudum*); Sturm, Deutschl. Flora **2**: 63. *pl. 17.* 1832.

Marchantia vittata Raddi, Mem. Soc. Ital. Modena **20**: 45. 1829.

Marchantia Syckorae Corda; Nees von Esenbeck, Naturg. Europ. Leberm. **4**: 97. 1838.

Marchantia oregonensis Steph.; Röll, Bot. Centralbl. **43**: 203. 1891.

Thallus pale to dark green, not glaucous, sometimes with a brownish or purplish median band on the upper surface, often more or less pigmented with purple on the lower surface, usually 0.75-1.25 cm. wide and 4-6 cm. long, repeatedly dichotomous, the successive forks usually 2 cm. or less apart; texture sometimes delicate, sometimes firm, but never leathery, margin entire or minutely denticulate; epidermis composed of cells with thin or slightly thickened walls, mostly 20-60μ long (averaging about 29μ) and 12-20μ wide (averaging about 16μ), papillae present near the margin or absent altogether; pores (with their surrounding cells) mostly 60-75μ long and 40-60μ wide, sometimes measuring as much as 90 x 65μ, surrounded usually by four rows of cells (two in each series), each row being usually composed of four cells, inner opening usually four-sided, the sides rarely concave throughout, each bounding cell usually projecting inward in the form of a rounded papilla with subparallel or converging sides, mostly with a resinous deposit; air-chambers low, more or less elongated, their boundaries indistinct when viewed through the epidermis, usually present everywhere (except close to the margin) but sometimes absent from the median region, rows of photosynthetic cells sometimes three cells long but often shorter; compact ventral tissue mostly twelve to twenty cells thick in the median portion, destitute of slime cells and sclerotic cells, the cell walls slightly thickened and showing distinct pits; ventral scales in three rows on each side of the thallus, median and marginal scales in distinct rows, laminar scales in a more indefinite row, scales often more or less pigmented with purple, the marginal scales close together though scarcely imbricated, usually projecting beyond the margin; appendages of median scales broadly orbicular, mostly 0.5-0.75 mm. long and 0.6-0.8 mm. wide, rounded to very bluntly pointed, sometimes apiculate, margin usually minutely and irregularly denticulate, sometimes (in hygrophilous forms) tending to be crenulate, cells showing a gradual decrease in size toward the margin, median cells subisodiametric, mostly 35-40μ in diameter, marginal cells mostly 20-25μ long and 14-16μ wide, sometimes smaller (10-16μ x 10μ), cells containing oil-bodies about 20μ in diameter, usually from five to ten on each appendage, restricted to submarginal (and, rarely, marginal) portions: male receptacle borne on a stalk 1-3 cm. long with two rhizoid-furrows, destitute of dorsal air-chambers, the disc mostly 0.7-1 cm. broad, shortly lobed or merely crenate, the lobes or rays mostly eight (rarely nine or ten), 2 mm. long or less, rounded at the apex with thin wavy margins, covered ventrally with densely imbricated scales in several rows: female receptacle borne on a stalk 2-7 cm. long, with two rhizoid-furrows and a single broad dorsal band of air-chambers, the disc mostly 0.8-1.3 cm. broad, deeply lobed, the lobes or rays spreading at maturity, mostly nine (sometimes ten or eleven), 3-5 mm. long, separated by subequal sinuses, terete, covered over with epidermal papillae; involucre deeply and irregularly lobed, the lobes long-acuminate and ciliate on the margins: spores yellow, 12-15μ in diameter, nearly smooth; elaters 3-5μ wide, bispiral: cupules deeply lobed, the lobes acute to acuminate, usually dentate to short-spinose on the sides, outer surface with epidermal papillae. (FIGS. 1, 2.)

Throughout the greater part of Europe and in the northern parts of Asia and North America *M. polymorpha* is the only representative of the genus and is exceedingly abundant. It grows in swamps and bogs, on rocks and walls near the ground, on banks and the sides of ditches, in gardens and greenhouses, and on the earth in fields and woods. It is perhaps most luxuriant in bogs and on steep rocky hillsides where a liberal supply of water is available. In the woods it is especially likely to occur where a fire has left a supply of charcoal behind. Toward the south other species of *Marchantia* make their appearance and *M. polymorpha* becomes less abundant. In many places it presents the appearance of being an introduced plant.

A search through the literature shows that the occurrence of *M. polymorpha* south of the equator has been doubted or denied by certain authors. Hooker,[5] for example, about fifty years ago,

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[5] See Handb. New Zealand Fl. 545. 1867.

stated that *M. tabularis* (i. e., *M. Berteroana*) was the southern representative of the northern *M. polymorpha,* thus implying that the latter species was absent from antarctic regions. Stephani[6] is even more definite when he describes the habitat of the species as "Europa, Asia et America septentrionalis." Other authors, however, cite definite stations for *M. polymorpha* from the Southern Hemisphere. It will be sufficient to mention in this connection the recent record by Schiffner[7] for Kerguelen Island, that by Kaalaas[8] for the Crozet Islands, and that by Howe[9] for South Georgia. In the opinion of the present writer the occurrence of the species in South America has been clearly established. Specimens from Ecuador, Bolivia and Patagonia have been carefully studied and have been found to agree in all essential respects with European and North American material. Specimens from Kerguelen Island, collected by the Challenger Expedition, and the specimens from South Georgia cited above have likewise been examined, and have been found equally convincing, but no further statements can be made from personal knowledge regarding the distribution of the species in other parts of the Southern Hemisphere.

On account of the abundance of *M. polymorpha* in the United States and northward it seems inadvisable to give a full list of the North American specimens which have been examined. It is enough to state that the species has been collected in Greenland and other parts of arctic America, in Alaska, in nearly every Canadian province and territory and in nearly every state of the Union. The specimens cited below are from tropical North America and from South America.

Federal District of Mexico: Cañada San Magdalena, Contreras, October, 1908, *Barnes & Land 455, 458* (Y.).

Oaxaca: near Miahuatlan, 1895, *E. W. Nelson 2530* (U. S.).

Puebla: banks along Avenida Hidalgo and path to barranca, Tezuitlan, October, 1908, *Barnes & Land 541, 542* (Y.); Santa Barbara, near Puebla, November, 1909, *Frère Nicolas 20* (Y.).

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[6] Bull. Herb. Boissier **7**: 393. 1899.

[7] Deutsch. Südpolar-Exped. **8**: 64. 1906.

[8] Nyt Mag. Naturv. **49**: 86. 1911.

[9] See Taylor, N. Sci. Bull. Mus. Brooklyn **2**: 62. 1914.

Vera Cruz: Orizaba, 1855, *F. Müller 2245* (N. Y., listed by Gottsche in Mex. Leverm. 268. 1863); Mirador, April, 1857, *C. Mohr* (N. Y.); Orizaba, January, 1892, *J. G. Smith* (N. Y.).

Jamaica: near Hardware Gap, July, 1903, *A. W. Evans 176* (Y.).

Ecuador: near Baños, *R. Spruce* (distributed in Hepaticae Spruceanae).

Bolivia: Sorata, February, 1886, *H. H. Rusby 3005* in part (N. Y., listed by Spruce as "*M.* nova species?" in Mem. Torrey Club **1**: 140. 1890).

Chile: Renca, near Santiago, February, 1901, *G. T. Hastings 318* (U. S.); Straits of Magellan, 1866-67, *A. Cunningham 105, 135* (N. Y.); Punta Arenas, November, 1895, *P. Dusén* (N. Y., first determined by Stephani as *M. Berteroana;* afterwards listed as "*M. tabularis*" in Bihang t. K. Sven. Vet.-Akad. Handl. 26^3, No. 17: 8. 1901); Cordilleras of Patagonia, February, 1897, *J. B. Hatcher* (Y., listed by the writer in Bull. Torrey Club **25**: 424. 1898); Punta Arenas, February, 1906, *R. Thaxter 64, 65* (H., Y.).

The following additional stations, recorded in the literature, are likewise of interest:

Costa Rica: Volcano of Poas, *H. Pittier 6021* (listed by Stephani in Bull. Soc. Bot. Belgique **31**: 180. 1892).

Colombia: Bogota, 1859, *A. Lindig 1700, 1701, 1717* (listed by Gottsche in Ann. Sci. Nat. Bot. V. **1**: 186. 1864).

Venezuela: Colonia Tovar, *Moritz 134* (listed, but erroneously ascribed to Colombia, in Syn. Hep. 789. 1847; also listed by Hampe in Linnaea **20**: 333. 1847).

Ecuador: Tunguragua, *R. Spruce* (listed in Trans. Bot. Soc. Edinburgh **15**: 560. 1885).

As its name implies, *Marchantia polymorpha* is an exceedingly variable species, and a full account of its numerous forms is given by Nees von Esenbeck.[10] He recognizes two principal varieties, A. *Communis* and B. *Alpestris,* and under each variety he describes a series of sub-varieties and groups of more inferior rank. A. *communis* is prevalent at lower altitudes but sometimes ascends to higher elevations in sheltered localities; B. *alpestris* is restricted to mountainous regions. A. *communis* is charac-

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[10] Naturg. Europ. Leberm. **4**: 65-71. 1838.

terized by a lax habit and by female receptacles having elongated rays and long slender stalks; B. *alpestris,* by a compact habit and by female receptacles having shorter rays and shorter and thicker stalks.

Nees von Esenbeck's varieties and subordinate groups are accepted without question in the Synopsis Hepaticarum, but later writers have largely neglected them. There are two, however, which appear from time to time in local lists and taxonomic works. One of these is A. *communis, α aquatica,* usually quoted as "var. *aquatica* Nees," and the other is B. *alpestris,* quoted as "var. *alpestris* Nees." The differences between these two so-called varieties are indeed striking. In var. *aquatica* the thallus shows a distinct median band on the upper surface usually pigmented with purple and associated with the absence of air-

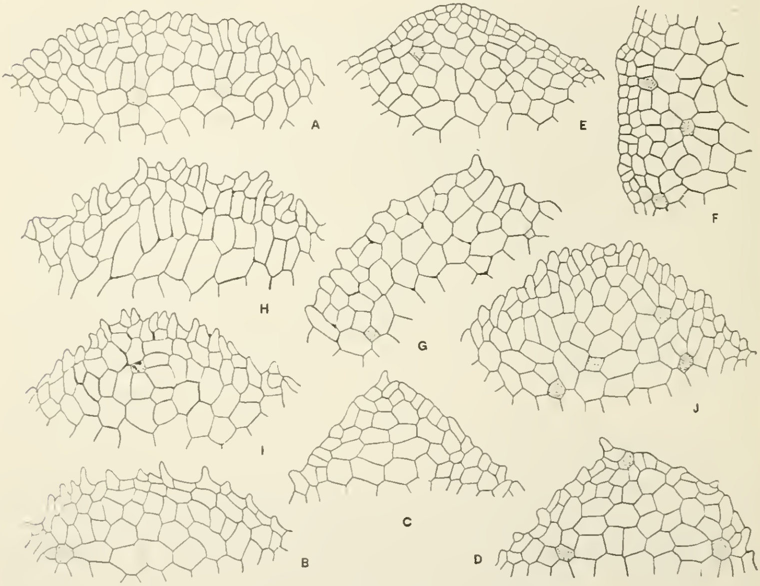

FIG. I. MARCHANTIA POLYMORPHA L.

Appendages of ventral scales, x 100; F represents the basal portion of an appendage; the other figures represent apical portions. A. Opdal, Norway, *J. Hagen,* in V. Schiffner's Hep. Europ. Exsic. *15,* type of var. *mamillata* Hagen. B-D. New Haven, Connecticut, *A. W. Evans.* E, F. Wilbraham, Massachusetts, *E. A. Chapin,* forma *aquatica.* G. Mount Hood, Oregon, *J. Röll,* type of *M. oregonensis* Steph. H. Oaxaca, *E. W. Nelson 2530.* I. Jamaica, *A. W. Evans 176.* J. Patagonia, *J. B. Hatcher.*

chambers, as Schiffner has pointed out; in var. *alpestris* the thallus is uniformly green on the upper surface, and air-chambers are everywhere present. In var. *aquatica* the margin of the thallus is entire or nearly so, and the upper surface completely lacks epidermal papillae or bears them very rarely; in var. *alpestris* the margin of the thallus is more or less denticulate from projecting cells, and epidermal papillae occur in greater or less abundance in the marginal portions. In var. *aquatica* the appendages of the ventral scales are entire or nearly so, and the spreading rhizoids are smooth; in var. *alpestris* the appendages are distinctly denticulate, and the spreading rhizoids tuberculate.

About fifteen years ago another so-called variety was distinguished by Hagen under the name var. *mamillata.* It was based on a supply of specimens collected by its author at Opdal in Norway and distributed by Schiffner in Hep. Europ. Exsic. *15.* Apparently Hagen himself did not publish his variety. Schiffner[11] did so, however, and quoted Hagen's original diagnosis, as follows: "Cellulae epidermicae et frondis dorsalis et carpocephali acute mamillosae." In commenting on this diagnosis Schiffner showed that the mamillose appearance, so strongly emphasized, was due to epidermal papillae and that these were restricted to the marginal portions of the thallus. He showed further that the female receptacles in all forms of *M. polymorpha* were mamillose in Hagen's sense. Var. *mamillata,* therefore, is based on exceedingly vague characters and has little or nothing to distinguish it from var. *alpestris.*

Although var. *aquatica* and var. *alpestris* are at first sight so distinct from each other they are connected by intermediate forms, and their differences seem to be associated with definite differences in environmental conditions. They represent, therefore, modifications rather than varieties in the taxonomic sense. Probably the most logical disposition to make of them is to regard them as forms, as Müller[12] has done, and to cite them as forma *aquatica* (Nees) K. Müll. and forma *alpestris* (Nees) K. Müll., respectively. Other forms, less distinct than these, might likewise be distinguished, but it would hardly be a profitable task to designate them by names.

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[11] Lotos 49: 93. 1901.

[12] Rabenhorst's Kryptogamen-Flora 6: 306. 1907.

Of the various synonyms quoted under *M. polymorpha* the first six require no special mention, since no question has arisen about them for many years. In fact three of these synonyms were never published adequately by their author at all, and nothing would now be known about them if Nees von Esenbeck had not included them among the synonyms of his varieties and forms of *M. polymorpha.* It is perhaps worthy of note, however, that *M. stellata* and *M. umbellata* were based on female and male specimens, respectively; showing how deep an impression the very different receptacles made on the early observers. The last three synonyms deserve a few words of comment.

The first, *M. vittata,* was described from specimens collected by its author on the island of Madeira. It is characterized by the presence of a longitudinal median band on the thallus, deep purple in color, and by a female receptacle bearing three to ten terete rays. The authors of the Synopsis Hepaticarum cite the species but do not number it, thus implying that they doubt its validity. They refer it with some question to one of the varieties of *M. polymorpha.* Although type specimens of *M. vittata* have not been available for study there can be little doubt that the species should be referred to *M. polymorpha* forma *aquatica,* on account of its median purple band. This conclusion is supported by the fact that Schiffner[13] quotes *M. polymorpha* var. *aquatica* definitely from Madeira, although he makes no mention of *M. vittata.* In fact the writer has found no references to the species later than the date of the Synopsis.

The next species, *M. Syckorae,* was based on female specimens collected by Syckora and by Corda in Bohemia. Nees von Esenbeck, without having seen specimens, gave a description of the species based on Corda's notes and figures. The features emphasized are the stellate female receptacles with terete rays and the monocarpous involucres, each consisting of two distinct membranes divided into six lanceolate acuminate lobes with serrate-dentate margins. In spite of the peculiarities in the involucre Nees von Esenbeck suspected that *M. Syckorae* was nothing but a form of *M. polymorpha,* and yet it is cited and numbered in the Synopsis Hepaticarum. Many years later Dědeček[14] definitely included *M. Syckorae* among the synonyms

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[13] Oesterr. Bot. Zeitschr. 51 : 116. 1901.

[14] Arch. Naturw. Landesdurchf. Böhmen, Bot. 5^4 : 20. 1886.

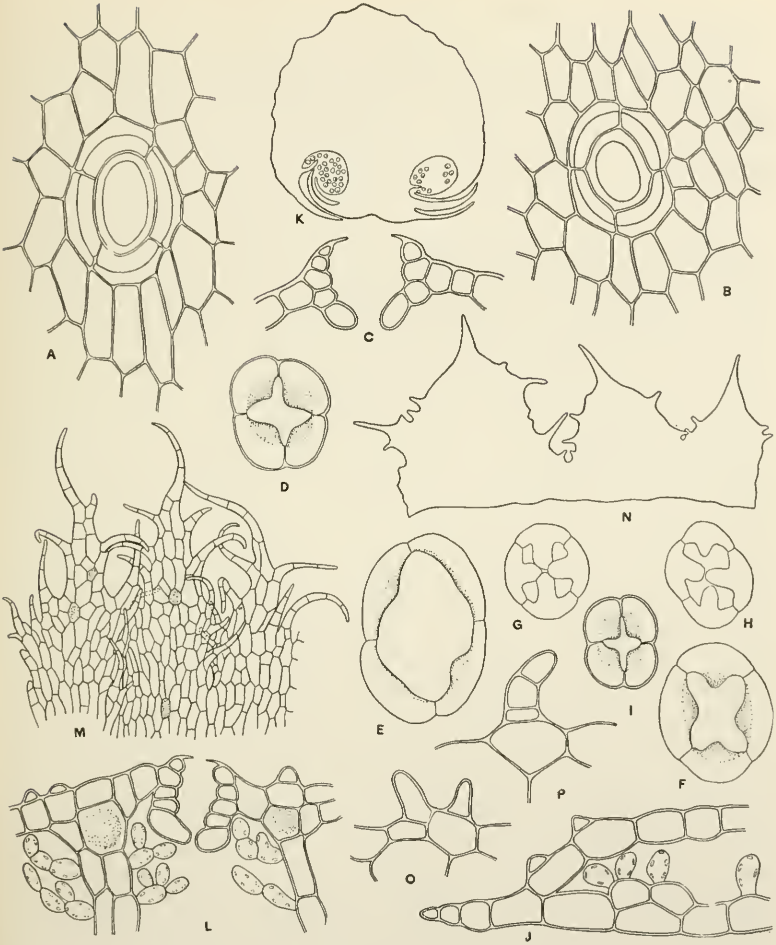

FIG. 2. MARCHANTIA POLYMORPHA L.

Anatomical details. A, B. Epidermal pores of thallus, surface view, x 225. C. Pore in cross-section, x 225. D-I. Inner openings of pores, x 225. J. Marginal portion of thallus, in section, showing two epidermal papillae, x 225. K. Stalk of male receptacle, cross-section near base, x 40. L. Female receptacle, section of part of disc, showing a pore and three epidermal papillae, x 225. M. Part of involucre, x 50. N. Part of cupule, showing three lobes, x 50. O, P. Epidermal papillae from cupule, in section, x 225. A, D. Opdal, Norway, *J. Hagen,* in V. Schiffner's Hep. Europ. Exsic. *15,* type of var. *mamillata* Hagen. B, I, J. Jamaica, *A. W. Evans.* C. Oaxaca, *E. W. Nelson 2530.* E, L-P. New Haven, Connecticut, *G. E. Nichols, A. W. Evans.* F-H. Wilbraham, Massachusetts, *E. A. Chapin,* G and H representing forma *aquatica.* K. Eberswalde, Germany, *A. W. Evans.*

of *M. polymorpha* and Schiffner[15] has since followed the same course.

The type material of the last synonym, *M. oregonensis,* consists of a series of male specimens collected on Mount Hood, Oregon, by J. Röll, in 1888. A portion of the type in the Underwood herbarium has been examined by the writer. In his original account of *M. oregonensis,* Stephani emphasizes the dentate and spinose appendages of the ventral scales and states that he knows no other *Marchantia* of temperate regions in which similar appendages occur. Howe[16] soon pointed out, however, that the appendages in many European and American specimens of *M. polymorpha* agreed with those of *M. oregonensis* and expressed the opinion that the peculiarity emphasized by Stephani had no specific significance. Fig. 1, G, drawn from *M. oregonensis,* fully supports Howe's statements. As a matter of fact the appendages are not deeply enough toothed to be called "spinose" or even "dentate"; it would be more accurate to describe them as denticulate or crenulate. In his Species Hepaticarum, published the same year as Howe's observations, Stephani[17] still maintains the validity of *M. oregonensis.* He describes the appendages as variously and remotely dentate-spinose and states that they are composed of small subequal cells. Here again Fig. 1, G brings out a slight inaccuracy, by showing that the marginal cells are distinctly smaller than the interior cells. In his critical notes he no longer emphasizes the features of the appendages but calls attention to the cruciate internal openings of the epidermal pores, stating that no other North American species has pores of this character. In the material studied by the writer no pores of a distinctly cruciate type were found; they agreed, rather, with the pores of *M. polymorpha* forma *alpestris,* as shown in Fig. 2, D. Since both of the distinctions relied upon by Stephani thus break down there seems to be no reason why *M. oregonensis* should not be considered a simple synonym of *M. polymorpha.*

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[15] Engler & Prantl, Nat. Pflanzenfam. 1^3: 37. 1893.

[16] Mem. Torrey Club 7: 62. 1899.

[17] Bull. Herb. Boissier 7: 531. 1899.

2. MARCHANTIA PLICATA Nees & Mont.

Marchantia (?) *plicata* Nees & Mont.; Montagne, Ann. Sci. Nat. Bot. II. 9: 43. 1838.

Marchantia lamellosa Hampe & Gottsche; G. L. & N. Syn. Hep. 527. 1846.

Marchantia vulcanica Spruce, Trans. Bot. Soc. Edinburgh 15: 559. 1885 (as synonym).

Thallus green, not glaucous, often more or less pigmented with purple on the lower surface, usually 1-1.5 cm. wide, often 6-8 cm. long or even more, occasionally dichotomous, the successive forks usually about 2 cm. apart, texture delicate, margin entire; epidermis composed of thin-walled cells, averaging about 20μ in length and 13μ in width, papillae absent; pores (with their surrounding cells) mostly 65-80μ long and 50-60μ wide, gradually decreasing in size toward the margin, the smallest measuring about 50 x 40μ, surrounded by three or (usually) four rows of cells (two rows being in the lower series), each row being usually composed of four cells, inner opening mostly four-sided, with slightly convex to distinctly concave sides, somewhat roughened by a resinous deposit; air-chambers low, isodiametric or somewhat elongated, their boundaries very indistinct when viewed through the epidermis, everywhere present (except close to the margin), rows of photosynthetic cells usually less than three cells long; compact ventral tissue mostly twenty to twenty-five cells thick in the median portion, destitute of slime cells and sclerotic cells, the cell-walls slightly thickened and with distinct pits; ventral scales in four to six rows on each side of the thallus, median and marginal scales in distinct rows, laminar scales in two to four indistinct rows, scales often pigmented with purple, marginal scales more or less imbricated and usually projecting beyond the margin; appendages of median scales orbicular-ovate to orbicular, mostly 0.65-0.9 mm. long and 0.65-0.8 mm. wide, somewhat narrowed toward the rounded and sometimes apiculate apex, margin minutely and irregularly denticulate or crenulate, a tooth sometimes consisting of an entire cell borne on a slightly projecting stalk cell, cells rapidly decreasing in size toward the margin, median cells mostly 70-90μ in length and 40-60μ in width, marginal cells only 25-50μ in length and 12-20μ in width, cells containing oil-bodies 15-30μ in diameter, usually about ten on each appendage, restricted to submarginal portions: male receptacle borne on a stalk 2-3 cm. long, with two rhizoid-furrows, destitute of dorsal air-chambers, the disc mostly 1-1.2 cm. broad (when well developed), deeply lobed, the lobes or rays mostly eight (sometimes nine or ten), the two basal rays usually separated by a wider sinus than the others, 2-4 mm. long, rounded at the apex and with thin wavy margins, covered ventrally with densely imbricated scales in several rows: female receptacle borne on a stalk 6-8 cm. long (when well developed), with two rhizoid-furrows and a single broad dorsal band of air-chambers, the disc mostly 1.2-1.6 cm. broad, deeply lobed, the lobes or rays spreading at maturity, mostly eleven (sometimes nine or ten), 5-6 mm. long, the two basal rays usually shorter than the others and separated by a wider sinus, rays terete, rounded at the apex, destitute of surface-papillae; involucre sometimes pigmented, deeply and irregularly lobed, the lobes long-acuminate and dentate to ciliate on the sides: spores pale yellow, 12-14μ in diameter, smooth or nearly so; elaters 3-5μ wide, bispiral: cupules deeply lobed, the lobes as in *M. polymorpha,* outer surface with epidermal papillae. (FIGS. 3, 4.)

The species seems to be confined to the high mountains of South America. The following specimens have been examined:

COLOMBIA: Boqueron, Bogota, *W. Weir* (N. Y.).

ECUADOR: Quito, December, 1847, *W. Jameson* (N. Y., listed by Mitten as *M. Berteroana* in Jour. Bot. & Kew Misc. 3: 361. 1851); Pichincha, *R. Spruce* (distributed in Hepaticae Spruceanae).

PERU: Cuzco, July, 1911, *H. W. Foote* (Y., listed by the writer as *M. lamellosa* in Trans. Conn. Acad. 18: 299. 1914); same locality, September, 1914, *Mr. & Mrs. J. N. Rose 19060* (N. Y., Y.); Ollantaytambo, May, 1915, *Cook & Gilbert 672* (U. S., Y.); San Miguel, Urubamba Valley, June, 1915, *Cook & Gilbert 1162* (U. S., Y.); Lucumayo Valley, June, 1915, *Cook & Gilbert 1321* (U. S., Y.).

BOLIVIA: between Chupé and Janacaché, province of Yungas, *A. d'Orbigny 209* (M., type); Sorata, February, 1886, *H. H. Rusby 3005* in part (N. Y., listed by Spruce as *"M. plicata* Nees?" in Mem. Torrey Club 1: 140. 1890); Songo, November, 1890, *M. Bang 910* (N. Y., U. S., Y., listed by Rusby as *M. polymorpha* in Mem. Torrey Club 4: 274. 1895); Sorata, September, 1901, *R. S. Williams 2144* (N. Y., Y.).

The type specimen of *M. lamellosa* was collected at the following locality:

VENEZUELA: Paramo de Mucuchies, *Moritz 45* (listed, but erroneously ascribed to Colombia, in Syn. Hep. 527. 1846; also listed by Hampe in Linnaea 20: 333. 1847).

The present species was based on a specimen without receptacles or gemmae. When originally described its generic position was considered doubtful, but the authors of the Synopsis saw clearly that it represented a *Marchantia* and suggested its relationship to *M. polymorpha.* Unfortunately the absence of receptacles made a positive conclusion impossible, and they were therefore obliged to place it among the species "incertae sedis." A portion of the type material from the Montagne herbarium, kindly forwarded by M. Paul Hariot, has been carefully com-

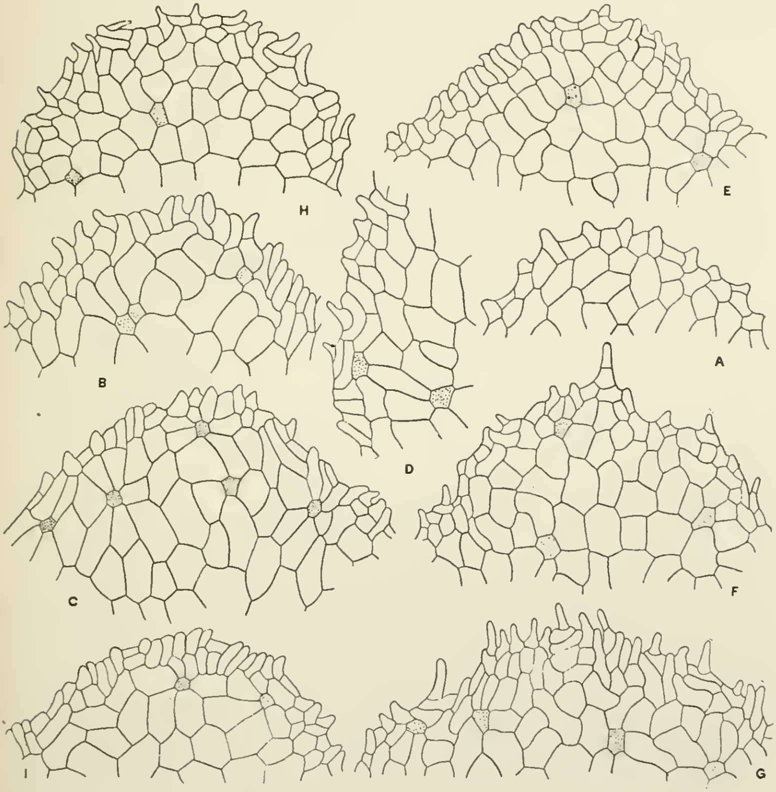

Fig. 3. Marchantia plicata Nees & Mont.

Appendages of ventral scales, x 100. D represents the basal portion of an appendage; the other figures represent apical portions. A. Ecuador, *W. Jameson.* B-D. Peru, *H. W. Foote.* E-G. Peru, *Cook & Gilbert 672, 1162, 1321.* H. Bolivia, *A. d'Orbigny,* type. I. Bolivia, *M. Bang 910.*

pared with the other specimens cited above. The epidermal cells are unusually delicate and are slightly smaller than the averages given, measuring perhaps $18 \times 10\mu$, but the epidermal pores and ventral scales agree very closely with those of the other specimens. It is clear, therefore, in the writer's opinion, that all the specimens cited represent the same species.

The original material of *M. lamellosa* has not been available for study, but the specimen from Colombia, listed above, was referred to this species by Mitten and is evidently the same as the specimens from Ecuador, Peru, and Bolivia. On the basis of this specimen and the full description in the Synopsis Hepaticarum, *M. lamellosa* is here reduced to synonymy. It should be noted, however, that Stephani considers it valid, so that this reduction is perhaps unwarranted. He ascribes to the species cruciate pores and papillate rays on the female receptacles. In one of the Peruvian specimens, No. 672, some of the pores are as cruciate as those of *M. oregonensis,* but other pores are not cruciate at all, so that a considerable range of variation is present. The lack of receptacles in these specimens makes it impossible to determine whether papillate rays are associated with pores which approach the cruciate condition, although the constant absence of papillae in all the fruiting specimens studied, which are clearly the same as No. 672, makes such an association improbable. Even if papillae occasionally occurred they would hardly afford a basis for a specific separation. Stephani cites *M. lamellosa* from the type locality and also from Ecuador (Chimborazo and Altar, *Hans Meyer*).[18] He cites *M. plicata* from the type locality, from Ecuador (Quito, *Ortoneda, Spruce*), from Colombia (*Lindig*), and from Venezuela (Merida, *Moritz*). It is probable that the Lindig specimens are those listed by Gottsche under *M. polymorpha* and that the Moritz specimens are those doubtfully referred by Hampe[19] to *M. Berteroana.* Of course, in the absence of the specimens themselves, this matter can not be definitely decided.

Although *M. plicata* and *M. polymorpha* are closely related species it is usually easy to distinguish them. Some of the differential characters, however, are vague and subject to variation. When *M. plicata* is well developed the thallus and the

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[18] See Meyer, In den Hoch-Anden von Ecuador 517. Berlin, 1907.

[19] Linnaea 20: 333. 1847.

sexual receptacles are larger than in the most robust forms of *M. polymorpha,* approaching or equalling in this respect the more southern *M. Berteroana.* The thallus also shows a tendency to fork at infrequent intervals, so that it presents the appearance of being more elongated than in *M. polymorpha.*

The lack of epidermal papillae on the rays of the female receptacle seems also to be a distinguishing character. In fact papillae of this type are restricted to the outer surface of the cupules. In spite of the large size of the thallus the epidermis of *M. plicata* is unusually delicate in texture and the air-chambers unusually low.

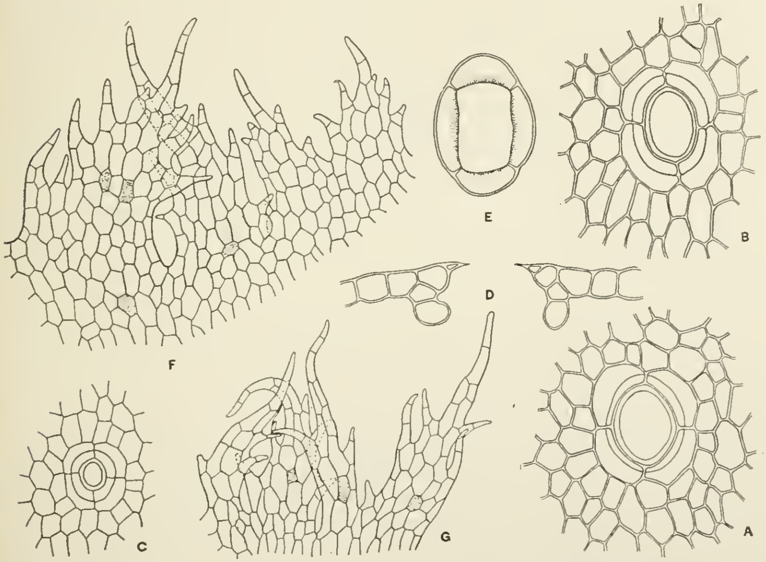

FIG. 4. MARCHANTIA PLICATA Nees & Mont.

Anatomical details. A-C. Epidermal pores of thallus, surface view, x 225. D. Pore in cross-section, x 225. E. Inner opening of pore, x 225. F, G. Two parts of the same involucre. A, B, D, E. Peru, *Cook & Gilbert 1162, 1321.* C. Bolivia, *A. d'Orbigny,* type. F, G. Colombia, *W. Weir.*

The ventral scales exhibit considerable variation with respect to size and amount of pigmentation. In typical examples the ventral surface is almost covered with purple scales, but this condition is by no means constant; the scales may only partially cover over the surface and the pigmentation may be very slight.

The crowded marginal scales, however, visible from above, seem to be a constant feature, although these scales may not be any more conspicuous than in *M. polymorpha.* The appendages of the ventral scales, as in other species, yield some of the most important characters (FIG. 3). The small marginal cells are exceedingly irregular, forming various angles with the periphery of the appendage and often projecting in the form of blunt teeth. Frequently a projecting cell will be borne on a broader basal cell, a two-celled tooth of a peculiar type being thus produced. Usually the difference in size between the marginal cells and the interior cells is very marked, but the difference is less when the appendages are poorly developed (FIG. 3, A). The apices of the appendages are especially variable. In some cases a distinct apical tooth two cells long is present, making the appendage apiculate (FIG. 3, F); in other cases the apical tooth is hardly distinguishable from the neighboring teeth (FIG. 3, G); in still other cases there is no indication whatever of an apical tooth (FIG. 3, H, I).

When the appendages are compared with those of *M. polymorpha* they are found to have many features in common. In both species they are similar in form and show a decrease in the size of the cells in passing from the middle to the margin; in both species the apex is variable and the margin is normally denticulate. In *M. plicata,* however, the cells are larger and the decrease in size more abrupt, the denticulation tends to be more pronounced, owing largely to the frequency of two-celled teeth, and the marginal cells tend to be more irregular. Although these differences are of a comparative nature and subject to variation, they will usually be found serviceable in separating the species.

3. MARCHANTIA BERTEROANA Lehm. & Lindenb.

Marchantia Berteroana Lehm. & Lindenb.; Lehmann, Pug. Plant. 6: 21. 1834.

Marchantia tabularis Nees, Naturg. Europ. Leberm. **4**: 71 (footnote). 1838.

Marchantia cephaloscypha Steph. Hedwigia **22**: 51. 1883.

Thallus green or bluish green, sometimes glaucous, often more or less pigmented with purple or brownish near the margin and on the lower surface, usually 1-1.5 cm. wide and 6-8 cm. long, variously dichotomous, the successive forks sometimes 2-3 cm. apart but often closer together, texture usually tough and leathery, margin entire or minutely and irregularly denticulate or crenulate, more or less plicate; epidermis composed of cells with thin or slightly thickened walls, mostly 20-60μ long (averaging about 32μ) and 16-24μ wide (averaging about 19μ), papillae absent; pores (with their surrounding cells) mostly 60-80μ long and 50-60μ wide, surrounded usually by six rows of cells (three in each series), each row being usually composed of four cells, inner opening cruciate, the bounding cells commonly four (rarely three or five), slightly roughened; air-chambers of medium height, usually a little longer than broad, their boundaries indistinct when viewed through the epidermis, present everywhere, rows of photosynthetic cells usually three or four cells long; compact ventral tissue about twenty-five cells thick in the median portion, destitute of slime cells and sclerotic cells, usually thin-walled and with indistinct pits; ventral scales in two rows, median and laminar, no marginal scales being present, scarcely imbricated, pale or brownish; appendages of median scales orbicular-ovate to broadly orbicular, usually somewhat narrowed toward the rounded apex, mostly 0.6-1 mm. in length and about the same in width, margin minutely and often regularly crenulate or denticulate from projecting cells, cells showing an abrupt decrease in size toward the margin, median cells mostly 60-85μ long and 20-40μ wide, marginal cells (in one, two, or three rows) mostly 12-20μ long and 8-12μ wide, cells containing oil-bodies about 20μ in diameter, about five on each appendage, restricted to submarginal portions: male receptacle borne on a stalk 1-5 cm. long with two rhizoid-furrows, destitute of dorsal air-chambers, the disc about 1 cm. in diameter, more or less deeply lobed when well developed, the lobes or rays mostly eight, usually 2-3 mm. long, rounded at the apex and with thin wavy margins, covered ventrally (except in the marginal portions) with imbricated scales in several rows, sinuses usually subequal in width: female receptacle borne on a stalk mostly 3-8 cm. in length, with two rhizoid-furrows and a broad dorsal band of air-chambers, the disc mostly 0.8-1 cm. broad, deeply lobed, the lobes or rays spreading at maturity, mostly nine, 2-3 mm. long, separated by subequal sinuses, terete, rounded, destitute of epidermal papillae; involucre much as in *M. polymorpha:* spores brownish yellow, mostly 8-10μ in diameter, smooth; elaters about 5μ wide, bispiral: cupules deeply lobed, the lobes as in *M. polymorpha,* outer surface with epidermal papillae. (Fig. 5.)

A widely distributed species, restricted (according to our present knowledge) to the Southern Hemisphere. The following South American specimens have been examined:

ARGENTINA: Buenos Aires, without date, *Twiedie* (H.); La Plata, collector and date unknown (H.).

CHILE: Concepcion, November, 1905, *R. Thaxter, 16, 66* (H., Y.); Port Corral, January, 1906, *R. Thaxter, 62, 74, 92* (H., Y.); Hermite Island, Cape Horn, 1843, *J. H. Hooker* (H.).

JUAN FERNANDEZ: without definite localities, 1830, *C. Bertero* (H., N. Y.), type); *H. N. Moseley* (N. Y., Challenger Expedition); 1901, *G. T. Hastings 218* (N. Y., U. S.).

FALKLAND ISLANDS: without definite locality, 1843, *J. D. Hooker* (H.).

The following specimens from other regions have likewise been examined:

ST. HELENA: without definite locality or date, *J. Melliss* (N. Y.); 1844, *J. D. Hooker* (N. Y.); February, 1890, *W. H. & A. H. Brown 264* (U. S., United States Eclipse Expedition to Western Africa, listed as *M. tabularis* by Stephani in Bull. Herb. Boissier 7: 1899).

CAPE COLONY: Table Mountain, *F. Krauss* (N. Y.); Montague Pass, *J. C. Bruetel* (N. Y.); without definite localities or dates, *W. H. Harvey* (N. Y.), *Capt. Rabenhorst* (Y.).

AUSTRALIA: Victoria, *Robertson 633* (N. Y.); Swan River, 1846, *J. Drummond* (H.); without definite locality, *F. von Müller* (H., Y.).

TASMANIA: without definite localities, 1823, *Lawrence* (N. Y.); 1838, *R. Gunn* (N. Y.); no date, *W. Archer* (N. Y.); western mountains, no date, *Lawrence* (N. Y.); Tasman Peninsula, roadside from Long Bay to Tarrand, February, 1899, *1956b* (H., distributed by E. Levier as *M. cephaloscypha*).

NEW ZEALAND: without definite localities, no date, *A. Sinclair* (N. Y.); 1881, *E. Craig* (Y.); no date, *J. Remy* (N. Y., distributed by C. Roumeguere as *M. nitida*); Waikehi, *A. Sinclair* (H.); Raipara, 1850, *S. Mossmann* (H.); Point Cooper, collector and date unknown (N. Y.); North Island, 1904, *W. A. Setchell 32* (Y.); Lord Auckland's Group, November, 1840, *J. D. Hooker* (H.); Campbell Island, November, 1840, *J. D. Hooker* (H.); without definite locality, date, or collector's name (B., type of *M. cephaloscypha*).

Other South American stations of interest, cited in the literature, are the following:

ARGENTINA: Staten Island, Tierra del Fuego, *C. Spegazzini* (listed by Massalongo in Nuovo Gior. Bot. Ital. **17**: 258. 1885).

CHILE: San Augustin and San Francisco del Monte, *F. J. F. Meyen* (listed in Syn. Hep.); Otway Gulf, *P. Savatier* (listed and figured as *M. tabularis* by Bescherelle and Massalongo in Compt. Rend. Miss. Sci. Cap Horn **5**: 247. *pl. 4, f. 17*. 1889).

The identity of *M. Berteroana* and *M. tabularis* was established by Schiffner, although Nees von Esenbeck, in proposing *M. tabularis,* recognized its close relationship with the older species. *M. Berteroana* was based on specimens collected by Bertero on the island of Juan Fernandez, while the type material of *M. tabularis* came from Table Mountain in Cape Colony. The Synopsis Hepaticarum recognizes both species; it cites *M. Berteroana* from Chile and St. Helena, as well as from the type locality, and gives Devil's Peak in Cape Colony as a second station for *M. tabularis.* Under *M. Berteroana* three varieties are recognized: α, from Juan Fernandez, *β, biflora,* from Chile; and *γ, anactis,* from Juan Fernandez and St. Helena. In α, according to the description, the rays of the female receptacle are one third longer than the involucres, the latter enclosing three to five flowers; in β, the rays are the same as in α but are fibrillose, while the involucres usually contain only two flowers; in γ, the rays do not project beyond the involucre at all.

In discussing *M. Berteroana,* Schiffner[20] points out that the differences relied upon by Nees von Esenbeck in separating *M. tabularis* are of no significance and that the same thing is true of the differential characters assigned to the three varieties of *M. Berteroana.* He points out further certain mistakes in the original description of this species and also in the description given in the Synopsis. He based his conclusions on a large series of original and authentic specimens, several of which have been studied by the present writer, and there seems to be no reason for doubting the accuracy of his observations.

Schiffner was apparently the first to give a satisfactory description of the scale appendages in *M. Berteroana.* He calls attention to the finely crenulate margin, to the border of very small cells in one or two rows, and to the sharp distinction in size between

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[20] Oesterr. Bot. Zeitschr. **46**: 41-44, 100-103. 1896.

the marginal cells and the cells which adjoin them. To *M. polymorpha* he assigns appendages which are minutely but sharply denticulate, and adds that the cells gradually increase in size in passing from the margin to the median portion. In most cases the distinctions given by Schiffner apply very definitely, but in the forma *aquatica* of *M. polymorpha* (FIG. 1, E, F) the appendages are usually destitute of distinct denticulations, the

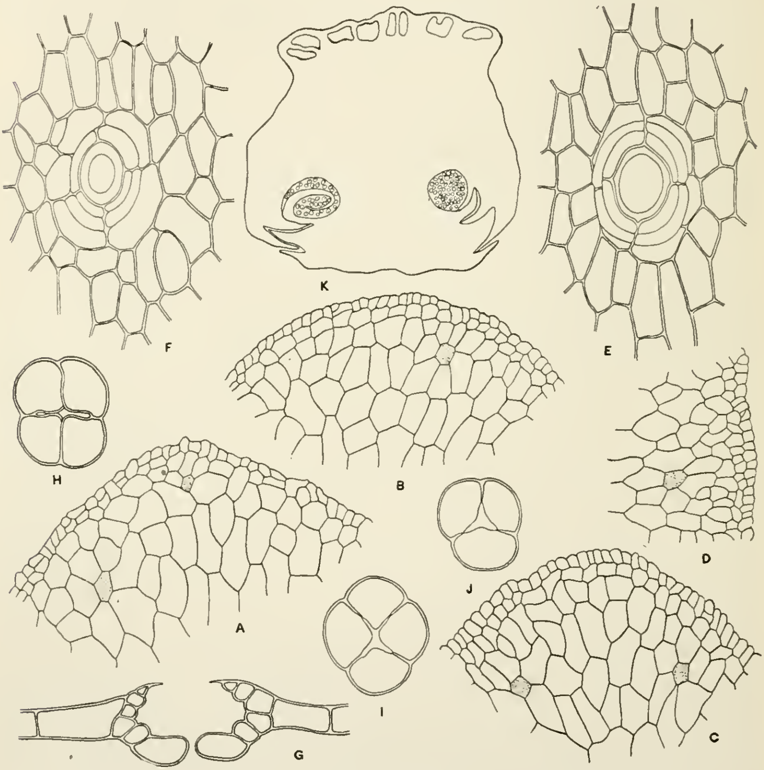

FIG. 5. MARCHANTIA BERTEROANA Lehm. & Lindenb.

Appendages of ventral scales and other anatomical details. A-D. Appendages of ventral scales, x 100: D represents the basal portion of an appendage; the other figures represent apical portions. E, F. Epidermal pores of thallus, surface view, x 225. G. Pore in cross-section, x 225. H-J. Inner openings of pores, x 225. K. Stalk of female receptacle, cross-section near base, x 40. A. Juan Fernandez, *G. T. Hastings 218.* B, E, G, H. Chile, *R. Thaxter 66.* C, D. Cape Colony, *Capt. Rabenhorst.* F, I-K. Australia, *F. von Müller.*

entire or crenulate margin closely simulating that of *M. Berteroana.* Even here, however, the gradual decrease in the size of the cells as the margin is approached is in contrast to the abrupt decrease found in *M. Berteroana.*

In habit and in general appearance *M. Berteroana* resembles *M. polymorpha* very closely, and it is not surprising that the early observers failed to distinguish it as a species. The thallus, to be sure, is more robust, it tends to be thicker and more leathery than in the northern species, and the rays of the female receptacle tend to be shorter, but these differences are not always pronounced. There are, however, several distinctive features, in addition to the scale-appendages, which deserve to be emphasized. In the first place *M. Berteroana* seems to lack marginal scales altogether. Sometimes the laminar scales form a vague double row, some of the scales being nearer the margin than the others, but even under these conditions there is quite a little space between the outermost scales and the margin. In most cases the row of laminar scales is more definite and the region without scales is consequently wider. In *M. polymorpha* the marginal scales are apparently always present, although they do not always attain the same degree of development. *M. Berteroana* is further distinguished by its cruciate epidermal pores, and by its lack of epidermal papillae on both thallus and female receptacle. The lack of marginal scales, the crenulate scale appendages, and the cruciate pores will serve also to distinguish *M. Berteroana* from *M. plicata,* although there is no evidence as yet that their ranges overlap.

The writer has fortunately been able to examine an original specimen of *M. cephaloscypha.* The species was based on gemmiparous material with young female receptacles collected somewhere in New Zealand, neither the date nor the collector's name being given. A few years later Stephani[21] referred to his species a series of specimens from various parts of Australia and was able to add the characters derived from mature female receptacles and ripe capsules. In his Species Hepaticarum,[22] in addition to New Zealand and Australia, he cites Tasmania, Fuegia, Patagonia and Chile as localities for the plant and notes that it is not

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[21] Hedwigia **28**: 265. 1889.

[22] Bull. Herb. Boissier 7: 391. 1899.

rare. Still later he[23] quotes stations on Juan Fernandez, the Chilean island of Chiloé, and the Falkland Islands. He therefore gives the species a very extensive distribution in the Southern Hemisphere. It has already been noted that he does not credit *M. Berteroana* to America at all, the only specimens which he cites being from Cape Colony, the Transvaal, and the island of St. Helena.

In his descriptions of *M. cephaloscypha* Stephani emphasizes the cruciate pores, the large scale-appendages bordered with very small cells, the nine-rayed female receptacles with smooth and terete rays, the eight-lobed male receptacles, and the spinose cupules. It will at once be noted that all of these features are found in *M. Berteroana.* There are, however, certain discrepancies between Stephani's descriptions and the account of *M. Berteroana* given above. He states, for example, in his original description that the cupules are contracted at base and apex and that the ventral scales are in three rows on each side of the thallus, one row of tongue-shaped scales being close to the margin. In his last description he still emphasizes the contracted apices of the cupules but makes no allusion to the three rows of ventral scales, perhaps because he has already given a triseriate arrangement of the scales as a generic character.

The type specimen shows that some of the specific characters emphasized by Stephani are based on misconceptions. The single cupule present, for example, is contracted at the throat but flares widely at the mouth. Even if the mouth itself were contracted this condition might easily be due to immaturity and figures of a young cupule of *M. polymorpha* by Mirbel,[24] in which the mouth is distinctly contracted, fully support this view. There are, moreover, no marginal ventral scales, although the margin, being irregularly crispate, produces the effect of scales. The appendages of the median scales are slightly crenulate and show one or two rows of marginal cells, the rays number nine in the female receptacle and are destitute of papillae, the surface of the cupule bears numerous papillae, and the pores are of the cruciate type. The writer therefore feels justified in considering *M. cephaloscypha* a simple synonym of *M. Berteroana.*

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[23] Kungl. Svensk. Vetensk.-Akad. Handl. 46^9: 5. 1911.

[24] Mém. Acad. Sci. 13: *pl. 4, f. 31, 32.* 1835.

SECTION II. **Chlamidium**

4. MARCHANTIA PALEACEA Bertol.

Marchantia paleacea Bertol. Opus. Sci. Bologna 1: 242. 1817.
Marchantia papillata β italica Raddi, Mem. Soc. Ital. Modena 19: 44. 1823.
Fimbriaria paleacea Corda; Opiz, Beitr. zur Naturg. 648. 1828.
Fegatella Michelii Corda, *l. c.* 649. 1828 (according to Nees von Esenbeck).
Marchantia nepalensis Lehm. & Lindenb.; Lehmann, Pug. Plant 4: 10. 1832.
Marchantia nitida Lehm. & Lindenb. *l. c.* 11. 1832.
Marchantia squamosa Raddi; Lehm. & Lindenb. *l. c.* 12. 1832 (as to the East Indian plant).
Marchantia tholophora Bisch. Nova Acta Acad. Leop.-Carol. 17: 989. 1835.
Marchantia calcarata Steph. Bull. Herb. Boissier 5: 98. 1897.
Marchantia planipora Steph. *l. c.* 98. 1897.

Thallus pale green, often glaucous, sometimes more or less pigmented with purple, especially near the margin and on the lower surface, usually 0.5-0.8 cm. wide and 2-4 cm. long, repeatedly dichotomous, the successive forks usually 1 cm. or less apart; texture firm but scarcely leathery, margin entire; epidermis composed of cells with more or less thickened walls, sometimes in two layers, mostly 35-70μ long (averaging about 43μ) and 20-40μ wide (averaging about 30μ), papillae absent; pores (with their surrounding cells) mostly 70-90μ long and 65-85μ wide, sometimes measuring as much as 140 x 100μ, surrounded usually by six (or seven) rows of cells (three in the upper and three or four in the lower series), each row being usually composed of four cells or the innermost row of the upper series of from four to eight cells, inner opening cruciate, the bounding cells smooth; air-chambers usually high, isodiametric or slightly elongated, their boundaries indistinct when viewed through the epidermis, present everywhere, rows of photosynthetic cells often six or seven cells long but sometimes shorter; compact ventral tissue mostly twenty to thirty cells thick in the median portion, the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells usually distinct, scattered, ten to twenty in a cross-section of thallus, more abundant in median region but not confined to this, slime-cells sometimes lacking, sometimes more or less abundant, especially toward the margin; ventral scales in two distinct rows, the laminar scales alternating with the median and only a little nearer the margin; appendages of median scales oblong, ovate, or ovate-orbicular, mostly 0.6-0.75 mm. long and 0.45-0.6 mm. wide, usually narrowed toward the rounded, obtuse or acute apex, margin entire or vaguely and irregularly denticulate or dentate, rarely with a basal lobe, cells showing a slight and gradual decrease in size toward the margin, median cells isodiametric to distinctly longer than broad, mostly 25-60μ long and 20-30μ wide, marginal cells mostly 30-40μ long and 12-20μ wide, very irregular, the long axis sometimes parallel with the margin and sometimes at an angle with it, cells containing oil-bodies sometimes absent altogether, when present about 20μ in diameter, one to three or more in number and indefinite in position: male receptacle borne on a stalk 5-7 mm. high, with two rhizoid-furrows, destitute of dorsal air-chambers, the disc 5-6 mm. broad, very shortly or sometimes (according to Schiffner) more deeply eight- (to twelve-) lobed, the lobes or rays rounded and with a thin wavy margin, ventral scales restricted to middle portion of disc: female receptacle borne on a stalk 2-4 cm. high, with two rhizoid-furrows and a single broad dorsal band of air-chambers, the disc about 0.5 cm. broad, usually nine-lobed, the lobes or rays spreading at maturity, 0.8-1.2 mm. long, separated by subequal sinuses or with the deep sinus between the basal ray broader than the others, flat, dilated at the truncate or emarginate apex, disc with a median hemispherical or papilliform protuberance about 0.5 mm. in diameter and nine distinct ridges corresponding with the rays; involucre much as in *M. polymorpha:* spores brownish yellow, about 34μ in diameter, with a narrow hyaline margin about 2μ wide, outer face bearing a series of low lamellae sometimes forming an indistinct reticulum; elaters mostly 6-8μ wide, bispiral; cupules with toothed lobes much as in *M. polymorpha,* but lacking epidermal papillae. (Figs. 6-8.)

A widely distributed species in tropical and subtropical regions. The following North American specimens have been examined:

Arizona: Huachuca Mountains, 1910, *L. N. Gooding 824* (N. Y.).

Puebla: Puebla, 1906, *Frère Arsène* (N. Y.); Honey Station, October, 1908, *Barnes & Land 507* (Y.); banks along Avenida Hidalgo and path to barranca, Tezuitlan, *Barnes & Land 544* (Y.); Santa Barbara, near Puebla, November, 1909, *Frère Nicolas 3* (Y.).

Vera Cruz: Orizaba, 1855, *F. Müller 2245* in part (N. Y.); walls of Lost River sink, Orizaba, November, 1908, *Barnes & Land 668* (Y.).

Guatemala: Coban, Alta Verapaz, 1310 m. alt., 1892, *H. von Tuerckheim 4960* (N. Y.).

Cuba: without definite locality, *C. Wright* (H., N. Y., Y., distributed in Hep. Cubenses as *M. domingensis*); La Perla, Oriente, 600-660 m. alt., February, 1911, *J. A. Shafer 9096* (N. Y., Y.); Monte Verde, Oriente, on walls of the ruined mansion of Lescaille, where Wright lived, August, 1913, *Brother Leon 4089* (N. Y.).

Jamaica: Whitfield Hall Plantation, December, 1896, *W. Harris 11063* in part (N. Y.); along path from Cinchona to Clyde River, July, 1903, *A. W. Evans 14* (Y.); vicinity of Cinchona, February, 1905, *C. E. Cummings 29, 31* (N. Y., Y.); Mabess Road, May, 1906, *D. S. Johnson 46* (Y.); Morce's Gap and vicinity, August, 1906, *A. W. Evans 462* (Y.).

The following specimens from Europe, the Azores, and Asia have likewise been examined:

France: Mentone, November, 1864, *I. T. Moggridge* (N. Y.).

Italy: without definite locality, *G. Raddi* (N. Y., labeled *M. papillata β italica*); Monte Oliveto, near Pegli in Liguria, May, 1851, *L. Caldesi* (N. Y.); near Genoa, May, 1855, *G. de Notaris* (N. Y., also distributed in Rabenhorst's Hep. Europ. *27*); Ripoli, near Florence, May, 1899, *E. Levier* (Y., Micheli's locality); Trezzo sull' Adda, province of Milan, July, 1899, *F. A. Artaria* (C. C. H.; also distributed in Schiffner's Hep. Europ. Exsic. *13*).

Azores: San Miguel 1865, *F. D. Godman* (N. Y.); August, 1894, *C. S. Brown, 365* (N. Y.), *366* (N. Y.); August, 1894, *W. Trelease 1320* (N. Y.), *1321* (N. Y.); May and June, 1898, *B. Carriero 713, 718* (Y.). The specimens collected by Brown and Trelease have been listed by Trelease in Rept. Missouri Bot. Gard. **8**: 187. 1897. The following specimens, however, although listed under *M. paleacea,* should be referred to *Conocephalum conicum* (L.) Dumort.: *C. S. Brown 367* (from San Miguel), *368* (from Fayal), *369* (from Pico) and *W. Trelease 1317* (from Terceira). A specimen collected by B. Carriero at Furnas, in 1888, has been reported by Schiffner in Oesterr. Bot. Zeitschr. **51**: 116. 1901.

China: Szechwan, no date, *E. Faber 1110* (N. Y.).

India (including Nepal): Northwest Himalayas, no date, *H. Falconer 1073* (N. Y., U. S., Y.); *J. F. Royle* (N. Y.); Nepal, *N. Wallich* (N. Y., types of *M. nepalensis, M. nitida,* and *M. squamosa*); Shagak Valley, 1847, *T. Thomson 1661, 1663* (N.

Y.); Kumaon, *Strachey & Winterbottom* (N. Y., listed by Strachey, as *M. paleacea* and *M. nitida,* in Cat. Pl. Kumaon, 234. 1906); Musooric (Northwest Himalayas), Arnigadh, December, 1895, *W. Gollan 210* (N. Y., Y., distributed by E. Levier as *M. nepalensis*).

Japan: Nagasaki, April-May, 1875, *R. Oldham* (N. Y., listed by Mitten, as *M. nitida,* in Trans. Linn. Soc. II. Bot. 3: 205. 1891); Kigo, August, 1877, *Ahlberg* (B. type of *M. planipora*); Yamakita, Spidzuoka, May, 1899, *Abbé Faurie* (Y., distributed as *M. nitida* in Hép. du Japon *82*); Tokyo, May, 1897, *K. Miyake 40* (C. C. H., Y., determined as *M. diptera*); Kuzunmura, August, 1898, *K. Okudaira 26* (C. C. H); Kyoto, August, 1900, *K. Miyake* (Y., determined as *M. planipora*); Mt. Futatabisan, near Kobe, April, 1903, *Abbé Faurie* (Y., distributed as *M. diptera* in Hép du Japon *1268*); Jigokudani, May, 1903, *S. Okamura* (C. C. H.); Kochi, May, 1904, *S. Okamura* (C. C. H.); Kanagawa, Sagami, no date, *M. Maeda 41* (Y.); Osaka, May, 1905, *S. Okamura* (C. C. H.); Ikku, May, 1908, *S. Okamura* (C. C. H.).

Java: Mt. Pangerango, April, 1894, *V. Schiffner* (Y., distributed as *M. nitida* in Iter Ind. *59*).

Within recent years *M. paleacea* has been recorded from the Caucasus, from Dalmatia, Spain and Portugal, and from Morocco. Although the writer has seen no specimens from any of these countries, there can be little doubt regarding the correctness of the determinations. Some of the records for *M. nitida,* however, are open to suspicion. This species has been reported from the Philippines, Tahiti, Samoa and New Zealand, as well as from the Fiji and Hawaiian Islands. Specimens from the first four of these localities, which have been determined as *M. nitida,* have been examined and are, in the writer's opinion, referable to other species. No specimens from either the Fiji or the Hawaiian Islands have been available for study.

Although *M. paleacea* is here reported from a number of North American localities it is remarkable that there are no earlier records for the species from America. In fact the only trustworthy records for *M. tholophora,* here considered a synonym of *M. paleacea,* are the following:

Oaxaca: near Oaxaca, *Sommerschu* (the type-locality); Chinantla, *F. Liebmann* (listed by Gottsche in Mex. Leverm. 1863).

It has already been noted that *M. paleacea* was distinguished by the Florentine botanist Micheli as long ago as 1729. His figure brings out clearly the general habit of the plant and many of the features of the cupules and female receptacles. The rays of the latter are shown to be flat at their extremities, and the center of the disc is marked by a distinct rounded elevation. In the only receptacles where the rays can be counted ten or eleven are represented, but one receptacle in profile shows only four rays, indicating that sometimes at least fewer than ten rays were present in the material figured. It is now admitted that the

Fig. 6. Marchantia paleacea Bertol.

Ventral scales, x 27. A-G represent median scales (with appendages); H-O, laminar scales (without appendages). A-D, H-J. Italy, *F. A. Arteria,* in V. Schiffner's Hep. Europ. Exsic. 13. E, K. Vera Cruz, *Barnes & Land 668.* F, L. Cuba, *C. Wright,* in Hep. Cubenses, as *M. domingensis.* G, M-O. Java, *V. Schiffner,* in Iter Ind. 59, as *M. nitida.*

normal number of rays is nine. Micheli, in his description, emphasizes the glaucous color of the thallus. The species is still abundant in the vicinity of Florence, where it was originally collected, and specimens from this region are among those cited above.

Bertolini's description is drawn from female plants, and he distinctly states that both male receptacles and cupules were unknown to him. His material came from the vicinity of Chiavari in Liguria. He adds very little to Micheli's account, but gives the number of rays definitely as ten and notes that their extremities are obtuse or almost truncate. Apparently his species was not very widely known at first because neither Raddi nor Lehmann and Lindenberg make any allusion to it. Raddi's *M. papillata β italica* was based on Micheli's description and figure and on specimens collected at Micheli's original locality. *M. nepalensis* and *M. nitida* were based on material collected by Wallich in Nepal and *M. squamosa* on two specimens, one collected by Wallich in Nepal and the other by Raddi in Brazil.

In 1835 Taylor[25] accepted *M. paleacea* as a species and referred to it not only the Italian specimens originally cited but also specimens from Nepal collected by Wallich. Although there seem to be no specimens in the Taylor herbarium labeled *"M. paleacea"*, there are two with a manuscript name of Taylor's from the Wallich collection. In one case *M. nitida* is given as a synonym and *M. squamosa* as a doubtful synonym, so that these specimens probably represent the *M. paleacea* of Taylor's paper. Unfortunately his figures and description do not correspond in all respects with authentic specimens of the species in question and have therefore given rise to considerable confusion. The most marked discrepancy is in his account of the female receptacles, where the number of involucres is given as four to six, instead of eight (corresponding with nine rays), but an error of this sort might easily be made if poor material was examined. Taylor's specimens are, indeed, imperfectly developed, but they show the thallus characters of *M. paleacea* very clearly, and his determination may therefore be considered correct.

In proposing *M. tholophora* as a species Bischoff makes no mention of *M. paleacea* or of the various species based on

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[25] Trans. Linn. Soc. 17: 378. *pl. 12, f. 3.* 1835.

Wallich's specimens, so that the works of Bertolini and of Lehmann and Lindenberg may have been unknown to him. His description was drawn from Sommerschu's material, collected near Oaxaca, Mexico, and is unusually detailed. The species is recognized as valid by subsequent writers, the authors of the Synopsis Hepaticarum placing it next to *M. nitida* and Stephani following their example. The original material has not been available for study. Bischoff's description, however, and the

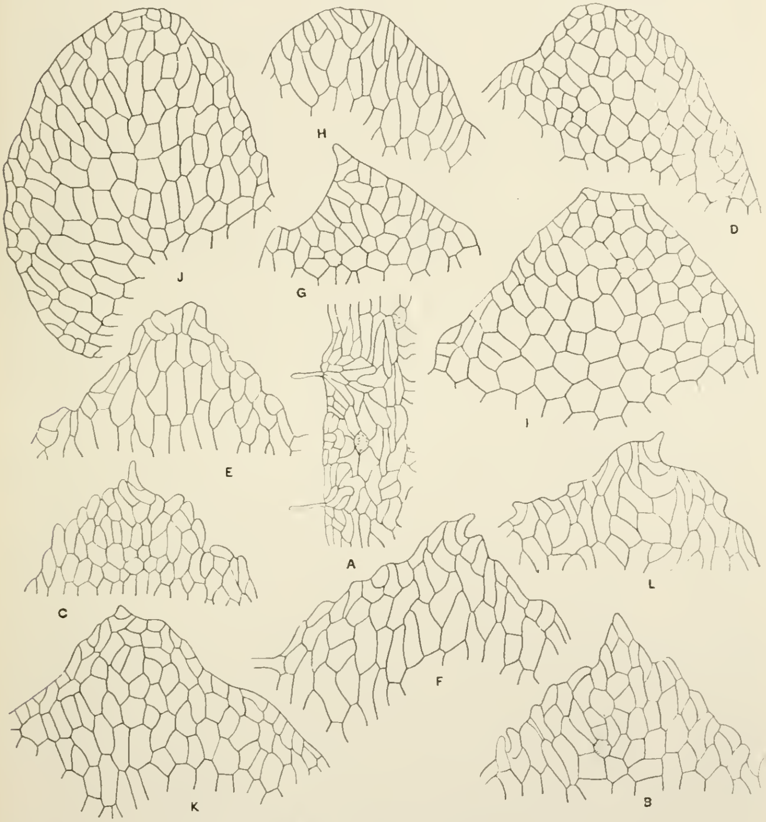

FIG. 7. MARCHANTIA PALEACEA Bertol.

Portions of ventral scales. A. Margin of basal portion of median scale, x 100. B-L. Appendages of median scales, x 100. A-C. Italy, *F. A. Artaria,* in V. Schiffner's Hep. Europ. Exsic. *13*. D. Azores, *F. D. Godman.* E, F. Vera Cruz, *Barnes & Land 668.* G, H. Cuba, *C. Wright,* in Hep. Cubenses, as *M. domingensis.* I-K. Nepal, *N. Wallich;* I, type of *M. nepalensis;* J, type of *M. nitida;* K, type of *M. squamosa;* L, Java, *V. Schiffner,* in Iter Ind. *59,* as *M. nitida.*

figure which he[26] afterwards published show almost beyond a doubt that the species represents a synonym of *M. paleacea.* This conclusion seems further warranted by the fact that the true *M. paleacea* is now known from several Mexican localities.

Nees von Esenbeck, in describing *M. paleacea,* places it in the section *Chlamidium* and calls especial attention to the features of the female receptacle. He gives the normal number of rays as nine and mentions the median protuberance of the disc and the dilated apices of the rays. Among the synonyms of the species he includes *M. nitida* without question, basing his opinion on specimens received directly from Lindenberg. He quotes a statement of the latter author to the effect that *M. nitida* is very close to the Italian *M. paleacea* and perhaps identical with it, accompanied by the remark that *M. paleacea* had not been seen by him when he published *M. nitida* as a new species. Nees von Esenbeck hesitates somewhat in the case of Taylor's *M. paleacea* but inclines toward the opinion that this plant also must be the same as Bertolini's species.

In spite of these statements *M. nitida* is reinstated as a valid species in the Synopsis Hepaticarum and Taylor's *M. paleacea,* so far as the Nepal specimens are concerned, is given as a synonym under it; the range of *M. paleacea* being again restricted to Italy. Both *M. nepalensis* and *M. squamosa* are likewise accepted as valid and these two species, together with *M. paleacea* and *M. nitida,* are included under the section *Chlamidium.* Many years later, in 1899, Stephani,[27] in recognizing these four species, placed *M. nitida* and *M. nepalensis* in his section with unsymmetrical receptacles, while he placed *M. paleacea* and *M. squamosa* in the section with symmetrical receptacles.

In 1898 doubt was again thrown on the validity of *M. nitida* by Schiffner,[28] who stated that it was probably synonymous with *M. paleacea.* Two years later he reaffirmed this idea and added that *M. calcarata* Steph., according to a specimen in his herbarium, was surely identical with *M. nitida.*[29] In the following year

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[26] Handb. Bot. Term. und Systemk. **2**: *pl. 55, f. 2727.* 1842.

[27] Bull. Herb. Bossier **7**: 402, 522. 1899.

[28] Conspect. Hepat. Archip. Indici 50. Batavia, 1898.

[29] Fl. de Buitenzorg **4**: 31. 1900. A specimen in the writer's herbarium, collected by the Abbé Faurie at Tokyo, Japan, and distributed (Hép. du Japon *2360*) under the name *M. calcarata,* represents *M. polymorpha.* Stephani himself now regards the true *M. calcarata* as a synonym of *M. diptera* Mont., a species which evidently requires further study.

he maintained still more definitely that *M. paleacea* and *M. nitida* were identical and stated further that in his opinion *M. nepalensis* also would have to be considered a synonym.[30] He criticised Stephani for placing *M. paleacea* in one section of the genus, while he placed *M. nepalensis* and *M. nitida* in another, thus implying that their relationship to the Italian species was at best remote.

The writer would agree with Schiffner in his reductions. Type specimens of *M. papillata β italica,* of *M. nepalensis,* and of *M. nitida* have all been available for study. The first and third are in good condition and show close agreement with each other and with the abundant material of *M. paleacea* from other localities. The type specimen of *M. nepalensis* bears very immature female receptacles, but the thallus characters are those of *M. paleacea* and there seems to be no reason for attempting to maintain the species as valid. Two other species quoted above among the synonyms of *M. paleacea* remain to be considered. The first of these is *M. squamosa.* Wallich's specimens of this species are clearly the same as *M. paleacea,* and since these specimens are the ones first quoted by Lehmann and Lindenberg, they might logically be considered the type. It is probable, however, that Raddi originally gave the name *M. squamosa* to his own Brazilian specimens, and this is apparently the view held by Stephani who quotes only the specimens from Brazil. Raddi's specimens have not been seen by the writer. If they should prove distinct from *M. paleacea* it might still be possible to maintain *M. squamosa* as valid. It is unfortunate that Raddi published nothing on his species himself. The second species to be considered is *M. planipora,* which the writer knows from a portion of the type material and from specimens sent by Professor Miyake. These specimens agree with *M. paleacea,* and the descriptions given by Stephani bring out no essential differences.

There is usually little difficulty in distinguishing *M. paleacea* even in the absence of receptacles. At the present time it is the only known North American species in which the epidermal pores constantly conform to the cruciate type. In this respect it agrees with *M. Bertcroana* of the Southern Hemisphere, a much larger plant with very different scale-appendages and terete rays on the female receptacle. Aside from the cruciate pores *M. paleacea*

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[30] Lotos 49: 92. 1901.

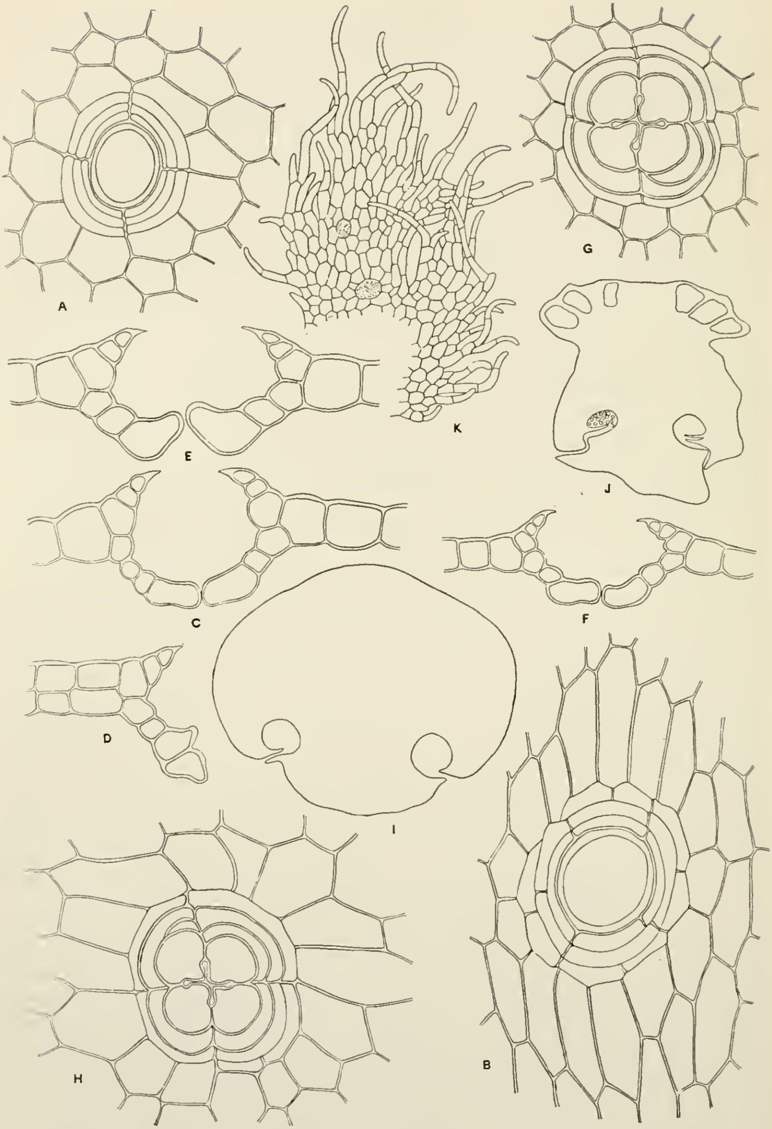

Fig. 8. Marchantia paleacea Bertol.

Anatomical details. A, B. Epidermal pores of thallus, surface view, x 225. C-F. Pores in cross-section; C, D, F, x 225; E, x 300. G, H. Pores, inner view, x 225. I. Stalk of male receptacle, cross-section, x 40. J. Stalk of female receptacle, cross-section, x 40. K. Part of involucre, x 50. A, C, D, G, J, K. Italy, *F. A. Artaria,* in V. Schiffner's Hep. Europ. Exsic. *13*. B, E, H. Vera Cruz, *Barnes & Land 668*. F. Java, *V. Schiffner,* in Iter Ind. *59*, as *M. nitida*. I. Puebla, *Frère Arsène*.

is distinguished from *M. polymorpha* by its somewhat smaller size, by its total lack of epidermal papillae, by having the pores bounded by six or seven rows of cells, by the presence of sclerotic cells, by the flattened rays of the female receptacles, by the lack of marginal scales and by marked differences in the appendages of the median scales. In *M. polymorpha* epidermal papillae are always present on cupules and female receptacles, the pores are surrounded by only four or five rows of cells, there are no sclerotic cells, the rays of the female receptacle are terete, and marginal scales are always present.

The features of the appendages in *M. paleacea* deserve particular attention (Fig. 7, B-L). When a long series is examined, it will be seen that they exhibit marked differences in their apices and margins, although they are almost constantly longer than broad and maintain an oblong or ovate form. The apex is sometimes rounded, sometimes truncate, and sometimes apiculate or even acute, while the margin may be entire throughout, variously toothed, or even provided with a basal lobe. A tooth, on its part, may be the slightest and vaguest projection of a marginal cell, it may be a distinctly projecting cell, or it may consist of a cell borne on a stalk-cell; in some of the broader teeth two adjoining cells may even be involved. It must be admitted, however, that large and complicated teeth are the exception. In commenting on the type specimen of *M. nitida* Schiffner states that the appendages are broadly ovate, less pointed at the apex and scarcely toothed, those of his Javan material being broadly cordate, abruptly pointed and with irregular and distant marginal teeth. These differences, which he considers of little importance, are shown by Fig. 7, J, L, and at first sight are somewhat striking. Since, however, equally extreme conditions are sometimes found on a single specimen, as shown by Fig. 7, G, H, it is evident that Schiffner did not underrate their value. The appendages also vary in the number of cells with oil-bodies which they show. In some cases no such cells are present; in one case as many as ten were counted; in the majority of cases there are from one to three. The gradual decrease in size between the median cells and the marginal cells is usually evident, although the actual measurements are not very different, and a distinct margin is never apparent as in *M. Berteroana*. It may be noted that Stephani assigns smaller marginal cells to *M. nepalensis, M. nitida,* and *M. tholophora,* while he states that the cells of *M. paleacea* are subequal in size, a specific difference which is not supported by actual comparisons. When contrasted with the appendages of *M. polymorpha,* those of *M. paleacea* are seen to be narrower, usually less toothed, and composed of larger cells, which show a less marked decrease in size between the median and marginal regions.

The male receptacles of *M. paleacea* seem to be infrequent. In the few cases seen the receptacles have been remarkably like those of *M. polymorpha,* although borne on shorter stalks. In other words the disc has been shortly eight-lobed with rounded rays and narrow sinuses. According to Schiffner the rays as they grow older become longer and give the disc a palmate appearance. If this is true the male receptacles exhibit a considerable range of variation. The cupules of *M. paleacea,* with their dentate, sharp-pointed lobes, likewise agree with those of *M. polymorpha* and its allies, except that the outer surface is free from epidermal papillae.

When well developed the female receptacle of *M. paleacea* consists of a disc with nine horizontal flat rays borne on an elongated stalk. In many cases the rays are about twenty degrees apart and present the appearance of being symmetrically disposed. Even here, however, the single plane of symmetry is marked by the sinus between the two basal rays, which is much deeper than the others. When the basal rays are separated by a sinus more than twenty degrees wide the plane of symmetry is more apparent and the disc does not show a radial appearance. Since the width of the sinus between the basal rays varies markedly it should not be made the basis for specific separations, although this has evidently been done in the past. The extremities of the rays are variously dilated and are truncate or even emarginate at the apex. In the center of the disc the hemispherical or bluntly conical protuberance is usually distinct, and the same thing is true of the nine rounded ridges extending from the protuberance to the beginnings of the rays. When the receptacle is young or, in some cases, when fertilization has not taken place, the rays do not spread horizontally but extend downward, and usually, under these circumstances, the median protuberance and the radiating ridges are only slightly developed. In fact they are not always distinct even when the rays have assumed a horizontal position. Although the normal number of rays in *M. paleacea* is nine, just as in *M. polymorpha,* deviations from this number sometimes occur, a reduced number being associated with poor development.

According to Prescher scattered slime cells of small size are present in the walls of the cupules of *M. paleacea* but are lacking altogether in the thallus and in the female receptacles. Although the thallus sometimes agrees with his account it does not always do so. Cases have been observed in which slime cells formed a rather conspicuous feature of the ventral tissue of the wings, an occasional cell of this character being present even in the thickened median region. In other cases, the slime cells were less abundant. In the male receptacles, which Prescher did not examine, slime cells are fairly numerous. It is evident from these observations that the presence or absence of slime cells can not be utilized in distinguishing *M. paleacea.*

5. **Marchantia breviloba** sp. nov.

Thallus pale green, more or less glaucous, sometimes a little pigmented with purple, especially near the margin and on the lower surface, mostly 0.5-0.8 cm. wide and 2-5 cm. long, repeatedly dichotomous, the successive forks usually 1-2 cm. apart, texture firm but not leathery, margin entire; epidermis composed of cells with somewhat thickened walls, sometimes in two layers mostly 45-90μ long (averaging about 65μ) and 20-40μ wide (averaging about 28μ), papillae absent; pores (with their surrounding cells) mostly 125-150μ long and 100-120μ wide, surrounded usually by six (or seven) rows of cells (three in each series or sometimes four in the outer series), innermost row of upper series usually composed of four cells, second row of four to eight cells and third row of eight or more cells, each row of lower series usually composed of four cells, inner opening usually four-sided (sometimes three-, five-, or six-sided), the sides being concave and forming acute angles with one another, bounding cells of pore more or less roughened with a resinous deposit; air-chambers usually high, more or less elongated, their outlines very indistinct when viewed through the epidermis, present everywhere, rows of photosynthetic cells often four or five cells long; compact ventral tissue mostly twenty or twenty-five cells thick in the median portion, the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells distinct, scattered, about forty in a cross-section, largely confined to median region, sometimes as much as 0.7 mm. in length, slime cells about 0.1 mm. in diameter, usually conspicuous (often three or four in a cross-section of thallus), scattered but more abundant toward the margin, sometimes present in the walls between air-chambers; ventral scales in two distinct rows, the laminar scales alternating with the median and only a little nearer the margin (a large portion of the ventral surface being free from scales); appendages of median scales ovate to orbicular, mostly 0.5-0.65 mm. long and 0.45-0.55 mm. wide, narrowed toward the rounded, obtuse, or apiculate apex, margin sinuate, sparingly and irregularly crenulate or denticulate from projecting cells, cells showing a gradual decrease in size toward the margin, median cells usually distinctly longer than broad, mostly 60-120μ long and 28-40μ wide, marginal cells mostly 30-50μ long and 18-25μ wide, irregular, the long axis usually forming an angle with the margin, rarely parallel with it, cells containing oil-bodies lacking: male receptacle borne on a stalk 1.5-2 cm. high, with two to four rhizoid-furrows and a single narrow dorsal band of air-chambers, the disc mostly 1-1.5 cm. broad, deeply six- (or seven-) lobed, the lobes or rays palmately disposed (the basal sinus being almost a straight line), mostly 2-5 mm. long and 1.5 mm. wide, rounded and with a thin wavy margin, ventral scales imbricated, mostly in two rows: female receptacle borne on a stalk 6-8 cm. long, with four rhizoid-furrows (except close to the base) and a single broad dorsal band of air-chambers, the disc mostly 0.6-0.8 cm. broad, usually eleven-lobed, sometimes seven- to nine-lobed, the lobes or rays short, 1 mm. long or less, flat, scarcely or not at all dilated at the truncate apex, basal sinus considerably broader than the others, upper surface of disc plane or with low ridges corresponding with the lobes; involucre ciliate, not lobed; spores yellowish brown, about 34μ in diameter, with a hyaline margin about 4μ wide, outer face bearing a few low lamellae, sometimes forming a very indistinct reticulum; elaters about 8μ wide, bispiral: cupules shortly and irregularly ciliate-dentate, the teeth sometimes adjoining and sometimes separated by sinuses of varying width, mostly two or three cells long and one or two cells wide at the base, epidermal papillae lacking. (Fig. 9.)

The following specimens of this species, which seems to be very local, have been examined:

Jamaica: without definite localities or dates, *Wilds* (N. Y., four specimens); Hardware Gap and vicinity, April, 1903, *W. R. Maxon 1115* (U. S., Y.); July, 1903, *A. W. Evans 175, 203* (Y.); Chestervale, July, 1903, *A. W. Evans 211* (Y.); vicinity of Cinchona, March, 1905, *C. E. Cummings 28* (N. Y., Y.); St. Catherine's Peak and vicinity, August, 1906, *A. W. Evans 441* (Y.). The specimens collected by Wilds include both

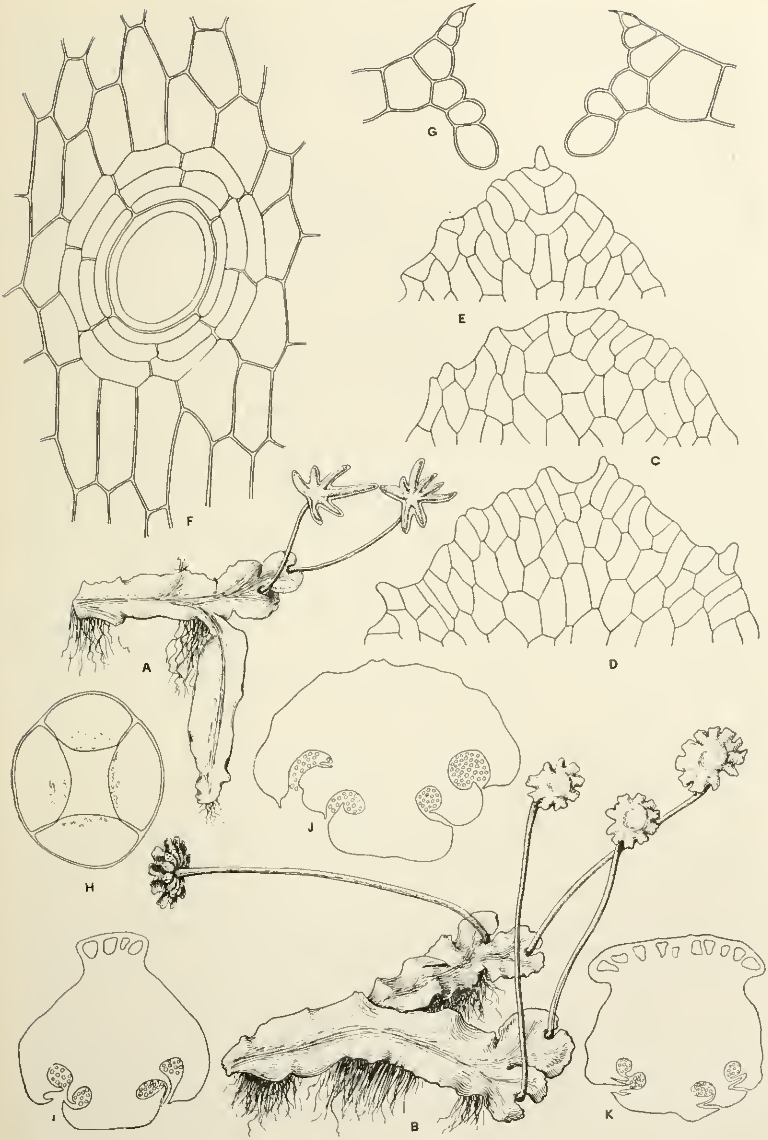

FIG. 9. MARCHANTIA BREVILOBA Evans

Plants, natural size, and various anatomical details. A. Male plant, x 1. B. Female plant, x 1. C-E. Appendages of ventral scales, apical portions, x 100. F. Epidermal pore of thallus, surface view, x 225. G. Pore in cross-section, x 225. H. Inner opening of pore, x 225. I, J. Stalk of male receptacle, cross-sections, x 40; I was cut near base; J, near apex. K. Stalk of female receptacle, cross-section, cut near base. A. Jamaica, *W. R. Maxon 1115*. B-D, F-K. Jamaica, *A. W. Evans 175*, type. E. Jamaica, *A. W. Evans, 203*.

female and gemmiparous material. Two, bearing the numbers 5 and 6, are labeled *"Marchantia conica"*; the other two bear no name. No. 175, collected by the writer, may be designated the type.

The thallus of *M. breviloba* bears a strong resemblance to that of *M. paleacea,* being of about the same size and similarly subject to pigmentation. The ventral scales and the appendages of the median scales in these two species likewise have certain features in common. The arrangement of the scales, for example, is very similar and the appendages agree in form, in the gradual decrease in the size of the cells in passing toward the margin, and in some of the peculiarities of the margin itself. Even the pores look a good deal alike when examined through a lens. A detailed examination, however, quickly brings out points of difference. In *M. breviloba* the pores are not of the cruciate type, the inner opening (so far as observed) being surrounded by evenly bulging cells and thus usually exhibiting a four-sided outline with concave sides and narrow angles; in *M. paleacea* the pores are distinctly cruciate. In *M. breviloba* the cells of the appendages are markedly larger than in *M. paleacea* and oil-containing cells seem to be constantly absent; in *M. paleacea* oil-containing cells can often be detected. In *M. breviloba* slime cells seem always to be numerous and conspicuous; in *M. paleacea* they are less frequent and may be absent altogether: this last difference, unfortunately, is one to be used with caution.

The differential characters yielded by the receptacles and cupules, in separating *M. breviloba* from *M. paleacea,* are even more marked than those derived from the thallus. In *M. breviloba* the male receptacle is borne on a long stalk with a distinct band of air-chambers and usually with four rhizoid-furrows; and the disc is unsymmetrically divided into six or seven elongated lobes, the basal sinus being much broader than the others and often approximating a straight line. In *M. paleacea* the male receptacle is borne on a very short stalk without air-chambers and with only two rhizoid-furrows; while the disc is very shortly and apparently radially divided into eight (or more) often indistinct lobes, the basal sinus being of about the same width as the others.

In *M. breviloba* the stalk of the female receptacle shows four rhizoid-furrows, and the disc is very shortly lobed, the lobes being usually more than nine and scarcely if at all dilated at the apex. In *M. paleacea* the stalk of the female receptacle shows only two rhizoid-furrows, and the disc is more deeply divided, the lobes being usually nine (or fewer) and more or less distinctly dilated at the apex; the upper surface of the disc, moreover, shows a median protuberance and nine ridges corresponding with the rays, these structures being very indistinct in *M. breviloba* or absent altogether. In *M. breviloba* the cupule is simply short-ciliate; in *M. paleacea* it shows a series of ciliate or dentate lobes.

There is no difficulty in separating *M. breviloba* from *M. polymorpha*. The new species is smaller, it lacks marginal ventral scales, the appendages of the median scales have larger cells and usually fewer marginal teeth, the epidermal cells are more complex being surrounded by more rows of cells, there are no epidermal papillae, the stalk of the male receptacle has air-chambers and usually more rhizoid-furrows, the disc is more deeply and more unsymmetrically lobed, the stalk of the female receptacle has more rhizoid-furrows, the disc is less deeply lobed, and the lobes are flattened instead of being terete. The difference in the cupules, already noted in connection with *M. paleacea*, would apply equally well in separating the species from *M. polymorpha*.

6. MARCHANTIA DOMINGENSIS Lehm. & Lindenb.

Marchantia domingensis Lehm. & Lindenb.; Lehmann, Pug. Plant. 6: 22. 1834.
Marchantia inflexa Nees & Mont.; Montagne, Ann. Sci. Nat. Bot. II. 9: 43. 1838.
Marchantia disjuncta Sulliv. Am. Jour. Sci. II. 1: 74. 1846.
Marchantia linearis G. L. & N. Syn. Hep. 529. 1847 (in part). Not Lehm. & Lindenb.
Marchantia martinicensis Spreng.; G. L. N. *l. c.* 531. 1847 (as synonym).
Marchantia Elliottii Steph. Bull. Herb. Boissier 7: 400. 1899.
Marchantia caracensis Steph. *l. c.* 526. 1899.

Thallus pale to dark green, not glaucous, slightly or not at all pigmented with purple, usually 4-6 mm. wide and 2-3 cm. long, dichotomous, the successive forks usually 1-1.5 cm. apart, texture delicate, margin entire; epidermis composed of cells with slightly thickened walls, sometimes in two layers, mostly 30-60μ long (averaging about 45μ) and 15-30μ wide (averaging about 23μ), papillae absent; pores (with their surrounding cells) mostly 90-130μ long and 70-80μ wide, surrounded usually by six (or seven) rows of cells (three or four in the upper and three in the lower series), the two lower rows of the upper series usually composed of eight (six to ten) cells apiece (more rarely of only three to five cells), the other rows of four (three to five) cells apiece, inner opening usually four-sided, more rarely three- or five-sided, with the sides straight or nearly so, the bounding cells more or less obscured by a resinous deposit; air-chambers of medium height, isodiametric or somewhat elongated, their boundaries sometimes distinct and sometimes vague when viewed through the epidermis, present everywhere, rows of photosynthetic cells often four or five cells long but sometimes shorter; compact ventral tissue about twenty cells thick in the median portion, the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells usually distinct, scattered, mostly five to thirty in a cross-section, more abundant in the median portion but sometimes present in the wings, in the latter case often distinctly visible without sectioning, slime-cells lacking; ventral scales in two distinct rows, the laminar scales alternating with the median scales and not much nearer the margin; appendages of the median scales broadly lanceolate to ovate, when well developed mostly 0.35-0.6 mm. long and 0.27-0.45 mm. wide but sometimes considerably smaller, apex apiculate, acute, or cuspidate, margin more or less densely denticulate or dentate, the teeth usually one or two cells long, cells showing a gradual and slight decrease in size toward the margin, median cells usually longer than broad, mostly 40-80μ long and 20-40μ wide, marginal cells mostly 20-40μ long and 15-20μ wide, irregular but the long axis usually at right angles or nearly so to the margin, cells containing oil-bodies apparently always lacking: male receptacle borne on a stalk 5 mm. long or less, with two to four rhizoid-furrows and a single broad dorsal band of air-chambers, the disc variable in size but mostly 6-8 mm. broad, deeply lobed, the lobes or rays usually four to six but sometimes two, three, seven or eight, palmately disposed, the basal sinus a very broad angle or a straight line, mostly 3-6 mm. long and 2-3 mm. wide, rounded, with a thin wavy margin extending across the basal sinus, ventral scales imbricated, in two or more rows; female receptacle borne on a stalk 1.5-2 cm. high, with two to four rhizoid-furrows and a single broad dorsal band of air-chambers, the disc mostly 5-7 mm. wide, the lobes or rays spreading at maturity, extending about half way from the margin to the center, normally seven but often only five or six, more rarely eight to eleven, slightly or not at all dilated at the truncate, irregularly crenate or slightly emarginate apex, upper surface of disc and rays usually plane but sometimes more or less convex, basal sinus broader than the others and sometimes forming a very obtuse angle; involucre very delicate, the margin minutely and often irregularly crenulate to short-ciliate, the teeth usually varying from one to three cells in length; spores brownish yellow, about 28μ in diameter, the outer face bearing a series of low irregular ridges not forming a network; elaters about 6μ wide, bispiral: cupules closely short-ciliate, the cilia mostly one to four cells long, outer surface without papillae. (FIGS. 10-12.)

A widely distributed species in the southern United States, the West Indies, Mexico, Central America, and Venezuela. The following specimens have been examined:

TENNESSEE: Etowah, June, 1909, *F. McCormick* (C. C. H., Y., listed as *M. disjuncta* by the writer in Bryologist 13: 33. 1910).

GEORGIA: west bank of Ocmulgee River, Hawkinsville, June, 1902, *R. M. Harper 1382a* (N. Y., U. S.); Samochechobee Creek, near Killen, Clay County, October, 1902, *R. M. Harper 1791b* (N. Y., U. S.); Flint River swamp, below Albany, Dougherty County, August, 1903, *R. M. Harper 1951e* (N. Y., U. S.).

FLORIDA: Devil's Millhopper, Alachua County, February, 1909, *R. M. Harper 14* (N. Y.); April, 1915, *N. L. T. Nelson 45, 46, 47, 51* (Y.).

ALABAMA: banks of the Alabama River near Claiborne, *W. S. Sullivant* (H., type locality of *M. disjuncta,* specimens distributed in Musc. Alleg. *286* and Hep. Bor.-Amer. *128*); Auburn, May, 1896, *L. M. Underwood* (N. Y., Y., distributed, as *M. disjuncta,* in Hep. Amer. *182*); June, 1897, *Earle & Baker 52* (N. Y.).

TEXAS: Fort Worth, 1887, *G. S. Thompson 10* (N. Y., U. S., listed as *M. disjuncta* by Underwood in Bot. Gaz. 20: 69. 1895); Hallettsville, May, 1892, *G. C. Nealley 59* (C. C. H., U. S.); Austin, March, 1909, *F. D. Heald* (Y.).

ARKANSAS: Fort Harvey, no date, *F. L. Harvey 2* (N. Y., listed as *M. disjuncta* by Underwood, *l. c.*).

MEXICO: without definite locality or date, *C. H. Schultz 1229* (B., listed as *M. papillata,* by Stephani in Bull. Herb. Boissier 7: 397. 1899).

HIDALGO: Tula, *C. G. Pringle 10675* (Y., distributed in Pl. Mex. under a manuscript name of Stephani).

Puebla: banks along Avenida Hidalgo and path to barranca, Tezuitlan, 1908, *Barnes & Land 553* (Y.).

Tamaulipas: near Victoria, June, 1907, *E. Palmer 446* (N. Y., Y.).

Vera Cruz: Orizaba and vicinity, 1855, *F. Müller 2373* (N. Y., listed as *M. disjuncta* by Underwood, *l. c.*); 1857, *C. Mohr* (N. Y., Y.); March, 1890, *W. Stone 114, 115* (N. Y., listed by Underwood, *l. c.*); 1892, *J. G. Smith* (N. Y., Y.); Cordova, 1885, *W. G. Farlow 18* (N. Y., listed as *M. tholophora* by Underwood, *l. c.* 70).

Guatemala: Black River, *S. Watson 295b* (H., N. Y., listed as *M. linearis* by Underwood, *l. c.* 69); near the Finca Sepacuite, Alta Verapaz, March and April, 1902, *Cook & Griggs 82, 255, 403* (U. S., Y.).

Bahamas: Fort Charlotte, New Providence, April, 1905, *L. J. K. Brace 3916* (N. Y., Y., listed as *M. chenopoda* by the writer in Bull. Torrey Club **38**: 206. 1911); New Providence, October, 1904, *L. J. K. Brace 873* (N. Y.).

Cuba: without definite localities or dates, *C. Wright* (distributed as *M. disjuncta* and *M. linearis* in Hep. Cubenses); San Andre, April 14, 1865, *C. Wright* (H., Y.); valley of the San Juan River, near Matanzas, March, 1903, *Britton, Britton & Shafer 326* (N. Y., Y.); Guines, Havana, March, 1905, *M. T. Cook* (N. Y., Y.); Almendares River, near Puentas Grandes, Havana, April, 1908, *Brother Leon 723* (N. Y., Y.); falls of the Habanilla and near Siguanea, Trinidad Mountains, Santa Clara, March, 1910, *E. G. Britton 4855, 5076* (N. Y., Y.); vicinity of Guane, Pinar del Rio, March, 1911, *Britton, Britton & Cowell 9770* (N. Y., Y.); vicinity of Pinar del Rio, March, 1911, *E. G. Britton 10017* (N. Y., Y.); Finca Guerrero, Rio Yayabo, St. Spiritus, Santa Clara, December, 1911, *Brother Clement 44* (N. Y., Y.); Banaos Hills, Santa Clara, August, 1913, *Brother Leon 4036* (N. Y., Y.); Ensenada de Mora, Oriente, March, 1912, *Britton, Cowell & Shafer 13005* (N. Y., Y.).

Santo Domingo: Azui, province of Seibo, November, 1909, *N. Taylor 281* (N. Y., Y.).

Jamaica: without definite locality or date, *N. Wilson 595, 611* (N. Y., listed as *M. disjuncta* by Underwood, *l. c.*); Hartford and adjoining properties, near Priestman's River, June, 1904, *W. R. Maxon 2535* (U. S., Y.); road from Holly Mount to Resource, February, 1905, *W. Harris 8876* (N. Y., Y.); vicinity of Mandeville, September, 1907, *E. G. Britton 429* (N. Y., Y.); February, 1910, *S. Brown 280, 282, 283* (N. Y., Y.); Kempsport and Roaring River Falls, March, 1908, *E. G. Britton 668, 708* (N. Y., Y.); Porus to Clarendon Park, September, 1908, *N. L. Britton 3785* (N. Y., Y.); Cokely, near Castleton, and Hope Gardens, January, 1914, *W. Harris* (N. Y.).

Porto Rico: Las Marias Road and vicinity of Mayaguez, March, 1906, *Britton & Marble 594, 613* (N. Y., Y.); Lares to San Sebastiano, April, 1913, *Britton & Marble 2797, 2803* (N. Y., Y.); Rio de Maricao, April, 1913, *E. G. Britton 2494* (N. Y., Y.); Ciales, August, 1913, *J. R. Johnston 940* (N. Y., Y.); between Arecibo and Utuado, July, 1901, *Underwood & Griggs 836* (U. S., Y.); March, 1914, *E. G. Britton 2074* (N. Y., Y.); Lares, June, 1901, *Underwood & Griggs 36* (U. S., Y.); June, 1914, *J. R. Johnston 2070* (N. Y., Y.); Monte Montoso, February, 1915, *Britton & Cowell 4177* (N. Y., Y.); La Juanita, near Las Marias, February, 1915, *E. G. Britton 3965* (N. Y., Y.); vicinity of Utuado, March, 1915, *E. G. Britton 5168, 5112* (N. Y., Y.).

St. Kitts: Bethesda, *J. C. Breutel* (N. Y., listed as *M. linearis* in Syn. Hep. 529 and as *M. domingensis* by Stephani in Bull. Herb. Boissier 7: 399. 1899); without definite locality, 1853, *Walwyn* (N. Y.); Old Road and Lambert Estate, September and October, 1901, *Britton & Cowell 481, 626* (N. Y., U. S., Y.).

Montserrat: mountain pass to Roches and Tar River, February, 1907, *J. A. Shafer 867, 871* (N. Y., Y.).

Guadeloupe: Morne Rouge, Gombeyre (Basse-Terre) and Morne Papillon, 1897-1900, *Père Duss 250, 251, 312, 392* (N. Y., Basse-Terre specimens listed as *M. disjuncta* by Schiffner in Oesterr. Bot. Zeitschr. 57: 51. 1907).

Dominica: without definite locality or date, *W. R. Elliott 1292* (B., type of *M. Elliottii*).

Martinique: without definite locality, date, or collector's name (M., received from Mérat, type of *M. inflexa*); without definite locality or date, *Sieber 378* (N. Y., probably type of *M. martinicensis*); St. Pierre and between Deux-Choux and Gros-Morne, 1899, 1900, *Père Duss 342, 393* (N. Y.); Morne Rouge, August, 1901, *Père Duss 578, 580, 581* (N. Y.); Deux-Choux, September, 1903, *Père Duss* (N. Y., determined as *M. caracensis* by Stephani).

St. Vincent: without definite localities or dates, *L. Guilding* (H., N. Y., specimens in the Taylor and Mitten herbaria, labeled "*March. linearis—chenopoda.*"):

Grenada: Annandale, St. George's, March, 1906, *W. E. Broadway* (N. Y.).

Trinidad: without definite locality, 1878-80, *A. Fendler* (N. Y., U. S., Y., distributed as *M. chenopoda*); Mareval Valley, 1913, *R. Thaxter* (H., Y.); La Lenia Valley, 1913, *R. Thaxter* (H., Y.).

Venezuela: Rio Cartude, Caracas, 1856, *Gollmer* (B., type of *M. caracensis*); Caracas, August, 1902, *A. F. Blakeslee*, (H., Y.).

The following stations, cited in literature, should also be noted:

Santo Domingo: without definite locality, date or collector's name (type).

Guadeloupe: without definite locality or date, *L'Herminier 69* (listed, as *M. linearis,* by Bescherelle in Jour. de Bot. 7: 193. 1893).

Martinique: without definite localities or dates, *C. Bélanger 124* (listed, as *M. linearis,* by Bescherelle, *l. c.*); *K. von Martius; C. Bélanger 24* in part, *374; Hahn, 774* (the last three listed, as *M. inflexa,* by Bescherelle, *l. c.*).

The type specimen of *M. domingensis* was collected in Santo Domingo, neither the date nor the collector's name being mentioned in the original publication. Unfortunately this specimen has not been available for study. In its absence the writer has been obliged to rely upon West Indian material determined as *M. linearis* and upon the type specimen of *M. inflexa.* These are referred to *M. domingensis* without question by Stephani and agree in all essential respects with the other specimens listed. The type specimens of *M. disjuncta, M. Elliottii* and *M. caracensis* have likewise been examined and show a similar agreement. The writer feels convinced, therefore, that the synonymy given above is correct.

The type specimen of *M. inflexa,* received from the Montagne herbarium, is very fragmentary but bears two female recep-

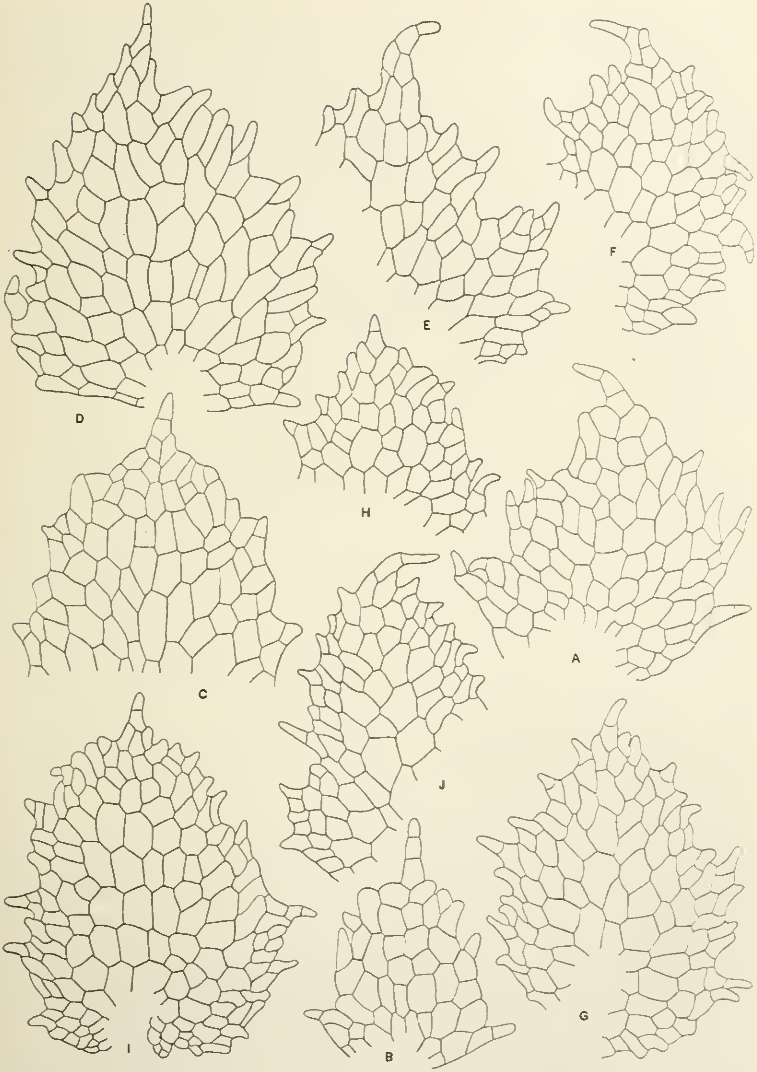

FIG. 10. MARCHANTIA DOMINGENSIS Lehm. & Lindenb.

Appendages of ventral scales, x 100. A, B. Alabama, *Earle & Baker 52.* C. Cuba, *C. Wright,* distributed in Hep. Cubenses, as *M. disjuncta.* D, E. Hope Gardens, Jamaica, *W. Harris.* F. St. Kitts, *J. C. Breutel,* specimen in the Mitten herbarium, labeled *M. linearis* and *M. chenopoda.* G. St. Kitts, *Britton & Cowell, 626.* H. Martinique, type of *M. inflexa.* I, J. Mareval Valley, Trinidad, *R. Thaxter.*

tacles: the first shows nine truncate rays clearly, the basal sinus being broader than the others; the second shows ten less clearly marked rays. The type of *M. disjuncta* agrees closely with the specimens distributed by Sullivant, by Austin, and by Underwood. They are well represented in the beautiful figures published by Sullivant,[31] and the female receptacles show a variable number of rays. The type of *M. Elliottii* bears numerous female receptacles, which show from five to nine rays apiece, the rays being plane or slightly convex and blunt. The type of *M. caracensis* bears both cupules and female receptacles, the latter showing five rays apiece. All of these specimens show the dentate scale appendages and other features characteristic of the species.

The thallus of *M. domingensis* is smaller and usually more delicate in texture than in any of the preceding species. In wet localities the photosynthetic layer is especially thin and the epidermis is rarely more than a single cell in thickness, so that plants growing under these conditions present an unusually fragile aspect. The epidermal pores, however, maintain their complex structure and form conspicuous whitish dots on the upper surface. Sometimes the boundaries of the air-chambers show distinctly through the epidermis, but they are usually indistinct. The structure of the pores is much the same as in *M. breviloba,* although the inner opening is bounded by straighter lines.

The sclerotic cells in the thallus exhibit a great deal of variability. When abundantly developed they occur both in the thickened median portion of the thallus and in the wings, those in the latter position showing distinctly as elongated brown spots when examined from underneath. The sclerotic cells appear to be separated from one another by parenchyma when a cross section of a thallus is examined. As a matter of fact, in the median portion of the thallus at least, they often form elongated strands running for a considerable distance, the acute ends of the cells slightly overlapping. There are many cases, however, where the sclerotic cells are very scantily developed. Sometimes there are none at all present in the wings although the median portion still retains them; sometimes even the median portion seems to

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[31] Mem. Am. Acad. II. 3: *pl. 3.* 1846.

lack them completely, although no specimens have yet been seen in which a careful examination failed to show traces of sclerotic cells in this region.

The appendages of the ventral scales (Fig. 10) have better developed teeth than in any other North American species of *Marchantia,* although the South American *M. papillata* is a close rival in this respect. The teeth are very irregular, the simplest being single cells which project as rounded or bluntly pointed processes. Between these simple teeth and irregular lobes, several cells long and wide, are all possible gradations. The apical tooth tends to be longer than the others, although this tendency is not always apparent. The median cells of the appendages are often longer than broad and a decrease in the size of the cells

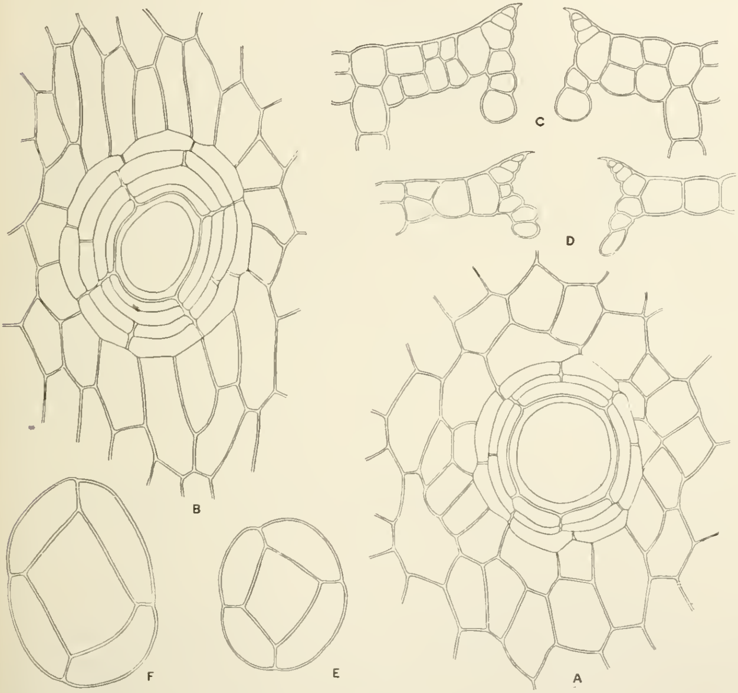

Fig. 11. Marchantia domingensis Lehm. & Lindenb.

Epidermal pores of thallus, x 225. A, B. In surface view. C, D. In cross-section. E, F. Inner openings. A, C, E. Texas, *F. D. Heald.* B, D, F. Cokely, near Castleton, Jamaica, *W. Harris.*

between the middle portion and the margin is distinctly evident. There is no definite border, however, as in *M. Berteroana.* Sometimes, in wet situations, the appendages remain very small, although even under these circumstances the marginal teeth form a conspicuous feature. The more sharply pointed apices, the larger and more irregular teeth, the larger marginal cells and the lack of cells containing oil-bodies will at once distinguish the appendages of *M. domingensis* from those of *M. polymorpha.*

According to the original description of *M. domingensis* the female receptacle is semicircular and ten-lobed to the middle, the lobes being dilated and emarginate-crenate at the apex. The Synopsis gives the number of lobes as seven to ten, while Stephani states that nine lobes are present. The original description of *M. inflexa* assigns nine to eleven lobes to the receptacle, while Sullivant gives seven to nine as the number of lobes in *M. disjuncta;* here again Stephani places the number of lobes definitely at nine, and gives the same number for *M. Elliottii.* In *M. caracensis,* however, he states that only five or six lobes are present. As a matter of fact the receptacles are exceedingly variable and it is not easy to decide what the typical or normal number of lobes really is. In the material from the mainland seven is perhaps the usual number but five lobes often occur and more than seven have been observed in several instances. In the West Indian material nine lobes are present more frequently, but seven or even only five lobes are not unusual. Sometimes the lobes seem to be subdivided, so that it is not always easy to count them except by means of the involucres which alternate with them. The lobes vary not only in number but in thickness. In some cases they are very thin and flat, in other cases thicker and convex. When the lobes are fleshy the center of the disc sometimes shows a low swelling, but it is usually plane, and the receptacle never shows the conspicuous median protuberance and radiating ridges which are so characteristic of *M. paleacea.*

The study of the involucre is beset with considerable difficulty on account of its extreme delicacy. This has apparently been the cause of considerable confusion in the published descriptions. In *M. domingensis,* for example, the involucre is said to be laciniate-ciliate or shortly fimbriate; in *M. inflexa,* laciniate; in *M. disjuncta,* sparingly dentate or subentire; in *M. caracensis,* shortly fimbriate. Fig. 12, E-J, brings out the range of variation observed by the writer. The nearest approach to an entire condition is seen in Fig. 12, E, although even here the margin is distinctly and closely crenulate; in Fig. 12, F, the crenulate condition is more pronounced, some of the teeth being two cells long; in Fig. 12, G, a crenulate portion directly adjoins a short-ciliate portion, in which the cilia are two or three cells long; in Fig. 12, H-J, taken from a single receptacle, the variation to be expected is shown with especial clearness, some of the marginal teeth or cilia being straight and some curved. In all probability the laciniate and fimbriate involucres of the descriptions have been the result of irregular tears in old material.

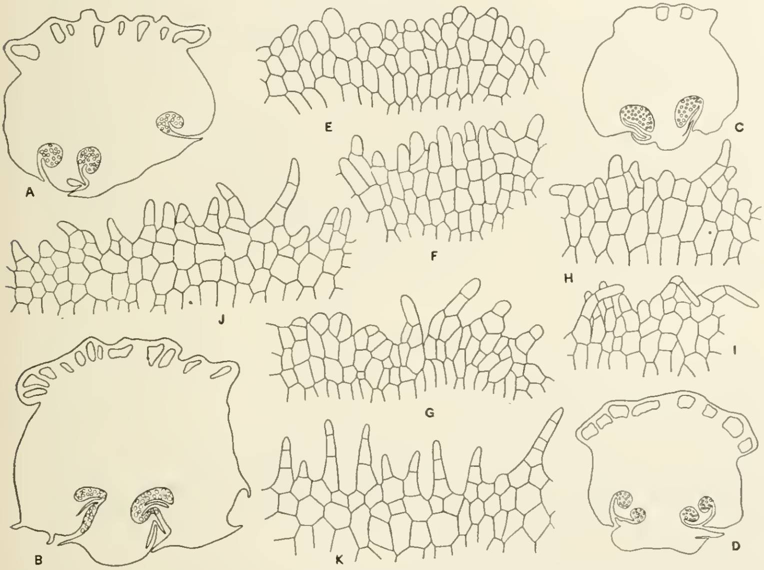

Fig. 12. Marchantia domingensis Lehm. & Lindenb.

Anatomical details. A. Stalk of male receptacle, cross-section, x 40. B-D. Stalks of female receptacles, cross-sections, x 40, C having been cut near base. E-J. Parts of involucres, x 100: H and I were dissected from a single involucre; J, from another involucre on the same receptacle. K. Part of cupule, x 100. A. Florida, *N. L. T. Nelson 47*. B, F. Texas, *F. D. Heald*. C, H-J. Jamaica, *E. G. Britton 668*. D. St. Kitts, *Britton & Cowell 626*. E. Alabama, *Earle & Baker 52*. G. Guatemala, *Cook & Griggs 82*. K. Cokely, Jamaica, *W. Harris*.

In the case of the male receptacle, Sullivant states that the number of lobes in *M. disjuncta* is normally seven, although some of his figures show six, four, or only three lobes. Stephani places the number at about eight in his account of *M. disjuncta* but makes no mention of the male receptacles in *M. domingensis, M. Elliottii* or *M. caracensis.* Apparently a good deal of variation is to be expected from varying environmental conditions, as Goebel[32] has recently noted, poorly developed material showing a reduced number of lobes. Even when only two rays are present the upper part of the stalk shows two rhizoid-furrows, although the lower part shows but one. The deeply lobed male receptacle will distinguish *M. domingensis* from all the preceding species except *M. breviloba.* In addition to its greater size this species differs from *M. domingensis* in the appendages of the ventral scales, which are larger and much less toothed; in the slime cells of the thallus, these structures being apparently never found in *M. domingensis;* in the less deeply lobed female receptacles; and in the distinctly ciliate involucres.

7. MARCHANTIA PAPILLATA Raddi

Marchantia papillata α brasiliensis Raddi, Mem. Soc. Ital. Modena 19: 44. 1823; 20: *pl. 6a, f. 3, 4.* 1829.

Marchantia platycnemos Schwaegr.; Gaudichaud, Freyc. Voy. Bot. 218. 1827 (as to the Brazilian plant).

Marchantia androgyna Nees; Martius, Fl. Brasil. 1: 308. 1833. Not L.

Marchantia subandina Spruce, Trans. Bot. Soc. Edinburgh 15: 561. 1885.

Thallus dull green, not glaucous, sometimes more or less pigmented with purple, usually 1.5-3 mm. wide and 0.8-1.15 cm. long, dichotomous, the forks usually only 1.5-3 mm. apart, texture firm, margin entire; epidermis composed of cells with more or less thickened walls, usually in a single layer, mostly 20-50μ long (averaging about 30μ) and 12-20μ wide (averaging about 15μ), papillae absent; pores (with their surrounding cells) mostly 50-70μ long and 40-45μ wide, surrounded usually by five (or six) rows of cells (two or three in the upper series and three in the lower series), each row usually composed of four cells (rarely of three or five), the lowest row of the upper series sometimes with from five to eight cells, inner opening usually four-sided (rarely with three or five sides), the sides concave,

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[32] Organographie der Pflanzen, 2d ed. 699. 1915.

bounding cells more or less obscured by a resinous deposit; air-chambers low, isodiametric or somewhat elongated, their outlines very indistinct when viewed through the epidermis, present everywhere, rows of photosynthetic cells usually two or three cells long; compact ventral tissue about fifteen cells thick in the median portion; the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells scattered, mostly fifteen to twenty in a cross-section, more abundant in the median portion but often present in the wings, sometimes clearly visible without sectioning, slime cells lacking; ventral scales in two rows, the row of laminar scales more or less irregular but tending to alternate with the median scales and not much nearer the margin; appendages of the median scales ovate, when well developed mostly 0.3-0.45 mm. long and 0.25-0.3 mm. wide but sometimes considerably smaller, apex apiculate, acute, or cuspidate, margin subentire or usually more or less closely denticulate or dentate, the teeth irregular, mostly one or two cells long, rarely larger and more lobe-like, cells showing a gradual and slight decrease in size toward the margin, median cells usually longer than broad, mostly 40-60μ long and 25-30μ wide, marginal cells mostly 30-45μ long and 15-25μ wide, irregular but usually with the long axis at right angles or nearly so to the margin, cells containing oil-bodies apparently always lacking, male receptacle borne on a stalk about 3 mm. long with two rhizoid-furrows, the disc about 0.8 cm. wide, deeply four- to eight-lobed, the lobes or rays palmately disposed (the basal sinus being very broad), about 3 mm. long and 1 mm. wide, rounded at the apex and with a thin wavy margin, ventral scales imbricated: female receptacle borne on a stalk 1.5-2 cm. long, with two rhizoid-furrows and a single broad dorsal band of air-chambers, the disc mostly 3-4 mm. broad, normally nine-lobed (but sometimes with five to eight lobes), the lobes or rays 1-1.5 mm. long and about 1 mm. wide, distinctly dilated at the truncate to emarginate apex, strongly convex on upper surface, basal sinus broader than the others, upper surface of disc with a low median protuberance; involucre very delicate, irregularly lobed and crispate, otherwise entire or slightly and irregularly crenulate; pores yellowish brown, about 26μ in diameter, outer face bearing a series of very low ridges not forming a network, margin narrow and often indistinct, less than 2μ broad; elaters about 8μ broad, bispiral: cupules sparingly and irregularly denticulate to short-ciliate, the teeth being projections of marginal cells or from one to four cells long, epidermal papillae lacking. (Fig. 13.)

The following specimens have been examined:

Brazil: Rio de Janeiro, without date, *G. Raddi* (N. Y., type); without date, *J. Milne* (N. Y.); without definite locality or date, *W. J. Burchell 1857* (N. Y.).

PARAGUAY: Paraguari, August, 1883, *B. Balansa* (N. Y., U. S., distributed in Pl. du Paraguay *4006,* and listed by Stephani in Rev. Bryol. **14**: 58. 1887).

PERU: near the Rio Huallaga, *R. Spruce* (type of *M. subandina,* distributed in Hepaticae Spruceanae).

BOLIVIA: Isapuri, October, 1901, *R. S. Williams 2145* (N. Y., Y.).

Although the writer has seen no specimens of *M. papillata* from other localities, the following records may be cited from the literature:

CUBA: "ad terram in locis humidis prope S. Marcos," *Ramon de la Sagra,* gemmiparous specimens (listed by Montagne in Ramon de la Sagra, Hist. Fis. Pol. y Natur. Cuba **9**: 290. 1845).

MARTINIQUE: without definite locality or collector's name (listed by Underwood in Bot. Gaz. **20**: 70. 1895); without definite locality or date, *A. Plée 1821* (listed by Bescherelle in Jour. de Bot. **7**: 193. 1893).

BRAZIL: Rio Janeiro, *C. Gaudichaud* (listed, as *M. platycnemos,* in Freyc. Voy. Bot. 218. 1827); Minas Geraes, *K. von Martius* (listed by Nees von Esenbeck in Naturg. Europ. Leberm. **4**: 109. 1838); "ad muros humidos aquaeductus, loco Corcovado dicto" near Rio de Janeiro, and "ad terram juxta flumen Rio Negro", *A. d'Orbigny* (listed by Montagne in D'Orbigny, Voy. dans l'Amér. Mérid. 7^2: 397. 1839).

.FALKLAND ISLANDS: without definite locality or date, *C. Gaudichaud* (listed, as *M. platycnemos,* in Freyc. Voy. Bot. 218. 1827).

The original *M. papillata* included two varieties, *α. brasiliensis* and *β. italica.* Nees von Esenbeck[33] soon showed, however, that the second variety was a synonym of *M. paleacea;* he therefore reserved the name *M. papillata* for the first variety, a course which has been followed by subsequent writers. He was also the first to recognize the fact that his Brazilian *M. androgyna* belonged to *M. papillata* and to include *M. platycnemos* among the synonyms of the same species. It is possible, however, that *M. platycnemos* ought still to be maintained as a species, at least in part. It was based on three specimens, the first from the

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[33] Naturg. Europ. Leberm. **4**: 101. 1838.

Marianne Islands in the Pacific, the second from the Falkland Islands, and the third from Brazil. The first specimen may be regarded as the type of the species since it is mentioned first. A portion of this specimen in the herbarium of the New York Botanical Garden shows that the type is distinct from *M. papillata,* as here understood, but that it is very close to *M. emarginata* and perhaps synonymous with it. Nees von Esenbeck's inclusion of *M. platycnemos* among the synonyms of *M. papillata* must therefore be considered as applying to a part only of Schwaegrichen's species as originally described.

Of Raddi's original figures, *f. 3* is said to represent male plants and *f. 4,* female plants. This is obviously an error, the receptacles shown under *f. 3* being clearly female. In *f. 3a* six receptacles are drawn, two showing six lobes apiece and one seven lobes, the number being doubtful in the other three. In *f. 3b* an enlarged receptacle with nine lobes is represented; the lobes show clearly the enlarged apices with more or less distinct emarginations, and no difference is brought out between the basal sinus and the others. The receptacles shown in *f. 4* are very doubtful and bear a disc which is scarcely lobed at all. Unless drawn from very immature material they probably belong to some other species than *M. papillata.* It should be noted, however, that the Synopsis describes the disc of the male receptacle as "subdimidiato excentrico marginibus repando-lobatis," thus evidently recognizing a male receptacle in Raddi's so-called female receptacle; but Stephani apparently discards this view, since he does not mention the male receptacles at all.

The specimen of *M. papillata,* quoted above as the type, is in the Mitten herbarium and was received from Hooker. It is very fragmentary but includes three female receptacles, two showing eight lobes apiece and the third, seven lobes. The dilated apices of the lobes and the broader basal sinus are clearly apparent. This specimen has been carefully compared with the other specimens cited and found to agree with them in all essential respects. Spruce compares *M. subandina* with both *M. papillata* and *M. Berteroana,* which he knew from description only. He ascribes to the species, however, a polyoicous inflorescence and monospiral elaters. Unfortunately the specimens which he distributed, although agreeing with his description in other respects, show a strictly dioicous inflorescence and bispiral elaters, so that his statements about the inflorescence and elaters must have been based on a misconception.

The thallus of *M. papillata* is even smaller than in *M. domingensis;* it is, in fact, the smallest American species known at the present time. So far as the structure of the thallus is concerned the agreement with *M. domingensis* is very close. Slime cells seem to be always lacking in both species and sclerotic cells are usually abundant and equally conspicuous. The appendages of the median scales, moreover, are essentially the same, although the marginal teeth in *M. papillata* exhibit a slightly wider range

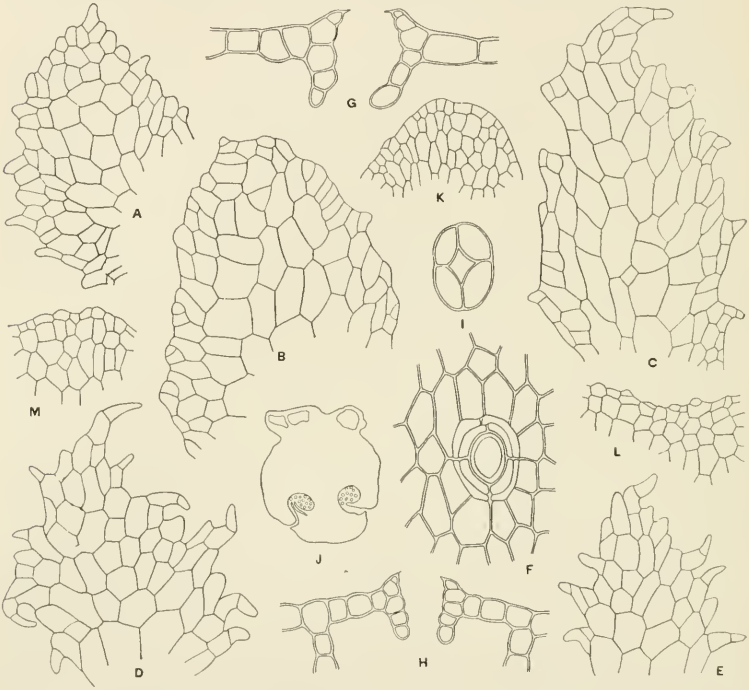

Fig. 13. Marchantia papillata Raddi

Appendages of ventral scales and other anatomical details. A-E. Appendages of ventral scales, B and C having been dissected from the same thallus, x 100. F. Epidermal pore of thallus, surface view, x 225. G, H. Pores in cross-section, x 225. I. Inner opening of pore, x 225. J. Stalk of female receptacle, cross-section, x 40. K-M. Parts of involucres, x 100. A. Brazil, *G. Raddi,* type. B, C, G, J, K. Paraguay, *B. Balansa 4006.* D-F, H, I. Bolivia, *R. S. Williams 2145.* L, M. Peru, *R. Spruce,* type of *M. subandina.*

of variability. There are, however, certain differences in the epidermal cells and pores which deserve some emphasis. The cells and pores are not only distinctly smaller than in *M. domingensis,* but the pores are constructed on a simpler plan, the opening being surrounded by fewer rows of cells and the number of cells in each row being less subject to variation. The cells bounding the inner opening tend to be more convex. It must be admitted that these differences are very slight and might not deserve much attention if they were not supported by other differences derived from the female receptacle.

The variability of the receptacles with respect to the number of lobes has already been commented upon in connection with the type specimen and becomes still more apparent from a study of the published descriptions. According to Nees von Esenbeck the usual number of lobes is seven, eight to ten being sometimes present; according to Spruce nine lobes are present in *M. subandina;* according to Schiffner, who studied Raddi's specimen in the Lindenberg herbarium, the normal number of lobes in *M. papillata* is six, a larger number being unusual; according to Stephani both *M. papillata* and *M. subandina* have nine lobes apiece. In the writer's opinion nine may be regarded as the normal number of lobes, although a smaller number frequently occurs. In the number of lobes, therefore, the species agrees on the whole with *M. domingensis.* The receptacle, however, is smaller; the lobes are more dilated and more frequently emarginate at the apex; the medium protuberance of the disc and the convexity of the lobes are more pronounced; and the involucre is less variable, being entire or nearly so and apparently never bearing elongated teeth or cilia. Just how constant these differences are can only be established by the study of more material. If they should be found to intergrade it might become necessary to reduce *M. domingensis* to synonymy under *M. papillata,* but the differences seem sufficient at the present time to justify the maintenance of both species as valid.

The group of species to which *M. domingensis* and *M. papillata* belong is well represented in paleotropic regions. Among the species which are referable to this group *M. emarginata* R. Bl. & N.,[34] *M. linearis* Lehm. & Lindenb.,[35] and *M. Schaden-*

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[34] Nova Acta Acad. Caes.-Leop. Carol. 12: 192. 1824.

[35] Lehmann, Pug. Plant. 4: 8. 1832.

bergii Steph.[36] may be especially mentioned. The first of these has a very extensive distribution and is reported by Stephani from China, the Himalayas, Japan, Java and the Philippine Islands; the second is known from various parts of India; the third, from the Philippine Islands only. These three species are closely related, and the differences brought out by Stephani are not very convincing. As indicated in the synonymy the authors of the Synopsis referred specimens of *M. domingensis* to *M. linearis,* an error first pointed out by Stephani. Since, however, *M. linearis* is so closely related to *M. emarginata* it will be sufficient to compare the two American plants with this latter species, a full description of which has been published by Schiffner.[37]

In size *M. emarginata* is comparable with *M. domingensis;* in the structure of the female receptacle, with *M. papillata.* It agrees with both species in the possession of sclerotic cells in the thallus; in the general features of the ventral scales; in the closely toothed appendages of the median scales; and in the structure of the involucre. Schiffner describes the latter as lobed and almost entire, but it is sometimes possible to detect a few short teeth, especially toward the outer extremities. A few differences in the structure of the thallus may be mentioned. In *M. emarginata,* for example, although sclerotic cells are present they are never so abundant or so conspicuous as they sometimes are in *M. domingensis.* The thallus is further distinguished by the possession of slime cells and, according to Schiffner, by the occasional presence of epidermal papillae. It would be unwise, however, to lay much stress on any of these differences, since the structures on which they are based are so very variable.

The female receptacle of *M. emarginata* shows the features described under *M. papillata* in an intensified form. The median protuberance is not only more pronounced, but the lobes themselves might almost be described as costate, while their apices are more markedly dilated and emarginate. These features are of course subject to variation. The male receptacles are distinguished by their long and slender stalks. The cupules are much the same as in two American species.

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[36] Bull. Herb. Boissier 7 : 524. 1899.

[37] Fl. de Buitenzorg 4 : 31. 1900.

8. MARCHANTIA BESCHERELLEI Steph.

Marchantia Bescherellei Steph. Rev. Bryol. **15**: 86. 1888.

Thallus dull green, not glaucous, slightly or not at all pigmented with purple, mostly 5-7 mm. wide and 2-3 cm. long, dichotomous, the forks 1-1.5 cm. apart, texture very delicate, margin entire, sometimes vaguely and irregularly plicate; epidermis composed of cells with very thin walls, in a single layer, mostly 40-70μ long (averaging about 50μ) and 20-35μ wide (averaging about 25μ), papillae absent; pores (with their surrounding cells) mostly 160-200μ long and 120-160μ wide, surrounded usually by seven or eight rows of cells, three or four in the upper series and four in the lower series, the two lower rows of the upper series usually composed of ten to twelve or even more cells apiece, the other rows of five or six cells, rarely of only four cells apiece, inner opening usually five- or six-sided, rarely only four-sided, with the sides strongly concave, resinous deposit slight; air-chambers low, somewhat elongated, their boundaries indistinct when viewed through the epidermis, present everywhere except close to the margin, rows of photosynthetic cells usually two or three cells long; compact ventral tissue mostly twelve to fifteen cells thick in the median portion, abruptly thinning out in the wings, the walls somewhat pigmented, slightly or not at all thickened, sclerotic cells scattered, sparingly developed, slime cells lacking; ventral scales in two rows, the laminar scales alternating with the median scales and not much nearer the margin; appendages of the median scales ovate, when well developed mostly 0.5-0.6 mm. long and 0.35-0.45 mm. wide but often smaller, apex acute, margin sparingly and irregularly dentate, the teeth in the basal portion often larger and sharper and sometimes lobe-like, cells showing a gradual and slight decrease in size toward the margin, median cells usually longer than broad, mostly 50-80μ long and 30-40μ wide, marginal cells mostly 30-50μ long and 15-25μ wide, irregular but usually perpendicular or nearly so to the margin, cells containing oil-bodies lacking: male receptacle borne on a stalk about 1 cm. long (in the only example studied), with two rhizoid-furrows and (apparently) with a single broad dorsal band of air-chambers, the disc 7 mm. broad, with four short and rounded lobes or rays with thin margins, basal sinus more than 180 degrees, the other sinuses narrow, ventral scales apparently in two rows: female receptacle borne on a stalk about 2 cm. long (in the only example studied), with two rhizoid-furrows and dorsal air-chambers apparently in two distinct bands, the disc about 7 mm. wide, with five short and rounded lobes or rays, upper surface of receptacle plane, basal sinus a straight line or nearly so; involucre delicate, closely and irregularly dentate, some of the teeth three or four cells long and two to four cells wide at the base, other teeth smaller: spores (according to Stephani) yellowish brown, 23μ in diameter, erose along the ridges, otherwise smooth. (FIG. 14.)

Known only from the following specimens:

BRAZIL: Rio Janeiro, *A. Glaziou 6348* (B., N. Y., type); *E. Ule 123* (B., listed by Stephani in Bull. Herb. Boissier **7**: 406. 1899).

The material of *M. Bescherellei* in the Boissier herbarium, portions of which have been examined by the writer, includes the female type specimens and the male specimens collected by Ule. A sterile specimen of the type material, in the Mitten herbarium, has likewise been examined. It will be noted that Spruce,[38] who published a list of Glaziou's specimens, makes no mention of No. 6348. According to the label on the specimen in the Mitten herbarium, Spruce thought that this number might perhaps represent a new genus of the Marchantiaceae, but he evidently reached no definite conclusion about it. Probably he had only sterile material at his disposal, because the female receptacle shows at once that Stephani was correct in referring the plant to the genus *Marchantia.* Unfortunately the specimens studied by the writer were very fragmentary and remained shriveled after long soaking in water. It was therefore impossible to gain from them an adequate idea of the species, and some of the statements made about the structure must be regarded as more or less tentative.

The texture of *M. Bescherellei* is exceedingly delicate and the thallus thins out abruptly in passing from the midrib to the wings. In the latter the ventral tissue becomes reduced, according to Stephani, to a single cell in thickness, and the marginal portion, where the entire thallus is only one cell thick, is four cells broad. Although the air-chambers are low the photosynthetic tissue is well developed and characteristic and the pores are large and complex.

The appendages of the ventral scales are composed of cells which show a gradual decrease in size in passing from the median portion toward the margin, resembling in this respect the appendages of *M. domingensis* and *M. papillata,* but the margin itself is

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[38] Rev. Bryol **15**: 33, 34. 1888.

very different in being much more sparingly toothed. Among the preceding species the appendages find their closest counterparts in *M. paleacea* and *M. breviloba.* Their apices, however, are more uniformly sharp-pointed, their teeth tend to be sharper, and their marginal cells are more frequently placed at right angles to the margin.

With regard to the female receptacle there are marked discrepancies between Stephani's original description and the later description of his Species Hepaticarum. According to the original account the disc is green, convex in the middle, five-lobed for one third the distance from margin to center, the lobes being rounded and shortly incised at the apex, plane and horizontal, delicate and beautifully reticulated. Doubt is thrown, however, upon the constancy of the five-lobed condition. The involucres are described as reddish, firm in texture, and shortly ciliate. According to the later account the disc is brownish green, delicate and veiny, plano-convex in the center, and nine-lobed, the lobes being plane, connate almost to the apex, rounded and very shortly incised. The involucre is said to be hyaline, small-lobed, irregularly and shortly fimbriate. In the only receptacle seen by the writer the disc is five-lobed, the two basal lobes being only about

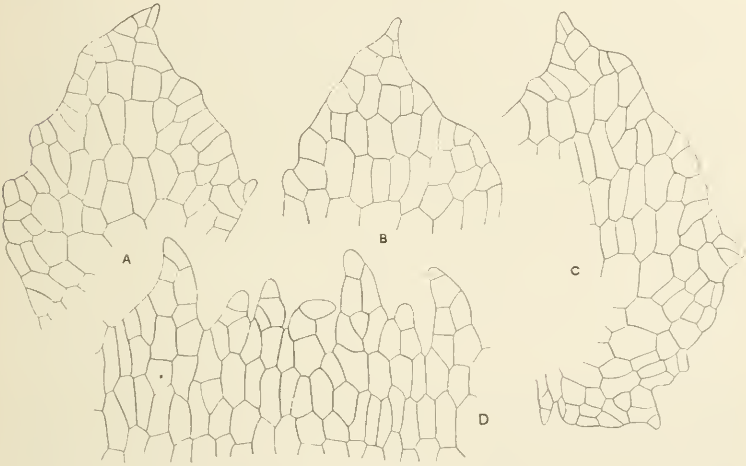

Fig. 14. Marchantia Bescherellei Steph.

Anatomical details. A-C. Appendages of ventral scales, x 100. D. Part of an involucre, x 100. Drawn from the type specimen.

half as broad as the other three lobes and the sinus being practically a straight line. The three broad lobes appear to be very shortly incised at the apex but they are actually only emarginate, the apparent incision being really filled by an extension of the membranous margin of the lobes. In other respects the lobes agree with Stephani's accounts. The involucre is distinctly toothed, but the teeth are scarcely long enough or sharp enough to be described as cilia or fimbriations. The discrepancy in the number of lobes which Stephani's accounts bring out might of course be due to a variability of the species, which could only become evident through the study of more extensive material.

It is unfortunate that the structure of the stalks of the receptacles must be left in doubt. In Stephani's original description the stalk of the female receptacle is said to bear two dilated dorsal lamellae but no mention is made of these in his later account, and nothing whatever is said about the structure of the stalk of the male receptacle. From the scanty supply of material available, it has been impracticable to prepare cross-sections of stalks, so that the writer is unable to confirm Stephani's statement or to add further details. If the stalk of the male receptacle bears a band of air-chambers the relationship might be with *M. domingensis.* If two bands of air-chambers are present in the stalk of the female receptacle, a relationship with *M. chenopoda* would be indicated, and it is worthy of note that Mitten referred Glaziou's type specimen to *M. brasiliensis* Lehm. & Lindenb., a species which is now included among the synonyms of *M. chenopoda* L. According to our present knowledge, however, the systematic position of the species can hardly be determined.

9. MARCHANTIA CHENOPODA L.

Marchantia chenopoda L. Sp. Plant. 1137. 1753.

Marchantia androgyna L. *l. c.* 1138. 1753 (in part); Swartz, Fl. Ind. Occ. 1882. 1806.

Chlamidium indicum Corda; Opiz, Beitr. zur Naturg. 647. 1828 (*nomen nudum*).

Marchantia Swartzii Lehm. & Lindenb.; Lehmann, Pug. Plant. 4: 9. 1832.

Marchantia cartilaginea Lehm. & Lindenb. *l. c.* 4: 31. 1832.

Marchantia brasiliensis Lehm. & Lindenb. *l. c.* 4: 32. 1832.

Grimaldia peruviana Nees & Mont.; Montagne, Fl. Boliv. in D'Orbigny, Voy. dans l'Amér. Mérid. 7^2: 53. 1839.
Marchantia peruviana Nees; G. L. & N. Syn. Hep. 538. 1847.
Marchantia Dillenii Lindb. Krit. Gransk. Hist. Musc. 47. 1883.

Thallus pale or yellowish green, sometimes more or less glaucous, usually tinged with purple or brownish on the lower surface, usually 4-7 mm. wide and 2-3 cm. long, dichotomous, the successive forks averaging about 1 cm. apart, texture varying from firm and often leathery to delicate, margin entire; epidermis composed of cells with slightly thickened walls, often in two layers, mostly 30-60μ long (averaging about 40μ) and 15-30μ wide (averaging about 22μ), papillae absent, slime cells often present, averaging about 60μ in diameter; pores variable in size, usually (with their surrounding cells) measuring 100-170μ in length and 80-130μ in width but sometimes considerably smaller, usually surrounded by seven rows of cells (four in the upper series and three in the lower), more rarely by six, eight or even nine rows, the two upper rows of the upper series and the two lower rows of the lower series composed of four to six cells apiece, the third row of each series usually of twice as many, and the fourth row of the upper series usually of a much larger number, sometimes of as many as eighteen, inner opening four- to six-sided with the sides straight or more or less concave, cell-walls mostly smooth throughout; air-chambers of medium height, isodiametric or somewhat elongated, their boundaries usually distinct but sometimes obscure when viewed through the epidermis, present everywhere, cells of partition walls sometimes including slime cells, rows of photosynthetic cells usually three or four cells long; compact ventral tissue mostly twenty to twenty-five cells thick in the median portion, the walls sometimes pigmented, more or less thickened and showing distinct pits, sclerotic cells usually distinct, scattered, mostly twenty to fifty in a cross-section, usually abundant in both median portion and wings, slime cells usually present, scattered, tending to be more abundant in the wings, rarely more than six or eight in a cross-section; ventral scales in two distinct rows, the laminar scales alternating with the median scales and not much nearer the margin; appendages of the median scales very variable, lanceolate to broadly ovate, when well developed mostly 0.45-0.65 mm. long and 0.3-0.4 mm. wide but sometimes considerably smaller, apex acuminate, acute or apiculate, margin entire or variously and irregularly toothed, the teeth rarely numerous and often restricted to the basal portion, cells of about the same size throughout or showing a slight and gradual decrease in size toward the margin, median cells usually longer than broad, mostly 60-90μ long and 25-40μ wide, marginal cells mostly 30-70μ long and 20-35μ wide, irregular, the long axis varying from parallel to perpendicular to the margin, cells containing oil-bodies usually absent, rarely one or two present: male receptacle borne on a stalk mostly 1-2 cm. long, with two rhizoid-furrows and no air-chambers, the disc mostly 0.8-1 cm. broad, deeply lobed, the lobes or rays mostly four, rarely five or six, palmately disposed, the basal sinus sometimes more than 180 degrees broad, the lobes mostly 5-7 mm. long and 1.5-2 mm. wide, rounded, with a thin wavy margin extending across the basal sinus, ventral scales imbricated, mostly in two rows: female receptacle borne on a stalk 2-4 cm. high, with two rhizoid-furrows and two narrow dorsal bands of air-chambers, the disc convex, mostly 6-8 mm. wide, shortly five-lobed, the lobes or rays convex, rounded and separated by shallow sinuses, the basal sinus much broader than the others and approximating a straight line; involucre firm, the margin sparingly dentate to closely ciliate or laciniate, the teeth or cilia varying from one to five cells in length, sometimes forking; spores brownish yellow, about 26μ in diameter, narrowly margined, the outer face bearing a few low ridges not forming a network; elaters about 6μ wide, bispiral: cupules closely short-ciliate, the cilia mostly two to four cells long, outer surface without papillae. (Figs. 15-20.)

A widely distributed species is tropical America. The following specimens have been examined:

Puebla: banks of Avenida Hidalgo and path to barranca, Tezuitlan, October, 1908, *Barnes & Land 537*.

Vera Cruz: Jalapa and vicinity, September, 1906, *Barnes & Land,* no number (Y.); July, 1908, *C. G. Pringle 15326* (Y., distributed in Pl. Mex. under a manuscript name of Stephani); November, 1908, *Barnes & Land 556, 614, 626a* (Y.); vicinity of Orizaba, November, 1908, *Barnes & Land 631, 670* (Y.).

Guatemala: without definite locality or date, *Godman & Sabin* (N. Y.); Santa Rosa, September, 1894, *Heyde & Lux 6293* (N. Y.); near the Finca Sepacuité, Alta Verapaz, March and April, 1902, *Cook & Griggs 83, 141, 394* (U. S., Y.); trail from Pangós to Sepacuité, Alta Verapaz, January, 1908, *Maxon & Hay 3111* (U. S., Y.); Coban, Alta Verapaz, *H. von Tuerckheim 6074* (N. Y.).

Costa Rica: Bagnar, Angostura, June, 1874, *O. Kuntze 2102* (N. Y.); la Verbena, Alajuelita, August, 1894, *A. Tonduz 15562* (N. Y., Y., distributed by E. Levier under a manuscript name of Stephani); Rio Turrialba, March, 1896, *J. D. Smith* (N. Y.); Cuesta de la Vieja, road to San Carbos, April, 1903, *Cook & Doyle 111* (U. S., Y.); Juan Vinas, April, 1903, *Cook & Doyle 301* (U. S., Y.); vicinity of La Palma, May, 1906, *W. R. Maxon 489* (U. S., Y.).

PANAMA: without definite locality or date, *B. Seemann* (N. Y.); Darien, April and June, 1908, *R. S. Williams 1083, 1084* (N. Y., Y.).

CUBA: without definite localities or dates, *C. Wright* (distributed in Hep. Cubenses).

JAMAICA: without definite localities or dates, *Fordyce, W. Wright;* Whitfield Hall, December, 1896, *W. Harris 11063* in part (N. Y.); Moody's Gap, March, 1895, *W. Harris 5671* (N. Y., U. S., Y.); vicinity of Cinchona, November, 1902, *F. S. Earle 397a* (N. Y., Y.); July, 1903, *A. W. Evans 248* (Y.); Mount Airy, trail to Tweedside, April, 1903, *W. R. Maxon 864* (U. S., Y.); Second Breakfast Spring, near Tweedside, April, 1903, *W. R. Maxon 880* (U. S., Y.); Morce's Gap, August, 1906, *A. W. Evans 405* (Y.); Cuna Cuna Gap, September, 1908, *E. G. Britton 990* (N. Y., Y.); March, 1909, *Britton & Howe 4032* (N. Y., Y.).

PORTO RICO: Adjuntas, March, 1886, *P. Sintenis 51* (N. Y., U. S., Y., listed by Stephani in Hedwigia 27: 294. 1888); road from Ponce to Adjuntas, July, 1901, *Underwood & Griggs 732* (N. Y., U. S., Y.); Military Road, north of Cayey, June, 1901, *Underwood & Griggs 278* (U. S., Y.); road from Utuado to Arecibo, July, 1901, *Underwood & Griggs 839* (U. S., Y.); near Cayey, July, 1900, *A. W. Evans 95* (Y.); between Ponce and Utuado, March, 1906, *Britton & Marble 778* (N. Y., Y.); Mount Morales, near Utuado, March, 1906, *M. A. Howe 1098* (C. C. H., N. Y., Y.); summit of Loma la Mina, Sierra de Naguabo, July, 1914, *J. A. Shafer 3337* (N. Y., Y.); La Juanita, near Las Marias, February, 1915, *E. G. Britton 3964* (N. Y., Y.); La Chiquita, near Maricao, February, 1915, *E. G. Britton 4099* (N. Y., Y.); *Britton & Cowell 4296* (N. Y., Y.); between Adjuntas and Ponce, March, 1915, *E. G. Britton 5367* (N. Y., Y.): Maricao, July, 1915, *F. L. Stevens 1844* (N. Y., Y.); Gigante, July, 1915, *F. L. Stevens 1797* (N. Y., Y.).

GUADELOUPE: without definite locality, 1874, *T. Husnot* (distributed in Pl. des Antilles *196*); Gombeyre, 1897-1900, *Père Duss 391* (N. Y.); Basse Terre, 1898 *Père Duss 253* (N. Y., determined as *M. brasiliensis* by Stephani).

DOMINICA: Laudat, 1903, *F. E. Lloyd 76, 78, 285* (N. Y., Y.).
MARTINIQUE: St. Pierre, 1899-1900, *Père Duss 390* (N. Y.,

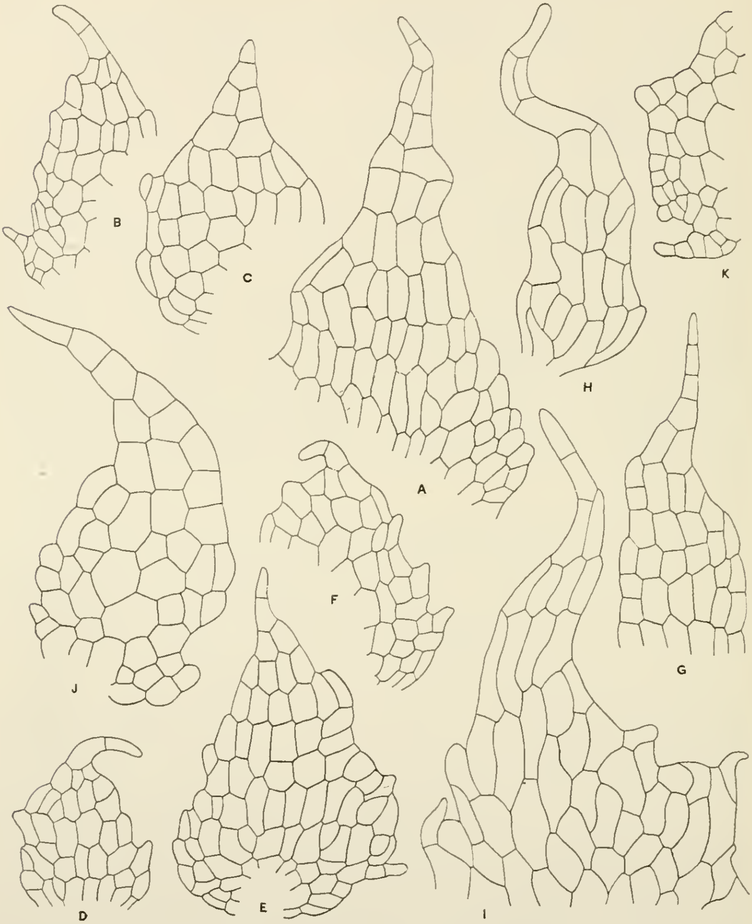

FIG. 15. MARCHANTIA CHENOPODA L.

Appendages of ventral scales, x 100; K represents the basal portion of an appendage. A. Vera Cruz, 1906, *Barnes & Land.* B-G. Vera Cruz, *Barnes & Land 614.* H, I. Vera Cruz, *Barnes & Land 626a.* J, K. Guatemala, *Cook & Griggs 83.*

determined as *M. brasiliensis* by Stephani); Carbet, 1899, *Père Duss 342 bis* (N. Y.); Morne Rouge, August, 1901, *Père Duss 581* (N. Y.).

GRENADA: Grand Etang, 1913, *R. Thaxter* (H., Y.).

VENEZUELA: near Caripe, *A. von Humboldt* (Y., specimen from the Hooker herbarium, labeled *"Humboldt 235,"* presumably the basis for the record in Nov. Gen. Sp. Plant. 7:99. 1825); without definite locality or date, *Funck & Schlim 337* (N. Y.).

COLOMBIA: Andes Bogotenses, *W. Weir* (N. Y.).

BRAZIL: Orgaos Mountains, *C. Gaudichaud* (N. Y., specimen from the Montagne herbarium, labeled simply *"Brasilia,"* presumably the basis for the record in Voy. Corv. la Bonité, Bot. 1:209. 1844-46); Morro Velho, no date, *G. Gardner 131* (N. Y.); Rio de Janeiro, no date, *J. Milne* (N. Y.); *A. Glaziou 17992* (N. Y., listed by Spruce in Rev. Bryol. 20:60. 1893); Jacobina, Mattogrosso, October, 1872, *O. Kuntze* (N. Y., sterile and somewhat doubtful); near Sao Paulo, April, 1905, *A. Usteri 1* (Y.).

ECUADOR: Baños, *R. Spruce* (listed in Trans. Bot. Soc. Edinburgh 15:562. 1885, and distributed in Hep. Spruceanae).

PERU: near Tarapoto, *R. Spruce* (distributed in Hep. Spruceanae); Ollantaytambo, May, 1915, *Cook & Gilbert 755* (U. S., Y.).

BOLIVIA: near Irupana, *A. d'Orbigny 226* (M., type of *Grimaldia peruviana*); Yungas, 1885, *H. H. Rusby, 3001, 3002, 3003, 3004* (N. Y., U. S., listed by Spruce in Mem. Torrey Club 1:140. 1890); 1892, *M. Bang 1545* (N. Y.); July, 1893, *P. Jay 71* (N. Y., Y.); Tumupasa, December, 1901, *R. S. Williams 2143* (N. Y., Y.).

GALAPAGOS ISLANDS: Albemarle Island, August, 1906, *A. Stewart 6876.*

The following additional stations, recorded in the literature, are likewise of interest:

OAXACA: Mirador and Comaltepec, *F. Liebmann* (listed by Gottsche in Mex. Leverm. 268. 1863).

VERA CRUZ: near Orizaba and at Cordoba, 1855, *F. Müller* (listed by Gottsche, *l. c.*).

COSTA RICA: near San José, *H. Pittier 6004, 6049;* Marais de la Palma, *H. Pittier 6018, 6024* (both listed by Stephani in Bull. Soc. Bot. Belgique 31:180. 1892).

JAMAICA: without definite locality or date, *P. Collinson* (type of *M. Dillenii*).

MARTINIQUE: Morne de la Calabasse, without date or collector's name (type, cited by Plumier); without definite locality, date, or collector's name (type of *M. cartilaginea*); without definite locality or date, *Hahn 1347; T. Husnot 197, 198* (the last three listed by Bescherelle in Jour. de Bot. 7: 193. 1893).

FRENCH GUIANA: near Cayenne, 1835-49, *Leprieur 1386* (listed by Montagne in Ann. Sci. Nat. Bot. IV. 3: 320. 1855).

VENEZUELA: Merida, *K. Goebel* (figured in Organographie der Pflanzen 258. *f. 157.* 1898).

COLOMBIA: Muzo, Fusagasuga and Puripi, 1859, *A. Lindig 1715, 1718, 1719, 1722, 1723* (listed by Gottsche in Ann. Sci. Nat. Bot. V. 1: 186. 1864).

PERU: Rio Huallaga, November, 1902, *E. Ule 527* (listed by Stephani in Hedwigia 44: 223. 1905).

BRAZIL: "Montagne d'Estrella," *G. Raddi* (cited by Raddi, see below); without definite locality or date, *F. Sellow* (type of *M. brasiliensis*).

The specimens recorded by Schiffner from the Fiji Islands (Leberm. Forschungsr. S. M. S. "Gazelle" 43. 1890) are described as having ciliate-dentate ventral scales and would probably now be referred to some other species.

The interpretation of *M. chenopoda* is beset with difficulties, and a history of the species may therefore be in place. The Linnaean description or diagnosis is very short and reads, "Marchantia calyce communi dimidiato palmato quadrifido." If the term "calyx" signifies the female receptacle this description would not apply accurately to any of the known American species, where a four-parted receptacle occurs only as an abnormality. If the term signifies the male receptacle there are several species to which the description might perhaps apply. In any case it would be quite impossible to identify a definite species by means of the Linnaean description alone.

Unfortunately the only synonym which Linnaeus quotes, the "Lichen anapodocarpos" of Plumier, is likewise insufficient to lead to a positive conclusion. Plumier[39] described his plant from material collected on the Morne de la Calabasse in Martinique. Linnaeus cites the original description and figure and also the

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[39] Traité des Fougères de l'Amér. 143. *pl. 142.* Paris, 1705.

later description and figure published by Dillenius.[40] Plumier's figure represents certain reproductive parts in detail and a thallus with a sinuate or vaguely lobed margin, branching occasionally by forking and apparently also by ventral outgrowths. From the tips of some of the branches the four-lobed receptacles on short stalks take their origin and clearly bring the growth of the branches to an end. In two cases—possibly in three—five-lobed receptacles are shown. In his text Plumier compares the appearance of the plant with that of the Indian fig and says that the upper surface is of a pale green color and roughened by minute elevated points. He compares the entire receptacle with a mushroom and states that one side of the disc is rounded, while the other shows four semicircular lobes, the whole resembling an inverted goose foot. He adds that each lobe opens longitudinally, and shows minute white "flowers" in the form of tubes. Each tube divides at the apex after a while into four parts which roll back and disclose an oval fruit filled with "seeds" like flour. It is clear from this account that he had female receptacles before him and that he saw the involucre, the pseudoperianth, the capsule, and the spores.

Dillenius took his figure directly from Plumier and did not know the plant itself. He tried to improve the figure, however, by indicating that the upper surface of the thallus was covered over with minute polygons as in related species. Lindberg[41] criticises the figure of Dillenius (and consequently that of Plumier) by stating that an autoicous inflorescence is shown, both male and female receptacles being represented on the thallus. This criticism is undeserved. The receptacles shown are all female, the dorsal surface being represented in some cases and the ventral in others. In his text Dillenius brought out the fact that the receptacles were all the same kind, although he incorrectly interpreted the fruit of Plumier as an anther and the flour-like seeds as pollen, a well-known error which he repeats in his interpretation of the reproductive parts in other bryophytes.

On the basis of Plumier's description and figures it becomes evident that the term "calyx" in the Linnaean diagnosis of *M.*

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[40] Hist. Musc. 531. *pl. 75, f. 5.* Oxford, 1741.

[41] Krit. Gransk. Dillen. Hist. Musc. 45. Helsingfors, 1883.

chenopoda refers to the female receptacle, and it has already been pointed out that a quadrifid female receptacle is not found normally in any known American species. Plumier's work indicates further, that the involucres and sporophytes of his plant are situated underneath the lobes, a condition which is likewise

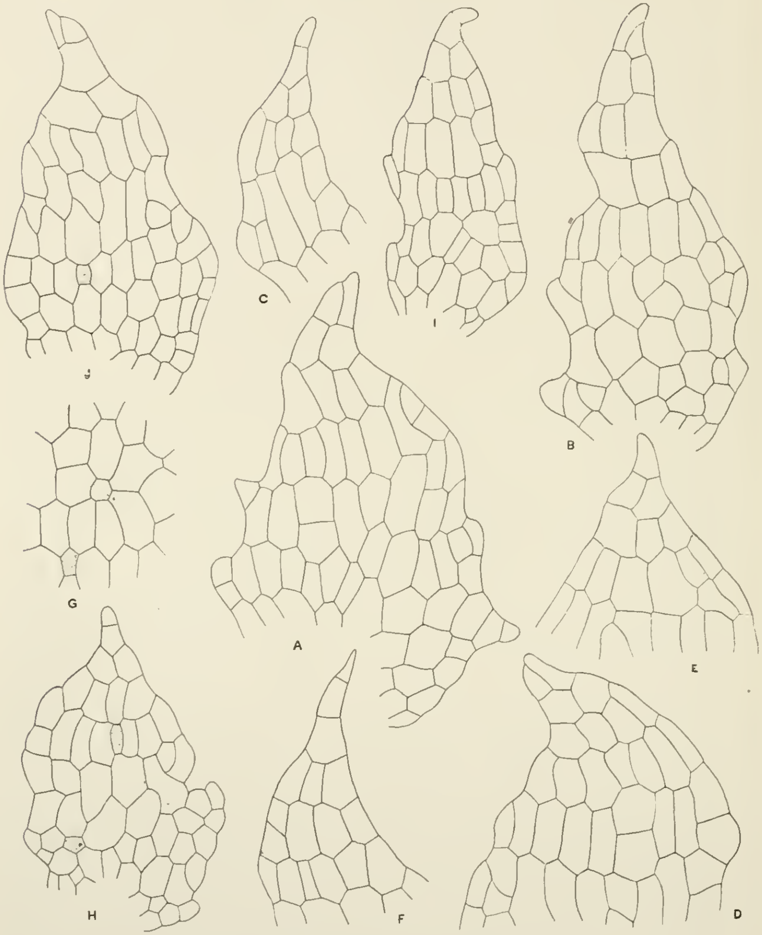

Fig. 16. Marchantia chenopoda L.

Appendages of ventral scales, x 100; G represents the median portion of an appendage with two cells containing oil-bodies. A-C. Cuba, *C. Wright,* in Hep. Cubenses. D, E. Jamaica, *A. W. Evans 258.* F, G. Jamaica, *W. R. Maxon 405.* H, I. Porto Rico, *F. L. Stevens 1844;* J. Guadeloupe, *T. Husnot,* in Pl. des Antilles *196.*

unknown among American species, where the involucres and sporophytes invariably alternate with the lobes. Since there are apparently no specimens of Plumier's plant in herbaria, it is clear that *M. chenopoda* L. represents an unidentifiable plant, and the logical course would be to give up the species altogether.

In the literature of the Hepaticae, however, *M. chenopoda* has an established place, and it seems justifiable to interpret it according to the descriptions of later writers. Even Plumier's figure gives us a little help because it shows that he occasionally observed a five-lobed receptacle, although he makes no mention of such a structure in his text. Since most subsequent writers ascribe to the species definitely a five-lobed receptacle, and since the species to which they assign the name is abundant in Martinique, it is quite probable that their *M. chenopoda* is the same as Plumier's plant. Unfortunately their descriptions and figures are not without discrepancies, and it becomes evident that Taylor at least did not distinguish between what is here called *M. chenopoda* and *M. domingensis*.

Apparently Swartz[42] was the first to describe the male receptacles. He states that they are subpeltate, unsymmetrical, palmate-quadrifid, plane and verruculose above (like the thallus), and convex below, the rays or lobes being linear, obtuse, and often unequal, with membranous, undulate margins. He cites no stations for the species although he implies that it occurs in Jamaica. Quadrifid receptacles are sometimes found in *M. domingensis,* but it is probable that Swartz had the true *M. chenopoda* before him, and his description is definitely cited in the Synopsis Hepaticarum.

Schwaegrichen,[43] in 1814, quotes *M. chenopoda* from Africa as well as from America, and F. Weber,[44] the following year, notes a similar extension of range. Neither writer adds anything significant to our knowledge of the species, and it is probable that their citation of African stations is based on incorrect determinations, since all subsequent writers restrict the range of *M. chenopoda* to America.

A few years later Raddi[45] extended the known range of the

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[42] Fl. Ind. Occid. 1880. Erlangen, 1806.

[43] Hist. Musc. Hepat. Prodr. 32. Leipzig, 1814.

[44] Hist. Musc. Hepat. Prodr. 103. Kiel, 1815.

[45] Mem. Soc. Ital. Modena 19: 44. 1823; 20: *pl. 6a, f. 1, 2.* 1829.

species into Brazil and stated that it occurred abundantly at the bottom of moist and mossy rocks on the "Montagne d'Estrella." According to his account *M. chenopoda* is distinguished from all the other species of *Marchantia* by its receptacles, which are truncate on one side. He adds that in the male receptacle the upper surface is plane and that the four parts or lobes are unequal in length, and he criticises Plumier for comparing this receptacle with a goose's foot; in his opinion it is more like the foot of a pigeon. Of course this criticism has no weight, since Plumier drew his account entirely from female receptacles. According to Raddi the disc of the female receptacle is strongly convex and either entire or very shortly divided, bearing on the lower surface four fleshy or rib-like swellings, between which are borne the capsules, much as in *M. polymorpha.* He notes further that the upper surface of the thallus is areolate and perforated by white vesicles and that the lower surface is violet except along the margin, where it is green. Although Raddi's specimens have not been available for study it is evident that he had the true *M. chenopoda* before him. Not only is his description unusually clear, but the species has since been collected in other Brazilian localities.

In 1835 Taylor published an account of the Marchantiaceae which had come under his observation. In his description of *M. chenopoda*[46] he comments on the inaccuracies of Plumier's figures and quotes them doubtfully, although it was upon Plumier's work that the species was primarily based. According to Taylor the female receptacle is hemispherical and divided into from eight to ten truncate laciniae, each bearing underneath a single involucre with ciliate or serrulate margins. He notes further that the stalk of the receptacle has two rhizoid-furrows and adds interesting statements about the scales on the vegetative thallus and about the cupules. The scales, in his words, have an entire and broadly ovate base, then a deep constriction at about the middle, and then a broadly ovate and ciliate expansion (the latter being what is now known as the appendage). In the cupules he speaks particularly of the serrate margin. It will be seen at once that Taylor's account of the female receptacle is very different from that of his predecessors, and the specimens in his herbarium show that it was drawn from *M. domin-*

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[46] Trans. Linn. Soc. 17: 379. *pl. 12, f. 2.* 1835.

gensis. His account of the male receptacle, however, agrees esentially with that of Swartz. Taylor cites *M. chenopoda* from Guadeloupe and St. Vincent as well as from Jamaica and Martinique.

Fig. 17. Marchantia chenopoda L.

Appendages of ventral scales, x 100. A, B. Venezuela, *Funck & Schlim.* C-E. Brazil, *A. Glaziou 17992.* F, G. Brazil, 1905, *A. Usteri 1.* H-J. Galapagos Islands, *A. Stewart 6876.*

In the Synopsis Hepaticarum emphasis is again laid on the receptacles. The female receptacle is said to be excentric, hemispherical, and about five-lobed, the lobes being obtuse, subcrenate and soon obsolete, with hyaline, denticulate involucres. The male receptacles are said to be unsymmetrical and palmately four- to five-parted. This account of the female receptacle agrees closely with that of Raddi and differs from that of Taylor. Both writers, however, are cited under the species. From Brazil several localities are enumerated, but the only West Indian stations given without question are on the island of Martinique. The Synopsis quotes three synonyms: *M. androgyna* (female plants only), *M. Swartzii*, and *Chlamidium indicum*. These may be considered in order.

Swartz apparently supposed that what he called *M. androgyna* was the same as *M. androgyna* L.,[47] a species based on two citations, the first from Dillenius[48] and the second from Micheli.[49] According to Swartz, who treats the plant very briefly, *M. androgyna* is related to *Reboulia hemisphaerica* (L.) Raddi; he describes the thallus as narrower than in that species and states that the male receptacles are perhaps sessile and that the female receptacles are subentire. Although he cites no actual material it is probable that he drew his description from Jamaican specimens collected by himself, these being definitely referred to by later writers.

Now the Dillenian species quoted by Linnaeus under *M. androgyna* has been the cause of a great deal of confusion. It was based on two entirely different plants, a fact which was first pointed out by Lehmann and Lindenberg in their discussion of the Asiatic *M. linearis* Lehm. & Lindenb.[50] They show clearly that the Dillenian *f. 3B*, which, as they state, is essentially the same as the figure by Micheli, represents *Grimaldia dichotoma* Raddi, a common species of the Mediterranean region. They show further that the Dillenian *f. 3A* and *f. 3C* represent a species of *Marchantia*, and they suppose that this species is the same as the *M. androgyna* of Swartz. The two figures in question were drawn from specimens collected in Jamaica by P. Collinson;

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[47] Sp. Plant. 1138. 1753.

[48] Hist. Musc. 520. *pl. 75, f. 3.* 1741.

[49] Gen. Nov. Plant. 3. *pl. 2, f. 3.* 1729.

[50] Lehmann, Pug. Plant. 4:9. Hamburg, 1832.

f. 3A shows a plant with numerous cupules and female receptacles, while *f. 3C* shows a small forking fragment with cupules only. The receptacles are so strongly convex that they appear conical and resemble those of *Conocephalum conicum* (L.) Dumort. In fact, according to Lehmann and Lindenberg, the

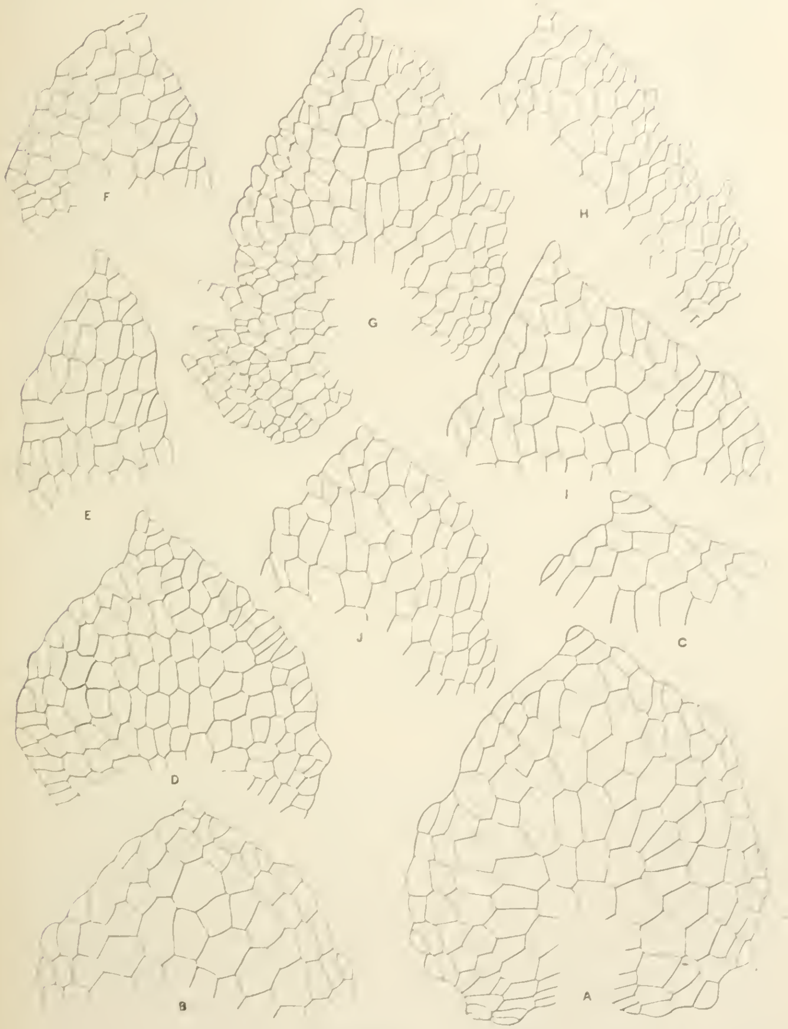

FIG. 18. MARCHANTIA CHENOPODA L.

Appendages of ventral scales, x 100. A-C. Peru, *Cook & Gilbert 755*. D-F. Bolivia, *A. d'Orbigny*, type of *M. peruviana*. G, H. Bolivia, *H. H. Rusby 3004*. I, J. Bolivia, *P. Jay 71*.

M. androgyna of Weber[51] is actually *Conocephalum conicum,* and the Linnaean name has been applied by other writers to such distinct species as *Preissia quadrata* (Scop.) Corda and *Reboulia hemisphaerica* (L.) Raddi.

Lehmann and Lindenberg's conception of *M. androgyna* Sw. was based on specimens collected by Swartz in Jamaica. Although they considered these specimens identical with those collected by Collinson they did not take up the name *M. androgyna* for the species, probably because the original *M. androgyna* L. was an aggregate. They described it instead under the new name *M. Swartzii.* The female receptacle, according to their account, is unsymmetrical, hemispherical, and subentire or obsoletely lobed, the lower surface and the stalk being villous. They state further that the upper surface of the thallus is green with many large pores bordered with white, and that the lower surface is brown with scales in the median portion; and they suggest that the male receptacles of Swartz's description may have been cupules only. So far as the descriptions go *M. Swartzii* and, consequently, *M. androgyna* Sw. do not differ in any essential respects from *M. chenopoda,* and the authors of the Synopsis are probably correct in citing these two species as synonyms of *M. chenopoda.* This view is supported by a fragmentary specimen in the Taylor herbarium, labeled *M. Swartzii* by Lehmann, which apparently represents *M. chenopoda,* although a positive conclusion can hardly be reached without sectioning the material.

A further difficulty in disentangling the synonymy is, however, encountered. Although Lehmann and Lindenberg considered Swartz's and Collinson's plants identical, this opinion was not shared by the authors of the Synopsis Hepaticarum. In quoting *M. Swartzii* as a synonym of *M. chenopoda* they take pains to exclude the Dillenian *f. 3* altogether, although *f. 3A* and *f. 3C* are definitely quoted by the authors of *M. Swartzii* in citing *M. androgyna* Sw. as a synonym of their species. Fortunately Collinson's material is preserved in the Dillenian herbarium and throws a little light on the subject. It was studied by Lindberg, who reached the conclusion that it represented a distinct and undescribed species. This he proposed as new under the name *M. Dillenii* Lindb. He assigns to

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[51] Spic. Fl. Goettingen. 168. Gotha, 1778.

the species a delicate pellucid thallus with indistinct areolae but with large pores, the thallus in *M. chenopoda* being thick and opaque with distinct areolae and small pores. He states further that the female receptacles are depressed-semiglobose, excentric and almost entire, the five lobes present being very short, thick,

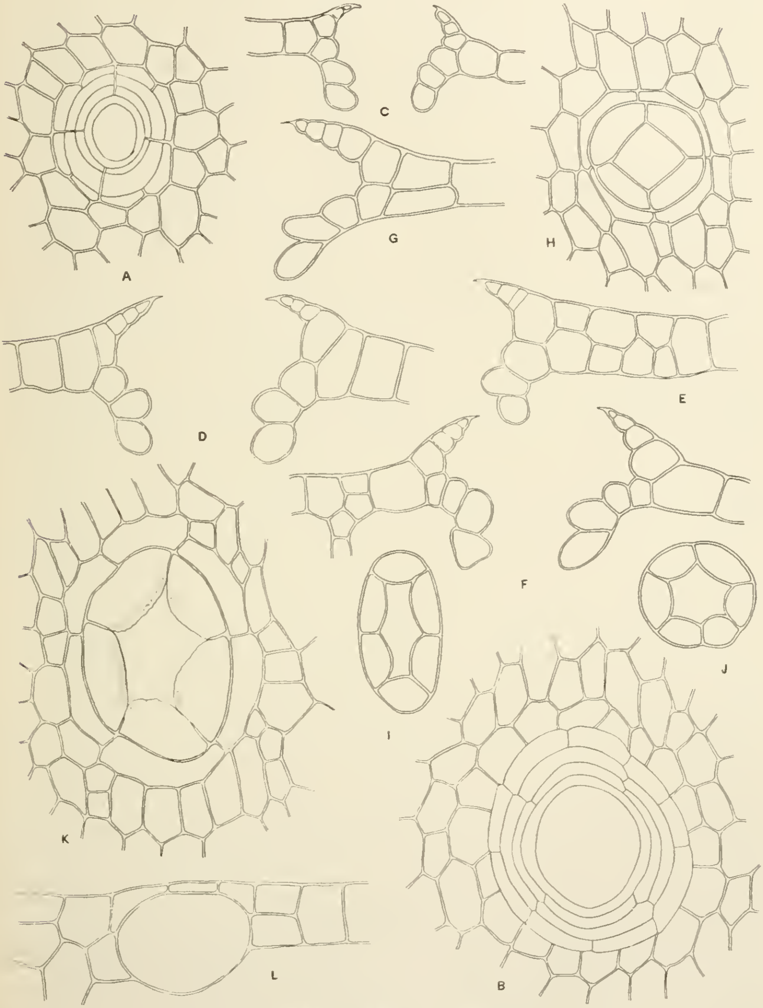

FIG. 19. MARCHANTIA CHENOPODA L.

Epidermal structures of thallus, x 225. A, B. Pores, surface view. C-G. Pores, cross-section. H-K. Pores, inner view. L. Slime cell, cross-section. A, C, H-J. Guatemala, *Cook & Griggs 83*. B, D, E, K, L. Jamaica, *W. R. Maxon 405*. F, G. Peru, *Cook & Gilbert 755*.

semicircular in outline and slightly incurved. The receptacles described are immature and do not therefore yield very satisfactory characters, but Lindberg's description, so far as it goes, would clearly apply to *M. chenopoda.* Even the characters drawn from the thallus easily come within the range of variation to be expected in so multiform a species, where both the texture and the size of the pores differ widely in different plants. The writer would therefore follow Stephani in reducing *M. Dillenii* to synonymy, even in the absence of Lindberg's type material.

The third synonym given in the Synopsis, *Chlamidium indicum,* is nothing but a *nomen nudum.* According to Corda it was based on No. 375 of Sieber's Flora Martinicensis. The Synopsis, however, in citing it as a synonym under *M. chenopoda,* states that it was based on No. 378. In the Mitten herbarium a specimen of No. 378 is preserved under the name *M. martinicensis.* This plant, which probably represents the type of the manuscript species *M. martinicensis* Spreng., is clearly referable to *M. domingensis,* as the authors of the Synopsis have already shown. Their citation of No. 378 under *Chlamidium indicum,* therefore, was probably an error or due to the fact that this number was a mixture; in any case Corda's species, in the absence of adequate publication, deserves no further attention.

If the work of Taylor is excepted it will be seen that writers up to the time of the Synopsis Hepaticarum (1847) were practically unanimous in assigning to *M. chenopoda* a subentire or shortly five-lobed female receptacle and a deeply four-cleft male receptacle. The same thing may be said of subsequent writers. Unfortunately identical or similar characters have been assigned to other species. Aside from *M. Dillenii,* which has already been alluded to, *M. cartilaginea, M. brasiliensis,* and *M. peruviana* may be mentioned in this connection. The first was based on material collected on the island of St. Vincent, no collector being named; the second on Brazilian material collected by Sellow; the third on Bolivian material collected by D'Orbigny.

In *M. cartilaginea* the male receptacles are said by the authors of the species to be slightly convex and borne on very short stalks, while the female receptacles are said to be minute and entire or obsoletely crenulate. Schiffner, who studied the type material, found that the female receptacles were immature and that the so-called male receptacles were nothing more than extremely young female receptacles. The distinctive characters of the species thus break down, and he reduced it to synonymy, retaining it as a var. *cartilaginea* (Lehm. & Lindenb.) Schiffn. under *M. chenopoda*. Stephani quotes it as a simple synonym. Their views are supported by the work of Prescher, who found the distribution of the slime cells the same in *M. cartilaginea* as in *M. chenopoda*.

In *M. brasiliensis* the male receptacle is described as peltate, angled and convex, the central portion being thickened and the margin plane and hyaline; the female receptacle is said to be hemispherical, symmetrical and entire. Here again Schiffner showed that the receptacles in the type specimen were immature and that the distinctive characters drawn from the male receptacles could be duplicated by young male receptacles of *M. chenopoda*. He therefore regards *M. brasiliensis* as synonymous with *M. chenopoda,* a view which the writer is disposed to share. Stephani, in maintaining the validity of the Brazilian plant, dwells on the symmetry of the female receptacle and describes it as strongly convex and very shortly four- to six-lobed. He adds that the entire appendages of the ventral scales can easily be distinguished from the dentate appendages of *M. chenopoda*. Since, however, he assigns both entire and toothed appendages to *M. chenopoda* in his detailed description of that species, and since the receptacles on some of the West Indian specimens referred by him to *M. brasiliensis* are distinctly unsymmetrical, his differential characters can not be regarded as having much significance.

In the original description of *Grimaldia peruviana* the female receptacle is said to be subglobose and crenate while the male receptacle is said to be discoid and sessile. Apparently on account of the characters of the so-called male receptacles Montagne continued to regard the species as a *Grimaldia* even after the authors of the Synopsis had correctly transferred it to *Marchantia*.[52] Probably the sessile structures which Montagne observed were immature female receptacles, but unfortunately the type specimen in his herbarium, a portion of which the writer has been able to examine, is sterile, so that these problematical organs could not be studied. The compound pores, however,

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[52] See Montagne, Sylloge 91. Paris, 1856.

and the cupules show conclusively that the species is a *Marchantia,* and the writer would go even further than Stephani did and reduce it to a synonym of *M. chenopoda.* This conclusion is strengthened by the fact that numerous specimens of *M. chenopoda* have been collected in Bolivia by subsequent explorers.

Although a wide range of variability is assigned to *M. chenopoda,* according to the writer's conception of the species, an equally wide range is assigned to *M. domingensis* and an even wider range to *M. polymorpha.* The structures which are perhaps most subject to variation are the epidermal pores, the slime cells, the appendages of the ventral scales and the involucres. The male receptacles and the female receptacles in most respects exhibit features of a more constant character.

In normal and well-developed specimens the pores are unusually large in the middle of the thallus and are only slightly smaller near the margin. In other cases the contrast in size between the median and marginal pores is much more marked; in still other cases even the median pores may be small or medium sized. Corresponding with these differences in size there are differences in the number of cells in the concentric rows around the opening, although the number of such rows is usually seven. The differences in number are found especially in the third and fourth rows of the upper series and in the third row of the inner series. In the fourth row of the outer series the variation is especially great. In small pores as few as four cells may be present, in large pores as many as eighteen cells, and all gradations between these extremes are to be expected. In the third row of each series similar but less marked differences are encountered. In the first and second row of each series four cells are normally present although three, five, six, or even seven cells sometimes occur.

The slime cells vary greatly in number and in distribution. In typical West Indian material they occur abundantly in the epidermis, in the walls of the air-chambers, and in the compact ventral tissue of the thallus. In other specimens they are rare in the epidermis or even absent altogether, although still persistent in the walls of the air-chamber and in the compact tissue; in still other specimens, and this seems to be especially true of material from Mexico, Central America and South America, they are restricted to the compact tissue, where indeed they may be

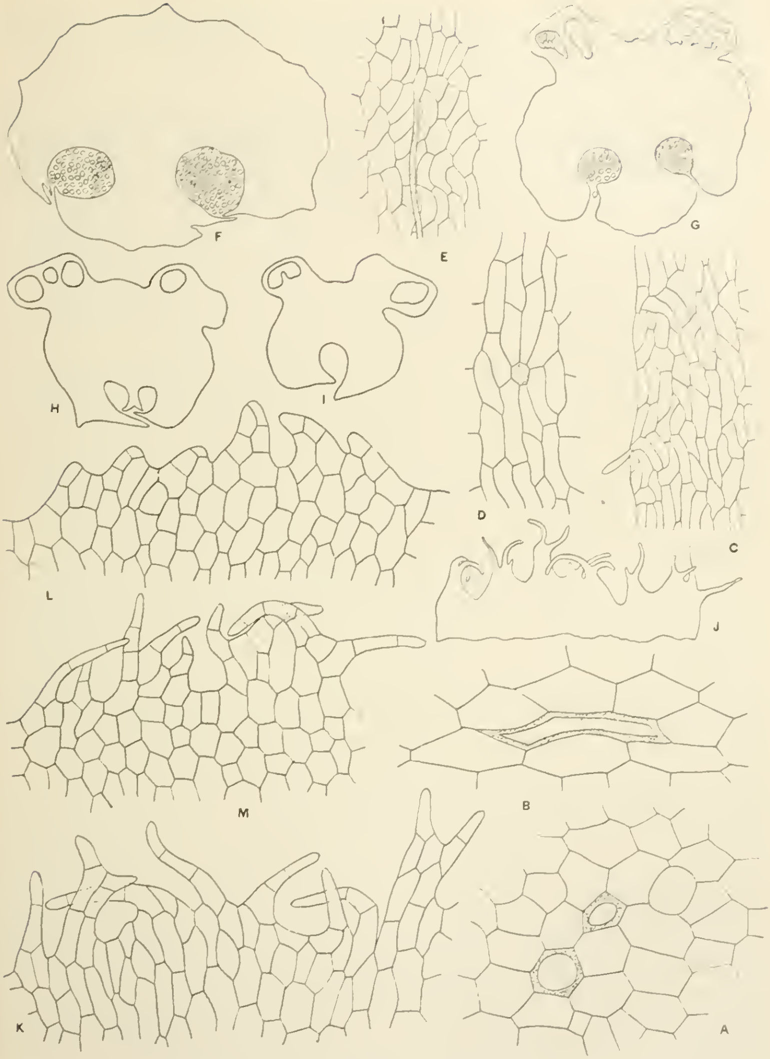

FIG. 20. MARCHANTIA CHENOPODA L.

Anatomical details. A. Cells from compact ventral tissue in cross-section, including two sclerotic cells and a cell containing oil-bodies, x 100. B. Cells from same tissue in longitudinal section, including a sclerotic cell, x 100. C-E. Cells from basal portions of median scales, x 100. F. Stalk of male receptacle, cross-section, x 50. G-I. Stalks of female receptacles, cross-sections, x 50: G, showing a stalk of average size; H, a slender stalk near the middle; and I, the same slender stalk near the base. J-M. Portions of involucres: J, x 40; L-M, x 100. A-G, J. Jamaica, *A. W. Evans 405, W. R. Maxon 880.* H, I. Panama, *R. S. Williams 1084.* K. Vera Cruz, *Barnes & Land 631.* L. Costa Rica, *Cook & Doyle 301.* M. Bolivia, *R. S. Williams 2143.*

very scarce. Since these different conditions grade into one another, it seems impossible to use them as a basis for the segregation of *M. chenopoda.*

Very striking variations are to be observed in the appendages of the median scales. If the series represented in FIGS. 15-19 is examined it will hardly seem possible at first that all can have been taken from a single species. The appendages shown exhibit four more or less distinct types, varying in shape, in the character of the margin, and in the size of the component cells. In the first type, shown by FIGS. 15, A-H, and 16, the appendages are narrowly ovate to lanceolate, tapering gradually to an acute or acuminate apex; the margin is either entire or provided with one or more vaguely defined and irregular teeth; and the cells are large, showing no marked differences in size between the median and marginal portions. In the second type, shown in FIGS 15, I, and 17, A, the appendages are larger than in the first type and tend to be more acuminate; the margin is more distinctly dentate, although the teeth are still irregular; and the cells are much the same as in the first type, except for the fact that the marginal cells in the basal portion tend to be smaller. In the third type, shown in FIG. 18, A-C, the appendages are broadly ovate and apiculate to abruptly acute; the margin is entire or vaguely and sparingly dentate or crenate toward the base; and the cells are everywhere large, much as in the first type. In the fourth type, shown in FIG. 18, D-J, the appendages have about the same form as in the third type, although they sometimes taper more gradually; but the margin is more irregular, varying from entire to distinctly and rather closely crenate, dentate, or even lobed in the basal portion; and the cells are distinctly smaller, often showing a definite decrease in size between the median and marginal portions. Cells containing oil-bodies are usually absent altogether, but one or two sometimes occur, as shown in FIG. 16, G, H, J. These have not been observed except in the first type of appendage.

Since the various types of appendage are more or less characteristic of definite regions, the first type, for example, being prevalent in the West Indies and the fourth in South America, the writer at first thought that distinct varieties with definite geographical ranges might be distinguished, using the appendicular differences as a basis. It soon became evident, however, that this was hardly possible. Many instances were noted where the range of one type overlapped that of another, and a few cases were observed in which appendages of two distinct types occurred on an individual thallus (Figs. 15, H, I; 17, A, B). It was impossible, moreover, to associate the differences in the appendages with other differences showing any degree of constancy. In the writer's opinion, therefore, the numerous types of appendage are to be regarded as a further evidence of the great variability of the species.

In the case of the involucres there is again great variability, although the extremes are perhaps less marked than in *M. domingensis.* Fig. 20, L, shows an involucre in which the teeth are scattered, short, and blunt; while in Fig. 20, J, K, M, the involucres shown bear crowded, long and slender teeth. It will be noted that some of the teeth are simple while others are more or less complex. Bifid teeth are especially common and often show widely divergent divisions. The involucres are firmer than in *M. domingensis,* the cell walls being sometimes distinctly thickened and pigmented with yellowish brown.

In North America the only species with which *M. chenopoda* is likely to be confused is *M. domingensis.* The two species are of about the same size, the structure of the epidermal pores is much the same in both, the sclerotic cells in the ventral portion of the thallus show a similar distribution and the male receptacles are very much alike in general appearance. There are, however, striking differences which usually make it possible to distinguish specimens even in the absence of female receptacles. In *M. chenopoda* slime cells can almost always be observed in the thallus and often occur in great abundance; the appendages of the ventral scales are often entire and are never very closely toothed; and the stalk of the male receptacle is destitute of air-chambers. In *M. domingensis* there are no slime cells in the thallus; the appendages of the ventral scales are closely toothed; and the stalk of the male receptacle bears a band of air-chambers.

If female receptacles are present other important differences may be observed. In *M. chenopoda,* the stalk bears two bands of air-chambers; there are normally only five lobes, these being very short; and the involucre is firm in texture, the margin varying from dentate to ciliate or laciniate. In *M. domingensis* the stalk bears a single band of air-chambers, there are usually more than five lobes, these being more or less elongated; and the involucre is very delicate in texture, the margin varying from crenulate to short-ciliate.

The features which distinguish *M. chenopoda* from *M. domingensis* will distinguish it also from the South American *M. papillata.* Another South American species to which it may be related is *M. Bescherellei,* the appendages and involucres of which might easily come within the range of variability exhibited by *M. chenopoda.* According to our present knowledge, *M. Bescherellei* is a more delicate species with lower air-chambers and thinner ventral tissue. There is no danger of confusing *M. chenopoda* with any of the other species recognized in the present paper.

Doubtful Species

1. MARCHANTIA SQUAMOSA Raddi; Lehm. & Lindenb. in Lehmann, Pug. Plant. 4: 12. 1832 (as to the Brazilian plant).

BRAZIL: without definite locality or date, *Raddi.*

Attention has already been called to this species and to its possible aggregate nature (see p. 261). Stephani's description agrees in most respects with *M. paleacea,* and it is possible that Raddi's specimens would now be referred to that species. If this should prove true it would mark an interesting extension of range.

2. MARCHANTIA QUINQUELOBA Nees, Naturg. Europ. Leberm. 4: 98. 1838.

WEST INDIES: without locality, date, or collector's name.

According to the full description given by Nees von Esenbeck this species is probably a form of *M. domingensis.* In any case there seems to be no reason for attempting to maintain it, since the original specimens (according to Stephani) are poorly developed and valueless.

3. MARCHANTIA PUSILLA Nees & Mont.; G. L. & N. Syn. Hep. 526. 1847.

CHILE: without locality, date, or collector's name.

This species was based on a single very immature specimen and is not represented in the Montagne herbarium. The original description throws little light on its affinities, and Montagne himself apparently had no faith in its validity since he does not mention it in his Sylloge (1856). Stephani therefore seems justified in repudiating it altogether.

4. Marchantia flabellata Hampe, Linnaea **20**: 235. 1847.

Venezuela: Galipan, without date, *Moritz 47b* (erroneously ascribed by Hampe to Colombia).

According to the brief original account the species is monoicous, the female receptacles are four-parted, and the male receptacles seven-parted. Although no specimens have been available the writer suspects that *M. flabellata* may represent a synonym of *M. domingensis.* Should this be established it would show that Hampe confused the male and female receptacles and incorrectly assigned a monoicous inflorescence to his species. Unfortunately the question must be left in doubt.

5. Marchantia Notarisii Lehm. Pug. Plant. **10**: 22. 1857.

Chile: near Valparaiso, without date, *W. Lehmann.*

Although Stephani at first threw doubt on the validity of this species, suggesting that it was probably synonymous with *M. chenopoda,* he afterwards listed it without question from the Chilean island of Chiloé, citing specimens collected by C. Skottsberg.[53] The original description of *M. Notarisii* is very full but is justly criticised by Gottsche[54] on account of its many ambiguities. It certainly seems to point to *M. chenopoda,* and the writer would refer it provisionally to that species. Unfortunately no specimens of *M. chenopoda* from Chile have been available for study.

Sheffield Scientific School,
Yale University.

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[53] Kungl. Sven. Vet.-Akad. Handl. **46**^{9}: 5. 1911.

[54] Bot. Zeit. **16** (Beil.): 28. 1858.

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[From BULLETIN OF THE TORREY BOTANICAL CLUB, 44: 191-222, *pl. 8, 29 text-figs.* 14 Ap 1917.]

Notes on the genus Herberta, with a revision of the species known from Europe, Canada and the United States*

ALEXANDER W. EVANS

(WITH PLATE 8 AND 29 TEXT FIGURES)

INTRODUCTION

The genus *Herberta* (or *Herbertus*, as it was originally spelled) was published by S. F. Gray in 1821.† It was named in honor of George Herbert, one of the patrons of Micheli, and was based on a single species, the *Jungermannia adunca* of Dickson. In common with Gray's other genera, *Herberta* was ignored by botanical writers until Carruthers called attention to it in 1865.‡ Although it has since been accepted more or less widely in both Europe and North America, a strong tendency has recently arisen to repudiate it. This is largely due to Gray's unfortunate practice of giving his generic names a masculine termination, even when he derived them from the names of persons. As Dumortier expresses it, they are the names of men and not of plants. Since, however, a change from a masculine to a feminine termination might readily be construed as the correction of an error in orthography, this objection seems hardly sufficient to justify the setting aside of Gray's genera altogether. From a scientific standpoint the claims of *Herberta* are fully as good as those of many other genera which are accepted without question, and the writer is therefore disposed to recognize it, at least for the present.

A year after the appearance of *Herberta*, Dumortier§ published his genus *Schisma*, including under it not only *J. adunca* but also *J. juniperina* Sw. and *J. concinnata* Lightf. Nine years later he added another species, *S. stramineum* Dumort.,|| but excluded *J. concinnata*, making it the type of his new genus *Acolea*. At

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* Contribution from the Osborn Botanical Laboratory.

† Nat. Arr. British Pl. 1: 705. 1821.

‡ Jour. Bot. 3: 300. 1865.

§ Comm. Bot. 114. 1822.

|| Syll. Jung. 76. 1831.

that time he was undoubtedly ignorant of Gray's writings. Many years afterwards, however, in his last published work on the Hepaticae,* he quotes Gray's generic names as synonyms, refusing to recognize them as valid on account of their masculine form. In the present instance he naturally maintains his genus *Schisma*. Gray's genera were likewise unknown to Nees von Esenbeck. In the first volume of his Naturgeschichte der europäischen Lebermoose, published in 1833, he accepted *Schisma* as valid (p. 107). In the third volume, published in 1838, he suggested that it might be considered a section of his genus *Mastigophora* (p. 573), although he continued to employ *Schisma* as a generic name. The inclusion of *Schisma* under *Mastigophora* would have been quite unwarranted on the basis of priority. The latter genus was not published until 1833, and its characters were completely revised in 1835. *Schisma* therefore antedates it by more than a decade. As originally defined *Mastigophora* was essentially the equivalent of the genus *Lepidozia* Dumort., although no species were definitely assigned to it; in its revised form it was made to include such species as *Jungermannia diclados* Brid. and *J. Woodsii* Hook. At the present time it is accepted by most writers in its revised form.

Nees von Esenbeck's provisional reduction was adopted definitely by the authors of the Synopsis Hepaticarum (1845), who went even farther than he and included both *Schisma* and *Mastigophora* under the genus *Sendtnera* of Endlicher,† a genus which had been proposed a few years earlier for the single species *Jungermannia Woodsii*. On account of the high position which the Synopsis holds in the literature of the Hepaticae the name *Sendtnera* was acknowledged for many years as the correct name for the combined genus. Now, however, both *Schisma* and *Mastigophora* are universally regarded as distinct, and the name *Schisma* is employed by those who refuse to sanction the use of the name *Herberta*.

Of the eighteen species of *Sendtnera* given in the Synopsis only six would now be included in the genus *Herberta*. In Stephani's recent monograph of the genus (under the name *Schisma*), pub-

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* Bull. Soc. Bot. Belgique **13**: 123. 1874.

† Gen. Plant. 1342. 1840.

lished in 1909,* seventy-one species are recognized. According to the information at hand four species have since been described, making seventy-five in all. This marked increase is due partly to the more extensive material at the disposal of recent writers and partly to their narrower interpretation of species. Of the seventy-one species admitted by Stephani nearly all have a very limited geographical range and no fewer than forty-seven are described as new. Taking into account the species of his monograph and those since published, two are restricted to Europe, thirteen to Africa (including the Azores), sixteen to Asia (including the Philippines), seven to various islands of the Pacific, ten to tropical North America, and twenty-six to South America; Stephani gives one species a wider range, including Samoa, Tahiti, Hawaii, Japan, and Himalaya. It is interesting to note that he accredits no species to North America north of Mexico, although *H. adunca*, a species which he restricts to Europe, has been repeatedly reported by American writers, not only from Alaska and British Columbia but also from the eastern United States.

The species of *Herberta* grow on rocks, on trees, and on the ground and sometimes form extensive mats or tufts. In the tropics they seem to be confined to higher altitudes, but the few species which occur in temperate and frigid regions sometimes descend to the level of the sea, this being true in both hemispheres. The plants are usually marked by a yellowish or brownish color, due to a pigmentation of the cell walls. In rare cases a reddish or purplish tinge is present, and in sheltered stations the pigmentation may be so slight that the plants appear green.

NOTES ON THE MORPHOLOGY OF THE GENUS

In its morphological features *Herberta* is one of the most clearly defined and natural genera of the Hepaticae. The gametophyte consists of a prostrate rhizome which gives rise to numerous secondary stems. These sometimes remain simple, even when they become comparatively long, and sometimes branch sparingly. The subequally bifid leaves are slightly incubous while the underleaves are strictly transverse, and yet, since the underleaves are nearly or quite as large as the leaves and similar to them in most

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* Spec. Hepat. 4: 1–30. 1909.

other respects, the shoots appear almost radial in structure. The inflorescence is invariably dioicous. The androecium is at first terminal on a secondary stem or one of its branches but soon proliferates, and the male shoot eventually shows a series of short intercalary androecia separated by equally short sections bearing normal leaves. The archegonia are likewise terminal on secondary stems. When fertilization takes place the growth of the female stem is usually brought to an end; when fertilization does not take place one or more subfloral innovations may be produced. The involucre is composed of crowded bracts and bracteoles, which are essentially alike and not very different from the leaves, while the perianth is deeply laciniate at the mouth and free or nearly so from the bracts. The calyptra and the sporophyte conform to the usual jungermanniaceous type.

The rhizome of *Herberta* was apparently overlooked by the older writers. Spruce,* however, calls attention to it and to the fact that it may bear rhizoids, while Stephani mentions its small diameter and copious branching. It tends, in fact, to be considerably more slender than the secondary stems, although both vary in size. In *H. juniperina*, for example, an average rhizome measures only 0.35 × 0.25 mm. in cross section, while a stem measures 0.5 × 0.35. The features of the rhizome are not easily made out in material where the secondary stems are well developed. The leaves are more or less disintegrated with age and it is difficult to demonstrate the relationship between the branches and the leaves. In most cases the leaves and underleaves are minute and widely separated. The leaves are practically transverse in their insertion and it would be difficult to distinguish them from the underleaves, if the rhizome did not show a slight dorsiventral flattening, the underleaves being of course situated on one of the flattened sides. Both leaves and underleaves are distinctly bifid. The rhizoids grow out normally from the basal cells of the underleaves, although they often occur on the leaves as well, but the rhizome itself is usually free from them. The branches are all intercalary and many of them spring from the axils of the underleaves. This position, however, is not constant; occasional branches tend to be lateral and do not show a definite relationship

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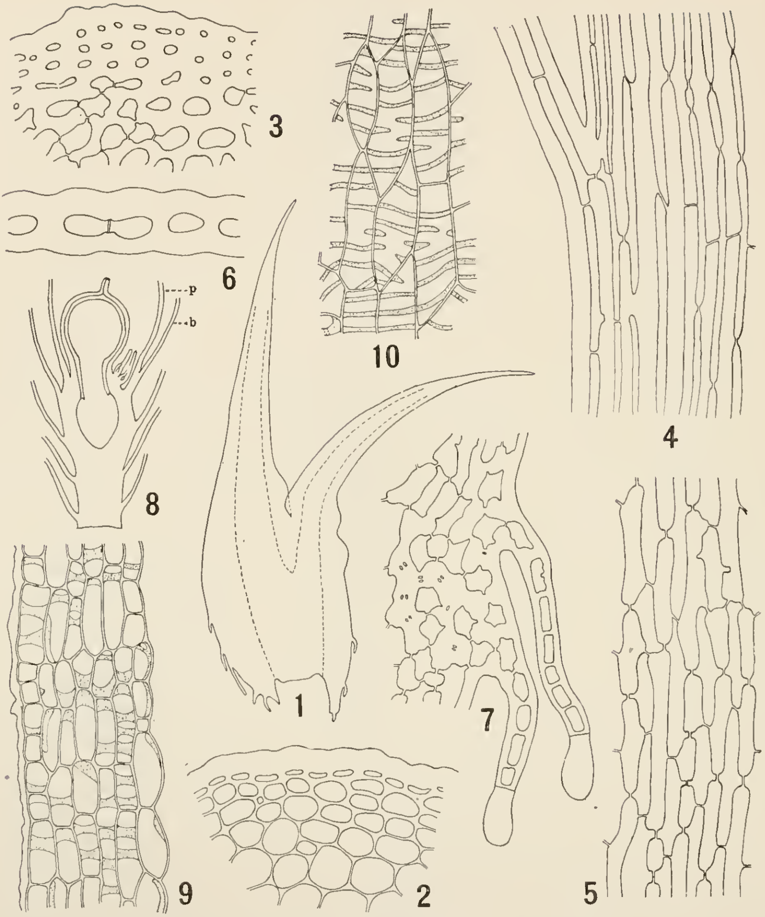
* Trans. Bot. Soc. Edinburgh **15**: 340. 1885.

to either leaves or underleaves. It is of course possible that their aberrant position is due to secondary displacements caused by inequalities of growth, but this could not be definitely determined from the material studied. The secondary stems are sometimes direct extensions of the creeping rhizomes, but it is usually possible to demonstrate their origin as branches. Even under these circumstances they usually bear small leaves at the base and only gradually give rise to the normal leaves. Sometimes the change is more abrupt, and all gradations may be present between the small-leaved prostrate rhizomes and the typical secondary stems with large leaves.

The secondary stems differ greatly in length in different species and even in the same species under varying conditions. In some of the robust tropical species a length of 25 cm. may be attained. The stems are usually ascending but are often pendulous and sometimes form conspicuous festoons hanging from the branches of trees. The branches are always intercalary, just as in the case of the rhizomes. The normal vegetative branches take their origin in the axils of underleaves and are rarely subdivided. In most cases they spread widely and show a flagelliform appearance, their leaves being distinctly smaller than those of the stem. When the growing point of a stem is injured, however, a ventral branch sometimes changes its direction of growth and assumes that of the stem, its leaves at the same time increasing in size. The same thing is true of the subfloral innovations, which may be either ventral or lateral in position. The growth of the stem is here brought to an end by the development of the archegonia. Rhizoids are often absent altogether from the secondary stems. When they occur they are usually restricted to the underleaves and leaves of the ventral branches, although the normal leaves and underleaves have the power of developing them.

The leaves (TEXT FIGS. 1, 14, 15, 21–25) and underleaves of the secondary stems present a great deal of uniformity throughout the genus. They are more or less deeply bifid with a narrow sinus and sharp divisions. In rare cases a leaf may be trifid instead of bifid, a peculiarity to which certain species seem to be more subject than others. The divisions are sometimes distinctly grooved but show little tendency to be complicate, both lying approximately in



FIGS. 1–10. HERBERTA JUNIPERINA (Sw.) Trevis.

1. Leaf, × 17. 2. Transverse section of a young stem, × 225. 3. Transverse section of a mature stem, × 225. 4. Longitudinal section of a mature stem, including the base of a leaf, × 225. 5. Cells from the basal vitta of a leaf, × 225. 6. Cells from the basal vitta of a leaf in transverse section, × 300. 7. Cells from the dorsal base of a leaf, showing cilia with slime papillae, × 225. 8. Longitudinal section of a young sporophyte and surrounding parts, × 17; *b*, innermost perichaetial bract; *p*, perianth. 9. Transverse section of the wall of a mature capsule, × 225. 10. Cells from the innermost layer of the wall of a mature capsule, × 225. FIGS. 1, 5–7 were drawn from specimens collected by the writer on Blue Mountain Peak, Jamaica, *242*; FIGS. 2–4, 6, from specimens collected by L. M. Underwood along the trail from Cinchona to Morce's Gap, Jamaica, *280*; the remaining figures, from specimens collected by W. Harris on the lower slopes of Sir John Peak, Jamaica, *11133*.

the same plane. At the base on each side a series of slime papillae or their vestiges can be demonstrated. These are sometimes sessile (TEXT FIG. 17) and sometimes borne on the tips of more or less evident teeth or cilia (TEXT FIG. 7; PLATE 8, FIG. 5). Occasionally slime papillae with their teeth are developed on the surfaces of the leaves and underleaves, as well as on their margins. The teeth vary from short stalks a cell or two long to broad and subdivided lobe-like structures. Except for the basal teeth associated with the slime papillae the margins are usually quite entire. In a few species, however, distinct teeth are present higher up, even beyond the region of the sinus, and these teeth show no evidences of slime papillae. Even when teeth of this character are present the upper parts of the divisions lack them completely. A vague serrulation, caused by projecting cells, may sometimes be discernible but seems to be a very exceptional feature.

Aside from the difference in insertion there are certain other slight differences between the leaves and underleaves. The leaves are usually curved backward and appear unsymmetrical when dissected from the stems and spread out flat. The curvature affects the ventral division more strongly than the dorsal division (PLATE 8, FIGS. 1–3); the latter in fact may be straight or nearly so while the ventral division is strongly curved (TEXT FIG. 1). In some species the curvature is much less pronounced than in others and may not be evident at all in explanate leaves (TEXT FIGS. 22–25); the lack of symmetry, however, still expresses itself in a difference of direction of the divisions and in a greater development of the basal portion on the dorsal side. The underleaves bend backward in a squarrose fashion and appear symmetrical when spread out, their straight divisions diverging equally and the basal portion being equally developed on the two sides. The leaves and underleaves are usually more or less imbricated. The divisions of the curved leaves and squarrose underleaves are thus crowded together along the ventral portion of the shoot, the plant acquiring a distinctly moss-like appearance.

The cells and especially the cell-walls yield some of the most distinctive characters of the genus. Most of the walls are strongly thickened and this applies even to the rhizoids when they become old. According to Goebel* excessive thickening of the cell walls in the bryophytes, which occurs especially in xerophilous species, is significant on account of the great power of imbibition which these walls possess. They readily absorb and retain water, and the rapidity with which most species of *Herberta* regain their normal appearance and consistency, when a dry tuft is deluged with water, is a striking phenomenon. In the cauline portions of the plant the cells are all elongated, although they never assume a truly prosenchymatous character. The outer or cortical region is distinguished from the inner or axial region by its deeper color and more strongly thickened walls. In the secondary stems the thickening at first takes place in the outermost layer of cells, the process continuing until the cell cavities become reduced to narrow canals (TEXT FIG. 2). The thickening is largely restricted to the outer or superficial walls and the layer presents the appearance of an epidermis with well-developed cuticle. In some cases the entire cortex consists of this outermost layer, the walls of the remaining cells showing only a slight degree of thickening (TEXT FIG. 26). This, however, is very unusual. In the majority of cases two or more additional layers take part in the formation of the cortical region; their walls become as markedly thickened as those of the outermost layer, the only difference being that the thickening is deposited uniformly on all the walls (TEXT FIG. 3). Even in the central region the thickening of the walls is sometimes very pronounced, though never so much so as in the cortical region. Since, moreover, the central cells are larger than the cortical cells, their cavities remain distinctly wider. The cells of the stem are everywhere connected by pits, which show clearly in both transverse and longitudinal walls (TEXT FIGS. 3, 4). They are just as evident in the superficial layer as elsewhere, the cells of this layer being connected with one another both longitudinally and tangentially, as well as with the cells of the layer next within. There is nothing, in fact, to indicate any essential difference in function between the superficial layer and the other cortical layers. In spite of the fact that the outer walls simulate a cuticle so strongly, they have the same powers of imbibition as the other walls and simply form part of the imbibing system of the stem. In the rhizomes the

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* See Organographie der Pflanzen, 2d ed. 553. 1915.

same distinction between cortical and central regions is apparent. There is perhaps a tendency for the cortical region to be thinner and for the cell-walls of the central region to be less thickened than in the secondary stems, but there are no essential differences between the two.

The leaf-cells in their more important features have long been familiar to students of the Hepaticae. Although forming a single layer as in most of the Jungermanniaceae the cells show a differentiation into elongated cells and more or less isodiametric cells (see, for example, PLATE 8, FIG. 4). The elongated cells form a median band extending from the line of insertion into the basal portion of the leaf. Somewhere below the sinus the band, or "vitta," as Stephani terms it, forks, one branch passing into each division. Here they may extend to the extreme apices or stop at a variable distance below them. The isodiametric cells form the rest of the leaf and are divided into three patches by the vitta and its branches, the two lateral patches extending from the base into the divisions on their outer sides and the median patch from the forking of the vitta into the divisions on their inner sides. Apparently the first allusion to the vitta is found in the original description of *H. dicrana* (Tayl.) Trevis.* In a critical note, quoted from Taylor, a "nerve" is spoken of which runs out into the divisions. Gottsche afterward described the vitta in other species, and Stephani lays especial emphasis on it in his recent monograph. In his opinion the vitta yields some of the best differential characters in distinguishing species. He considers the basal portion (below the forking) to be constant in size for a given species, and he finds an equal constancy in the length of the branches. Unfortunately it is not always easy to determine the exact lateral boundaries of the vitta or the points where the branches terminate in the divisions of the leaves. Although the median cells of the basal portion are markedly different from the cells near the margin of the leaf, there is sometimes a gradual transition between the vitta and the marginal portion, and a similar transition may exist between the cells of the vitta and the marginal and apical cells of the divisions. Two observers, in consequence, might obtain different results in measuring the same

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* Syn. Hep. 239. 1845.

leaf. A case in point is found in *H. adunca.* According to Stephani the branches of the vitta come to an end below the apices of the divisions; according to K. Müller they extend to the apices. At the same time the value of the vitta from the standpoint of taxonomy must not be overlooked, and Stephani deserves credit for utilizing it.

The cells of the vitta present a number of interesting peculiarities, not only in their structure at maturity but also in their development, especially in the way in which the thickenings of the wall are deposited. Gottsche, in his account of *H. juniperina*,* noted some of these peculiarities many years ago, but subsequent allusions to them have been very scanty. According to Gottsche each basal cell of the leaf, after treatment with caustic potash and iodide of zinc, reveals a spiral of eight to fifteen turns representing a thickening of the secondary layer of the wall. In a later account† of the same species he gives the number of turns as fifteen to twenty-two.

By treating young leaves with potash it is easy to demonstrate the presence of the bands of thickening described by Gottsche, not only in the basal portion of the leaf but elsewhere, and they clearly represent a stage in the development of the cell wall (TEXT FIG. 11). The writer has found it impossible, however, to show that the bands form a continuous spiral. They seem to be rather in the form of separate rings or partial rings, an occasional ring being branched. When the rings are incomplete the gaps occur on the free walls of the cell and never on the vertical walls, which separate the cell from its neighbors. Even under these circumstances, however, the bands of thickening extend partially across the free walls and leave only the median portion thin throughout. The bands of one cell do not lie opposite the bands of adjoining cells but tend to alternate with them. The vertical walls show a zigzag appearance where they meet the free walls, each angle of the zigzag marking the position of one of the bands. In the irregular cells between the vitta and the margin the bands are more irregular than in the cells of the vitta and rarely if ever form complete rings. In other respects they are essentially the same.

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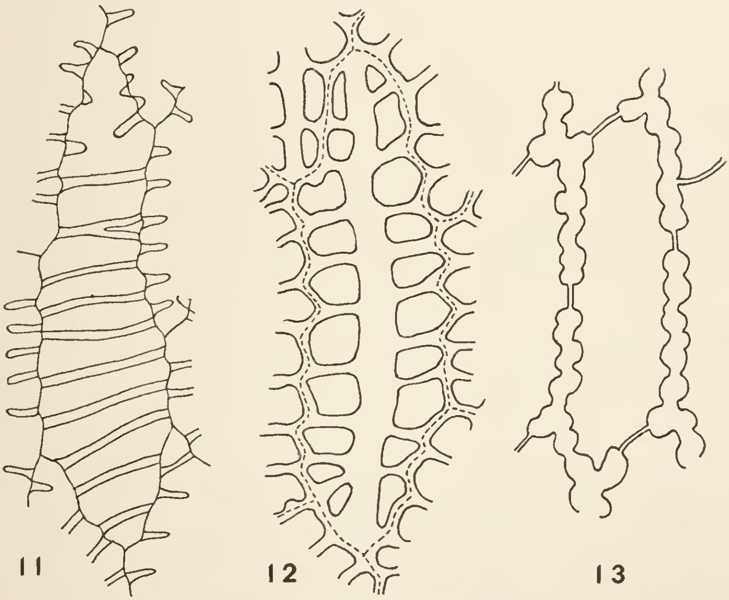
* Rabenhorst, Hep. Eur. *210*, accompanying text.

† Mex. Leverm. 138. 1863.

The bands of thickening just described soon become united by median bands laid down on the free walls (Text fig. 12). These leave a series of thin places on each side, which show at first angular outlines. Almost simultaneously the bands on the vertical walls increase in thickness and become connected by deposits laid down between them, the result being that these walls acquire a continuous layer of thickening except for an occasional pit. At first the original bands are thickened more conspicuously than the intermediate regions and the vertical walls appear distinctly scalloped when examined in optical section (Text fig. 13). But the conditions just described are temporary. The thin places in the free walls are gradually filled up by deposits of thickening, becoming rounded as they diminish in size, and the depressions between the scallops along the vertical walls become obliterated



Figs. 11–13. Herberta juniperina (Sw.) Trevis.

11. Very young cell from the basal vitta of a leaf, surface view, × 1,000. 12. Somewhat older cell from same vitta, surface view, × 1,000. 13. Still older cell from same vitta, optical section, × 600. The figures were all drawn from specimens collected by L. M. Underwood along the trail from Cinchona to Morce's Gap, Jamaica, *280*.

in much the same way. The entire cell-cavity is eventually lined by a uniformly thick layer of deposit, the only thin places left being the pits in the vertical walls (TEXT FIGS 5, 6). Even some of the pits may be obliterated with age. When this takes place the deposit either fills the pit-chamber altogether or bridges it across, leaving a minute vestige of the chamber next to the closing membrane (TEXT FIG. 7). When the cells are mature it is sometimes possible to detect evidences of the original bands of thickening and of the scallops along the vertical walls, but the free walls present an absolutely uniform appearance. Although the thickenings look very much as if they were formed by the coalescence of trigones and intermediate thickenings, it is clear from their method of development that they are not directly comparable with the trigones and intermediate thickenings of other Hepaticae.

Although the description just drawn from *H. juniperina* probably applies in its essential features to the entire genus, the details are not always as clear in some of the other species. In *H. adunca*, for example, it is difficult to demonstrate bands of thickening except in the basal portion of the vitta, and it is doubtful if they ever form complete rings. The scalloped appearance of the vertical walls is likewise much less evident. Possibly the more indefinite conditions found are associated with the fact that the thickening of the walls in *H. adunca* is usually much less marked than in *H. juniperina*.

The leaf surface in *Herberta*, the so-called cuticle of authors, is striolate or verruculose. The roughness is sometimes very apparent and sometimes made out with difficulty. Whether differences in the degree of roughness yield constant differential characters in separating species is perhaps doubtful, although such differences seem very striking when certain species are compared.

The androecia in *Herberta* are relatively short and usually include from four to eight pairs of bracts, those at the upper and lower ends being somewhat transitional in character. The male plants tend to produce smaller leaves than female plants or vigorous sterile plants, and although the bracts are considerably larger than the leaves borne between the successive androecia, they scarcely equal in size the normal leaves on female individuals. Several years ago Schiffner made the remarkable discovery that antheridia occur not only in the axils of the bracts but also in the axils of the bracteoles.* In order to determine whether this phenomenon was widespread among the Ptilidioideae, to which group *Herberta* is usually assigned, he examined species of several other genera. The closely related *Mastigophora*, however, was the only one in which he was able to observe antheridial bracteoles. In the case of *Herberta* the bracteoles differ from the bracts in about the same way that the ordinary underleaves differ from the leaves. Both bracts (TEXT FIG. 20; PLATE 8, FIGS. 8, 9) and bracteoles are more or less imbricated and have a broad inflated pocket at the base enclosing a cluster of two or more antheridia. The pocket does not involve the entire width of the basal region but leaves a narrow flattish or revolute strip on each side. In the inflated portion the cells are broader and much paler than ordinary cells, and the thickenings of the walls are more irregular in outline and less strongly developed. The divisions, sinus, and margins are much the same as on ordinary leaves.

The perichaetial bracts (PLATE 8, FIGS. 10, 11) and bracteoles are essentially alike. They occur in three or four closely crowded series and increase somewhat in size toward the perianth, only the apical portion of which projects beyond them. Those of the innermost series, when viewed from the outer surface, show two rounded ridges in the basal portion, separated by a narrow median groove. A marginal band on each side is flat or slightly concave. The divisions are much the same as on ordinary leaves but the margins are much more toothed, the teeth being irregular and extending higher up, sometimes almost to the apices of the divisions. Occasionally minute and irregular paraphyllia (PLATE 8, FIG. 12) with marginal papillae are found among the bracts. According to Spruce the bracts closely embrace the perianth but are free from it throughout their entire length; according to Stephani they are coalescent with the perianth up to a considerable height. A longitudinal section through a young sporophyte and surrounding parts (TEXT FIG. 8) shows that Spruce was essentially correct. Any coalescence which may be present is so slight as to be practically negligible. Between the innermost bracts and bracteole and the leaves below the involucre there is a gradual transition.

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* Untersuchungen über Amphigastrial-Antheridien und über den Bau der Andröcien der Ptilidioideen. Hedwigia 50: 146–162. *f 1–39* 1910.

The perianth of *Herberta*, when well developed, clearly supports the theory that three floral leaves take part in the formation of this organ (PLATE 8, FIG. 13). It is split for nearly half its length into six slender laciniae, essentially like divisions of leaves, every alternate split being a little deeper than the others. These deeper splits mark the boundaries of the three coalescent leaves. In the undivided portion of the perianth a cross section shows that six rounded ridges are present, separated by six rounded grooves (PLATE 8, FIG. 14). Three alternate grooves are deeper than the others and correspond with the three deeper splits at the mouth of the perianth. The innermost bracts and bracteoles, each with its two dorsal ridges separated by a groove, are closely appressed to the ridges and grooves of the perianth. The laciniae of the perianth bear numerous slime-papillae and often teeth. The slime papillae occur not only along the margins of the laciniae toward the base but also on the inner surface of the perianth. Here they sometimes form short rows and sometimes show no regular arrangement. The surface papillae are occasionally borne on the tips of short teeth or along the margins of narrow and irregular ridges. In some cases the perianth is not developed normally. More than six laciniae, for example, may be present at the mouth, or one of the splits may extend to the very base; sometimes both of these abnormalities may be seen in a single perianth. An increase in the number of laciniae is not surprising, since ordinary vegetative leaves with three divisions sometimes occur, and the deep split might plausibly be interpreted as a place where coalescence had failed to take place.

The wall of the capsule is described in its essential features by Spruce. It is composed of from five to seven layers of cells (TEXT FIG. 9) and shows a thickness of 70–100 μ. This is considerably more than in most of the leafy Hepaticae studied by Andreas.* In *Plagiochila asplenioides* (L.) Dumort., for example, where the wall is composed of seven or eight layers, the thickness is only 55 μ, while in *Chiloscyphus polyanthus* (L.) Corda, where the wall is composed of five layers, the thickness is only 25 μ. It is less, however, in *Herberta* than in *Pleurozia purpurea* (Lightf.)

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* Ueber den Bau der Wand und die Oeffnungsweise des Lebermoossporogons. Flora **86**: 161–213. *pl. 12+f. 1–25.* 1899.

Lindb.; in this species, according to Andreas, the wall is composed of seven or eight layers and has a thickness of 130 μ. In all these forms he describes local thickenings in the cells of all the layers. In the innermost layers the thickenings are in the form of half rings extending across the inner tangential wall (see TEXT FIG. 10) In the other layers they are in the form of bands on the radial walls. Even here, however, the bands sometimes extend to a greater or less extent along the tangential walls. According to Andreas the structure of the capsule wall in the leafy Hepaticae shows comparatively little variation, and the genus *Herberta* agrees on the whole with his account. It might be added that the valves are covered on the outside by a granular wax-like deposit, and that secondary splits sometimes occur in one or more of the four primary valves.

Many years ago Spruce* described the occurrence of rudimentary shoots on the leaves of *Herberta*. According to his account they arise singly or in pairs from the cells of the vitta in the basal portion of the leaves and never in the divisions. These shoots have not been observed by the writer and are probably developed under exceptional conditions. They represent the only type of vegetative reproduction known in the genus. As Spruce's figures clearly show, the shoots bear three ranks of small bifid leaves and show no signs of dorsiventrality. They resemble in many respects the adventive shoots borne on the leaves of certain species of *Plagiochila*, although they are much less abundantly produced.

REVISION OF THE SPECIES KNOWN FROM EUROPE, CANADA AND THE UNITED STATES

According to most recent writers on the Hepaticae the genus *Herberta* is represented in Europe by only two species. The first of these is *H. adunca* (Dicks.) S. F. Gray, the type of the genus; the second, *H. Sendtneri* (Nees), sometimes known as *H. straminea* (Dumort.) Trevis. The range of *H. adunca*, according to available records, is restricted to Norway, the Faroe Islands and the British Isles; the range of *H. Sendtneri* is even more circumscribed, being accredited only to the Austrian and Bavarian Alps.

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* On the branch-bearing leaves of *Jungermannia juniperina*, Sw. Phytologist 2: 85, 86. 1844. [Illust.]

In thus restricting the range of the latter species, writers differ markedly from Dumortier.* He considered that his *Schisma stramineum*, under which he included *S. Sendtneri* Nees as a synonym, grew in Scotland, as well as in Austria and Germany. His species, in fact, was based on Scottish material. Apparently his only recent follower is Lett,† who admits both *H. adunca* and *H. straminea* as members of the Scottish flora.

Botanists have long recognized the fact, however, that *H. adunca* includes two well-marked forms. These were distinguished by Gottsche,‡ as long ago as 1862, under the names, *α Dicksoniana* and *β Hutchinsiae*. He applied the first name to the plant with shorter, erect-spreading leaves, having straight acuminate divisions, and the second to the plant with longer leaves, hooked when dry and squarrose when moist, having lanceolate, incurved divisions. He considered that *α Dicksoniana* was primarily a plant of Scotland while *β Hutchinsiae* was primarily a plant of Ireland, and yet he made no attempt to restrict the range of either form definitely. Carrington,§ in taking up the name *β Hutchinsiae*, implies that all the Irish specimens are referable to this form and states that the species grows at much lower altitudes in Ireland than in Scotland. He adds that both forms grow in Scotland, the form with ovate or ovate-lanceolate leaves being restricted to higher and exposed mountains. This form is clearly Gottsche's *α Dicksoniana*, although Carrington does not call it by this name. He includes under it Dumortier's *S. stramineum* as a synonym and calls attention to the fact that it approaches *H. Sendtneri*. Although subsequent British writers have paid little attention to Gottsche's names, Schiffner has recently revived them and applied them to specimens in his exsiccatae.||

From a careful study of European specimens referred to *H. adunca*, the writer has reached the conclusion that Gottsche's two so-called forms represent two distinct, but closely related, species. The form *α Dicksoniana*, as its name implies, represents the type of *Jungermannia adunca* Dicks. In the absence of Dickson's original

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* Bull. Soc. Bot. Belgique 13: 125. 1874.

† Hepat. British Isl. 177. 1902.

‡ Rabenhorst, Hep. Eur. *210*. 1862.

§ Trans. Bot. Soc. Edinburgh 7: 454. 1863.

|| Hep. Eur. Exsic. *403–407*. 1912.

material, the statement is supported by Scottish specimens in the Taylor herbarium, received from Hooker, and by the fact that Dickson's plant was collected "in alpibus Scoticis." The type of Dumortier's *Schisma stramineum* was likewise collected "in alpibus Scotiae" and, in the complete absence of all of Dumortier's types, his species may be regarded as a simple synonym of *H. adunca.* The second form, *β Hutchinsiae,* is described below as a new species under the name *H. Hutchinsiae* (Gottsche). In certain respects the true *H. adunca,* as thus restricted, resembles *H. Sendtneri* more strongly than it does *H. Hutchinsiae.* This would account for the fact that Dumortier failed to distinguish between his *Schisma stramineum* and *H. Sendtneri.* The latter species, however, is clearly distinct, and there is no evidence that its range extends beyond the mountains of Austria and Germany.

With regard to the North American specimens which have been referred to *H. adunca,* there has likewise been confusion. There are apparently two species represented, but neither agrees with typical *H. adunca.* The plant from the eastern United States seems to be new and is described below under the name *H. tenuis;* the plant from the Pacific Coast, on the contrary, seems to be referable to *H. Hutchinsiae.* The Alaskan material of this species is unusually satisfactory because it shows androecia, perianths, and sporophytes, all of which are exceedingly rare in European material. The four species considered in the present paper may be distinguished as follows, only vegetative characters being used:

Leaves mostly 1.2–2 mm. long and 0.45–0.9 mm. wide.

Leaves bifid about one half; divisions broad, slightly or not at all curved, acute to acuminate; vitta not distinct, the cells in the divisions mostly 20–40 μ long.

Basal portion of leaves normally entire. 1. *H. adunca.*

Basal portion of leaves sparingly and coarsely toothed. 2. *H. Sendtneri.*

Leaves bifid two thirds to four fifths; divisions narrow, strongly curved, long-acuminate; vitta distinct, the cells in the divisions often 50–70 μ long; basal portion of leaves entire or nearly so. 3. *H. Hutchinsiae.*

Leaves mostly 0.9–1 mm. long and 0.3–0.35 mm. wide, bifid two thirds to three fourths; divisions narrow, slightly or not at all curved, long-acuminate; vitta distinct, the cells in the divisions often 50–70 μ long; basal portion entire or sparingly and coarsely toothed. 4. *H. tenuis.*

1. HERBERTA ADUNCA (Dicks.) S. F. Gray

Jungermannia adunca Dicks. Plant. Crypt. Brit. **3**: 12. *pl. 8, f. 8.* 1793.

Jungermannia juniperina β Hook. Brit. Jung. *pl. 4.* 1812 (in part).

Herberta adunca S. F. Gray, Nat. Arr. Brit. Pl. **1**: 705. 1821.

Schisma aduncum Dumort. Comm. Bot. 114. 1822.

Jungermannia juniperina β adunca Lindenb. Nova Acta Acad. Leop.-Carol. **14** (suppl.): 35. 1829 (in part).

Schisma stramineum Dumort. Syll. Jung. 76. 1831; Bull. Soc. Bot. Belgique **13**: 125. 1874 (in part).

Schisma juniperinum β Nees, Naturg. Europ. Leberm. **1**: 108. 1833.

Sendtnera juniperina β Nees; G. L. & N. Syn. Hep. 239. 1845.

Sendtnera straminea Nees, *l.c.* 240. 1845.

Sendtnera adunca α Dicksoniana Gottsche; Rabenhorst, Hep. Eur. *210* (accompanying text). 1862.

Herberta straminea Trevis. Mem. R. Ist. Lomb. III. **4**: 396. 1877 (in part).

Herberta adunca var. *straminea* Cooke, Handb. Brit. Hepat. 70. 1894.

Herberta adunca var. *alpina* Macvicar, Student's Handb. Brit. Hepat. 340. 1912.

Herberta adunca α Dicksoniana Schiffn. Lotos **60**: 53. 1912.

Yellowish or brownish green, often tinged with red or purple, sometimes slightly glossy, growing in more or less extensive mats, or scattered among other bryophytes: secondary stems erect or ascending, sparingly and irregularly branched, rigid, mostly 5–10 cm. long but sometimes shorter, about 0.25 mm. (or fourteen cells) wide and 0.18 mm. (or ten cells) thick, the cells everywhere with strongly thickened walls: leaves imbricated, more or less secund, unsymmetrical, ovate, mostly 1.2–1.4 long and 0.45–0.6 mm. wide, bifid about one half, the divisions (in explanate leaves) slightly or not at all curved, acute to acuminate, mostly 0.6–0.7 mm. long and 0.27–0.35 mm. wide at base, margin normally entire; vitta usually indistinct even in the basal region, extending for a short distance into the division but coming to an end considerably below the apex, undivided portion usually 0.2–0.3 mm. long and wide; cells of vitta mostly 35–60 × 22 μ in the basal portion and 20–40 × 20 μ in the divisions, marginal cells in basal portion about 22 μ in diameter, cells between margin and vitta about 24 μ in diameter; thickenings distinct, in the vertical walls mostly 8–10 μ wide; cuticle scarcely striolate: underleaves similar to the leaves but squarrose and symmetrical: male inflorescences borne in an interrupted series in the upper part of a stem; bracts mostly in five or six pairs, similar to the leaves except for the broad basal pocket extending nearly to the sinus, margin normally entire; bracteoles similar to the bracts; antheridia mostly two or three in each axil: female inflorescence not seen. [TEXT FIGS. 14–20.]

The following specimens have been examined:

NORWAY: Drivandefossen Waterfall, Lyster, Bergen Stift, August, 1900, *B. Kaalaas* (listed by Kaalaas in Nyt. Mag. f. Naturv. 40: 247. 1902; distributed as *H. adunca α Dicksoniana* in Schiffner's Hep. Eur. Exsic. *465*); Söndfjord, Bergen Stift, July, 1903, *E. Jörgensen* (distributed as *H. adunca α Dicksoniana* by Schiffner, *l.c. 464*); Frafjord near Stavanger, July, 1899, *E. Jörgensen* (distributed as *H. adunca α Dicksoniana* by Schiffner, *l.c. 463;* specimens from same locality listed by Kaalaas, *l.c.* 33: 224. 1893).

FAROE ISLANDS: Syderö, Bordö and Vaagö, May and June, 1896, *C. Jensen* (these are among the specimens listed by Jensen in Bot. Faer. 1: 127. 1901).

SCOTLAND: Ben Lawers, 1803, *W. J. Hooker* (listed as *Jungermannia juniperina β* by Hooker in Brit. Jung. *pl. 4.* 1812); Craig Chailleach, *G. E. Hunt;* same locality, June, 1900, *S. M. Macvicar;* Camlochan, July, 1843, *W. Gardiner;* Stuichd-an-Lochain, July, 1842, *W. Gardiner;* near summit of Ben More, July, 1897, *H. N. Dixon* (var. *alpina* Macvicar); Glengyle, June, 1895, *Stirling & Kidston;* Ben Vorlich, July, 1901, *S. M. Macvicar* (listed in Ann. Scottish Nat. Hist. 1902: 114); Ben Udlaidh, June, 1903, *S. M. Macvicar*.

WALES: Snowden Mountain, June, 1915, *A. H. Graves.*

In Ingham's Census Catalogue of British Hepatics, published in 1913, *H. adunca* is quoted from the following provinces: South Wales, North Wales, Lakes, East Highlands, West Highlands, North Highlands and North Isles. It is quoted also from eleven county divisions in Ireland. It is probable that some of these records, especially those from Ireland, are based on *H. Hutchinsiae.*

Most of the earlier writers not only failed to distinguish *H. Hutchinsiae* from *H. adunca* but considered the combined species a mere variety or form of the Jamaican *H. juniperina* (Sw.) Trevis. (*Jungermannia juniperina* Sw.). Hooker was apparently the first to advance this idea. In the text accompanying *pl. 4* of his British Jungermanniae he recognized *J. juniperina* as a member of the British flora and included *J. adunca* under the variety "β," to which he did not even give a definite name. "After a most careful examination of Mr. Dickson's *J. adunca*, compared with others of *J. juniperina*, which I have received from Dr. Swartz," he adds in a critical note, "I am unable to find any characters which can induce me to keep them separate." He then calls attention to the larger size of the Jamaican plant and to the greater readiness with which it regains its original appearance when immersed in water but clearly regards these features of but little moment. Weber* protested against Hooker's treatment of *J. adunca* and maintained it as a valid species, in which he was followed by both S. F. Gray and Dumortier. The majority of contemporaneous writers, however, followed the example of Hooker, and the Synopsis Hepaticarum, in 1845, went so far as to cite Scottish specimens under *Sendtnera juniperina* β, without even mentioning *J. adunca* as a synonym. When Gottsche, nearly twenty years later, distinguished between his α *Dicksoniana* and β *Hutchinsiae*, he pointed out in addition the most marked differences between *H. adunca* and *H. juniperina;* and, since this time, both species have been almost universally recognized.

Among the characters of *H. adunca* which Gottsche emphasized was the lack of teeth on the leaves and underleaves. He pointed out the fact that young leaves sometimes showed five to eight primordial papillae at the base, these structures representing the rudiments of teeth, but of actual teeth he found no development. Although this description will apply to the vast majority of leaves, it will not apply to all. An occasional leaf will show one or perhaps two teeth in the basal region. Such a tooth usually consists of a single cell, serving as a stalk for a papilla, but it sometimes attains a length of several cells and becomes more lobe-like in appearance. The occurrence of these teeth, in view of their infrequency and

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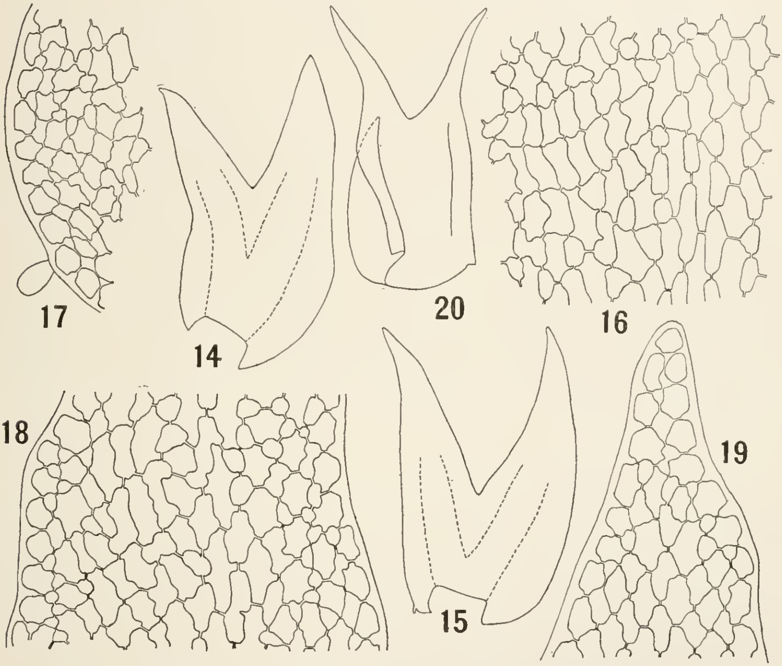
* Hist. Musc. Hepat. Prodr. 54. 1815.

irregularity, is doubtless more or less abnormal. The same thing may be said of the trifid leaves and of the blunt divisions which occasionally come to light, when a large series of leaves is examined.

Although Dickson's original figures show perianths and mature capsules, these organs seem to be very rarely produced.



Figs. 14–20. Herberta adunca (Dicks.) S. F. Gray

14, 15. Leaves, × 40. 16. Cells from the basal portion of a leaf, showing the basal vitta on the right, × 225. 17. Dorsal base of a leaf, × 225. 18. Cells from the upper part of a dorsal leaf-division, × 225. 19. Cells from the apex of the same division, × 225. 20. Perigonial bract, × 40. Figs. 14, 16–19 were drawn from Norwegian specimens collected by E. Jörgensen and distributed in Schiffner's Hep. Europ. Exsic. *464*; Figs. 15, 20, from Norwegian specimens collected by B. Kaalaas and distributed in the same exsiccatae *465*.

Hooker stated definitely that the only fruiting plants he had seen were Scotch specimens furnished by Dickson. Pearson* did not know fruiting plants at all; his description and figures of the bracts and perianths were drawn from Cuban specimens referred to *H. juniperina*, his idea being that the reproductive parts in this

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* Hep. British Isles 100, 101. *pl.* 36, *f. 11, 12.* 1900.

species would not differ appreciably from those of *H. adunca.* Perianths were likewise unknown to Stephani, although he quotes from Kaalaas a brief description of bracts, perianths and capsule. Whether Kaalaas actually saw these structures in *H. adunca* is, however, doubtful. The description quoted by Stephani was taken (with certain arbitrary changes) from the account of the *genus* given by Kaalaas,* the account of the species merely stating that the reproductive organs were "ut in genere." According to Macvicar female plants are frequent, but perianths are unknown in the British Isles. He quotes Hooker's statement about Dickson's fruiting plants but suggests that there was probably some mistake on Dickson's part. If this idea could be substantiated there would be no evidence left that *H. adunca* had ever been found in fruit. It is to be hoped that further explorations may be rewarded by the discovery of the missing parts, although a persistent sterility would not be surprising in the present genus, where other well-marked species apparently produce neither archegonia nor antheridia.

2. **Herberta Sendtneri** (Nees) comb. nov.

Schisma Sendtneri Nees, Naturg. europ. Leberm. **3**: 575. 1838.

Jungermannia Sauteriana Hüben. & Genth, Deutschl. Leberm. *108*. 1839 (*nomen nudum*); G. L. & N. Syn. Hep. 240. 1845 (as synonym).

Sendtnera Sauteriana Nees; G. L. & N. Syn. Hep. 240. 1845.

Schisma stramineum Dumort. Bull. Soc. Bot. Belgique **13**: 123. 1874 (in part). Not 1831.

Herberta straminea Trevis. Mem. R. Ist. Lomb. III. **4**: 396. 1877 (in part).

Brownish green, not glossy, growing in more or less extended mats: secondary stems erect or ascending, sparingly and irregularly branched, rigid, mostly 5–8 cm. long, about 0.35 mm. (or fifteen cells) wide and 0.3 mm. (or twelve cells) thick, the cells everywhere with strongly thickened walls: leaves imbricated, more or less secund, broadly ovate, mostly 1.2–1.6 mm. long and 0.75–1.1 mm. wide, bifid one half or a little more, the divisions (in explanate leaves), slightly or not at all curved, acute to acuminate, mostly 0.6–0.9 mm. long and 0.4–0.55 mm. wide, margin irregu-

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* Nyt Mag. f. Naturv. **33**: 223. 1893.

larly toothed near the base, the teeth mostly two to five on each side, sometimes small, sometimes larger and lobe-like; vitta indistinct even in the basal region, extending into the divisions but soon coming to an end, undivided portion about 0.25 mm. long and 0.35 mm. wide; cells of vitta mostly 40–70 × 18 μ in the basal portion and 30–40 × 16 μ in the divisions, marginal cells in the basal portion about 14 μ in diameter, cells between margin and vitta about 16 μ in diameter; thickenings distinct in the vertical walls, mostly 4–6 μ wide; cuticle distinctly striolate-verruculose, especially near the base: underleaves similar to the leaves but shorter and more symmetrical: inflorescence unknown.

The following specimens have been examined:

AUSTRIA (TIROL): Kleiner Rettenstein near Jochberg, *A. Sauter* (distributed as *Sendtnera Sauteriana* in Rabenhorst's Hep. Europ. *33a*); near Kitzbühel, August, 1882, *J. Breidler*; Rosskogl, *F. Arnold* (distributed as *Sendtnera Sauteriana* in Gottsche & Rabenhorst's Hep. Europ. *422*); Sellraintal, August, 1912, *H. von Handel-Mazzetti* (distributed as *H. straminea* in Schiffner's Hep. Europ. Exsic. *468*).

Müller and other writers cite the species from Bavaria and Salzburg, as well as from Tirol.

The present species bears a strong resemblance to the true *H. adunca* and it is not at all surprising that botanists have sometimes had difficulty in distinguishing them. Both normally grow in broad mats, their color is much the same except for the fact that *H. Sendtneri* seems never to be tinged with red or purple, their leaves are equally imbricated and divided to about the same extent, their divisions are less curved than in most species of the genus, and the vitta is poorly defined in both, the branches coming to an end far below the apices of the leaves. At the same time they exhibit excellent differential characters. The leaves in *H. Sendtneri* are relatively broader than in *H. adunca*, the same thing is true of the leaf-divisions, and the thickenings in the leaf cells are less conspicuous, those in the vertical walls being only about half as wide. The most striking differences between the two species, however, are to be found in the basal teeth. In *H. adunca*, as already noted, basal teeth are either absent altogether or else occur as a rare abnormality. In *H. Sendtneri* they form a conspicuous feature of the species. It is true that they may not be present on every individual leaf. Nevertheless, if a series of leaves is examined, the majority will show the basal teeth clearly. Some of the teeth consist of single cells, but most of them are three to ten cells long and often two to four cells wide at the base. Occasionally an even larger, lobe-like tooth is present. Although the basal teeth are almost always marginal it is sometimes possible to demonstrate a surface tooth.

3. **Herberta Hutchinsiae** (Gottsche) sp. nov.

Jungermannia juniperina β Hook. Brit. Jung. *pl. 4.* 1812 (in part).

Sendtnera adunca β Hutchinsiae Gottsche; Rabenhorst, Hep. Eur. *210* (accompanying text). 1862.

Herberta adunca β Hutchinsiae Schiffn. Lotos **60**: 54. 1912.

Yellowish or brownish green, sometimes tinged with red or purple, often somewhat glossy, growing in more or less extensive mats or in pendent tufts, sometimes mixed with other bryophytes: secondary stems erect, ascending or pendulous, rigid, mostly 5–10 cm. long but sometimes shorter, about 0.25 mm. (or fourteen cells) wide and 0.2 mm. (or twelve cells) thick, the cells everywhere with thickened walls, although showing a fairly marked difference between cortical and median regions: leaves imbricated, strongly secund, unsymmetrical, narrowly ovate, mostly 1.2–1.5 mm. long and 0.45–0.5 mm. wide, the divisions strongly curved and more or less divergent, acuminate to long-acuminate, mostly 0.8–1.2 mm. long and 0.2–0.25 mm. wide; margin normally entire; vitta distinct, extending far out into the divisions but hardly to the apices, undivided portion mostly 0.15–0.18 mm. long and 0.25–0.3 mm. wide; cells of vitta mostly 30–75 × 14–18 μ in the basal portion and 25–50 × 18–20 μ in the divisions, marginal cells in the basal region mostly 16–20 μ in diameter, cells between margin and vitta mostly 18–24 μ in diameter; thickenings distinct, in the vertical walls about 6 μ wide; cuticle faintly but distinctly striolate-verruculose: underleaves similar to the leaves but symmetrical, squarrose, and with straight divisions: male inflorescences normally borne in an interrupted series in the upper part of a stem, more rarely on a lateral or ventral branch; bracts and bracteoles mostly in four to six series, similar to the leaves but with straighter and less divergent divisions and a broad basal pocket, about 1 mm. long and 0.45 mm. wide, margin subentire to sparingly and irregularly denticulate; antheridia mostly two or three in each axil: female inflorescence apparently always terminal on a stem, often with one or more subfloral innovations; bracts and bracteoles similar, in about three series, those of the innermost series mostly 2.5–3.5 mm. long and 0.7–0.9 mm. wide, suberect and appressed to the perianth, bifid a little more than one half with slender, acuminate, subparallel divisions, margin copiously and shortly denticulate or dentate to or just above the level of the sinus, otherwise entire; bracts and bracteole of the other series a little shorter and often squarrose, the divisions usually more or less divergent, the margin varying from denticulate to coarsely and irregularly dentate; paraphyllia occasionally present, small and irregular; perianth ovate, not contracted at the mouth, about 3.5 mm. long and 0.8 mm. wide, divided for about half the length into six lanceolate, long-acuminate divisions, papillae numerous along the margins of the divisions near the base and on the inner surface of the perianth, usually sessile but sometimes borne on very short stalks: capsule brown, oval, about 1 mm. in diameter, splitting usually into six to eight valves; spores brown, about 25 μ in diameter, minutely echinulate; elaters brown, usually with two loose spirals, rarely with three, about 10 μ wide. [Plate 8.]

The following specimens have been examined:

Norway: Lyse near Stavanger, July, 1897, *E. Jörgensen* (distributed as *H. adunca β Hutchinsiae* in Schiffner's Hep. Eur. Exsic. *466;* specimens from the same locality listed by Kaalaas, as *H. adunca,* in Nyt. Mag. f. Naturv. **40**: 247. 1902).

Scotland: Moidart, Inverness, 1898, 1899 and 1901, *S. M. Macvicar* (listed as *H. adunca* in Jour. Bot. **37**: [3]. 1899; specimens from same region distributed as *H. adunca β Hutchinsiae* in Schiffner's Hep. Europ. Exsic. *467*); without definite locality or date, specimen from Hooker herbarium; Ben Vorlich, July, 1901, *S. M. Macvicar;* Ben Lavigh, July, 1901, *R. H. Meldrum.*

England: Borrowdale, Cumberland, July, 1844, *Mr. Brown;* April, 1893, *W. H. Pearson.*

Wales: Craig-y-can, Merioneth, May, 1877, *C. J. Wild & W. H. Pearson* (distributed as *H. adunca* in Carrington & Pearson's Hep. Brit. Exsic. *42*).

Ireland: Bantry, *Miss Hutchins;* Killarney, *B. Carrington* (distributed as *Sendtnera adunca β Hutchinsiae* in Rabenhorst's Hep. Europ. *210*); Brandon Mountain, *D. Moore* (distributed as "*Sendtnera juniperina* Nees = *Sendtnera adunca* Dickson" in Gottsche & Rabenhorst's Hep. Europ. *491*); same locality, no date, *W. Mitten,* several specimens; same locality, 1881, *D. Mc-*

Ardle; Mangerton Mountain, no date, *W. Mitten;* Mt. Cromaglown, *R. Spruce;* without definite locality or date, specimen from the Hooker herbarium.

ALASKA: Sitka, collector and date unknown (specimen received from Lindberg, in the Austin herbarium); Yes Bay, August, 1895, *T. Howell 1810* (listed as *H. adunca* by the writer in Proc. Wash. Acad. Sci. **2**: 309. 1900); Hot Spring, Baranof Island, June, 1899, *W. Trelease 1525a, 1808* (Harriman Expedition, listed as *H. adunca* by the writer, *l.c.*); Metlakatla, May, 1913, *R. B. Wylie 76, 97; T. C. Frye 109* in part; Ratz Harbor, June, 1913, *T. C. Frye 309;* Saltery Cove, June, 1913, *T. C. Frye 320;* Nichols Bay, June, 1913, *T. C. Frye 384;* Morse Cove, June, 1913, *T. C. Frye 446;* Brownson Bay, June, 1913, *T. C. Frye 470; A. S. Foster 517;* Augustine Bay, July, 1913, *T. C. Frye 561; A. S. Foster 677;* Port San Antonio, July, 1913, *T. C. Frye 605, 649;* Aats Bay, July, 1913, *T. C. Frye 925.* The specimens of Frye, Foster, and Wylie were collected under the auspices of the Kelp Investigation Expedition of the United States Bureau of Soils. They have already been listed by the writer, as *H. adunca*, in Bull. Torrey Club **41**: 601. 1915.

BRITISH COLUMBIA: Fraser Reach, Princess Royal Island, June, 1899, *F. V. Coville & T. H. Kearney* (Harriman Expedition, probably the basis for Osgood's record of *H. adunca* in U. S. Dept. Agric. Biol. Surv. Bull. 21: 14. 1901); Port Renfrew, August, 1902, *S. A. Skinner* (listed as *H. adunca* by the writer in Postelsia 1906: 228); Ucluelet, 1909, *J. Macoun 2* (specimens from same locality distributed as *H. adunca* by Miss Haynes in Amer. Hepat. *72* and by Macoun in Can. Liverworts *83*); Swanson Bay, May, 1913, *T. C. Frye 1174* (Kelp Expedition).

The specimens collected by Miss Hutchins at Bantry, Ireland, and now preserved in the Mitten herbarium at the New York Botanical Garden, should be considered the type of the species.

The following records for *H. adunca* from Alaska should also be noted: without definite locality, date or collector's name (listed by Underwood in Zoe **1**: 366. 1891); St. Paul Island, Pribolof Islands, *C. H. Merriam* (listed by Merriam in Proc. Biol. Soc. Washington **7**: 150. 1892). Underwood's record was probably based on Lindberg's specimens cited above. Merriam's record, however, was based on specimens in the United States National Herbarium, which, in the writer's opinion, represent a slender form of *Anthelia julacea* (L.) Dumort. This species is now known from several localities in Alaska, and additional specimens, essentially like those of Merriam, were collected on St. Paul Island, in 1897, by T. C. Kincaid (*49*).

The narrower and more deeply divided leaves of *H. Hutchinsiae*, with their more slender and strongly curved divisions will usually distinguish the species from *H. adunca* at a glance. In doubtful cases the distinct vitta extending far out into the divisions will decide the determination. The more gradual tapering of the divisions is clearly brought out by counting their width in cells. In *H. Hutchinsiae*, if the counts are made at a distance of 0.2 mm. from the apices, the divisions are found to have a width of from two to four cells; in *H. adunca* the corresponding counts will usually give from five to eight cells. Counts at the bases of the divisions are much less conclusive, on account of the fact that the divisions in *H. Hutchinsiae* are relatively longer, the bases thereby being often as wide as in *H. adunca*.

Among the specimens listed above, those from Norway are somewhat aberrant. Although some of the shoots conform closely to the type, others bear leaves which are considerably larger. One of the largest leaves measured had a length of 2.4 mm. and a width of 0.95 mm.; another, a length of 2 mm. and a width of 1 mm. The dorsal divisions of these measured, respectively, 1.2 × 0.45 mm. and 1.05 × 0.4 mm. Since these leaves are relatively broader than is usual, it might appear at first sight as if the large-leaved shoots approached *H. adunca*, but the distinct vittae present would seem to preclude this idea. In all probability they represent shoots developed under unusual conditions, perhaps exceptionally favorable from a nutritive standpoint; the large leaves might then be regarded as abnormal.

The androecia in *H. Hutchinsiae* are not absolutely constant in position. In normal cases they are borne on the secondary stems just as in *H. adunca*. Under these circumstances an androecium usually proliferates at the apex and then produces a new androecium after a short series of vegetative leaves. In several instances, however, androecia on ventral or lateral branches have been observed. These are apparently never produced unless the growth of the main male axis is brought to an end in some way, possibly through the failure of an androecium to proliferate, possibly through an accident of some sort. In either case a branch tends to take the place of the main axis and to assume its functions, precisely as a ventral branch of a sterile axis or a subfloral innovation would do. When, therefore, an androecium is borne on a branch of this character, its position can not be regarded as typical.

These considerations gain in significance when *H. Hutchinsiae* is compared with *H. dicrana* (Tayl.) Trevis., a closely related species of the Himalayas. The writer's knowledge of this species is largely based on specimens received from Levier and collected by Decoly and Schaul (*782*) near Kurseong in Sikkim-Himalaya, in May, 1899. These specimens contain both male and female plants and are of especial interest because they served as the basis for Schiffner's statements regarding the androecia of *H. dicrana.** He notes their occurrence on the ends of branches, their small size, the small number of bracts (about four pairs) which they bear, and the fact that they are sterile at the apices. The branches which bear the androecia are ventral and vary greatly in length. Sometimes the development of the antheridia brings the growth of the branch to an end, but a sterile proliferation of the androecium often occurs. The formation of the male branches seems to be a perfectly normal process and is not preceded by a cessation of growth of the main stem as in *H. Hutchinsiae.* It follows, therefore, that what occurs abnormally in the northern species has become normal in the Himalayan species. It should be noted, however, that ventral androecia are not absolutely constant even in *H. dicrana.* One example was observed where the androecium was borne on a main stem; it had somewhat larger bracts and bracteoles than the ventral androecia but resembled them in other respects. Aside from the difference in the position of the androecia, *H. dicrana* resembles *H. Hutchinsiae* very closely. The leaves and underleaves, the bracts and bracteoles, and the perianths are much the same in the two species, although the divisions of the leaves in *H. dicrana* usually are less strongly curved. The latter species, moreover, is slightly larger, the leaves are less crowded and the thickening of the cell-walls is less pronounced.

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* Hedwigia **50**: 148. 1910.

4. **Herberta tenuis** sp. nov.

Schisma juniperinum Sulliv. Musc. Alleg. *258*. 1846. Not Dumort.

Sendtnera juniperina Sulliv.; A. Gray, Man. 689. 1848. Not Nees.

Herberta adunca Underw. Bot. Gaz. **14**: 195. 1889. Not S. F. Gray.

Yellowish or brownish green, rarely tinged with red, growing in more or less extensive mats: secondary stems erect or ascending, sparingly and irregularly branched, rigid, mostly 2–4 cm. long, about 0.15 mm. (or ten cells) wide and 0.13 mm. (or nine cells) thick, outer layer of cells with strongly thickened walls, interior cells with slightly thickened walls: leaves scattered to loosely imbricated, subsquarrose to slightly secund, a little unsymmetrical, subovate, mostly 0.9–1 mm. long and 0.3–0.35 mm. wide, bifid two thirds to three fourths, divisions (in explanate leaves), divergent, slightly or not at all curved, long-acuminate, mostly 0.6–0.7 mm. long and 0.15–0.18 mm. wide, margin entire or with an occasional basal tooth; vitta distinct, extending far out into the divisions but not to the apices, undivided portion about 0.1 mm. long and 1.5 mm. wide; cells of vitta mostly 20–55 × 14 μ in the basal portion and 20–35 × 14 μ in the divisions, marginal cells in the basal region about 14 μ in diameter, in the divisions about 17 μ, cells between margin and vitta about 20 μ; thickenings distinct but not so strongly developed as in most species, in the vertical walls mostly 3–4 μ wide; cuticle minutely striolate-verruculose: underleaves similar to the leaves but symmetrical; inflorescence unknown. [TEXT FIGS. 21–29.]

The following specimens have been examined:

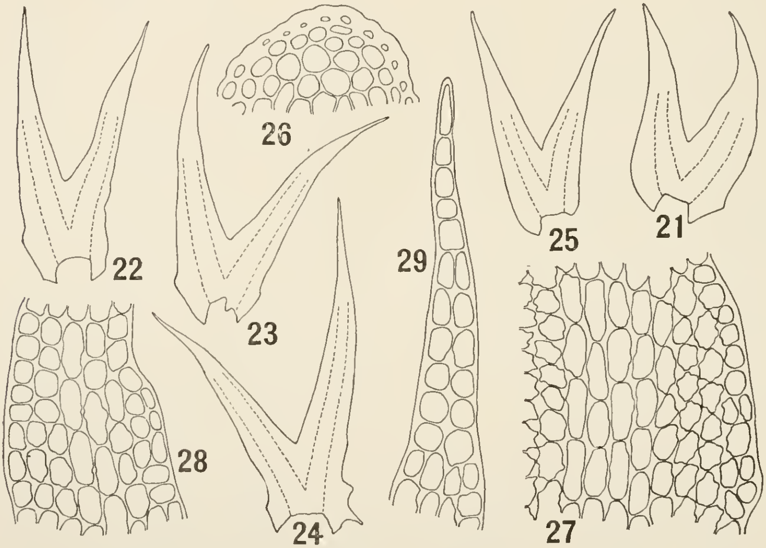
NEW YORK: Kaaterskill Falls, Catskill Mountains, *C. H. Peck* (listed by Peck, as *Sendtnera juniperina*, in Rep. New York State Mus. Nat. Hist. **19**: 70. 1866; both "Cauterskill" Falls and High Peak, Catskill Mountains, are mentioned here); Austin's Hep. Bor.-Amer. *82*, distributed as *Sendtnera juniperina*, is also *H. tenuis* and may possibly include some of Peck's material, the label reading: "Catskill Mountains, New York, *Peck*, Greenwood Mts., N. J., *Aust.;* also in the Alleghanies southward."

NEW JERSEY: Greenwood Mountains, Passaic County, November, 1866, *C. F. Austin* (listed by Britton, as *H. adunca*, in Cat. Pl. New Jersey 351. 1889); Austin's Hep. Bor.-Amer. *82* (see above) is probably made up largely of material from this locality.

Pennsylvania: Stony Creek, Somerset County, *F. Wolle.*

Virginia: summit of White Top Mountain, Washington County, May, 1892, *A. M. Vail & E. G. Britton 9, 91*, and numerous unnumbered specimens; same locality and date, *J. K. Small 77, 79* (listed by Small & Vail, as *H. adunca*, in Mem. Torrey Club 4: 193. 1894).

West Virginia: Tibbs Run, Monongalia County, September, 1892, *C. F. Millspaugh 1659* (listed by Millspaugh, as *H. adunca*, in Prelim. Cat. Fl. W. Va. 496. 1892); Quarry Run, Monongalia County, 1903, *A. LeR. Andrews.*



Figs. 21–29. Herberta tenuis Evans

21–25. Leaves, × 40. 26. Transverse section of a mature stem, × 225. 27. Cells from the lower part of a leaf, including the vitta just above the forking, × 225. 28. Cells from the upper part of a dorsal leaf-division, × 225. 29. Cells from the apex of a division, × 225. Fig. 21 was drawn from specimens distributed in Austin's Hep. Bor.-Amer. *82;* the remaining figures, from the type specimen.

North Carolina: "in montibus Carolinae," *F. Michaux* (listed by Michaux, as *Jungermannia sertularoides*, in Fl. Bor. Amer. 2: 278. 1803), the label reading as follows: "Junga sertularoides Rich. Fl. b. Am. a Jung. trichophylla vox aut non distincta! Hb. Hooker"; "in montosis editissimis Carolinarum," 1843, *A. Gray & W. S. Sullivant* (distributed, as *Schisma juniperinum*, in Sullivant's Musc. Alleg. *258*, and listed by Sullivant, as *Sendtnera juniperina*, in A. Gray, Man. 689. 1848); top of Black Mountain, June, 1850, *L. Lesquereux;* Grandfather Mountain, August, 1891, *J. K. Small 32* (also distributed, as *H. adunca*, in Underwood & Cook's Hep. Amer. *126*); Grandfather Mountain, September, 1901, *G. F. Atkinson 11420, 11501* (listed by Andrews, as *H. adunca*, in Bryologist **17**: 59. 1914); near Shulls Mills, Blue Ridge Mountains, September, 1901, *G. F. Atkinson 12054* (listed by Andrews, *l.c.*).

Dr. Small's specimen from North Carolina, No. 32, may be designated the type.

Two additional records for *H. adunca* from the eastern United States may likewise be noted, namely: Carbon County, Pennsylvania, *E. A. Rau* (listed by Porter in Cat. Bryoph. & Pteridoph. Pennsylvania 9. 1904), and mountains of western North Carolina, 1907, *A. J. Grout* (listed by Grout in Bryologist **12**: 54. 1909). In all probability these records were based on *H. tenuis*.

The present species is closely related to *H. Hutchinsiae* but is considerably smaller. Although at first sight the small size might appear to be due to poor development, the study of a large series of specimens from many localities shows pretty conclusively that this is not the case. The size is of course subject to more or less variation, as in all species of *Herberta*, but the measurements of the leaves given in the description represent a fair average of the more robust plants studied, and are only about two thirds as great as the corresponding measurements in *H. Hutchinsiae*. The difference in size is brought out with especial clearness by counting the width of the basal portion in cells between the vitta and the margin. In *H. Hutchinsiae* such a count would give from five to seven cells; in *H. tenuis* from three to five cells. Aside from the difference in size the slightly curved or straight divisions in *H. tenuis* and the thinner cell-walls will distinguish the species from *H. Hutchinsiae*, where the divisions are normally strongly curved and the thickening of the cell-walls much more distinctly marked.

The basal teeth in *H. tenuis*, although an inconstant feature, deserve a few words of comment. When they occur there may be one or, rarely, two teeth on each side, and the underleaves tend to produce them more frequently than the side-leaves. The teeth are of fair size, often involving several cells, and may be rounded or sharp. In the latter case they are especially conspicuous (TEXT FIG. 24). It has already been noted that teeth form an important feature of the leaves in *H. Sendtneri*, whereas in *H. adunca* and *H. Hutchinsiae* the margin is normally entire. *H. tenuis* occupies an intermediate position in this respect, the teeth being less frequent than in *H. Sendtneri* but more frequent than in either of the other species.

The present paper is based largely on material in the herbarium of Yale University. This has been supplemented by specimens from the Taylor herbarium at Harvard University and from the herbarium of the New York Botanical Garden. Additional specimens have been received from Professsr A. LeRoy Andrews of Cornell University, from Mr. S. M. Macvicar of Invermoidart, Scotland, and from Mr. C. Jensen of Hvalsö, Denmark. The writer would express his sincere thanks to all who have aided him in his work.

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Explanation of plate 8

HERBERTA HUTCHINSIAE (Gottsche) Evans

FIGS. 1–3. Leaves, × 40.

FIG. 4. Cells from the lower part of a leaf, showing the basal vitta, × 225.

FIG. 5. Cells from the dorsal base of a leaf, showing two rudimentary teeth, × 225.

FIG. 6. Cells from the upper part of a dorsal leaf-division, × 225.

FIG. 7. Cells from the apex of the same division, × 225.

FIGS. 8, 9. Perigonial bracts, × 40.

FIG. 10. Perichaetial bract from next to the last pair, × 27.

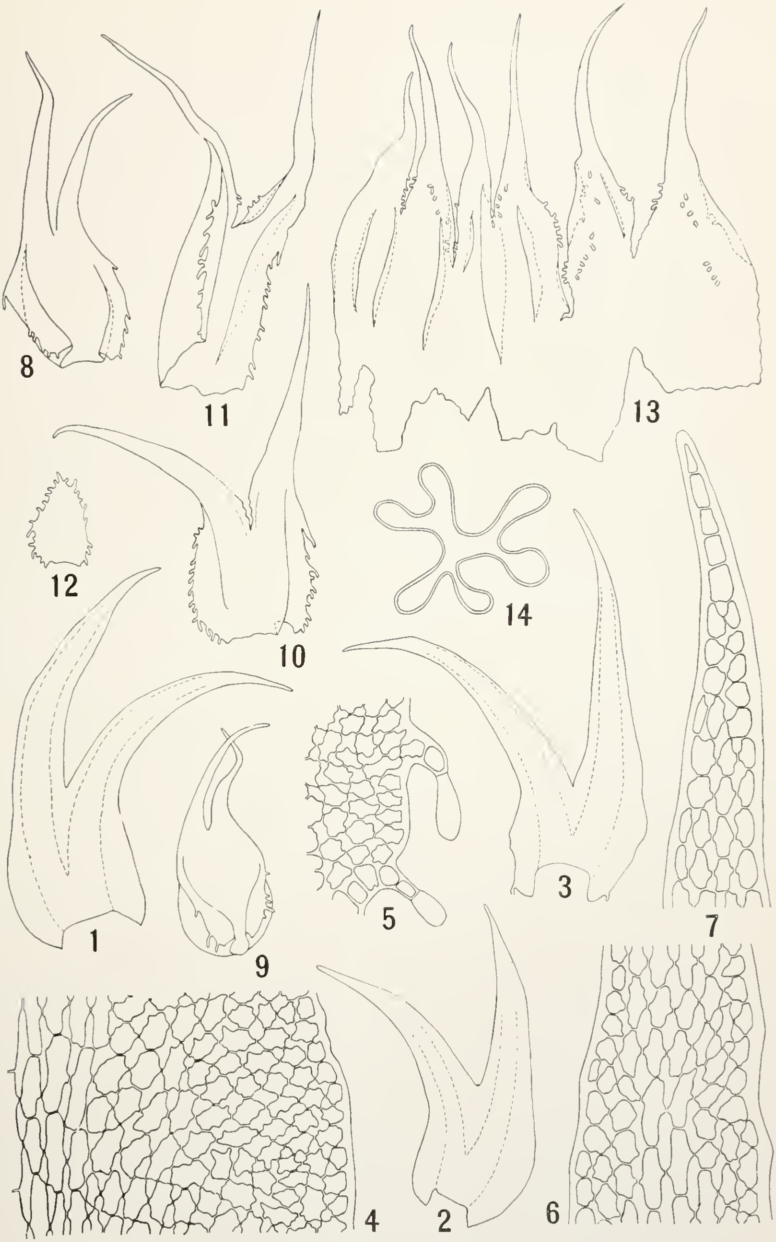
FIG. 11. Perichaetial bract from the innermost pair of the same involucre, × 27.

FIG. 12. Paraphyllium from the same involucre, × 27.

Fig. 13. Perianth, spread out flat, × 27.

FIG. 14. Transverse section of perianth, × 40.

FIG. 1 was drawn from Irish specimens collected by B. Carrington and distributed in Rabenhorst's Hep. Europ. *210*; FIG. 2, from Scottish specimens collected by S. M. Macvicar and distributed in Schiffner's Hep. Europ. Exsic. *467*; the remaining figures, from specimens collected by T. C. Frye at Port Antonio, Alaska, *649*.



HERBERTA HUTCHINSIAE (Gottsche) Evans

[Reprinted from The Bryologist, Vol. XX, No. 4, July 1917]

PRELIMINARY LIST OF ARIZONA HEPATICAE[1]

Alexander W. Evans

Very few species of Hepaticae have been reported from Arizona. The first records for the state were made in 1895 by Underwood,[2] who noted the occurrence of *Marchantia polymorpha* and *Reboulia hemisphaerica*, without citing definite stations. Four additional species have since been reported by the writer, as follows: *Plagiochasma rupestre* and *P. Wrightii*, in 1915;[3] *Frullania mexicana*, also in 1915;[4] and *Marchantia paleacea*, in 1917.[5] Of these six species, *Marchantia paleacea*, although not endemic to Arizona, is known from no other stations in the United States.

The following list is based largely on the collections made by G. E. Nichols, while participating in the International Phytogeographic Excursion in America. This has been supplemented by the material in the herbarium of the New York Botanical Garden and by specimens kindly communicated by W. A. Cannon, D. S. Johnson, F. Shreve, and J. J. Thornber. Although future collections will undoubtedly lengthen the list appreciably, it is hardly to be expected that many conspicuous species remain to be discovered.

1. Riccia glauca L. Bear Canyon, Santa Catalina Mountains, 1913, *G. E. Nichols.*

2. Riccia sorocarpa Bisch. Cherry Creek, Santa Catalina Mountains, 1913, *G. E. Nichols;* summit of Mt. Lemmon, Santa Catalina Mountains, *F. Shreve.*

3. Ricciella fluitans (L.) A. Br. Soldier Canyon, Santa Catalina Mountains, 1913, *G. E. Nichols;* Sabino Canyon, Santa Catalina Mountains, *F. Shreve.*

4. Targionia hypophylla L. Bright Angel Trail, bottom of Grand Canyon, 1913, *G. E. Nichols;* Sabino Canyon, Santa Catalina Mountains, *J. J. Thornber;* Miller Canyon, Huachuca Mountains, *F. Shreve.*

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Bot. Gaz. **20:** 69, 70. 1895.

[3] Bull. Torrey Club **42:** 279, 295. 1915.

[4] Bryologist **18:** 88. 1915.

[5] Trans. Connecticut Acad. **21:** 254. 1917.

5. Plagiochasma rupestre (Forst.) Steph. Without definite locality or date, *H. H. Rusby;* Soldier Canyon, Santa Catalina Mountains, 1913, *W. A. Cannon;* same locality, *G. E. Nichols.*

6. Plagiochasma Wrightii Sulliv. Nogales, 1902, *D. T. MacDougal.*

7. Grimaldia californica Gottsche. Cottonwood Springs and Soldier Canyon, Santa Catalina Mountains, 1913, *G. E. Nichols;* Bear Canyon and Sabino Canyon, Santa Catalina Mountains, *F. Shreve.* The specimens are all sterile, so that their determination must be considered provisional.

8. Reboulia hemisphaerica (L.) Raddi. Willow Spring, 1890, *E. Palmer 535;* Huachuca Mountains, *J. G. Lemmon 210; L. N. Goodding 752;* Soldiers Canyon, Santa Catalina Mountains, *G. E. Nichols;* Sabino Canyon, Santa Catalina Mountains, *J. J. Thornber;* same locality, *F. Shreve;* Clearson's Mill, Graham Mountains, *F. Shreve.*

9. Asterella californica (Hampe) Underw. Bright Angel Trail, bottom of Grand Canyon, 1913, *G. E. Nichols.* The specimens seem to be dioicous, but the absence of carpocephala makes their determination doubtful.

10. Conocephalum conicum (L.) Dumort. Frye Canyon, Graham Mountains, 1914, *F. Shreve.*

11. Marchantia paleacea Bertol. Huachuca Mountains, 1910, *L. N. Goodding 824.*

12. Marchantia polymorpha L. Miller's Canyon and Wickersheim's Cabin, Huachuca Mountains, 1909, *L. N. Goodding 111, 362.*

13. Fossombronia longiseta Aust. Cherry Creek, Santa Catalina Mountains, 1913, *G. E. Nichols.*

14. Plagiochila asplenioides (L.) Dumort. North side of Mt. Lemmon, Santa Catalina Mountains, 1912, *D. S. Johnson.*

15. Cephaloziella Hampeana (Nees) Schiffn. Cottonwood Springs, Santa Catalina Mountains, 1913, *G. E. Nichols.*

16. Cephaloziella myriantha (Lindb.) Schiffn. Bear Canyon, Santa Catalina Mountains, 1913, *G. E. Nichols.*

17. Cephaloziella papillosa Douin. Bear Canyon, Santa Catalina Mountains, 1913, *G. E. Nichols.*

18. Scapania undulata (L.) Dumort. Marshall Gulch, Santa Catalina Mountains, 1912, *D. S. Johnson.*

19. Radula complanata (L.) Dumort. Bear Canyon, Santa Catalina Mountains, 1913, *G. E. Nichols.*

20. Frullania mexicana Lindenb. North side of Mt. Lemmon, Santa Catalina Mountains, 1912, *D. S. Johnson.*

21. Anthoceros laevis L. Xero-montane Garden and Sabino Canyon, Santa Catalina Mountains, 1914, *F. Shreve.*

Of the species listed Nos. 1–12 belong to the Marchantiales, Nos. 13–20 to the leafy Jungermanniales, and No. 21 to the Anthocerotales. The large proportion of thalloid forms is an interesting feature of the flora and indicates its strongly xerophilous character. Many of these forms are able to pass through long periods of drought in a quiescent state and then to recover and resume their growth when conditions become more favorable. In some cases the dry plants are so inconspicuous that it is almost impossible to detect them. In discussing the hepatic flora of western California, Campbell[6] calls attention to many interesting peculiarities of xerophilous species, and his remarks would apply equally well to the hepatic flora of Arizona.

The state of Arizona is bounded by Mexico, California, Nevada, Utah, and New Mexico, while its northeastern corner meets the southwestern corner of Colorado. The Hepaticae of Nevada and Utah are almost unknown, so that it is impossible to make profitable comparison between the hepatic floras of these states and that of Arizona. The Hepaticae of California, however, are known to us through the thorough and comprehensive work of Howe,[7] who recognizes eighty-six species, inclusive of the Anthocerotes. For Colorado the writer[8] has listed forty-one species, while Standley[9] has reported twelve species from New Mexico. The Hepaticae of Mexico were long ago described by Gottsche,[10] and only scattered references to them have since been published. Perhaps four hundred species would be a conservative estimate for the entire country. Of the twenty-one species listed from Arizona, fifteen have been recorded from California, nine from Colorado, five from New Mexico, and twelve from Mexico. These figures would indicate a close relationship between the species of Arizona and those of California and Mexico. The number of Arizona species known from New Mexico is surprisingly small and would probably be increased by careful exploration. A closer relationship between the species of these two states is certainly to be expected.

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[6] Torreya **4**: 81–86. 1904.

[7] The Hepaticae and Anthocerotes of California. Mem. Torrey Club **7**: 1–208. *pl. 88–122.* 1899.

[8] Preliminary list of Colorado Hepaticae. BRYOLOGIST **18**: 44–47. 1915.

[9] Hepaticae of New Mexico. BRYOLOGIST **18**: 81–83. 1915. Additional notes upon New Mexican Hepaticae. BRYOLOGIST **19**: 64, 65. 1916.

[10] De mexikanske Levermasser. Kongel. Danske Vidensk. Selsk. Skr. V. Naturv. og Math. Afd. **6**: 97–380. *pl. 1–20.* 1863.

[From the BULLETIN OF THE TORREY BOTANICAL CLUB, 44: 389-403. 10 Au 1917]

Mechanics of movement in Drosera rotundifolia*

HENRY D. HOOKER, JR.

CONTENTS

I. INTRODUCTION

Plant growth is defined technically as any permanent change of shape or size produced by the activity of the plant (*cf.* Jost, '13, p. 339; Pfeffer, '06, p. 1). The movements of *Drosera* tentacles, being reactions to stimuli, are determined by the activity of the *Drosera* plant. Moreover, bending is accompanied by a permanent elongation of the convex side of the tentacle and unbending by a corresponding increase in the length of the concave side (Hooker '16). These movements are therefore phenomena of growth. The term "growth" obviously includes a number of processes, which may be determined by changes in the amount of protoplasm, cell-wall material or osmotically active substances.

II. EXPERIMENTAL DATA

1. OSMOTIC CONCENTRATION

In order to obtain a more detailed knowledge of the growth which brings about the movement of *Drosera* tentacles, the con-

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* Contribution from the Osborn Botanical Laboratory.

centration of osmotically active material dissolved in their cells was measured by plasmolysis. For this purpose solutions of potassium nitrate and glucose were prepared. The osmotic concentration of plant cells may be compared with the concentrations of these substances in terms of their relative osmotic values. Consequently osmotic concentrations will be measured in atmospheres as follows:

Atmospheres	Solutions of KNO_3 in percentages	Solutions of glucose in percentages
5	1.43	3.85
6	1.71	4.62
7	2.00	5.40
8	2.29	6.17
9	2.57	6.95
10	2.86	7.71
11	3.14	8.48
12	3.43	9.25
13	3.71	10.02
14	4.00	10.80
15	4.29	11.58

Tentacles of the *Drosera* were removed from the leaf with forceps, placed in prepared solutions, mounted and examined under the high power of the microscope. Plasmolysis was found to be most readily detected in slightly pigmented cells, and whenever possible tentacles with stalks composed of such cells were selected. In case aggregation occurred, the first traces of plasmolysis were much more difficult to make out. Tentacles were treated and examined when straight; just after bending in response to a tactile stimulus; when fully bent; during unbending; and when again straight. The first procedure was to place tentacles in each of the prepared potassium nitrate solutions and to examine them for traces of plasmolysis. The results obtained by this general orientation were repeated and verified by numerous subsequent experiments both with potassium nitrate and with glucose solutions. The data given with glucose solutions were practically identical throughout with the results furnished by the potassium nitrate solutions. The final data given below are expressed in terms of the most concentrated solution that failed to plasmolyze.

The epidermal cells on the pedicels of the tentacles have strongly cutinized outer walls which are impermeable to salt and sugar solutions. The solution reaches the inner cells of the tentacle by way of the gland at the apex and the broken end at the base where the tentacle was formerly attached to the leaf blade. In many cases it was found necessary to puncture the cuticle in several places with a needle, or else to cut the pedicel into segments with a razor, in order to give the solutions access to all the cells of the tentacles.

1. *Straight tentacles.*—Examination of over thirty normal marginal tentacles with potassium nitrate and of twenty with glucose solutions showed the cells of the apical half of the pedicel to have a higher osmotic concentration than the cells of the basal half. The latter ranged from eight to nine atmospheres; the former from nine to eleven. In a few instances the cells on the dorsal and ventral surfaces of the basal portion of the pedicel had a higher osmotic concentration than the cells on the flanks. De Vries ('86, pp. 4, 5) found that the cells of *Drosera* tentacles were plasmolyzed by a three per cent. solution of potassium nitrate, but not by a two per cent. solution. This is seen to hold for all the stalk cells excepting those at the apical end just below the gland.

2. *Bending tentacles.*—The glands of numerous tentacles were stimulated by rubbing with a fine brush and after fifteen to twenty minutes, when the tentacles had bent through an angle of 90° to 120°, they were removed and placed in a two per cent. potassium nitrate solution. This treatment did not cause the tentacles to unbend. They were then mounted in some of the same solution and covered with a supported cover-glass. Since the tentacles were curved, the different effect of the solution on the convex and concave sides of the tentacle could be observed. In nearly all cases where the movement was rapid, the two per cent. potassium nitrate solution had plasmolyzed the cells in the bent region on the convex or abaxial side, while the cells on the concave or adaxial side showed no effect. Similar results were obtained by using a 5.4 per cent. glucose solution. Examination of fifty tentacles with potassium nitrate and of thirty-five with glucose showed the osmotic concentration in the abaxial cells to be from six to eight atmospheres, in the adaxial cells from eight to nine atmospheres. The osmotic concentration of the cells on the convex side had therefore diminished during bending; that of the cells on the concave side

had remained practically unchanged. The greatest diminution in the osmotic concentration of the cells on the convex side was observed in those tentacles that reacted most rapidly. In a few cases of exceptionally slow movement no diminution was observed, the osmotic concentration being either eight or nine atmospheres. The osmotic concentration of the cells in the upper half of the stalk was found to be the same as in the unbent tentacle.

3. *Bent tentacles.*—Tentacles were stimulated by placing small flies on their glands, and after bending had proceeded as far as possible the tentacles were removed and examined. In twenty-five tentacles treated with potassium nitrate solutions and fifteen tentacles treated with glucose solutions, the cells at the base of the pedicel and in the bent region had an osmotic concentration of nine to eleven atmospheres, there being no difference between the two sides of the tentacle. The cells of the apical portion of the pedicel were found to have an osmotic concentration of ten to thirteen atmospheres. In a few exceptional cases the cells in the latter region appeared to have a higher osmotic concentration, but the detection of plasmolysis was particularly difficult because these cells were smaller than the basal cells and their contents were strongly aggregated.

4. *Unbending tentacles.*—Twenty tentacles in process of unbending were examined with potassium nitrate solutions and the results were checked by the examination of twelve more with glucose solutions. The osmotic concentration of the cells in the basal half of the pedicel was from eight to ten atmospheres; in the apical half from nine to eleven. No difference was observed in the osmotic concentrations of the cells on the concave and convex sides.

5. *Unbent tentacles.*—Eighteen tentacles which had become straight after completing a reaction were examined and found to be similar in osmotic concentration to the normal tentacles before reaction.

The experimental data given above are summarized in the following table:

Three significant facts should be noted, namely:

1. The osmotic concentration of the pedicel cells increases from the base to the apex.

Tentacles	Straight	Bending	Bent	Unbending	Unbent
Basal half of pedicel:					
Abaxial side	8–9	6–8	9–11	8–10	8–9
Adaxial side	8–9	8–9	9–11	8–10	8–9
Apical half	9–11	9–11	10–13	9–11	9–11

2. During rapid bending the osmotic concentration of the abaxial cells in the growing region decreases.

3. When the tentacles are bent, the cells have a higher osmotic concentration than at any other time.

2. RABDOIDS

Rabdoids were first discovered by Gardiner ('85) in *Drosera dichotoma*, and he states that in *Dionaea*, *Drosera rotundifolia* and other species of *Drosera* rabdoids occur which resemble those of *Drosera dichotoma*. Gardiner described the rabdoid as a body, usually spindle-shaped or acicular, which occupies such a position that it stretches diagonally across the cell from end to end, the two extremities being imbedded in the cell protoplasm. They were present in all the epidermal cells of *Drosera dichotoma* leaves except the gland cells and the cells immediately beneath the glands. In the bending region of those tentacles capable of movement they were larger in the epidermal cells on the abaxial side than on the adaxial side where they were very small or apparently absent. When these cells lost their turgidity the rabdoids contracted and separated into two or more parts, but regained their spindle shape when turgidity was restored. A sudden blow on the cover glass also caused the rabdoids to assume a spherical form.

The presence of rabdoids in the epidermal cells of *Drosera rotundifolia* leaves was confirmed. They occur in all the epidermal cells of the petiole, of the leaf blade and of the basal portion of the tentacles, including the bending region. Each cell contains a single rabdoid, rarely two rabdoids, situated near the outer wall and parallel with it. After a leaf has fed on insects, the rabdoids are distinctly larger than before. When plants are deprived of insectivorous food for any considerable period, the rabdoids dwindle until they are barely noticeable. Sudden shocks produced by tapping the cover glass or gradual pressure sustained for a considerable period of time cause the rabdoids to alter their shape.

They contract at each end so that they have the appearance of dumb-bells, and finally separate into several disk-shaped parts. In extreme cases they separate into a large number of droplets which exhibit Brownian movement. No marked difference was observed in the size of the rabdoids on opposite sides of the tentacle in the bending region, and no alteration was visible during movement. The function of the rabdoids is not apparent. It seems probable, however, that they are connected in some way with the process of secretion, rather than with the mechanics of movement. Gardiner ('85) suggested that they might be reserve material or some substance used up during secretion. This seems to be borne out by the fact that they are of protein composition according to Tunmann ('13, p. 481).

3. Unbending by plasmolysis

Although a two per cent. solution of potassium nitrate usually plasmolyzes the cells on the convex side of a bending tentacle, this does not cause the tentacle to become straight (see De Vries, '86, p. 5). More concentrated solutions produce unbending. For a short time after the tentacle is fully bent complete plasmolysis still causes unbending, but when the tentacle has been bent a considerable period and during unbending, plasmolysis does not alter its shape.

The xylene experiment which W. H. Brown ('12, '16) made on *Dionaea* and *Mimosa* was tried on *Drosera* tentacles, but no positive results were obtained. Bent and bending tentacles were killed in boiling water, treated with 95 per cent. alcohol, absolute alcohol and xylene. No unbending ensued. This may indicate a difference between the mechanics of movement in *Drosera* and in such plants as *Dionaea* and *Mimosa*. However, the failure of the experiment may have been owing to faulty technique, although the description of the process by Brown ('16, p. 78) was followed in detail.

III. DISCUSSION

1. Increased turgidity as the means of movement

The straightening of bent tentacles by plasmolysis shows the cell elongation, which is the immediate cause of bending, to be a passive stretching of the walls by turgidity. This conclusion is corroborated by direct observation. During bending the cells on the convex side in the curved region as seen under the microscope are noticeably distended, the outer walls appearing in optical cross-section as arcs extending between the end walls. A simple way of demonstrating this is afforded by mounting a straight tentacle in a one per cent. solution of tartaric acid, covering it with a supported cover glass and examining under the microscope. Tartaric acid as well as dilute solutions of many other organic and mineral acids induce rapid and violent bending. The acid enters the tentacle through the broken end of the pedicel at the base, where it was formerly attached to the leaf-blade, and affects the bending region directly, for inflexion proceeds even when the gland has not been stimulated in any way either by being touched or by coming in contact with the acid solution.* Gardiner ('85) observed that in well-inflected tentacles of *Drosera dichotoma* the cells on the convex side at the bending point are very turgid. It must be borne in mind that turgidity is the external manifestation of a balance between two antagonistic factors; one factor due to the presence of osmotically active substances in solution tends to increase the volume of the cell and to stretch the wall; the other factor due to the elasticity of the cell-wall tends to compress the cell contents. An increase in the size of the cell under such circumstances follows either from an increase in the amount of osmotically active material or from a diminished elasticity of the cell-wall, unless simultaneous changes in permeability interfere.

(*a*) *Osmotic concentration*

The experimental data show that during bending the osmotic concentration in the cells on the abaxial side of the pedicel in the growing region falls from eight or nine to six or eight atmospheres. It is at once evident that the elongation of the cells is not the result of an increase in the amount of osmotically active material. Exact data concerning the increase in length of the abaxial side

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* The bending produced in detached tentacles by this means is frequently astonishing. The tentacle may bend around completely on itself until it forms a spiral. It is known that stimulation of the glands of *Drosera* tentacles is followed by the secretion of an acid. Is it possible that the impulse which is conducted from the gland down the pedicel to the base of the tentacle and which there starts movement is the acid secreted by the gland diffusing from cell to cell?

during bending is given in a previous paper (Hooker, '16). An average of eleven measurements taken in the region of most active growth shows the increase to be about 27 per cent. of the original length. In one typical example (*ibid. f. 6*), cells on the abaxial side (*ibid.* Table III, segment 5) in the bending region grew from 0.45 mm. to 0.57 mm., an increase of 26.6 per cent. Assuming the other dimensions of the cell to remain unaltered, the increase in volume of the cells in this region would be proportional to the increase in length. An increase in volume must be accompanied by a corresponding decrease in osmotic concentration. Thus if the original concentration were eight atmospheres, we should expect as the result of an increase in volume of 26 per cent. an equivalent decrease in osmotic concentration, that is a fall from eight to six atmospheres. When it is considered that the measurements of osmotic concentration were taken before bending was completed, and that soon after the tentacle is bent the cells restore their original osmotic concentration, a process that must commence soon after bending begins, we see that the maximum decrease in osmotic concentration observed is amply accounted for by the increase in volume of the growing cells. The maximum decrease observed was approximately 25 per cent.; the increase in length averaged 27 per cent.; the correspondence is well within the limits of probable error. The alteration of osmotic concentration is therefore a result of the growth of the cells, and not a determining factor of their elongation.

No marked change in the osmotic concentration of the cells on the adaxial side of the bending tentacle was observed at any time. The slight elongation or compression which these cells experience during bending is probably insufficient to make a change of osmotic concentration perceptible. The irregularity in the nature of the alterations on the concave side of the tentacle indicates that this side takes no active part in the bending, but is either stretched or compressed according to the mechanical conditions that happen to prevail in the base of the pedicel. Gardiner ('85) states that the cells on the concave side of well-inflected *Drosera dichotoma* tentacles lose their turgidity at the bending point. No distinct evidence of loss of turgidity by the cells on the concave side of inflected *Drosera rotundifolia* tentacles was observed, however.

The external walls appear in optical cross-section as straight lines extending between the end walls.

(*b*) *Permeability*

It is of course possible that the elongation of the cells on the convex side of inflected tentacles might be caused by increased osmotic pressure, if the detection of the increased osmotic concentration were rendered impossible by a simultaneous increase in the permeability of the cells to the plasmolyzing solutions. The possibility that such is the case here is ruled out by two considerations. Firstly, the determinations of osmotic concentration made with an electrolyte, potassium nitrate, were confirmed by determinations made with a non-electrolyte, glucose. It is highly improbable that there should occur a differential change in permeability of such a nature as to permit increased diffusion of both potassium nitrate and glucose, which at the same time would not permit increased diffusion of the osmotically active material within the cell. Secondly, the correspondence between the increased volume of the elongating cells and the decreased osmotic concentration indicated by experiments cannot be disregarded, since it offers a direct and simple interpretation of the experimental data.

(*c*) *Cell-wall elasticity*

Since there is no evidence that the permeability is altered, and since the osmotic concentration decreases during bending, the increased turgidity of the elongating cells must be due to a decrease in the elasticity of their cell-walls. It is evident that irreversible changes take place in the cell-wall, for the increased size of the cell-wall is soon rendered permanent, probably by the deposition of new cell-wall material. This is shown by the fact that after bending is completed, the cells on the convex side lose their excess turgidity. The distended outer walls become flat, yet the tentacle remains bent. At this stage plasmolysis no longer causes unbending. Gardiner ('85) states that in *Drosera dichotoma* the cells on the concave side not only lose their turgidity after bending is finished, but become flaccid. These irreversible changes in the cell-wall apparently begin soon after bending starts, for when a bending tentacle is forcibly straightened, the distended outer cell-walls do not always return to their original condition, but are frequently crumpled or wrinkled. The rate of change in the cell-wall properties undoubtedly increases during the inflexion. In the same way the decrease in osmotic concentration which results from the increase in volume of the elongating cells is soon compensated for by the formation of new osmotically active material, as is shown by the equality of osmotic concentration on opposite sides of the tentacle a short time after it has become fully bent. This process too is probably initiated soon after inflexion begins, with the result that no marked difference in osmotic concentration is noticeable on opposite sides of tentacles which bend slowly. In the last analysis, therefore, the growth which causes the inflexion of *Drosera* tentacles is the activity of the protoplasm in manufacturing cell-wall substance and osmotically active material.

2. COMPARISON WITH GEOTROPIC MOVEMENTS

The movement of *Drosera* tentacles is seen to be brought about by the same mechanism found in geotropically reacting organs, where Kraus ('82, p. 87) and Noll ('88, p. 511) observed a decrease in the osmotic concentration of the cells on the convex side of roots and stems, which was particularly evident in case of rapid bending. The subject is well summed up by Jost ('13, p. 580) in the following paragraph, and his remarks apply to the bending of *Drosera* tentacles with equal felicity:

> In all cases that have been more carefully studied, the immediate cause of the bending is a difference of growth in length on opposite sides. The surface growth of the membranes here as elsewhere is preceded by stretching due to turgidity, and this is gradually made permanent by growth. If an organ be plasmolyzed at the beginning of the geotropic bending it again becomes straight, but later the curvature is permanent. The stretching is unequal in amount on the two opposite sides. This difference might consist in an increased osmotic pressure on the convex side and diminished osmotic pressure on the concave side, but this is by no means the case; the pressure on the concave side seems rather to remain unchanged, while that on the convex side diminishes during bending. This result is not so astonishing when we consider that the rate of growth does not depend directly on the amount of osmotic pressure, but that this latter frequently depends on the increase in cell-volume. The unequal stretching of the opposite sides due to turgidity must therefore be connected with an alteration in the elasticity of the cell-walls, the convex side becoming more extensible. Of course in unicellular organs (in sporangiophores of the Mucorineae, for example), the bending must depend solely on a change in the elasticity of the cell-wall.

3. ALTERATION OF CELL-WALL ELASTICITY

In the opinion of Noll ('95, p. 65) the change in the plasticity of the cell-wall is analogous to the gradual change that takes place in a strung bow, which after having been left strung a long time does not return completely to its original shape when unstrung. This plastic change does not involve any permanent diminution of elasticity, however, for the bow returns to its new shape after bending. The source of energy for this change in plasticity is found in the stored energy of elastic tension. The change from a condition of elastic tension to a plastic alteration of shape is compared by Noll ('95, pp. 79–81) to changes produced in rubber by vulcanization, during which process any elastic deformations that happen to be present are transformed in a greater or less degree to permanent alterations of shape. In bending plant organs he assumes that the protoplasm secretes one or more substances which act on the cell-wall as vulcanizing sulphur acts on crude rubber.

The correlation between the molecular structure and the physical properties of metals, which has been discovered in recent years by metallographists, offers a more satisfactory interpretation of the changes in the physical properties of the cell-wall. The alteration of the strength, ductility and elasticity of metals produced by mechanical treatment and by heat are based on changes in molecular structure, which consist in the rearrangement of the relative amounts of the phases that enter into the composition of the metal. Two phases are usually present, a crystalline phase and an amorphous phase that cements the crystals together. The strength and ductility of a metal are found to be increased and the elasticity diminished by an increase in the amount of the amorphous phase and a decrease in the amount of the crystalline phase. Conversely the elasticity would be increased and the strength and ductility diminished by an augmentation of the crystalline phase and a decrease in the amorphous phase. It is probable that changes in the elasticity of plant cell-walls are also produced by alterations in the molecular structure. The cell-wall is undoubtedly a mixture of phases in heterogeneous equilibrium. It seems plausible that changes in elasticity are effected by a readjustment between these phases. Possibly an amorphous and a crystalline phase are present, in which case an increase in the proportion of the former to the latter would decrease the elasticity and the reverse change would restore the original properties. Whatever changes in molecular structure actually occur, they must be controlled and regulated by the activity of the protoplasm.

4. AUTOTROPIC NATURE OF UNBENDING

(*a*) *Comparison of autotropic with hydrotropic stimulus*

When roots are exposed to a hydrotropic stimulus, greater evaporation takes place from the cells of the drier side and this tends to increase their osmotic concentration. The resulting inequality of osmotic concentration or changes which this induces on opposite sides of the root constitute the stimulus that released the hydrotropic reaction, which consists in bending toward the source of moisture by faster growth on the side with the higher osmotic concentration (Hooker, '15). It is characteristic of hydrotropic reactions that small differences in the relative moisture on opposite side of the exposed root, and consequently small differences in osmotic concentration are sufficient to produce changes that release a reaction. On the other hand the exposure must be prolonged, for the reaction does not commence until the roots have been subjected to a hydrotropic stimulus for at least six hours. Bending proceeds much more slowly than in geotropic reactions.

The autotropic unbending of *Drosera* tentacles as well as of geotropically bent roots and shoots resembles hydrotropic reactions in several respects. The unbending is produced by growth on that side of the organ that tends to have the higher osmotic concentration during bending. The reaction does not begin until some time after the bending, and it proceeds at a very much slower rate. During this process no difference of osmotic concentration was ever observed in opposite sides of the tentacle, which indicates that the formation of osmotically active material keeps pace with the increase in volume of the growing cells.

(*b*) *Internal changes that follow bending*

In a discussion of the autotropic unbending of tendrils, Fitting ('03, p. 612) expresses the opinion that the unbending may be a response to a new stimulus produced by "the inequality of conditions, of pressure-distribution, tissue-tension, etc., which are established in the cells on opposite sides of the originally straight organ as a result of an attempted or executed reaction."

The inequality of conditions that should constitute the autotropic stimulus may be found in the changes produced by the difference of osmotic concentration observed in bending roots and tentacles, since just such a difference induces an analogous reaction in hydrotropically stimulated roots. It has been emphasized elsewhere (Hooker, '16, p. 21) that the increase in the rate of growth which produces the unbending of *Drosera* tentacles proceeds in the same manner as that which causes bending, in both cases commencing near the base and extending apically. Moreover, the amount of growth that occurs during unbending is nearly the same in amount and is distributed in much the same manner as during bending, so that the unbent tentacle is straight and reaches approximately the same position it held before the reaction. This nice regulation is intelligible when we consider that the changes resulting from the decrease in osmotic concentration during bending are directly proportional to the increase in volume of the growing cells. It is not to be denied that other factors may coöperate in producing the autotropic reaction, but the striking similarity with hydrotropic reactions indicates that the effects of the difference in osmotic concentration during bending are most significant.

When an insect is caught and digested, the unbending of the tentacle is postponed a considerable time, occasionally several days. It would appear that the absorption of food material through the gland inhibits the reaction to the inequality of conditions produced by the bending. All the cells of the tentacle from base to apex are generally aggregated while food is being absorbed. According to Gardiner ('85) the state of aggregation is accompanied by a loss of water and he found that the injection of water into the tissue stopped aggregation at once and restored the cells to their normal condition. This probably accounts for the fact that the osmotic concentration in the cells of bent tentacles is higher than under any other circumstances. When absorption ceases, aggregation stops and the tentacles unbend in the normal manner. This is brought about by increased turgidity of the cells on the concave side. Without doubt the same factors found to determine bending are involved in the unbending, but the process is so slow that it resembles ordinary plant growth. It does not seem probable that this deferred reaction can be a direct response to changes produced by a difference of osmotic concentration which existed during bending, but is now completely effaced. In these cases unbending is probably a response to changes taking place as the result of a cessation of absorption and the end of the aggregated condition. Nevertheless the effects of the difference in osmotic concentration are conditioning factors of the unbending reaction, for an accelerated rate of growth on the adaxial side of the tentacle occurs only after previous bending.

IV. SUMMARY

The osmotic concentration in cells of *Drosera rotundifolia* tentacles was measured by plasmolysis in potassium nitrate and glucose solutions. Measurements were made on straight, bending, bent and unbending tentacles. The osmotic concentration in the cells on the abaxial side of the stalk, in the growing region, was found to diminish during bending; no change was observed on the adaxial side. The decrease in osmotic concentration is accounted for by the increase in volume of the cells, and is therefore considered an effect and not a cause of their elongation. There is no indication that changes in permeability occur.

The elongation is produced by a decrease in the elasticity of the cell-walls, and is later fixed by growth. The movement of tentacles is therefore brought about by the same mechanism found in geotropically reacting organs, where a decrease has been observed in the osmotic concentration in the cells whose growth causes bending.

Similarities between hydrotropic reactions and autotropic unbending of tentacles and of geotropically bent roots indicate that the growth on the concave side which brings about the unbending is a response to changes resulting from the difference in osmotic concentration present during bending. As in hydrotropic reactions, growth takes place on the side with the higher osmotic concentration.

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LIEBIG'S LAW OF THE MINIMUM IN RELATION TO GENERAL BIOLOGICAL PROBLEMS[1]

THE Law of the Minimum has never been accurately defined, although the idea that it involves is relatively simple. Professor B. E. Livingston says in a recent paper[2] that "this principle is still quite incomplete logically and its statement will assuredly become much more complex as our science advances." In order to get a clear understanding of the law so that it may be stated accurately, we will begin with a simple application to chemical reactions.

One molecule of KOH reacts with one molecule of HCl to form one molecule of KCl and one of H_2O. If only one molecule of KOH is present, only one molecule of KCl can be formed, no matter how many molecules of HCl are present; and likewise if only one molecule of HCl is present, only one molecule of KCl can be formed, no matter how many molecules of KOH are present. By considering the weights of the reacting substances, the situation is somewhat complicated: 56.1 grams of KOH react with 36.5 grams of HCl to form 74.6 grams of KCl and 18 grams of H_2O. In round numbers 3 parts by weight of KOH and two of HCl give 4 parts by weight of KCl and one of H_2O: 3/4 gr. of KOH and

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[1] Paper read before the Biological Club of Yale University, April 19, 1917.

[2] *Plant World*, 20: 1–15, 1917.

1/2 gr. of HCl are necessary to form a gram of KCl. Let us call these fractions, 3/4 and 1/2, the specific reactive weights of KOH and HCl in respect to the formation of a unit quantity of KCl. Suppose x amount of KOH and y of HCl are given. If x and y are divided by their respective specific reactive weights, we get $\frac{4}{3}x$ and $2y$. The smaller of these quantities is a direct measure of the weight of KCl that can be formed from x KOH and y HCl. If, for example, x and y are both equal to three grams, four grams of KCl can be obtained.

These facts can be generalized. If A, B and C are substances which react to form S and u A, v B and w C are necessary for the formation of a unit amount of S, then u, v and w may be called the specific reactive values of A, B and C, respectively. They may be weights, volumes, numbers of molecules or what not. In any particular case, where pA, qB and rC are reacting, the amount of S formed is the smallest of the fractions p/u, q/v, r/w. When the amounts of the reacting substances are divided by their specific reactive values, the smallest quantity so obtained is equal to the amount of the product formed.

This conclusion is directly applicable to the problem of fertilizers. It is known that most of the higher plants must obtain seven elements in combined form from the soil. They are S, P, N, K, Ca, Mg and Fe. If αS, βP, γN, δK, ϵCa, ζMg and ηFe are required for a unit amount of growth in some particular plant, say wheat, and if aS, bP, cN, dK, eCa, fMg and gFe are present in a particular soil in available form, the maximum amount of wheat that can be grown in that soil will be the smallest of the fractions a/α, b/β, c/γ, d/δ, e/ϵ, f/ζ, g/η. In this case α, β, γ, etc., may be called specific growth values for the plant under consideration. When the available amounts of the essential inorganic food constituents are divided by their respective growth values, the smallest quantity obtained gives the maximum amount of growth possible.

It was in this connection that Liebig[3] first formulated the Law of the Minimum which, as commonly stated,[4] says that "the yield of any crop always depends on that nutritive constituent which is present in minimum amount." The use of the term minimum is not strictly accurate, as can be seen from the example of KOH and HCl. If three grams of each are present, the amount of KOH determines the yield of KCl, although both HCl and KOH are present in equal amount. However, the above statement of the law is convenient because of its simplicity.

A much broader application of the Law of the Minimum was indicated by the work of F. F. Blackman, whose conclusions are summarized in his paper on "Optima and limiting factors."[5] Blackman called attention to the complexity of the process of carbon assimilation, the rate of which depends on at least six factors—

1. Temperature,
2. Light intensity,
3. Carbon-dioxide supply,
4. Water supply,

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[3] "Die Chemie in ihre Anwendung auf Agricultur und Physiologie," 7te Auflage, 2: 225, 1862.

[4] *Cf.* F. Czapek, "Biochemie der Pflanzen," 2: 841, 1905.

[5] *Annals of Botany,* 19: 281–295, 1905.

5. Chlorophyll,
6. Enzymes.

Where it is possible to vary one of these factors independently of the rest, its effect on the rate of assimilation can be measured, under suitable conditions, and a curve plotted. In this way a temperature-assimilation curve, a light-assimilation curve and a carbon-dioxide-assimilation curve can be constructed. The other factors are more difficult to control. The following curves were constructed by Blackman and Smith[6] from a study of the rate of assimilation in *Elodea.*

The light curve and the carbon-dioxide curve are straight lines. The rate of assimilation varies directly with the intensity of light and the supply of carbon dioxide. The temperature curve shows that the rate of assimilation is an exponential function of the temperature. In fact the process of assimilation obeys van't Hoff's law of reactions for temperatures under 30° C. Above this, the rate of assimilation

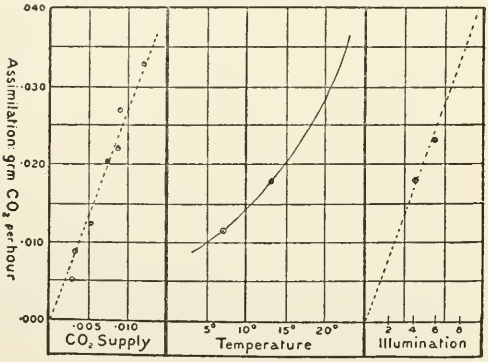

Fig. 1. Effect of external factors on assimilation in *Elodea.* (After Blackman and Smith.)

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[6] *Proc. R. Soc., B.,* 83: 389–412, 1910.

at first rises and then falls off, the process being complicated at high temperatures by a "time factor." The same effect has been observed at high light intensities, and with strong concentrations of carbon-dioxide which have a narcotic effect.

Disregarding these complications, we will confine our attention to the first parts of these curves. The ordinates of all three curves are the same, namely, rates of carbon assimilation, which can be measured in terms either of CO_2 absorbed or of sugar produced. The former happens to be the more convenient measure. At any given temperature, the rate of assimilation which is a function of that particular temperature can be determined directly by the curve and is equal to a certain distance measured off from the origin on the Y-axis. Similar distances are given for any definite supply of carbon dioxide and for any degree of illumination. In any actual environmental complex, where the temperature, light and carbon-dioxide supply are known, the rate of assimilation is equal to the shortest distance measured on the Y-axis. This is stated as a general principle by Blackman as follows: "When a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest' factor." The factor which gives the shortest distance on the Y-axis—that is, the "slowest" factor, he calls the limiting factor.

As a matter of fact the carbon assimilation of green plants is usually limited by the seasonal variation in temperature and the diurnal variation in light, the CO_2 content of the air being constant. Nothing has been said of the other factors that effect carbon assimilation—the water supply, chlorophyll and enzymes. These so-called "internal" factors, as well as the "external" factors, are governed by the Law of the Minimum. Of the internal factors, water and chlorophyll are present in excess in healthy green plants, the amount of assimilatory enzymes being the only probable limiting factor.

It is not necessary to adduce additional examples to show that the Law of the Minimum is a *universal* law, affecting not merely the concentration of reacting substances, but *all* factors that in any way influence a reaction or process. The law is applicable to physical, chemical and geological as well as biological problems.[7] An interesting instance of its application to a problem in physics is the determination of the magnitude of a thermionic current. This varies with changes in temperature, and also with changes in the voltage applied. The temperature formula gives one value, the voltage formula may give another; the lesser value determines the current flowing. The application of the Law of the Minimum has been worked out in many cases and has been of great use in the interpretation of complicated relations; but it has been recognized as a law and has been consciously applied by plant physiologists and physiological chemists only.[8] Without doubt it can be used to advantage in many problems

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[7] A timely application may be made which is worth bearing in mind. The efficiency of a nation at war is subject to the Law of the Minimum. Defeat, in the last analysis, may be attributed to the effect of some limiting factor.

[8] *Cf.* the work of L. B. Mendel, T. B. Osborne and their pupils.

of the physiology, morphology and ecology of both plants and animals.

The Law of the Minimum must be taken into account in all experimental work, for which it serves both as a precaution and a guide.[9] When investigating the effect of an external factor such as temperature, light, etc., on any given process, it is necessary to keep all other variable factors constant, and then to determine the effect of changes in the factor under consideration. What results might be obtained when this method is used in studying carbon assimilation? Suppose the CO_2 supply and the light are kept constant, while the temperature is varied. If the CO_2 supply is such that it becomes a limiting factor when the temperature rises above 10° C. then the rate of assimilation will rise with the temperature up to this point, but will remain constant at all higher temperatures, until the destructive effect of the high temperature is manifested and the curve again falls off. Above 10° C. variations in the temperature have no apparent effect under these experimental conditions. But if the CO_2 supply is increased so as to permit more rapid assimilation, then the temperature curve can be extended. Negative results from such an experimental method are therefore without significance. It is not enough that the experiment be conducted under constant conditions; the constant factors must not interfere in any way with the carrying out of the process; that is, they must not be limiting factors. On the other hand, it is a simple matter to determine by the shape of the curve whether any other factor than the one under investigation is

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[9] *Cf.* B. E. Livingston, *loc. cit.*

a limiting factor. Such is always the case when a break occurs in the curve; usually the curve rises at first and later runs parallel with X-axis. Such curves were obtained by Miss Matthaei[10] in studying the carbon assimilation of cherry laurel at varying temperatures with unit light intensity. The problem is much more complicated, however, when variation of one factor is accompanied by changes in one or more other factors. This complication arises in plotting the temperature curve for enzyme activity. The curve rises at first according to van't Hoff's law of reactions, but eventually a maximum value is reached and the curve falls off. At some point near the end of the ascending portion of the curve a break occurs: for all temperatures below this point, temperature is the limiting factor and determines the activity of the enzyme; for all temperatures above this point, not temperature, but the amount of enzyme is the limiting factor. The higher temperatures cause a permanent inactivation or decomposition of the enzyme so that its activity is conditioned only secondarily by the temperature. There is also a time factor involved here; the longer the tem-

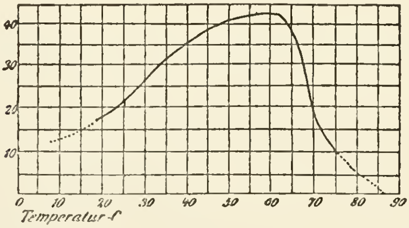

Fig. 2. Effect of temperature on the activity of malt diastase. (After Kjeldahl.)

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[10] *Phil. Trans.*, B, 196: 47–105, 1904.

perature acts, the more the enzyme is decomposed, within certain limits. The study of the action of salt solutions on permeability, growth, etc., involve even greater complications produced by the interrelation of conditioning factors.

In order to get an accurate statement of the Law of Minimum, it is necessary to get away from the custom of discussing causes, however difficult this may be.[11] The idea of causation invariably indicates *incomplete analysis.* A biological phenomenon is dependent not on a single variable, but on a complex or constellation of factors, as we have seen in the case of carbon assimilation. It should be discussed therefore in terms of all the conditioning factors, not in terms of that one which temporarily happens to be a limiting factor. The term "function" is valuable in this connection. The amount of carbon assimilation is a function of the temperature; it is another function of the illumination, etc. With this idea of function in mind, the Law of the Minimum may be stated in the following form. *When a quantity is dependent on a number of variable factors and must be a function of one of them, the quantity is that function which gives the minimum value.* Expressed in plain English this means that a chain is no stronger than its weakest link. The Law of the Minimum is only too obvious. Its application is often so self-evident that it is made as a matter of course.

But the most interesting thing about the law is not how it works, but when it does not work. There is a fundamental discrepancy between the Law of the Minimum and

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[11] *Cf.* B. E. Livingston, *loc. cit.*

Galton's Law of averages. In the current text-books on genetics and plant physiology[12] the following ingenious explanation of Galton's Law is given. Assume that the size of a bean is determined by only five variables, each of which must occur in one of two categories; in one case the size of the bean will be increased by one unit of size, in the other it will be decreased by the same amount. Considering all the possible permutations of these five variables, we get the following arrangement:

I	II	III	IV	V	Sum	I	II	III	IV	V	Sum
+	+	+	+	+	+ 5	+	+	−	−	−	− 1
+	+	+	+	−	+ 3	+	−	+	−	−	− 1
+	+	+	−	+	+ 3	+	−	−	+	−	− 1
+	+	−	+	+	+ 3	+	−	−	−	+	− 1
+	−	+	+	+	+ 3	−	+	+	−	−	− 1
−	+	+	+	+	+ 3	−	+	−	+	−	− 1
+	+	+	−	−	+ 1	−	+	−	−	+	− 1
+	+	−	+	−	+ 1	−	−	+	+	−	− 1
+	+	−	−	+	+ 1	−	−	+	−	+	− 1
+	−	+	+	−	+ 1	−	−	−	+	+	− 1
+	−	+	−	+	+ 1	+	−	−	−	−	− 3
+	−	−	+	+	+ 1	−	+	−	−	−	− 3
−	+	+	+	−	+ 1	−	−	+	−	−	− 3
−	+	+	−	+	+ 1	−	−	−	+	−	− 3
−	+	−	+	+	+ 1	−	−	−	−	+	− 3
−	−	+	+	+	+ 1	−	−	−	−	−	− 5

The beans will be of six sizes, + 5, + 3, + 1, — 1, — 3, — 5, and out of a very large number (n), $n/32$ will be + 5, $5n/32$ will be + 3, $10n/32$ will be + 1, $10n/32$ will be — 1, $5n/32$ will be — 3, and $n/32$ will be — 5. The six sizes are in the ratio 1 : 5 : 10 : 10 : 5 : 1. If we plot the sizes of the various classes of beans against the fre-

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[12] E. Baur, "Einführung in die experimentelle Vererbungslehre," 2^{te} Auflage, 1914. L. Jost, "Vorlesungen über Pflanzenphysiologie," 3^{te} Auflage, 1913.

quency of their occurrence, we get an approximation to the familiar curve of normal error. For the sake of simplicity, the number of variable factors was made five and the number of categories in which each might occur was limited to two. If the variables and the categories are made sufficiently numerous, the curve of normal error can be approximated within any desired degree of exactitude. It is unnecessary to point out the empirical fact that when the sizes, weights, etc., of organisms or their parts are divided into classes and the classes are plotted against the number of individuals in each class, the resulting curve approaches the normal curve of error, if a sufficiently large number of individuals are used. Exceptional instances of curves with more than one maximum, or only parts of curves, are easily accounted for and for convenience will be left out of consideration. Since the empirical data bear out the conclusions arrived at by the above procedure, the explanation may be considered valid.

However, the explanation involves the addition of the values of the various factors, which is in reality averaging them, since their value is measured in terms of net gain or loss. Although this process of averaging the various factors involved is borne out by comparing the results with empirical data, it is done, nevertheless, in contradiction to the Law of the Minimum. According to this law $n/32$ should be $+1$ and $31n/32$ should be -1, because *all* the factors are $+1$ in only one permutation, and -1 occurs in all the others and would be a limiting factor. The curve that would result if the Law of Minimum held would start from one at the upper end of the scale of sizes, weights or what not and would rise with great rapidity toward the lower end, where it would reach its maximum. This kind of curve is not the rule.

Every case where Galton's Law holds is a case where the Law of the Minimum does not hold. The resultant size or weight of an organism, which is a measure of its growth, shows that this is not determined by the limiting factor of its environment, but represents some sort of average between all the factors involved. In other words, a process of compensation or integration has taken place, the factors giving the largest values being utilized to some extent at least to alleviate the influence of the limiting factor—a utilization of surplus to cover deficit. Individual processes obey the Law of the Minimum; but the grand total is governed by what may be termed a principle of integration.

The means by which this integration is brought about are not hard to find. At least four important processes are at work in living organisms to this effect, namely—

1. Responses to stimuli,
2. Development,
3. Evolution,
4. Biotic succession.

A few examples will illustrate the way in which integration is effected by each of these. A seedling placed upside down is in the wrong position with respect to the center of the earth, its source of light, and moisture. Position with respect to gravity may be considered to be the limiting factor here; but the germinating rootlet is positively geotropic and bends toward the earth; the young shoot is negatively geotropic and bends away from the earth. In this way these responses to the geotropic stimulus counteract the influence of the limiting factor. Roots behave similarly in response to moisture content of the soil; stems and leaves in response to light.

In plants it is hard to draw a line between simple responses to stimuli and morphogenic responses which involve permanent changes of form and structure. The difference between sun leaves and shade leaves is a familiar example of a morphogenic response. The shape, size and structure of the leaf here counteract the limiting factor light. Again, plants which are shaded by others so that they receive insufficient light usually become etiolated, that is, the stems and leaf-petioles in many cases increase in length until some portion of the plant is brought to a position where it receives adequate illumination. Here again the limiting factor is light, and the result of etiolation is to overcome its effect.

Evolution is likewise an integrating process. Its results are not accomplished in the individual, but in the race, and are called adaptations. Adaptations are means of avoiding the effects of limiting factors.

Another means of integration is seen in biotic succession. Here the integration extends over a considerable period of time and its benefits do not accrue to the individual or the race, but to succeeding generations and different species. The integrative effect in succession may be largely produced by the death and decay of an association resulting in the accumulation of humus. Thus both xerophytic and hydrophytic plants prepare the way for a mesophytic flora. The limiting factor here is water, which is too scarce in the one case and too abundant in the other. By the accumulation of humus, the properties of the soil are so altered that a more favorable water supply is offered to later generations, and in this way the effect of the limiting factor is counteracted.

All these processes which bring about integration between the relations of living organisms to the factors of the environment that determine their growth and activity are evidently based on a single fundamental principle, to which Professor L. J. Henderson has applied the appropriate misnomer teleology.[13] Wherever integration is found in the factors influencing the individual, the race or the association, it is possible to define a closed system. Such a system includes all the factors which can be integrated, that is, all the possible limiting factors for any given process. These systems may focus about a single cell, an organ, an organism or a group of organisms. They are inclusive. The life of a plant, for example, is determined by a complex of factors between which integration is found to occur. At the same time the functional activity of the root system is determined by another complex of integrated factors, and the functional activity of the leaves by still a different set. Since the life of the root system is dependent on the products of the activity of the leaves, these represent members of the complex which conditions the growth and function of the root system. Such internal factors as enter into the complex of factors centering about the life of a portion of an organism are likewise subject to integration.

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[13] The order of nature, 1917.

In this way the condition of the root system affects the leaves and the condition of the leaves affects the root system. Correlations are therefore manifestations of the principle of integration.

The organic world can be analyzed into systems of various orders, those of a higher order being inclusive of, or divisible into, systems of a lower order. These systems are invariably overcoming the effects of limiting factors. The limiting factor is the stimulus to which the system reacts. The reaction places the organism in a more efficient relation with its environment, but no matter how many reactions are carried out, there is always some limiting factor left, and so the organism is kept constantly busy. The end result is to approximate more or less closely some kind of average of all the resources at its disposal.

I think it might be possible to go even further and get a quantitative measure of the degree to which the process of integration has been carried, by considering the number of factors integrated and how close an approximation to the normal curve of error had been obtained. Such a quantitative measure would likewise be an index of the stage of evolution that an organism had reached.[14] At the very least, the Law of the Minimum or the principle of limiting factors offers a sound basis from which such intangible processes as behavior, correlations, evolution and ecological succession[15]

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[14] Our criterion of ''degeneracy'' in a living organism is based essentially on a decrease in the number or range of factors between which integration is possible.

[15] For an application of the principles enunciated in this paper to plant ecology see G. E. Nichols, *Plant World,* Sept., 1917.

can be viewed with a clear perspective, if it is not the only scientifically accurate point of view from which to attack such problems.

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THE INTERPRETATION AND APPLICATION OF CERTAIN TERMS AND CONCEPTS IN THE ECOLOGICAL CLASSIFICATION OF PLANT COMMUNITIES[1]

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During the past seven years much of the writer's study has been along the line of local physiographic plant ecology, and the need has constantly been felt of some logical and adequate, yet at the same time simple and to a certain extent elastic scheme which could be readily adapted to the ecological classification of the vegetation of any region. The groundwork for such a classification is afforded by the principle of succession, the fundamental bearing of which on the relationship and evolution of plant communities has been indisputably established by the work of Cowles (7, 8, 9, 11), Whitford (24), Clements (3, 4), Moss (16, 17) and others. The principal object of the present paper is to outline a plan of classification which it is thought will recommend itself because of its lack of complexity and because of the readiness with which it can be applied, and in this connection to express the writer's views regarding the interpretation and application of certain ecological terms and concepts. Incidentally, several new terms, or rather combinations of terms already in use, are introduced, which it is thought will prove serviceable by very reason of their simplicity of interpretation and application. The scheme of classification itself is by no means wholly new or original. It is the outgrowth, and perhaps not a very radical modification, of the classification originally devised by Cowles (8).

THE UNIT OF VEGETATION WITH REFERENCE TO HABITAT

The association. From the standpoint of physiographic ecology (synecology) the association, in the last analysis, repre-

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[1] Contribution from the Osborn Botanical Laboratory.

sents the fundamental unit of vegetation. The association may be defined as: any group or community of plants, taken in its entirety, which occupies a common *habitat* (see Cowles 6, p. 939). In terms of dynamic plant geography it may be further defined as: any stage in a given successional series.

Uniformity of habitat, then, affords the criterion of the association. The word habitat commonly has been applied somewhat loosely, but from an ecological standpoint it is desirable that it should be delimited as precisely as possible. As conceived by the writer, the habitat may be defined as: any unit area in which the combined influence of the various external factors which determine the ecological aspect of the vegetation is such as to produce an essentially uniform *environment*. It is the environment which determines the ecological aspect of a plant community. The nature of the environment, in turn, is determined by a complex of physical and chemical factors which, in a general way, may be classified as (1) climatic, (2) edaphic, and (3) biotic. (1) The *climatic factors* comprise all those atmospheric conditions through whose widespread uniformity the character of the regional climate is determined. These include: (a) atmospheric humidity, (b) precipitation, (c) temperature, and (d) light. (2) The *edaphic factors* include all conditions which are attributable, directly or indirectly, to soil or topographic agencies. Their influences may be exerted either through the medium of the ground or through that of the atmosphere. The ground influences are attributable to: (a) soil factors (the physico-chemical nature of the soil, and the ground-water relations); (b) slope factors (the inclination of the ground's surface, i.e., the degree to which it departs from the level); and (c) dynamic physiographic agencies, where these are operative (as seen in the phenomena of erosion and deposition). The edaphic atmospheric influences are seen in the local modification of the climate associated with differences in exposure, which in turn are attributable to variations in topography: thus, a north-facing slope commonly possesses a somewhat different "local climate" from a south-facing slope; similarly, the "local climate" of a ravine differs from that of an exposed hillside; etc. While such local atmospheric dissimilarities represent merely modifications of the climate of the region, a distinction may well be drawn between these *local climatic factors*, which in the main are attributable to edaphic influences, and the *regional climatic factors.* For the sake of convenience, any area in which the combined influence of the various edaphic factors is essentially uniform throughout may be termed an *edaphic unit area.* (3) The *biotic factors* include all conditions which, directly or indirectly, are attributable to plant or animal agencies. Their influence is seen (a) in the ameliorating effect of humus on the water relations, etc. of the soil, and (b) in the effect of shade, as it inhibits the development of intolerant plants, modifies the evaporating power of the air, etc. (in this connection, see Cowles, 11).

In view of the foregoing remarks, the habitat may be further defined as any unit area in which the combined influence of climatic, edaphic, and biotic factors is essentially uniform throughout. Giving the term this precise interpretation, it becomes evident at once that many an area, such as a pond, a ravine, or a salt marsh, which only too frequently is characterized as a "habitat," should be regarded rather as a series of habitats. The various factors which, as above indicated, are responsible for the local variations in the nature of the environment and for the consequent delimitation of distinct habitats, in other words, the edaphic and the biotic factors, taken collectively, may be termed the *habitat factors,* in contrast to the *regional climatic factors,* the influence of which is widespread and essentially uniform throughout the region.

Although the nature of the habitat affords the actual criterion, plant associations, as a rule are most readily distinguished in terms of their vegetation; thus, in the case of a pond: the *Nymphaea* association, the *Scirpus-Typha* association, etc.

Floristic subdivisions of the association. In its ecological aspect an association is essentially homogeneous throughout. Floristically, however, it is commonly subject to more or less variation. Where the variation concerns the dominant species (*facies*) it is often possible to distinguish different *consociations,* i.e., subdivisions of the association "characterized by a single dominant" (Clements 4, p. 129). Where the variation concerns species of secondary importance it is similarly possible to distinguish different *societies*. Thus, a deciduous forest may be essentially uniform in its structure throughout, so far as the dominant species are concerned; or certain species may dominate locally, giving rise to more or less distinct consociations. Similarly, the herbaceous or shrubby vegetation in such a forest may, and usually does, vary locally, giving rise to more or less distinct societies. In the case of both the consociation and the society, the floristic composition of the vegetation affords the sole criterion, although there may also be slight but relatively inconsequential variations in the habitat. The consociation and the society, then, represent floristic and not ecological units.

The association-type. The nature of any given habitat is determined by a number of more or less definite, though not always tangible factors. Wherever, within a given climatic region, a given set of habitat factors is duplicated, the same type of habitat is the result. To express it algebraically: if it is assumed that the nature of a given habitat, H_1, is determined by the combined influence of the factors, A_1, B_1, C_1, and D_1, and if this fact be expressed by the equation $H_1 = f(A_1, B_1, C_1, D_1)$, then wherever the combination of factors A_1, B_1, C_1, D_1 recurs, the value of H will be the same. Of course, the exact application in practice of this criterion of the habitat would necessitate a vastly more accurate knowledge of the factors which determine its nature than is actually available, so that as a matter of fact the parallels must be based to a large extent on superficial observations. But, in a general way, numerous parallel series of habitats may be distinguished in every region. In comparing two neighboring ponds, for example, the habitat occupied by the *Nymphaea* association in the one may duplicate the habitat occupied by the *Nymphaea* association in the other; or the habitat of the *Scirpus* association in the one may duplicate the habitat of the *Typha* association in the other; etc. Similarly, the individual habitats occupied in different Connecticut salt marshes by the *Spartina glabra* association are essentially similar throughout; and so on. Habitats which thus are equivalent to one another may be referred to a common *habitat-type.*

In any given region, owing largely to the existence of these parallel series of habitats, there have been developed correspondingly numerous parallel series of associations. Different individual associations which are correlated with the same type of habitat and which as a result agree with one another in their ecological aspect, i.e., which are ecologically equivalent, even though they may differ in their floristic composition, may be considered as belonging to a common association-type. Thus, the *Nymphaea* association in one pond is obviously the ecological homologue of the *Nymphaea* association in a neighboring pond, while the *Scirpus* association in the one may similarly correspond to the *Typha* association in the other. In the same way, an oak forest association in one locality may represent the equivalent, from an ecological standpoint, of a hickory forest association in another locality; and so on. It will be seen that, unlike the association, the association-type is a more or less abstract conception. It may be simply defined as: a type of plant association which is correlated with a given type of habitat. The term association-type has already been used by Schröter (20) in a sense analogous to that here proposed.

The exact delimitation of association-types of course presents many difficulties, but in a general way it is possible to group the innumerable individual associations of a region into a comparatively small number of association-types. To a limited degree it is possible to refer to these association-types in terms of the habitat (or of the edaphic unit area) thus: rock face association-type,—middle beach association-type. But such a method of nomenclature, while desirable in theory, has its limitations in practice, owing in part to the difficulty of finding expressions which even in a general way are descriptive of the habitats concerned (especially when biotic factors are taken into account) in part to the deficiency of our knowledge concerning the habitat factors. It is therefore usually necessary, just as in naming the associations, to resort to the vegetation for titles; thus:

submersed aquatics association-type, water lily association-type, oak-hickory association-type, etc.

It should perhaps be added that the conception of the habitat-type and of the association-type need not necessarily be confined to any given climatic region. This is exemplified particularly well by the association-types of salt marshes, which in temperate regions are essentially uniform in their ecological aspect under various climatic conditions. In general it can be stated, from the standpoint of dynamic plant geography, that in comparing the association-types in regions having different types of climate, the highest degree of parallelism is exhibited between the more primitive (i.e., the more xerophytic or more hydrophytic) association-types; and that, conversely, the least parallelism is exhibited between the more ultimate (i.e., the more mesophytic) association-types. In comparing association-types in regions having similar types of climate, on the other hand, the parallelism also extends to these more ultimate association-types.

THE SUCCESSIONAL RELATIONS OF PLANT ASSOCIATIONS

Geologic versus contemporaneous successions. Cowles (11) has defined three types of succession: regional successions, which are attributable to widespread climatic changes; topographic successions, which are associated with changes in topography resulting from erosion and deposition; and biotic successions, which are due to plant and animal agencies. Regional successions, on the one hand, extend over long periods of time; biotic successions, on the other, take place with comparative rapidity. According to Cowles, "If, in their operation, regional agencies are matters of eons, and topographic agencies matters of centuries, biotic agencies may be expressed in terms of decades. . . . So rapid is the action of the biotic factors that not only the climate, but even the topography may be regarded as static over large areas for a considerable length of time" (11, p. 172). Now it is of course true that along actively eroding and depositing streams and coasts topographic agencies may operate with sufficient rapidity as to institute marked changes within a comparatively short period of time: along streams such rapid changes are commonly associated with the erosion of ravines in uncompacted rock and the building up and destruction of flood plains; along the coast they are associated with the erosion of bluffs in uncompacted rock, and the development or destruction of coastal swamps (e.g., salt marshes), beaches and sand dunes. In this connection, see especially Cowles (7, 8). But, in the large, rapid changes such as these are the exception rather than the rule. Over much the greater part of the earth's surface the changes due to topographic agencies are consummated so slowly that their influence on the vegetation, like that of climate, becomes apparent only when geologic periods of time are taken into account. It is indeed open to question whether in the main the successions due to topographic agencies do actually take place more rapidly than those due to changes in climate. In the glaciated regions of the eastern United States, for example, the land surface for the most part has undergone little alteration since the recession of the continental ice sheet; yet during this period it is generally agreed that there have ensued .profound climatic changes, which have been accompanied by correspondingly great transformations in the character of the vegetation (in this connection, see Nichols 18, pp. 237, 245, 249).

If account is taken of the three types of succession defined by Cowles, then it is evident at once that vegetation can never attain a condition of equilibrium. As Cowles (8, p. 81) aptly phrases it, "we have a variable approaching a variable rather than a constant." While conceding, however, the far-reaching importance of the climatic and topographic changes which have ensued and which will continue to ensue in geologic time, it seems to the writer that, in attempting to solve the relatively contemporaneous problems of dynamic plant geography, much more is to be gained than lost by postulating the climatic conditions of the present, and by ignoring topographic changes, except in so far as these manifestly proceed with sufficient rapidity as to become effective within the present climatic era.

then, the climate to be a regional constant, it follows that the ecological aspect of an association is the direct combined function of the habitat factors. Carrying the process a step further, it seems obvious that, with certain exceptions like those noted in a preceding paragraph, all of the habitat factors are relatively constant except those which are due to plant and animal agencies. It would follow, therefore, that the ecological aspect of an association is the direct combined function of these biotic factors alone. Now, with these deductions in mind, it might perhaps be expected to follow that through the gradual amelioration of the habitat, brought about by the progressive reaction of the biotic factors, the culminating member of every successional series throughout a given climatic region would be the same, the only difference between them being in point of the time when this ultimate condition is reached. But in this connection must be taken into account Liebig's *Law of the Minimum*, which states in effect that: if any reaction or process is the combined function of several factors (or variables), the extent to which the reaction or process may be carried is limited by the effect of that factor which possesses a minimum value, or which is present in relatively minimal amount. The application of this law to ecological problems has already been suggested by Adams (1) and Hooker (15); and herein lies the explanation of what the writer proposes to term the *edaphic climax association.*

The edaphic climax association. Disregarding for the moment the influence of biotic factors, it may be stated, on the basis of Liebig's Law, that in every habitat the degree of mesophytism which it is possible for the vegetation to attain is conditioned by the limiting edaphic factor. Where all the necessary edaphic factors are sufficiently represented, the highest degree of mesophytism permitted by the climate is capable of attainment. But the limiting influence of any one factor may prevent succession from proceeding beyond a certain stage.

The exact limiting factors of course vary with the habitat and are not easy of analysis, except in a very superficial way. A few illustrations, however, may be suggestive. In the case of a precipitous cliff, in a very general sense, the steepness of the slope may be regarded as the limiting factor. Along a bleak, exposed seacoast, wind, or perhaps better the absence of quiet air, may similarly represent the limiting factor. Most commonly, unavailability of sufficient water, to whatever causes this may be due, is the direct limiting factor.

In a measure, of course, the favorable influence of certain habitat factors, may compensate (or integrate) the limiting effect exerted by others. On precipitous slopes in rock ravines, for example, the factor "water runs off quickly" may be offset to such an extent by the factor "atmospheric humidity is great" that a mesophytic bryophyte flora is able to establish itself; but the factor "no foothold for roots," which may be the chief obstacle to the development of a forest cover here, cannot be wholly compensated by any other factor. Most important of all habitat factors in their compensating influence are those due to plant and animal agencies, particularly humus accumulation and shade as they affect the water relations of the habitat (see Cowles, 11). The significance of these factors in relation to succession is universally recognized, and in some cases their compensating influence is sufficient to completely offset the effect of the limiting factor: in other words, through the cumulative effect of biotic factors the habitat may become so modified that it becomes possible for the climax association-type of the region to develop. But elsewhere, in varying degree, the influence of the limiting factor is too pronounced to be completely overcome, and succession becomes permanently arrested at a stage less mesophytic than the regional climax. In the case of a swamp which has originated through the filling in of a lake by vegetable débris, for example, it is quite conceivable that, as a result of the gradual upbuilding of the substratum through the accumulation of humus, the habitat might eventually come to approximate that of uplands. But here again a limiting factor, which might be designated "decomposition of humus when exposed to air," ordinarily prevents the upbuilding process from proceeding beyond a certain point. It should be added, although it is perhaps quite obvious, that the effect of certain edaphic limiting factors is in turn modified by climatic factors. In a *Sphagnum* bog, for example, the *Sphagnum* tends to grow upward above the original water level, and in cool humid regions like coastal New Brunswick and Nova Scotia (see Ganong, 12) raised bogs may thus be developed; but in less humid regions the evaporating power of the air represents a limiting factor which, in varying degree, inhibits this upward growth of the moss.

The fact seems clear, then, as has already been suggested, that the climax of a successional series in any edaphic unit area is controlled largely by the influence of some limiting factor, and it therefore follows that the nature of the climax association may vary with the nature of the soil or of the topography. The term edaphic climax association may be defined as: the most mesophytic association which is capable of development in any given edaphic unit area through the progressive reaction of the various habitat factors. In a favorable situation, the habitat climax association coincides with the regional climax association-type.

The term edaphic climax association may be used either (1) in point of time, with reference to a specific successional series, i.e., with reference to the series of associations which follow one another in a given edaphic unit area; or, (2) in point of spatial relations, with reference to the group of associations which comprise an *association-complex* (see the following section), where these are genetically related. Used in the latter sense, it suggests the successional relationship which exists between the various associations of the complex. One can refer to such edaphic climax associations as these in terms of the physiographic unit area concerned: thus, trap cliff climax, rock ravine climax, bog climax, salt marsh climax.

One of the most forcible illustrations of the edaphic climax concept with which the writer is familiar is afforded by the New Jersey pine-barrens (see Taylor, 23; Harshberger, 14). This well-known phytogeographic area is situated in the midst of a region whose climate is capable of supporting a highly mesophytic forest. The portion of the coastal plain which it occupies has been uninterruptedly out of water and presumably covered with vegetation since upper Miocene times; yet in spite of this fact, today it is still occupied by a series of associations which, while they represent "an old and climax condition, ancestrally infinitely more ancient than anything in the surrounding area" (23, p. 242), nevertheless, with reference to the climax association-type of the region, must be classed as primitive. It is significant that this particular series of edaphic climax associations has apparently maintained itself in spite of changes in climate A stronger argument in favor of the potency of edaphic factors in limiting succession could hardly be conceived.

A similar noteworthy example of a widespread edaphic climax is seen in the natural prairie of western Long Island (see Harper, 13). Although, like the pine-barrens, situated in a region of deciduous forests, this area, some 50 square miles in extent, at least during the present climatic era apparently has never become forested, and there is no reason to believe that under the present climatic conditions, even if left undisturbed, it would undergo any appreciable changes in the future.

The association complex. Sometimes the nature of the habitat is essentially uniform throughout a given area, but more often, within an area which from a physiographic or some other standpoint it is desirable to treat as a unit, several different habitats are represented. Thus, for example, in the case of a pond, very largely as the result of differences in the depth of the water, there are numerous distinct types of habitat. Similarly, a salt marsh, a flood plain, a ravine, a rock hill, a sand plain, or a burned area may include a series of habitats which it is desirable to treat collectively. Any such series of habitats may be designated collectively as a *habitat-complex.* The term may be defined as: a group or series of habitats which occupy a unit area and are alike with reference to one or more habitat factors.

The conception of the habitat-complex, like that of the habitat-type is capable of algebraic expression. In the case of a pond, for example, let it be roughly assumed that P = pond, an area which it is desired to treat as a unit. Let A = the habitat factor "ground permanently covered by water;" and, for the sake of simplicity, let B = the habitat factor "depth of water." Then, according as B varies, $P = A(B)_1 + A(B)_2 + A(B)_3$, etc. In other words, all the habitats of the area P are alike with reference to the habitat factor A, and the series of habitats thus embraced may therefore be regarded as constituting a habitat-complex with reference to this factor. As another illustration, let it be assumed that B = an area which has been burned over; let F = the factor "fire;" and let H = the factor "humus destruction." Then, according as H varies, $B = F(H)_1 + F H_2 + F(H)_3$, etc. The area B may thus be regarded as a habitat-complex with reference to the habitat factor F.

Intimately associated with the habitat-complex is the association-complex. The relation between the two is analogous to that between the habitat-type and the association-type. In a pond, for example, correlated with the various individual habitats which comprise the habitat-complex, is a corresponding series of associations: the association of submersed aquatics, the *Nymphaea* association, the *Scirpus-Typha* association, etc. Similarly, in a salt marsh, there may be as many different associations as there are habitats. And just as the habitats in such unit areas, taken collectively, may be referred to as a habitat-complex, so the group of associations which occupies the habitat-complex may be designated as an association-complex. An association-complex may therefore be defined as: a group or series of associations which occupies, and forms a unit with respect to, a habitat-complex. The various ways in which the term association-complex can be applied need hardly be suggested. The associations of any area, taken collectively, may be so designated. The concept finds its most significant application, however, in relation to the *edaphic formation* which will be discussed in the following section.

The association-complex may be referred to in terms of the habitat-complex concerned; thus: pond association-complex (or simply pond complex), salt marsh association-complex, flood plain association-complex, burn association-complex, etc.

The classification of associations. In classifying plant associations, they should first of all be grouped with reference to the developmental relations of the habitats concerned; in other words, with reference to the successional relations of the associations themselves The further classification of the association-complexes thus defined is discussed in subsequent paragraphs.

(*To be continued.*)

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THE INTERPRETATION AND APPLICATION OF CERTAIN TERMS AND CONCEPTS IN THE ECOLOGICAL CLASSIFICATION OF PLANT COMMUNITIES. II

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THE UNIT OF VEGETATION WITH REFERENCE TO PHYSIOGRAPHY

The edaphic formation. As has been stated earlier, from an ecological point of view the fundamental unit of vegetation is the association, the ecological aspect of which is determined by the habitat. Now in any given climatic region the habitats are not distributed indiscriminately. They are grouped, as has just been suggested, into more or less definite complexes, the boundaries of which are determined primarily by the physiographic features of the region. In brief, the various habitat complexes are associated with specific physiographic unit areas. From the standpoint of the physiography of the region as a whole, these habitat-complexes determined by physiography represent edaphic divisions of a higher order than the habitat; and likewise, from the standpoint of the physiographic ecology of the region concerned, the association-complexes which occupy these physiographic divisions represent vegetational divisions of a higher order than the association. Just as a ravine, a salt marsh, a rock hill, or a sand-plain may be regarded in its entirety as a physiographic entity, so its vegetation, taken in its entirety, is to be regarded as an entity from the standpoint of physiographic ecology. In other words, just as the association can be regarded as a unit with reference to a specific physiographic unit area, so the association-complex, where it is determined by physiography, can be regarded as a unit with reference to the physiography of the region This physiographic unit of vegetation may be designated the edaphic formation. The edaphic formation may be defined as: an association-complex which is related to a specific physiographic unit area.

The developmental concept of the edaphic formation. The so-called developmental concept of the formation was first suggested by Moss who, in his account of the geographical distribution of the vegetation of Somerset (16, p. 12; *fide* Clements, 4, p. 118), states that: "The series of plant associations which begins its history as an open or unstable association, passes through intermediate stages, and eventually becomes a closed or stable formation, is in this paper termed a plant formation."[1] In a later paper (17, p. 36) he defines the [edaphic] formation as comprising "the progressive associations which culminate in one or more stable or chief associations [= edaphic climax associations], and the retrogressive associations which result from the decay of the chief associations, so long as these changes occur on the same habitat." This concept of the formation has been adopted by the Committee for the Survey and Study of British Vegetation (see 21, p. IX), and the edaphic formation is so interpreted by the writer, except that he would substitute "physiographic unit area" for "habitat" in the definition just quoted.

By some ecologists the edaphic climax association alone is treated as a formation. In the opinion of the writer, however, not the edaphic climax association, but rather the entire association-complex should be regarded as constituting the physiographic unit of vegetation: the edaphic formation. The edaphic climax association represents merely the culminating phase of a specific successional series: the most mesophytic type of vegetation capable of attainment in a specific physiographic unit area. It is the indicator, so to speak, of the degree of mesophytism which is attainable within the edaphic formation. As Moss expresses it (16, 17), it is the "chief" association of a successional series. It should be stated once more that the edaphic climax association of an edaphic formation may or may not coincide with the regional climax association-type.

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[1] The term formation is used by Moss in the sense that the term edaphic formation is used by the writer.

Primary and secondary edaphic formations. The term *secondary* is here used with reference to edaphic formations in which the vegetation has been modified by factors other than those which are attributable to biotic (not including human) or physiographic agencies. Formations whose vegetation has not been so modified are regarded as primary. Secondary edaphic formations commonly arise through the partial or complete destruction of the original vegetation by fire, lumbering operations, or cultivation.

The edaphic formation-type. In any climatic region, owing largely to the existence of numerous parallel series of physiographic unit areas, there have been developed correspondingly numerous parallel series of edaphic formations. Different individual formations which are correlated with the same type of physiographic unit area may be referred to a common edaphic formation-type; thus: ravine formation-type, rock hill formation. type, sand plain formation-type, etc. Like the association-type, the edaphic formation-type is an abstract conception. It may be defined as a type of edaphic formation correlated with a given type of physiography. As in the case of the association-type, the conception of the edaphic formation-type may be extended beyond the boundaries of a given climatic region. Thus, the ravine, or the flood-plain, or the salt marsh formation-type of one region may resemble that of another; etc. Edaphic formation-types are referred to in terms of the physiographic unit area concerned, as has been done above.

The classification of edaphic formations. Although worked out from a somewhat different point of view and therefore somewhat differently formulated, the developmental concept of the edaphic formation was one of the fundamental features of Cowles' physiographic classification of plant associations (8, 9). Cowles was the first to fully appreciate the significance of physiography in relation to the local distribution of plant associations. "The keynote," he writes (9, p. 8), "is that each particular topographic form has its own peculiar vegetation. This is due to the fact that the soil conditions upon which plants depend are determined by the surface geology and the topography." He further states that, "From the standpoint of the vegetation the topographic relations are more important than the geological. . . . all kinds of soils may have the same kind of vegetation when placed in similar topographic conditions, whereas the same soil may show many diverse types of vegetation."

In classifying the edaphic formations within a given climatic region, topography, as related to the physiographic history of the region, is of fundamental importance. For, using this as a basis, it is possible to bring out the developmental relations of the physiographic unit areas involved, in much the same way that the classification of associations with reference to the phenomenon of succession brings out the developmental relations of the habitats concerned. It should be reiterated however, that while the contemporaneous features of the physiography of any region are the result of progressive development in the geologic past, from the standpoint of present-day physiographic ecology, with the exception of the relatively few areas in which changes manifestly are taking place rapidly, the physiography can be regarded as stable. That, on the whole, from the viewpoint of dynamic physiographic ecology, soil is of subsidiary importance to topography in determining the character of the vegetation seems obvious. But that soil may also exert a far-reaching influence on the ecological character of the vegetation is emphasized by the survey of vegetation set forth in "Types of British Vegetation" (21) where the formations are classified primarily with reference to soil. In general, then, the writer would classify the edaphic formations (1) with reference to topography, and (2) with reference to soil.

The edaphic formation-complex. The edaphic formations of any area, taken collectively, may be regarded as an edaphic formation-complex. And just as the association-complex of a physiographic unit area constitutes an edaphic formation, so the edaphic formation-complex of any climatic region constitutes a *climatic formation.*

THE UNIT OF VEGETATION WITH REFERENCE TO CLIMATE

The climatic formation. Climatic factors determine the larger features of the plant covering of the earth. Owing to widespread differences in climate, there are correspondingly widespread differences in the general ecological aspect of vegetation. The vegetation of any region in which the essential climatic relations are similar or uniform throughout, taken in its entirety, is here regarded as constituting a climatic formation. The climatic formation, then, bears a similar relation to the climate of the earth that the edaphic formation bears to the physiography of a climatic region; a similar one to that which exists between the association and the habitat-complex of a physiographic unit area. In other words, if the association is the ecological unit of vegetation from the standpoint of the habitat, and the edaphic formation is a unit from the standpoint of physiography, then the climatic formation is a unit from the standpoint of climate. Individual climatic formations are usually designated by combining the name of the geographic region concerned with that of the climax association-type of the formation; thus: the deciduous forest formation of eastern North America, the Great Plains short-grass formation, the sage-brush desert formation of the Great Basin.

The developmental concept of the climatic formation. Clements (4, pp. 3, 124–127) has adopted the developmental concept of the formation with reference to the climatic formation (in which sense he uses the word formation). He states that, "The unit of vegetation, the climax formation, is an organic entity. As an organism, the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life-history of a formation is a complex, but definite process, comparable in its chief features with the life-history of an individual plant. The climax formation is the adult organism, the fully developed community, of which the initial and medial stages are but stages of development. . . . A formation, in short, is the final stage of vegetational development in a climatic unit. It is the climax community of a succession which terminates in the highest life-form possible in the climate concerned. . . . It is delimited chiefly by development, but this can be traced and analysed only by means of physiognomy, floristic and habitat."

It will be seen from the foregoing quotation that Clements regards as the climatic formation what from the writer's point of view would be termed the regional climax association-complex (or association-type). It is the opinion of the writer that the climax association-complex should not be so regarded, but that the entire edaphic formation-complex of the region, or, as before stated, the vegetation of the region in its entirety, should be considered as constituting a unit from the standpoint of regional physiographic ecology. It seems more logical to regard the climax communities of the region, like other ecologically parallel series of communities, as belonging to a common association-type. As the most mesophytic type of vegetation attainable under the existing climatic conditions, the climax association-type may be looked upon as the climatic indicator, but not as the climatic formation. To sum up, the vegetation of any region having an essentially uniform climate throughout, taken in its entirety, constitutes a climatic formation, the general ecological aspect of which is determined by that of the climax association-type of the region.

The advisability of using the terms: edaphic formation and climatic formation. In a review of Clements' "Plant Successions," Tansley (22, p. 203) objects that if the concept of formation is restricted to a climax stage determined by climate, then "it leaves out of account the establishment of permanent communities of distinct life-form owing to edaphic conditions or to conditions determined by biotic reaction on the soil. It was to cover cases of this kind that Schimper introduced the term edaphic formation, and if its use be not allowed it is difficult to see how we are to classify such communities." Schimper (19, p. 161) says that "two ecological groups of formations should be distinguished—the climatic or district formations, the character of whose vegetation is governed by atmospheric precipitations, and the edaphic or local formations, whose vegetation is chiefly determined by the nature of the soil."

It is the opinion of the writer that the only logical way to reconcile the divergent views of various authorities regarding the interpretation of the word formation is to retain the classification of Schimper, distinguishing between edaphic formations on the one hand and climatic formations on the other, but modifying Schimper's concept to harmonize with the developmental concept as set forth in preceding paragraphs of this paper.

The climatic formation-type. On different portions of the earth's surface, owing to the existence of various parallel types of climate, there have been developed correspondingly numerous parallel types of climatic formation. Thus, as delimited on Schimper's map (19, map 3), the sclerophyllous woodland formation of southern California is paralleled by the sclerophyllous woodland formation of the Mediterranean region and that of South Africa. Similarly, the short-grass formation of North America finds its ecological counterparts in the grassland formations of Russia and China. Different individual climatic formations which have thus developed in response to the same type of climate and which as a result agree with one another in their ecological aspect, even though they differ (as they usually do) in their floristic composition, are to be considered as belonging to the same climatic formation-type. Like the association-type and the edaphic formation-type, the climatic formation-type is an abstract conception. It may be defined as: a type of climatic formation correlated with a given type of climate. While, in practice, their exact delimitation is of course a matter of considerable difficulty, in a general way it is possible to divide the vegetation which clothes much of the earth's surface into a relatively small number of formation-types.

Brockmann-Jerosch and Rübel, in their universal classification of plant communities (2) have distinguished four vegetation-types (lignosa, prata, deserta, and phytoplankton) and have further subdivided the plant formations of the earth into fourteen formation-classes and seventeen formation-groups. They do not, however, restrict the use of these terms to climatic formations: under prata, for example, are included the salt marshes and fresh marshes of forested regions, as well as the climatically-conditioned grassland formations. The word formation-type, from the standpoint of regional physiographic ecology, is here used only with reference to climatic formations. Schimper (19) has used the term in this sense, distinguishing three chief types of climatic formations (woodland, grassland, and desert) as well as various types of subordinate rank. Climatic formation-types, like climatic formations, are best designated in terms of the ecological aspect of the vegetation, as has been done in the illustrations cited above.

The climatic formation-complex. In treating the vegetation of any large area, such as the continent of North America, where more than one type of climate and correspondingly numerous different climatic formations are represented, the term climatic formation-complex may be used to include collectively the climatic formations of the entire area. The climatic formations comprising the complex may be genetically related in point of geologic time, as in the glaciated parts of eastern North America, but the term does not necessarily imply such a relationship. The climatic formation-complex of the earth, taken in its entirety, might be regarded as forming a *terrestrial formation.*

The application of the law of the minimum in regional physiographic ecology. In applying the Law of the Minimum to problems in local physiographic ecology, climatic factors need not be taken into account since they are essentially constant throughout the region. The variable factors are edaphic; they are due, directly or indirectly, to variations in either soil or topography. In dealing with problems in regional physiographic ecology, however, where the climatic factors also are variable, these of course are of paramount importance. Precipitation, the evaporating power of the air, temperature, and light afford the chief limiting factors, the factors which determine the general aspect of the vegetation in a climatic formation.

Even here, however, the edaphic limiting factors, at least in some cases, may be of great significance, and it need be only suggested that in an accurate analysis these, as well as the climatic limiting factors, must be considered.

SUMMARY

By way of summary, it may be stated that the fundamental unit of vegetation is the association. The associations of a unit physiographic area, taken collectively, constitute an edaphic formation. The edaphic formations of a unit climatic area, taken collectively, constitute a climatic formation. The climatic formations of the earth, taken collectively, may be said to constitute the terrestrial formation. The association is a unit determined by habitat, the edaphic formation a unit determined by physiography, the climatic formation a unit determined by climate, while the terrestrial formation might be said to be a unit determined by the atmosphere. "The conception of a formation as an ecological genus and an association as an ecological species" (Cowles 10, p. 150) may be further amplified. If the association is regarded as an ecological species and the edaphic formation constitutes an ecological genus, then the climatic formation may be said to represent an ecological family, while the terrestrial formation might be regarded as a unit of a still higher order.

In the preceding pages the various ecological units of vegetation have been treated as an ascending series. Starting with the fundamental unit, the association, the units of a higher order have been treated in the order of their increasing complexity. Their relative rank and their relation to one another is brought out by the following synopsis.

- The terrestrial formation: = the climatic formation-complex of the earth
  - The climatic formation: = the edaphic formation-complex of a climatic unit region
    - The edaphic formation: = the association-complex of a physiographic unit area
      - The association: = the plant-complex (community) of a unit habitat

THE SCHEME OF CLASSIFICATION IN PRACTICE

Outline classification of the vegetation of northern Cape Breton Island. The practical application of the classification of plant communities according to the concepts enunciated in the foregoing pages will now be illustrated by a specific example. The vegetation of the area selected has been under investigation for four summers, and a full account of the writer's observations and conclusions here is in the course of preparation. Northern Cape Breton lies in the transition zone between the two great climatic formations of eastern North America: the deciduous forest climatic formation and the northeastern evergreen coniferous forest climatic formation, and, owing largely to differences of elevation, both of these are well developed, the former on the lowlands and the latter on the highlands. The scheme adopted in classifying the various edaphic formations which comprise the deciduous forest climatic formation here, is outlined below. Such a scheme, it should be borne in mind, answers much the same purpose in the realm of physiographic ecology as an analytical key in the realm of systematic botany. The classification has been carried as far as the ecological genus, i.e., as far as the group of associations which comprises an edaphic formation.

The Vegetation of Northern Cape Breton

The deciduous forest climatic formation

I. The regional climax association-type
II. The edaphic formation-complex of the region
  A. Primary formations of the xerarch successional series
    1. The formation-types of ordinary uplands
      a. The association-complexes of exposed rock outcrops
      b. The association-complexes of talus
      c. The association-complexes of glacial drift
    2. The formation-types of uplands along streams
      a. The association-complexes of rock ravines
      b. The association-complexes of open valleys
      c. The association-complexes of boulder plains
      d. The association-complexes of flood plains
    3. The formation-types of uplands along the seacoast
      a. The association-complexes of sea-bluffs and headlands
      b. The association-complexes of shingle beaches
      c. The association-complexes of sandy beaches and dunes

B. Secondary formations of the xerarch successional series
        a. Association-complexes due to cultivation
        b. Association-complexes due to fire
        c. Association-complexes due to logging
C. Primary formations of the hydrarch successional series
    1. The formation-types of inland lakes and swamps
        a. The association-complexes of permanent lakes and ponds
        b. The association-complexes of periodic ponds
        c. The association-complexes of well-drained swamps
        d. The association-complexes of undrained swamps
        e. The association-complexes of poorly drained swamps
    2. The formation-types of lakes and swamps along the seacoast
        a. The association-complexes of salt and brackish marshes
        b. The association-complexes of brackish ponds
D. Secondary formations of the hydrarch successional series

The northeastern evergreen coniferous forest climatic formation

I. The regional climax association-type
II. The edaphic formation-complex . . . . etc.

Explanatory remarks. In attempting to make an ecological analysis of the climatic formation of a given region it seems logical that the subject matter be first arranged under two heads: (I) The regional climax association-type, and (II) The edaphic formation-complex of the region. This division has already been employed by Cooper (5), although he did not distinguish the edaphic formations as such. An understanding of the regional climax association-type, representing as it does the highest degree of mesophytism permitted by the climate, is prerequisite to the adequate interpretation of subordinate association-types and of successional relations. The term edaphic formation, given its developmental concept, of course includes the successions.

The various edaphic formations which comprise the regional edaphic formation-complex are next assembled into two successional series which, adopting the terminology suggested by Cooper (5, p. 11), are termed respectively the xerarch and the hydrarch series. The term xerarch, to quote Cooper "is applied to those successions which, having their origin in xerophytic habitats, such as rock shores, beaches, and cliffs, become more and more mesophytic in their successive stages; [the term hydrarch] to those which, originating in hydrophytic habitats, such as lakes and ponds, also progress toward mesophytism." The formations of these two series are further grouped as primary and secondary.

Considered next with reference to the larger topographic features[2] of the region, the edaphic formations of the xerarch series are divided into three groups: (1) The formation-types of ordinary uplands; (2) The formation-types of uplands along streams; (3) The formation-types of uplands along the seacoast. The edaphic formations of the hydrarch series are similarly grouped under two heads: (1) The formation-types of inland lakes and swamps; (2) The formation-types of lakes and swamps along the seacoast. They might equally well be divided into four groups: (1) The formation-types of glacial lakes and swamps; (2) The formation-types of sink-hole lakes and swamps; (3) The formation-types of river lakes and swamps; (4) The formation-types of coastal lakes and swamps; except that river lakes and swamps are scarcely represented in this region.

Finally, the association-complexes which comprise the various edaphic formations are further grouped with reference to whatever specific physiographic unit areas it seems best to distinguish. Under this head are considered the character and the successional relations of the individual associations and association-types. This latter part of the scheme in particular is so elastic and so capable of modification that it may be readily adapted to the special requirements of any region and to the individual views of any investigator.

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A new Lejunea from Bermuda and the West Indies*

ALEXANDER W. EVANS

(WITH PLATE 24)

The species described below is not uncommon in the West Indies and is perhaps to be expected in Florida and Mexico. It seems to be most abundant at low altitudes, without being strictly coastal in its distribution. The material at first examined, which was scanty and incomplete, was confused with *L. glaucescens* Gottsche, and some of the Bermuda specimens have been listed under this name by the writer.† More abundant material has since been available and has shown conclusively that the species is amply distinct.

Lejeunea minutiloba sp. nov.

Pale or dull green, often somewhat brownish with age, scattered or growing in depressed mats: stems about 0.1 mm. in diameter, copiously and irregularly branched, the branches obliquely to widely spreading, often with slightly smaller leaves than the stem but not microphyllous: leaves contiguous to loosely imbricated, the lobe widely spreading, slightly falcate, plane or slightly concave, broadly ovate, when well developed about 0.5 mm. long and 0.45 mm. wide, dorsal margin usually arching partially or wholly across the axis, then strongly outwardly curved to the broad and rounded apex, ventral margin straight or slightly outwardly curved, margin entire or vaguely and minutely crenulate from projecting cells; lobule in the form of a minute triangular basal fold, consisting of only a few cells, the apex represented by a single projecting cell tipped with a hyaline papilla; cells of lobe averaging about 13 μ in diameter at the margin and $25 \times 20\ \mu$ in the median and basal portions, thin-walled but with minute trigones and occasional intermediate thickenings, cuticle smooth: underleaves distant, orbicular, about 0.2 long, bifid about one half with erect, triangular, acute, obtuse or rounded divisions, rounded at the base, margin as in the leaves: inflorescence autoi-

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* Contribution from the Osborn Botanical Laboratory.

† Bull. Torrey Club 33: 131. 1906.

cous: ♀ inflorescence sometimes borne on a leading branch, sometimes on a more or less abbreviated branch, innovating on one side, the innovation sometimes sterile, sometimes with a second ♀ inflorescence; bracts obliquely spreading, varying greatly in size, distinctly complicate, lobe oblong to obovate, when well developed about 0.45 mm. long and 0.3 mm. wide but often considerably smaller, margin as in the leaves, lobule ligulate, rounded at the apex, about 0.16 mm. long and 0.06 mm. wide; bracteole mostly obovate, about 0.4 mm. long and 0.25 mm. wide, bifid one third or a little more with erect, acute, obtuse, or rounded divisions, margin as in the leaves; perianth obovoid, when well developed about 0.5 mm. long and 0.35 mm. wide, terete in the lower half, distinctly five-keeled above, narrowed toward the base, truncate or slightly retuse at the apex and with a short but distinct beak: ♂ inflorescence usually occupying a short branch and not proliferating, bracts closely imbricated, in two or three pairs, strongly inflated, shortly bifid with a crenulate, strongly arched keel and rounded divisions; bracteole usually single at base of inflorescence, smaller than the underleaves, bifid: capsule about 0.2 mm. in diameter.

BERMUDA: on rocks and stones, Church Cave and vicinity, July, 1900, *M. A. Howe 7;* February, 1908, *S. Brown 504, 505;* September, 1912, *E. G. Britton 1088;* on rocks and stones, Walsingham, June, 1900, *M. A. Howe 3;* September, 1905, *E. G. Britton 286;* gully, Tuckerstown, September, 1905, *E. G. Britton 323;* February, 1908, *S. Brown 516;* on bark and roots, Abbott's Cliff, September, 1912 and 1913, *E. G. Britton 888, 931, 932* (in part), *933, 1867;* on bark, without definite locality, 1908, *S. Brown 559a.*

CUBA: in a ravine and on roots of royal palm, San Luis, Oriente, April, 1909, *N. L. Britton 2327, 2329;* on shaded limestone, Tropical Park, Puentes Grandes, Havana, August, 1911, *Brother Leon 2739.*

PORTO RICO: on trunk of a tree, near Rio Piedras, January, 1899, *Mr. & Mrs. A. A. Heller 147;* near Bayamon, July, 1901, *Underwood & Griggs 892;* vicinity of Coamo Springs, March, 1906, *M. A. Howe 1371;* on bark and on earth, Lares to San Sebastian, April, 1913, *Britton & Marble 2799, 2800;* at base of tree, vicinity of Ponce, March, 1913, *Britton & Shafer 1747;* on bark, Candalaria, near Bayamon, February, 1914, *E. G. Britton 1521.*

ST. THOMAS: on banks and stones, St. Peter, February, 1913, *Britton & Marble 1251, 1254, 1255;* on stones, Crown, February, 1913, *Britton & Marble 1365.*

No. 1365 from St. Thomas may be designated the type; a slight admixture of *L. pililoba* Spruce is present.

In the genus *Lejeunea* the lobule when typically developed consists of an inflated sac, ovate in outline, more or less involute along the free margin, and tipped by a single projecting cell with a hyaline papilla at its proximal base. The same general type of lobule is found in several other genera of the Lejeuneae, such as *Rectolejeunea*, *Ceratolejeunea*, and *Crossotolejeunea.* Unfortunately, in certain species of *Lejeunea*, the lobule often fails to show its typical structure and appears reduced in size or otherwise variously modified. In some cases a prolonged search may be necessary before inflated lobules can be demonstrated at all, and it is not unusual for poorly developed lobules to be associated with plants bearing perianths. In the species here proposed as new no inflated lobules whatever have been seen, although many plants, both with and without perianths, have been examined. The lobule in all cases observed has been in the form of a minute basal fold, consisting of only a few cells. It seems safe to assume, therefore, that lobules of this reduced type represent a constant feature of the species.

With respect to size, the leaves, perichaetial bracts and perianths of *L. minutiloba* exhibit a considerable range of variation, and on slender stems and branches the leaves may be scarcely half as large as on robust stems. The small bracts and perianths are associated especially with short female branches, the size varying approximately with the length of the branch. The smallest bracts and perianths, therefore, are usually to be found on branches which bear a single vegetative leaf in addition to the bracts. The underleaves and bracteoles are much less subject to variation in size than the leaves and bracts; they vary markedly, however, in the character of their apices. These are sometimes acute or even apiculate, sometimes obtuse, and sometimes broadly rounded.

Among related species it will be sufficient to mention *L. floridana* Evans and *L. glaucescens* Gottsche. The first is still known from Florida only, but the second is widely distributed in tropical and subtropical America. Both species are somewhat larger than L. *minutifolia*, the leaves being often 0.7 mm. in length, but they agree with it in inflorescence and in having small orbicular underleaves. In both species, however, the lobules are frequently inflated and conform closely to the usual *Lejeunea* type. L. *floridana* is further distinguished by its much larger perichaetial bracts (often 0.8 mm. in length), by its more shortly bifid underleaves and bracteole, and by the crenulate keels of its perianth, projecting upward as horns. In L. *glaucescens*, the bracts approximate those of L. *minutifolia* in size but the lobules are usually distinctly pointed.

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Explanation of plate 24

LEJEUNEA MINUTILOBA Evans

The figures were drawn by the writer from the type specimen and prepared for publication by Mr. H. D. Rhynedance.

FIG. 1. Part of plant with two perianths, ventral view (male inflorescence not shown), × 45.

FIG. 2. Lobule of a stem leaf, × 250.

FIG. 3. Cells from the apex of a lobe, × 335.

FIG. 4. Cells from the middle of a lobe, × 335.

FIG. 5. Underleaf, × 110.

FIGS. 6–8. Bracts and bracteole from a single involucre, × 55.

FIGS. 9–11. Bracts and bracteole from a second involucre, × 55.

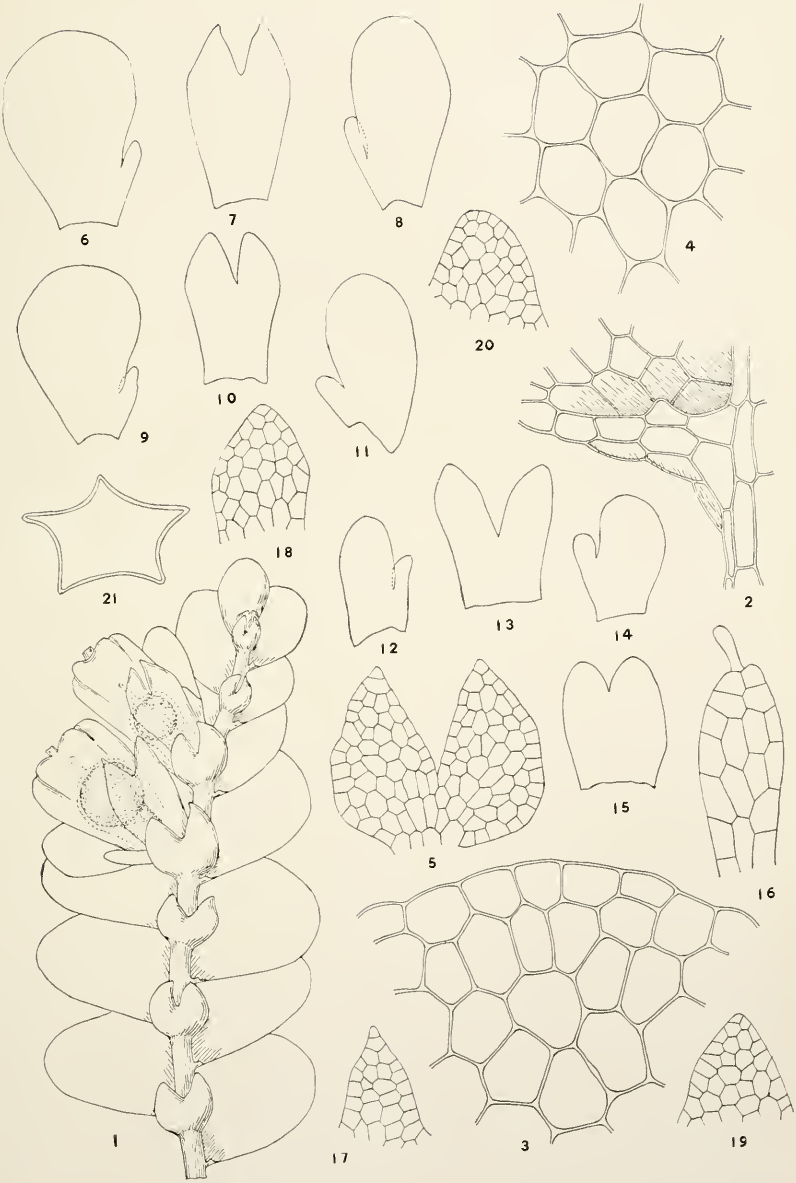
FIGS. 12–14. Bracts and bracteole from a third involucre, × 55.

FIG. 15. Bracteole from a fourth involucre, × 55.

FIG. 16. Lobule of a perichaetial bract, × 250.

FIGS. 17–20. Apices of various bracteole-divisions, × 110.

FIG. 21. Transverse section of a perianth in upper fourth, × 55.



LEJEUNEA MINUTILOBA Evans

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STUDIES ON THE RELATIVE PHYSIOLOGICAL VALUE OF SPECTRAL LIGHTS

I. Apparatus

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INTRODUCTION

The present paper is concerned primarily with a description of an apparatus by means of which spectral lights of equal radiant energy content can be obtained and comparative work of wide range carried out. Before proceeding to a description of this apparatus it seems best to point out, as briefly as possible, why such an apparatus is essential.

Against much of the work that has been done on the study of the relative physiological value of spectral lights the objection can be raised that sufficiently accurate methods of experimentation and description have not been employed. Speaking more particularly of the work which has been done on the "color vision" of animals other than man, and excluding the early investigations in which colored light was obtained by means of filters, screens, etc., much inaccuracy is found in those in which spectral light is used. By observing the influence of an entire dispersion spectrum on the aggregation of organisms results are obtained which leave much to be desired quantitatively. Also, in much of the work indefinite and inadequate terms of description are used, in that, e.g., one light is said to be brighter than another, as measured by the human eye, or equally bright, etc. This mode of description is purely subjective. Only qualitative facts are learned when a spectrum is viewed as a whole and this method does not enable us to say by how much one light is brighter than another, brightness being a quantitative conception only when measured photometrically.

It is therefore not permissible to compare the "color vision" of an organism to that of the normal human eye or of the color blind eye following the use of such inadequate methods. In a recent paper Hess (1) attempts to give an objective, quantitative comparison with the human eye, by comparing the influence of different colored lights on lower organisms with the influence of these same lights on the pupillar reflex of man. In this work, however, Hess makes use of a method, in addition to using colored glasses, against which objections may be raised. He varied the absolute intensity of his source, thus changing the luminosity of the colored lights, until a just perceptible change in the size of the pupil was observed. The relative results which he obtained with different colored lights he compared with those obtained on lower organisms. But this is an analytic rather than a synthetic method. Furthermore, it gives rise to physiological (subjective) differences in the apparent relative brightness value of lights of different color (Purkinje phenomenon). To have observed the comparative amount of change in size of the pupil with colored lights of the same intensity would have given more reliable results.

To return to the objections against the descriptive qualitative comparisons of colored lights as judged by the human eye, it is well known how variable such comparisons are likely to be on account of the variable physiological factors involved. In the first place the state of adaptation (light or dark) of the human retina is all important in the judgment of the relative luminosity of lights of different color. In the second place the absolute intensity of the colored lights must be considered, for the part of the spectrum of apparent maximum brightness shifts as the intensity of illumination is changed, being higher in a strong than in a weak spectrum. Luminosity or apparent brightness, as Troland (2) points out, is a psychological variable which cannot be expressed in physical units. It depends upon the absolute value of retinal illumination and upon the general state of sensitivity of the visual system.

But the chief fault which we have to find is the failure on the part of many investigators to take the unequal distribution of energy into consideration. It seems evident, to obtain quantitative results on a purely objective basis which will permit of comparisons being made exclusive of subjective sensations and which will allow a conclusive correlation of facts, that any comparative investigation of the influence of spectral lights must take into consideration this unequal distribution of radiant energy in the spectrum. The quantity of this radiation in the various colored lights should be ascertained, corrections made for the unequal distribution or, what is better still, the lights of various wave-lengths be made quantitatively equal by equating the radiant energy in them.

It is true that psychologists and physicists are not unanimous regarding the respective merits of photometry (equation of brightness) and of radiomicrometry (equation of radiant power) in the standardization of colored lights. This is due to the fact that they are primarily interested in light as it influences the human eye.

Photometric standardization (heterochromatic photometry) is a method which gives us quantitatively exact information about different colored lights, although as Parsons (3) says

> Photometry is one of the most faulty of physical measurements, chiefly, to use a paradox, because it is in most cases, not really physical, but physiological.

But a word should be said regarding the question of a photometric standardization of colored lights for comparative work on "color vision," and its seeming inadequacy. In the study of human vision it is essential that the brightness value of colored light stimuli be known and that work be done with visual stimuli of different wave-length but of equal brightness (spectral energy at constant luminosity). The use of such equally luminous stimuli for studying the stimulating value of different wave-lengths on lower organisms would give us quantitative results of interest but of questionable value except in so far as we wished to note the effects on other sensitive protoplasm of lights which are "equally bright" to the human eye. But the problem of visibility (to the human eye) is one that requires a measurement of the radiant energy content and a correction for the same. It deals with luminosity at constant spectral energy. In the work of Nutting (4), (5), Thürmel (6), Ives (7) and Nutting (8) we have the results of the study of this "visibility of radiation," which expresses the relative sensibility of the retina to light of different wave-lengths but of equal energy (Nutting (9)).

Now in man, as Troland (2) says

> To determine the effect of stimulus intensity we may take any constant wave-length and try our experiment with different values of the intensity, or to find the influence of wave-length, we may select a definite intensity and vary the wave-length. In this latter procedure we are obliged to equate the intensities of the qualitatively different lights which we use.

This latter problem, viz., the determination of the influence of wave-length, is the one that we are primarily interested in when we make a comparative study of the stimulating value of colored lights. We are therefore obliged to equate (either directly, or later by corrections) the radiant energy, in order to have a quantitative unit for the comparison of qualitatively different light, or for the sake of working with objective, not subjective, units of light.

We believe then, to repeat, that in the study of the evolution of color vision, or of the comparative investigation of the stimulating efficiency of spectral lights, it is absolutely essential that the distribution of the energy in the spectrum be considered, whether it is believed that it will affect the results obtained or not. This is just as important as is the necessity of having as pure and saturated lights as possible. Although it has long been recognized that the sensation of color brightness (the indication of the stimulating value to the human eye) must be due to a combination of wave-length and energy, and the curve for the distribution of this energy known (10), even the recent work on the investigation of the relative efficiency of different wave-lengths has, with few exceptions, failed to take this matter into consideration. Loeb and Wasteneys (11), (12), for instance, do not even refer to the possible influence of the unequal distribution of energy in the spectrum on the results which they obtained. This objection, among others, may also be made to the work of Hess (13).

The disregard of this matter is, however, not universal. Hertel in various investigations (14), (15), (16), determined, with a thermopile and galvanometer, the energy content of the lights of different wave-length which he used. Kniep and Minder (17), also using a thermopile and galvanometer, measured the absolute energy in their colored lights, and equated it (see p. 629 ff.). These investigators used filters for obtaining their colored lights, although they attempted to throw out the infra red and ultra violet rays. (See p. 634.) Blaauw (18, see pp. 271 ff.), corrected for the unequal distribution of radiant energy by means of calculations of its amount in the spectrum which he used, and Mast (19) referred to the importance of considering the amount of radiant energy.

In the work of Laurens (20), Day (21) and Gross (22) a real beginning was made in the study of the relative stimulating value of lights of different wave-length but of equal radiant energy content.[1] Comparative psychologists also have recognized the importance of radio-

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[1] This work was done at the Harvard Zoölogical Laboratory and the credit for its inception should be given to Prof. G. H. Parker.

metric determinations of lights used in studying the color vision of animals (23), (24), (25) and (26).

Mast (27) in his recent paper clearly recognizes the necessity of considering the amount of radiation in the various spectral lights, and says (p. 489) that,

> To ascertain the relation between wave-length and stimulating efficiency it is . . . . necessary to make correction for the unequal distribution of energy in the spectrum.

Such corrections were made. No objection can be raised against the physical accuracy of this method, but certainly, as Ives (7) points out, the measurement of the intensity of radiation directly at the eye-slit is the ideal one since it eliminates the determination of corrections. This is the actuating motive which prompted the construction of the apparatus which will now be described.

AN APPARATUS DELIVERING SPECTRAL LIGHTS OF EQUAL RADIANT ENERGY CONTENT[2]

The first problem was to decide upon an instrument with which to measure the radiant energy in the spectral lights. It was our intention, as above outlined, not to obtain data for the construction of the curve representing the distribution of energy in the spectrum, but after having ascertained the energy contained in different parts of the spectrum to equate this so that it had a certain unit value throughout.

For the measurement of radiation or of the radiant energy content of light, there are a number of physical instruments. For articles dealing with the description and application of these the following, among others, may be cited: Coblentz (28), (29), Schmidt (30), Pfund (31), (32), (33), (34), Day (21) and Kunz and Stebbins (35).

We finally decided to use a Hilger thermopile and a Broca galvanometer. The thermopile which we have has a sensitive area of 20

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[2] It gives us great pleasure to express our thanks to the following: Prof. H. S. Uhler of the Physical Laboratory, Yale University, for advice and assistance with the spectroscopic part of our apparatus; Prof. A. H. Pfund of the Physical Laboratory, Johns Hopkins University, for advice concerning the radiant energy measuring apparatus; Prof. H. A. Bumstead of the Physical Laboratory, Yale University, for the loan of a radiomicrometer; Prof. J. B. Watson of the Psychological Laboratory, Johns Hopkins University, for advice on general matters of apparatus—spectroscopic and energy measuring; and Prof. Philip E. Browning of the Kent Chemical Laboratory, Yale University, for the generous way in which he has placed a spectrometer at our disposal.

mm. × 1.5 mm. and a resistance of 2.8 ohms. The galvanometer has a resistance of 10.17 ohms, period 10 seconds, deflection in millimeters at 1 meter for 1 micro-amp 415, and deflection in millimeters at 1 meter for 1 micro-volt 40.81. The resistance was reduced by connecting the coils in parallel.

In order to control the sensitivity of this apparatus, readings of the radiation from a 16 c.p. Standard carbon lamp, burning always on 100 V, were taken. By means of the control magnet, the sensitivity of the galvanometer was varied until deflections of 400 mm., scale at 1 meter, were obtained.

In addition to this apparatus we have a Franz Schmidt and Haensch radiomicrometer (Schmidt (30) and Coblentz (29)) lent to us by Professor Bumstead.

Before proceeding to the description of our final apparatus for obtaining colored lights a brief reference may be made to one which was finished and then discarded for what will be obvious reasons. This apparatus was based on the plan of the light generators used by Laurens, Day and Gross (20), (21), (22). The light from a Nernst glower (220 V.) was passed through a lens, emerging as a parallel beam. To prevent over-heating a circulating water-cell was placed between the glower and the lens. Later this was given up because it lengthened the focal distance, in favor of a blast of compressed air emerging from a wing-tip burner, directed against the front face of the lens. Aside from the objection of cooling the glower and thus reducing the intensity of light, the glower was made to buckle backward, due to the unequal heating on the front and back surfaces. This happened although the lower connecting wire of the glower was suspended in a cup of mercury. The parallel rays of light were directed upon one of the faces of a large 60 degree angle prism-bottle (10.5 cm. by 10.5 cm.) filled with carbon bisulphide and placed at the angle of minimum deviation. The spectrum thus obtained was focussed by a converging lens and bands of light of the desired wave-lengths were obtained by placing a micrometer slit, opened to the appropriate width, at the focal plane of the converging lens.

This apparatus had the advantage of yielding a spectrum of large size and of great brilliancy. But it was found impossible to obtain with it pure and saturated light when the bands were examined with a spectrometer.

Since this large spectrometer was not successful we decided to obtain our spectral lights by passing white light through a Hilger constant deviation type spectrometer. At first we used the Nernst glower as a source. It was soon found, when we came to measure the radiant energy of the shorter wave-lengths, that more than one such glower was going to be necessary to give a light containing the unit energy content which, from preliminary experiments we had selected as being most satisfactory. By means of this apparatus we were able to obtain eight consecutive colored lights, each 30 wave-lengths broad, extending from 430 $\mu\mu$ to 670 $\mu\mu$ and containing the same amount of energy (see table 1). The glowers were clustered together and so connected by switches, with their ballasts, that any number, from one to five, could be burned at the same time. For the lights of shorter wave-length a mirror was placed behind the glowers so that their reflected image was focussed on the slit of the collimator.

TABLE 1

Showing the conditions under which the eight lights, each 30 wave-lengths wide and equal in radiant energy content were obtained

NUMBER	RANGE OF WAVE-LENGTHS	NUMBER OF NERNST GLOWERS	WIDTH OF SLIT IN TELESCOPE
			mm.
1	430–460	5 (+ mirror)	4.5
2	460–490	4 (+ mirror)	3.7
3	490–520	2	2.8
4	520–550	1	2.3
5	550–580	1	1.9
6	580–610	1	1.6
7	610–640	1	1.3
8	640–670	1	1.0

These eight lights were perfectly satisfactory but for the inconvenience occasioned by burning five glowers so closely together and the consequent bending and displacement. We therefore decided to use a 1000 watt gas-filled Mazda lamp, burning on a 110 V city circuit, the variations occasioned by the fluctuations in the intensity of this current being nullified by the large number of determinations of the radiant energy content which were always made. Furthermore we soon came to the conclusion that eight such lights were not all that we desired, for since we wished to study the relative stimulating value of the various wave-lengths in the spectrum, as well as to find the wave-lengths of maximum stimulating efficiency, it was deemed necessary, in order to be able to say, with an approach to accuracy, where the region of maximum stimulating efficiency was, to work with a smaller number of wave-lengths. But it is difficult, under our conditions, to work with bands of light less than 30 wave-lengths wide. We decided therefore to increase the number of lights, keeping each 30 wave-lengths wide, but, beginning with a band of light extending from 420 μμ to 450 μμ, to advance through the spectrum by 10 wave-length steps. The twenty-three lights thus obtained are listed in table 2.

TABLE 2

A summary of all the conditions necessary for obtaining twenty-three lights, each 30 wave-lengths wide and equal in radiant energy content

NUMBER	RANGE OF WAVE-LENGTHS IN μμ	POSITION AT WHICH DRUM MUST BE SET	WIDTH OF SLIT	DISTANCE ON DRUM	RANGE OF WAVE-LENGTHS ON EITHER SIDE OF D LINE	DISTANCE FROM LAMP TO SLIT
			mm.	*cm.*		*cm.*
1	420–450	434.0	4.8	12.90	549–641	9.0*
2	430–460	444.0	4.5	11.70	552–636	10.0*
3	440–470	454.0	4.3	10.70	555–632	13.0*
4	450–480	464.0	4.0	9.80	557–628	14.0*
5	460–490	474.0	3.7	9.15	559–625	2.5
6	470–500	484.0	3.4	8.40	561–622	4.0
7	480–510	494.0	3.1	7.80	563–619.5	6.0
8	490–520	504.0	2.8	7.20	565–617	7.5
9	500–530	514.0	2.6	6.70	566.5–615	9.5
10	510–540	524.0	2.5	6.25	568–613	11.5
11	520–550	534.0	2.3	5.85	569.5–611	13.0
12	530–560	544.0	2.1	5.50	570.5–609.5	14.5
13	540–570	554.0	2.0	5.20	571.5–608	16.0
14	550–580	564.0	1.9	4.90	572.5–607	17.5
15	560–590	574.5	1.8	4.60	573.5–606	19.0
16	570–600	584.5	1.7	4.30	574.5–605	20.5
17	580–610	594.5	1.6	4.10	575.5–604	22.5
18	590–620	605.0	1.5	3.90	576–603	24.5
19	600–630	615.0	1.4	3.60	576.5–602	26.5
20	610–640	625.0	1.3	3.50	577–601.5	28.5
21	620–650	635.0	1.2	3.30	577.5–601	30.5
22	630–660	645.0	1.1	3.10	578–600.5	32.5
23	640–670	655.0	1.0	2.95	578.5–600	34.5

* With reflector.

The lamp is enclosed in an asbestos lined, blackened box (see fig. 1), through an aperture in the front of which the light emerges to enter the slit *S*, kept at constant width, of the collimator. The back of the box is open and holes are bored in the top and bottom for ventilation. The light-box and spectrometer, with the exception of the ocular end of the telescope, are surrounded by heavy black curtains, reaching almost to the ceiling of the room. In order to obtain colored lights of the desired number of wave-lengths, diaphragms of appropriate width (twenty-three in number, one for each light), are placed at the focal point, directly behind the cross hairs, in the telescope, thus converting the spectrometer into a monochromatic illuminator. These diaphragms consist of cylindrical tubes of blackened cardboard adjusted to fit snugly inside the telescope tube, in the ocular end of each of which a disk of blackened cardboard, with a slit of appropriate width and 8

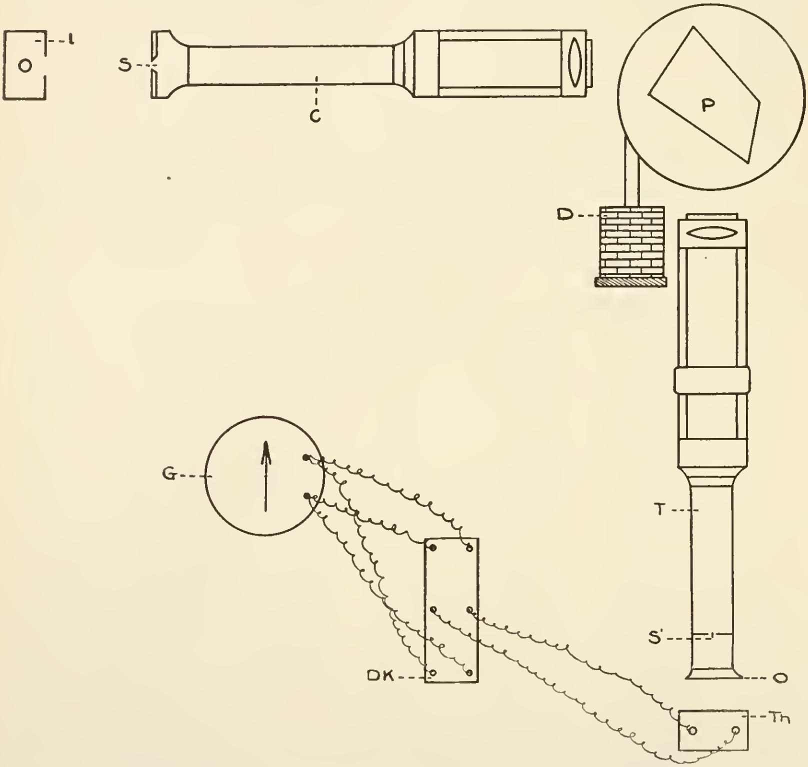

Fig. 1. *L*, lamp in box; *S*, collimator slit; *C*, collimator; *P*, prism; *D*, wave-length drum; *T*, telescope; *S'*, slit in telescope just behind cross-hairs; *O*, ocular; *Th*, thermopile; *DK*, double-key; *G*, galvanometer.

mm. high is fastened. The width of each slit is such as to allow 30 wave-lengths to pass. As is well known, in the prismatic spectrum the dispersion increases as the wave-length diminishes so that at the violet end a certain number of wave-lengths occupy a wider space than they do at the red end. A wide diaphragm is therefore necessary at the violet end and a narrow one at the red end to let through the same number of wave-lengths. The correct width was determined with the aid of the sodium line as follows: Given a desired range of wave-lengths, e.g., 460 $\mu\mu$ to 490 $\mu\mu$ (see no. 5, table 2); the distance on the wave-length drum between the scale marks 460 and 490 was first measured with a strip of paper and the middle point determined. (This middle point, in this case 474, gives the position at which the drum must be set in order that the desired wave-lengths, 460 $\mu\mu$ to 490 $\mu\mu$, pass). The middle point of the measuring strip of paper was then placed at 589 on the drum and an equal distance measured off on each side of this, thus determining the range of the wave-lengths on either side of the D line, in this case 559 to 625. The diaphragm, with a slit of arbitrary width, was then placed in position in the telescope and the points noted on the drum at which the D line (sodium flame) disappeared when the drum was rotated. The width of the diaphragm slit was then adjusted so that the D line just disappeared when the indicator on the drum pointed to 559 and 625 respectively. Since equal revolutions of the wave-length drum rotate the prism through equal angles this procedure assures that light ranging from 460 $\mu\mu$ to 490 $\mu\mu$ will pass when the diaphragm is in place and the drum set at 474. The width of the diaphragm slit was thus determined for each of the twenty-three lights.

Having procured the colored lights the next step was to equate the radiant energy in each. This was done by varying the distance between the lamp and the collimator slit of the spectrometer until the desired deflection of the galvanometer was obtained. A direct proportionality was found to exist between the bands, as indicated by their middle points, and this distance (see table 2).

The intensity of the first four lights was increased by placing a spherical reflector, obtained from the Spencer Lens Company, behind the lamp. The spectrometer was placed so that the collimator slit was at a distance of 9 cm. from the lamp, and the reflector adjusted so that the reflected image of the lamp filament was focussed on the slit. At this distance a radiant energy content equal to the amount chosen as our unit value was obtained for light no. 1 (420 $\mu\mu$ to 450 $\mu\mu$).

The radiant energy of the next three lights was then equated by moving the spectrometer away from the lamp, without disturbing the position of the reflector.

Table 2 gives a complete summary of all the conditions necessary for duplicating our apparatus and verifying our measurements. The range of wave-lengths for each light, the point at which the wave-length drum must be set, the width of the diaphragm slit in the telescope, the distance measured on the drum between the end-points of the range of wave-lengths, the range of the wave-lengths in question on either side of the D line used in determining the width of the slit, and the distance between the lamp and the slit of the collimator.

CONCLUSION

It seems of sufficient interest to restate briefly the advantages of the apparatus which we have described.

That it is perfect in the direction for which we have been arguing is not contended, but it certainly represents a distinct advance over anything that has been described for the comparative study of the relative physiological value of colored light in an equal energy spectrum. The degree of error involved is, in our opinion, of much smaller magnitude than the relative degree of sensitivity in the physiological work contemplated.

By means of the apparatus, in the first place, a series of brilliant colored lights of high purity and saturation are obtained, each of which is a band including a fairly small number of wave-lengths, the same for all, and equal in radiant energy content. Therefore no corrections are necessary for this factor. Furthermore, the entire apparatus is easily adjusted and any light obtained with ease. By it an exact specification of the intensity of the various spectral lights is given, the experimental conditions are rendered reproducible and an exact repetition of the experiments made possible.

We are at present engaged in a series of investigations dealing with the relative stimulating values of these lights on lower organisms and on the eyes of higher forms, as well as the study of chlorophyll assimilation and decomposition. But there are various causes which make the completion of any but a small part of this work in the immediate future doubtful. Owing to the conditions occasioned by the great war it is impossible to obtain a spectrometer from England. The spectrometer which we are at present using is borrowed from the chemical department of the College and we have the unrestricted use of it only during the vacations, thus retarding our progress. Furthermore extra work which we have both agreed to undertake during the coming college term will leave us little time for research.

Since it is highly improbable, therefore, that we can publish anything in the near future concerning results obtained with our apparatus, we are desirous of publishing a preliminary description of it so as to afford those who are interested in similar studies the benefit of our experience in the construction of an apparatus fulfilling what we consider the necessary physical conditions for the study of the relative stimulating value of spectral lights.

SUMMARY

The reasons are stated why the study of the relative stimulating value of different colored lights should be carried out with a high degree of exactness for all, even the lowest forms. This involves the use of pure "monochromatic" lights, directly measurable in terms of energy and preferably made equal in radiant energy content, thus doing away with the necessity of making corrections for this.

An apparatus is described which delivers lights of equal radiant energy content. Each light is a band 30 wave-lengths wide. The lights now obtained are twenty-three in number and extend, by steps of 10 wave-lengths, from 420 $\mu\mu$ to 670 $\mu\mu$. The apparatus used for equating the radiant energy content in the different lights is also described.

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BRIEFER ARTICLES

APOGAMY IN PHEGOPTERIS POLYPODIOIDES FÈE, OSMUNDA CINNAMOMEA L., AND O. CLAYTONIANA L.

Apogamous embryos developed on prothallia of *Phegopteris polypodioides* Fèe, *Osmunda cinnamomea* L., and *O. Claytoniana* L. in cultures on Prantl's and Knop's full solutions and certain modifications of the Prantl's solution. About 6 months after the spores had been sown, the first cases of apogamy were observed in cultures of *Phegopteris polypodioides* on Prantl's solution with NH_4 NO_3 omitted. The spores from which the prothallia developed had been collected during the summer from a plant growing on a lawn in Ithaca, New York. The plant did not appear in a normal, healthy condition, doubtless owing to the unfavorable conditions under which it was growing. After the spores were sown upon the nutrient solutions, the cultures were placed before an east window, where the conditions of light and temperature were approximately the same for all. Once each week the prothallia were transferred to fresh nutrient solutions.

The prothallia, upon which the apogamous embryos developed, were heart-shaped and developed archegonia but no antheridia. The apogamous embryo in most cases originated as a slight swelling of the archegonial cushion, either on the dorsal or ventral side, at some point near the notch or at the center of the cushion. This swelling gradually increased until a dome-shaped cellular mass was formed, from which the apogamous embryo developed. The parts of the embryo usually appeared in the following order: the leaf or leaves, root, and stem. However, in one case a root appeared before any other member. No foot was formed. In some cases, beside leaves, proliferations, either filamentous or slightly expanded at the apices, developed from the cellular mass. October 7, 1916, two series of cultures on the Prantl's and Knop's full nutrient solutions and modifications of the Prantl's solution were made. Fresh spores from the same plant at Ithaca, New York, as well as spores of the same species secured through the kindness of Dr. A. H. GRAVES from Brooklin, Maine, were used. As soon as the spores were sown upon the nutrient solutions, one series was placed in the greenhouse in bright light, while the other series was kept in the laboratory before an east window. The prothallia were not transferred to fresh solutions, but were allowed to remain upon the original solution on which the spores had been sown. A luxuriant growth of algae developed in all of the cultures, which added to the unfavorable growing conditions.

March 9, 1917, in both series of cultures, apogamous embryos were observed on the prothallia which developed in Knop's full solution from spores collected in Maine. Archegonia were developed on many of the heart-shaped prothallia, while in some of the cultures on the smaller prothallia antheridia were present. Some of the archegonia appeared aborted. In most cases the apogamous embryos developed in the manner which has previously been described. However, a few cases of peculiar development were observed. Multicellular hairs or outgrowths formed at the base of the first leaf or leaves of the young sporophyte, or at various places on it.

On one prothallium a long cylindrical outgrowth several cells in thickness developed from the cellular mass along with the leaves of the apogamous sporophyte. As growth proceeded, this outgrowth broadened out into a one-celled prothallium-like structure, after which it again assumed the cylindrical shape bearing tracheids; at its apex it tended to return to the prothallium structure. On another prothallium an outgrowth which had developed from the notch of the prothallium and projected as a narrow process broadened at the apex, forming a slightly notched prothallium.

The only cases of apogamy on prothallia developed from spores collected at Ithaca, New York, occurred in the culture of Knop's full solution which had been kept in the laboratory. Most of the apogamous embryos originated from cellular masses formed on the prothallia, but on one prothallium a cylindrical outgrowth bearing tracheids developed from the cells in the notch. At the apex of this long cylindrical process a cellular mass was formed, from which the leaves, root, and stem of the apogamous embryo developed.

Two series of cultures of *Osmunda cinnamomea* and *O. Claytoniana* were made at the same time, in the same manner, and placed under the same conditions as the cultures of *Phegopteris polypodioides*. Apogamous embryos were observed March 9, 1917, on the prothallia in the following solutions: Prantl's full solution, Prantl's solution with NH_4NO_3 omitted, and Prantl's solution with $MgSO_4$ omitted. Some of the apogamous embryos developed from cellular masses; others originated as cylindrical outgrowths containing tracheids, from the notch of the prothallia, bearing at their apices cellular masses which gave rise to the leaves, root, and stem of the sporophyte. On one prothallium an apogamous sporophyte formed near the notch, while at its base a lobe of the prothallium developed, on which in turn occurred an apogamous embryo. In the latter the root developed first. Only three cases of apogamy were observed in *Osmunda Claytoniana* in Prantl's solution with K_2SO_4 omitted. In two cases the sporophytes developed from a mass of cellular tissue, while the third arose as an outgrowth in the notch of the prothallium. A further study will be made of these apogamous forms.—ELIZABETH DOROTHY WUIST, *Osborn Botanical Laboratory, Yale University.*

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NOTES ON NEW ENGLAND HEPATICAE,—XIV.[1]

ALEXANDER W. EVANS.

IN 1915 Warnstorf[2] described and figured as a new species, under the name *Sphenolobus ascendens,* a specimen collected by Miss Lorenz at Waterville, New Hampshire. The specimen had been sent him as *Scapania glaucocephala* (Tayl.) Aust., but he failed to find the *Scapania* and suggested that there might have been an error in the determination. The Waterville material had been named by the writer, and had served as the basis for his observations on *S. glaucocephala,* published in 1909.[3] In view of a possible error this material has been carefully reëxamined, but there seems to be no reason for revising the original determination. Mixed with the *Scapania,* however, are several other species of Hepaticae, such as *Cephalozia curvifolia, Jamesoniella autumnalis, Harpanthus scutatus,* and *Lophozia porphyroleuca.* The last species occurs as a slender gemmiparous form and is not abundant, but the few plants present agree with Warnstorf's description and figures of *Sphenolobus ascendens.* The writer would therefore regard the *Sphenolobus* as a synonym of the *Lophozia.*

During the past two years Miss Lorenz[4] has recorded a number of species additional to the hepatic floras of Maine, New Hampshire, and Vermont, respectively. These species, with a single exception, were found by Miss Lorenz herself. The additions for Maine, collected on Mt. Ktaadn, are *Cephaloziella bifida, C. byssacea* (listed as *C. Starkii*), *Gymnomitrium corallioides, Lophozia Kunzeana, Nardia Geoscyphus,* and *Scapania dentata.* The only addition for New Hampshire, collected along the Connecticut River at Claremont, is *Riccia arvensis.* The additions for Vermont, collected at various localities, are *Riccia arvensis, R. Frostii* (first record for New England), *Ricciella crystallina, Cephalozia macrostachya, Lophozia heterocolpa, L. longidens,* and *Radula tenax.*

Attention should likewise be called to an interesting observation

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Hedwigia **57**: 63. *f. 2.* 1915.

[3] RHODORA **11**: 194. 1909.

[4] Bryologist **20**: 43–45. 1917; Vermont Bot. & Bird Clubs, Joint Bull. **2**: 14. 1916; Joint Bull. **3**: 7, 8. 1917.

by Howe[1] on *Riccia Lesenriana.* According to his studies this species, published by Austin in 1869, is a synonym of *R. Beyrichiana* Hampe, published by Lehmann in 1838. The species, therefore, should bear the earlier name.

In the present series of Notes the following three species are recorded from New England for the first time: *Scalia Hookeri, Harpanthus Flotowianus,* and *Calypogeia fissa.* The distinctive features of these species are discussed, further mention is made of *Riccia Frostii,* and several additions to local state floras are given.

1. Riccia Frostii Aust. Bull. Torrey Club **6**: 17. 1875. *R. Watsoni* Aust. *l. c.* *R. Beckeriana* Steph. Bull. Herb. Boissier **6**: 374. 1898. Clayey banks of the Connecticut River, Ascutneyville, Weathersfield, Vermont, July 15, 1916 (*A. Lorenz*). The species has a wide distribution in North America and the following stations may be cited from the literature: Genessee Falls, Rochester, New York, 1868 (*P. T. Cleve*); near Painesville, Ohio (*H. C. Beardslee*); Illinois (*J. Wolf*); Bloomington, Indiana (*C. L. Black*); banks of the Missouri River, St. Charles, Missouri (*C. H. Demetrio*); Manhattan, Kansas (*W. A. Kellerman*); South Dakota (*Williams*); Great Falls, Montana (*F. W. Anderson*); Colorado (*J. Wolf*); near Denver, Colorado (*C. C. Parry, E. Bethel*); Idaho (*J. B. Leiberg*); Nevada (*S. Watson*). The last named specimen, sent to Austin by C. C. Frost, should be regarded as the type of the species.

In 1898 Heeg[2] announced the occurrence of the species from the following localities in the Old World: Sarepta, Russia (*A. Beeker*); Vienna, Austria (*A. Pokorny*); Gorelevo, Fatjanova and Polovinka, Siberia (*H. W. Arnell*). In 1912 Massalongo[3] recorded it from two stations in Italy, namely: Sermide (*A. Manganotti*) and Francolini, province of Ferrara (*A. Fermioli*). In 1913 it was reported by Schiffner[4] from the vicinity of Makó, Hungary (*J. Györffy*) and from Mesopotamia, Asia Minor (*H. von Handel-Mazzetti*). Stephani considered the Russian specimens distinct from *R. Frostii,* describing them as new under the name *R. Beckeriana,* but K. Müller[5] reduces Stephani's species to synonymy, maintaining that it comes within the range of variability to be expected in a species.

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[1] Bryologist **20**: 33. 1917.

[2] Bot. Notiser 1898: 24.

[3] Atti R. Ist. Veneto **71**: 852. *f.* 7. 1912.

[4] Oesterr. Bot. Zeitschr. **63**: 455. 1913.

[5] Rabenhorst's Kryptogamen-Flora **6**: 210. *f. 138.*

In the absence of fresh material the writer has been unable to make a satisfactory study of the present species, but the published descriptions and figures bring out most of its essential characters clearly. Aside from the works of Heeg, Massalongo, and K. Müller, already alluded to, reference may be made to Underwood's account in the 6th edition of Gray's Manual, to Howe's critical observations in connection with the Hepaticae of California,[1] and to Miss Black's comprehensive morphological study.[2] Howe emphasizes the features of the spores, which distinguish the species from all known California *Ricciae.* He describes them as narrowly margined, 45–55 μ in maximum diameter, and covered over almost uniformly "by numerous short, delicate, wavy ridges which rarely anastomose." These peculiarities will serve equally well to separate *R. Frostii* from the other New England species of *Riccia,* in all of which the ridges on the spores form regular meshworks.

Whether *R. Frostii* should be retained in the genus *Riccia* or transferred to *Ricciella* is not altogether clear. The green tissue contains intercellular canals which extend, in some cases at least, from the compact ventral tissue to the dorsal surface. Whether they are always continuous for this entire distance, or whether they are occasionally subdivided by transverse or oblique partitions is not brought out by the descriptions. In any case the canals are broader than in typical species of *Riccia,* and instead of being bounded by only four cells in section view are bounded by several to many cells. In these respects they resemble the marginal canals described by Juel [3] in the case of the European *R. Bischoffii* Hüben. Since the median canals in this species are of the narrow type, Juel contends that it shows the *Riccia* structure in the median portion and the *Ricciella* structure in the wings, thus forming a connecting link between the two groups and making it unnecessary to recognize *Ricciella* as a genus. In typical species of *Ricciella,* however, the intercellular spaces are in more than one layer, so that the genus might still be maintained on the basis of this feature. In the case of *R. Frostii,* unfortunately, this criterion can not at present be applied, and it therefore seems wisest to retain the species in *Riccia,* even if certain writers have considered it a *Ricciella.*

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[1] Mem. Torrey Club **7**: 32. 1899.

[2] The morphology of *Riccia Frostii,* Aust. Ann. Bot. **27**: 511–532. *pl. 37, 38.* 1913.

[3] Über den anatomischen Bau von *Riccia Bischoffii* Hüb. Svensk Bot. Tidskr. **4**: 160–166. *pl. 7 + f. 1–5.* 1910.

2. Scalia Hookeri (Lyell) S. F. Gray, Nat. Arr. British Pl. **1**: 705. 1821. *Jungermannia Hookeri* Lyell; Sowerby, Engl. Bot. **36**: *pl. 2555.* 1814. *Mniopsis Hookeri* Dumort. Comm. Bot. 114. 1822. *Lejeunea Hookeri* Spreng.; Linnaeus, Syst. Veg. ed. 16, **4**: 234. 1827. *Gymnomitrium Hookeri* Corda; Opiz, Beitr. zur Naturg. 651. 1829. *Mniopsis acutifolia* Dumort. Syll. Jung. 75. 1831. *Haplomitrium Hookeri* Nees, Naturg. der europ. Leberm. **1**: 111. 1833. *H. Cordae* Nees, *l. c.* **1**: 112. 1833. On damp rocks, in a mat of *Pellia Neesiana* (Gottsche) Limpr., Huntington Ravine, Mt. Washington, New Hampshire, about 4800 feet altitude, August 7, 1917 (*A. W. E.*). New to America.

It is a great satisfaction to be able to record this rare and distinct species, representing a monotypic genus, as a member of our flora. Unfortunately the material collected is exceedingly scanty, consisting of a few antheridial shoots, but the plant is so different from all other northern Hepaticae that there is little danger of mistaking it. *S. Hookeri* was supposed to be confined to Europe, where it is widely distributed without being anywhere abundant. It was originally discovered in 1812 by Charles Lyell in the New Forest, Hampshire, England, near the southern coast, and is now known from several other localities on the British Isles and also from Norway, Sweden, Finland, Denmark, Germany and Austria. In the northern part of its range it sometimes descends to the sea level; in the southern part it seems to be confined to higher altitudes. The plants usually grow singly or in small tufts and are difficult to detect in the field. In most cases they occur scattered among other bryophytes, species of *Riccardia* or *Pellia* being perhaps their most common companions.

Full descriptions of *Scalia Hookeri*, many of them accompanied by figures, are available,[1] and the species served as the basis for an important monograph by Gottsche,[2] a work which ranks as a classic in the literature of hepaticology. It is therefore unnecessary to describe the plant in detail. It is hoped, however, that the following brief account of its more distinctive features may prove of interest.

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[1] See, for example, the following: Hooker, British Jung. *pl. 54.* 1814; Carrington, British Hep. 1. *pl. 1, f. 1.* 1874; Lindberg, Rev. Bryol. **12**: 33–36. 1885; Pearson, Hep. British Isles, 427. *pl. 189.* 1901; Warnstorf, Kryptogamenfl. der Mark Brandenburg **1**: 134. *f. 1.* 1902; K. Müller, Rabenborst's Kryptogamen-Flora **6**: 399. *f. 227.* 190 ; Macvicar, Student's Handb. British Hep. 88. *f. 1–8.* 1912; C. Jensen, Danmarks Mosser **1**: 60. *f. 1–3.* 1915.

[2] Anatomisch-physiologische Untersuchungen über *Haplomitrium Hookeri* N. v. E., mit Vergleichung anderer Lebermoose. Nova Acta Acad. Leop.-Carol. **20**: 267–398. *pl. 13–20.* 1843.

The gametophyte consists of a pale subterranean rhizome which branches sparingly and from which the erect leafy shoots arise. Both the rhizome and the leafy shoots are wholly destitute of rhizoids. Slime papillae, however, are produced in abundance. The leafy shoots are mostly 0.5–1 cm. high and are usually unbranched. The leaves are composed of thin-walled cells and vary in shape, some being entire and others variously incised or lobed. The shoots, in the upper part at least, are radial and show no evidence of dorsiventrality; in other words their broad leaves are in more than three ranks and no distinction can be drawn between lateral leaves and underleaves. The lack of dorsiventrality distinguishes *Scalia* from all other genera of the Hepaticae, but in Stephani's opinion[1] this distinction is more apparent than real. According to his observations the leafy shoots are dorsiventral in the lower part, the leaves being in three ranks and showing a differentiation into lateral leaves and underleaves. This differentiation is not one of form or of size but simply of insertion, the lateral leaves being obliquely attached to the stem while the underleaves are transverse. Stephani notes further that the radial structure of the shoot appears only in connection with the sexual organs and that many other leafy genera show a similar approach to a radial condition in their reproductive shoots. However this may be, the shoots of the *Scalia* present a very distinctive appearance and bear a strong resemblance to mosses, their upper leaves being closely crowded.

Most authors assign a dioicous inflorescence to *S. Hookeri*, but Stephani states that it is sometimes monoicous and may be always so. These statements are criticised by Warnstorf and there seems, indeed, to be very little to support them. The antheridia are conspicuous from their large size and bright orange color. They are borne on short stalks and arise irregularly all around the stem, showing no definite relation to the leaves. The archegonia, sometimes as many as ten, are developed near the tip of a shoot, but the apical cell itself does not take part in the formation of an archegonium, even though its activities are brought to an end. No perianth is developed, the protection of the sporophyte being secured by a large and fleshy calyptra, the neck of the fertilized archegonium being in the usual apical position and the unfertilized archegonia remaining at the base.

The sporophyte shows the usual differentiation into foot, stalk and

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[1] See Mém. Herb. Boissier **16**: 43. 1900.

capsule, the stalk attaining (according to Lindberg) a length of 1–3 cm. The capsule is oblong-cylindrical, 1.5–2 mm. in length and 0.6–0.75 mm. in diameter. The wall consists of a single layer of cells, except in the apical region, and splits at maturity into four valves, although these may remain more or less united. The cells of the wall are thin-walled, except for a median annular band in each cell, extending longitudinally. This type of thickening recurs in the closely related tropical genus *Calobryum* Nees[1] but otherwise seems to be unique. In all other genera of Hepaticae, where annular or half-annular bands of thickening have been described, the bands run in a general transverse direction. The elaters are for the most part long and bispiral, although some of those which remain attached to the tips of the valves are unispiral throughout more or less of their length. The spores are densely verruculose.

The genera *Scalia* and *Calobryum* constitute a very natural group, to which Goebel[2] has given the name Calobryaceae. This group represents, in the opinion of most writers, the highest development attained by the anacrogynous Jungermanniales. The genus *Calobryum* in fact, as Goebel emphasizes, is not anacrogynous at all, the archegonia forming a definite apical group on the broadened tip of the female shoot. Of course this does not imply that the acrogynous Jungermanniales are descended from the Calobryaceae. The group, as Cavers[3] states, appears "to form a blindly ending line of development," the probable origin of the true Acrogynae being in some less highly differentiated form.

3. HARPANTHUS FLOTOWIANUS Nees, Naturg. der europ. Leberm. **2**: 353. 1836. *Jungermannia Flotowiana* Nees, Flora **16**: 408. 1833. *J. convoluta* Hüben. Hep. Germ. 60. 1834. *J. vogesiaca* Hüben. *l. c.* 149. 1834 (as synonym). *Lophocolea vogesiaca* Nees, Naturg. der europ. Leberm. **2**: 348. 1836. *Pleuranthe olivacea* Tayl. Jour. Bot. **5**: 282. 1846. On damp, earth-covered rocks, mixed with other Hepaticae, Valley Way, Mt. Madison, New Hampshire, about 4700 feet altitude, July 9, 1917 (*A. W. E.*). New to New England.

The present species, which is the type of the genus, was based on material collected in the Riesengebirge, close to the boundary between Silesia and Bohemia. It is now known also from various other parts

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[1] See Andreas, Flora **86**: 204. *f. 23, 24.* 1899.

[2] Ann. Jard. Buitenzorg **9**: 21. 1891.

[3] New Phytol. Reprint **4**: 99. 1911.

of Germany and Austria, as well as from Norway, Sweden, France and Great Britain. Lindberg and Arnell report it further from various localities in Siberia. For the most part it is alpine or subalpine in its distribution although it sometimes descends to the sea level in the northern part of its range.

In North America its distribution is still very incompletely known. According to the Synopsis Hepaticarum (1845) it was collected by Vahl in Greenland, but there seem to be no other reports about its occurrence on the island. In 1889 Underwood[1] showed that *Pleuranthe olivacea* Tayl., which had been redescribed and figured by Sullivant in the second edition of Gray's Manual (1856), was a synonym of *Harpanthus Flotowianus.* Taylor's species was based on material in the Hooker herbarium, collected by J. Drummond in "North America" and presumably coming from somewhere in western Canada. In 1890 Pearson [2] cited the species vaguely from the "Rocky Mountains (*Bourgeau*)," and Underwood, in his account of the Hepaticae in the 6th edition of Gray's Manual, included *H. Flotowianus*, reproducing Sullivant's figures of *Pleuranthe olivacea.* At the end of the description the words "extra limital" appear, but Underwood [3] repudiated these two years later, stating that they had been added without his knowledge and that he had reason to believe that the species would be found in the northern United States. At the same time he reported it from Labrador (*Waghorne*), the specimens cited having come from Battle Harbor. In 1891 he had already recorded the plant from British Columbia.[4] This record was apparently based on specimens in his herbarium collected by J. Macoun in the "mountains of the Gold Range, north of Griffin Lake," in August, 1889,[5] although no statement to this effect is made. In 1900 the writer [6] detected the *Harpanthus* among the specimens brought back by the Harriman Alaska Expedition and listed the following stations: Hot Spring (*Trelease*), Orca (*Trelease*), Port Wells (*Trelease*), and Yakutat (*Brewer & Coe*). In 1904 [7] he reported the

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[1] Bot. Gaz. **14**: 196. 1889.

[2] List Canadian Hep. 18. 1890.

[3] The Hepaticae of Labrador. Bull. Torrey Club **19**: 269, 270. 1892.

[4] Zoe **1**: 366. 1891.

[5] See Macoun, Cat. Canadian Pl. **7**: 28. 1902.

[6] Proc. Washington Acad. **2**: 306. 1900. Through an unfortunate oversight *H. Flotowianus* is not mentioned in the writer's recent "Report on the Hepaticae of Alaska," published in Bull. Torrey Club **41**: 577–616. 1915.

[7] Minnesota Bot. Studies **3**: 142. 1903.

species from Grand Marais, Minnesota (*Holzinger*), but this record proves incorrect, the specimens in question representing a large form of *H. scutatus* (Web. f. & Mohr) Spruce. In 1906[1] he reported a new station for the plant from British Columbia, namely: Comox, Vancouver Island (*J. Macoun*). These scanty records seem to exhaust the list, and it will be seen that the stations from Greenland, Labrador, and New Hampshire are the only ones definitely known from eastern North America.

The genus *Harpanthus*, according to our present knowledge, is composed of only two species, *H. Flotowianus* and *H. scutatus*, the latter being widely distributed in northern regions and reaching a much lower latitude than *H. Flotowianus*. The genus is characterized by succubous, bifid leaves; large, lanceolate underleaves, usually undivided although sometimes sparingly toothed; ventral, intercalary branches, those bearing the sexual organs being very short; a rudimentary, erect perigynium, the sporophyte being partially imbedded in the swollen tip of the female branch; small involucral leaves and a short perianth, terete in the lower part. In *H. scutatus* the ventral position of the branches seems to be constant; in *H. Flotowianus* an occasional lateral branch of the *Frullania* type is produced.[2] In its general habit the genus bears a strong resemblance to *Lophocolea* and *Chiloscyphus*. Its systematic position is intermediate between *Heteroscyphus* and *Geocalyx*, both of which have bifid succubous leaves and short sexual branches, ventral in position. In *Heteroscyphus*, however, there is a well-developed perianth and no perigynium (just as in *Lophocolea* and *Chiloscyphus*), whereas in *Geocalyx* there is no perianth and a well-developed perigynium.

Sporophytes are rare in *H. Flotowianus*, but it is usually not difficult to determine sterile material. The conspicuous lanceolate underleaves at once indicate the genus *Harpanthus*, while the somewhat larger size and the blunt lobes of the leaves will serve to separate it from *H. scutatus*. The leaves, to be sure, are subject to considerable variation. The apical sinus, although usually distinct, is sometimes scarcely apparent, while the lobes vary from rounded to more or less acute. Even if acute lobes are present, however, they are in the minority, while the lobes of the leaves in *H. scutatus* seem to be constantly acute. The latter species is further distinguished by the fact

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[1] Postelsia 1906: 225.

[2] See Evans, Ann. Bot. **26**: 12. *f. 15.* 1912.

that the underleaves are often coalescent on one side with a leaf; in *H. Flotowianus* they are constantly free. The two species differ finally in habitat. *H. scutatus* prefers logs or dry rocks, rarely ascending to a high altitude, while *H. Flotowianus* grows on damp rocks or in subalpine bogs.

Schiffner[1] recognizes two modifications of the species, which he designates as forma *typica* and var. *uliginosus*, respectively. He admits, however, that they intergrade. In the forma *typica*, to which the Mt. Madison specimens might be referred, the stems are more or less prostrate, and the lobes of the leaves are often sharp. In the var. *uliginosus*, the stems are more or less erect, and the lobes of the leaves are mostly rounded. Forma *typica* grows in somewhat drier localities and occasionally produces reproductive organs; var. *uliginosus* grows in deep swamps and is always sterile. Full descriptions of the species, with figures, may be found in European manuals.

4. Calypogeia fissa (L.) Raddi. On banks, Mt. Washington Carriage Road, New Hampshire, near the three mile post, August 7, 1917 (*A. W. E.*); on shaded earth, Triple Falls, Randolph, New Hampshire, August 23, 1917 (*A. W. E.*); Vineyard Haven, Martha's Vineyard, Massachusetts, August, 1917 (*H. E. Greenwood*). New to New England. In 1907[2] the writer published an account of *C. fissa*, giving a full synonymy of the species. At that time he was able to cite only two stations, namely: Lafayette, Louisiana (*Langlois*), and Devonshire Marsh, Bermuda (*E. G. Britton*). Nichols[3] has since listed the species from Barrasois, Cape Breton, Nova Scotia, and the three following stations may now likewise be placed on record: Magnolia Swamp, Mt. Pleasant, District of Columbia (*M. B. Waite*); Gainesville, Florida (*N. L. T. Nelson*); and Boston Mountains, Swain, Arkansas (*W. H. Emig*). It is clear from these citations that the species is widely distributed in North America. Its range in Europe is equally extensive, and it has also been reported from Japan.

The species is characterized by shortly bidentate leaves and by wide and deeply bifid underleaves, the lobes of which are blunt or sharp and usually bluntly unidentate on the sides. When these features are at all constant, as in the material from Bermuda, the plant is easily distinguished from the closely related *C. Trichomanis* (L.) Corda. Unfortunately this is not always the case. In some

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[1] Lotos **48**: 332. 1900. [2] Bryologist **10**: 29. 1907. [3] Bryologist **19**: 42. 1906.

specimens only a few of the leaves are bidentate and the underleaves are sometimes narrower, less deeply divided, and not dentate on the sides. These deviations are more likely to be found on slender branches and apparently indicate a reversionary tendency. At the same time they show that *C. fissa* is to be looked upon as a "kleine Art," even by those who recognize its validity as a species.

The additions to local state floras, not already mentioned on the preceding pages, are as follows: —

For Maine: *Diplophyllum gymnostomophilum,* Round Mountain Lake and vicinity, Franklin County (*A. Lorenz*).

For New Hampshire: *Pellia Fabroniana,* Beaver Falls, Colebrook, and Stewartstown (*A. L. Andrews & A. W. E.*); *Cephalozia macrostachya,* Eagle Lake, Mt. Lafayette (*A. Lorenz*); *Frullania Selwyniana,* Stewartstown and Colebrook (*A. L. Andrews & A. W. E.*); *Lophozia badensis,* Beaver Falls, Colebrook (*A. L. Andrews & A. W. E.*); *L. heterocolpa,* Beaver Falls, Colebrook (*A. L. Andrews & A. W. E.*), and Alpine Cascade, Berlin (*A. W. E.*); *L. Kaurini,* Beaver Falls, Colebrook, and Lime Pond, Columbia (*A. L. Andrews & A. W. E.*); *Anthoceros crispulus,* Cornish (*C. C. Haynes*) and Compton (*A. Lorenz*); *A. Macounii,* Compton (*A. Lorenz*). The specimens of *A. crispulus* from Cornish have already been reported under the name *A. punctatus*[1] and have served as the basis for the record in the writer's Revised List.[2] The sign "+" in the list should therefore be transferred to *A. crispulus.*

For Vermont: *Marsupella Sullivantii,* Mt. Mansfield (*A. Lorenz*).

For Massachusetts: *Cephalozia Francisci,* Granville (*A. Lorenz*); *C. macrostachya,* Woods Holl (*H. E. Greenwood*); *Lophozia inflata,* Sandwich (*G. E. Nichols*) and Stillriver, Harvard (*H. E. Greenwood*); *Nardia crenuliformis,* Granville (*A. Lorenz*); *Radula obconica,* Mt. Washington (*A. Lorenz*); *Scapania dentata,* Sheffield (*A. Lorenz*).

For Connecticut: *Pallavicinia Flotowiana,* Salisbury (*A. Lorenz*); *Sphenolobus exsectaeformis,* Lantern Hill, North Stonington (*A. Lorenz*).

The census of New England Hepaticae now stands as follows: total number of species recorded, 189; number recorded from Maine, 138; from New Hampshire, 149; from Vermont, 129; from Massachusetts, 117; from Rhode Island, 79; from Connecticut, 143; from all six states, 60.

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[1] RHODORA **7**: 58. 1905.

[2] RHODORA **15**: 26. 1913.

Probably the most obvious characteristic of the forest vegetation as a whole is the extreme variety of species composing many of the associations and the general dissimilarity between it and the usual upland type lying westward and mostly outside of the county. One may clearly observe this transition in going from Ann Arbor to Detroit. The change is abrupt and takes place a short distance west of Ypsilanti or some twenty miles west of the Detroit River, where the rolling morainal topography changes to the level glacial lake basin of which Wayne County, except the small northwest portion, is a part. The change is apparent in the shrubs and herbs, but particularly in the trees that now remain either scattered or grouped in woodlots. Many of the trees show by their age that they were part of the heavy and nearly unbroken forest which existed less than a century ago. People who remember the forest as it existed fifty years ago testify that there was an abundance of such trees as black walnut, whitewood *(Lirodendron Tulipifera)* and others which would have made the individuality of the forest more strongly marked then than at present. This type of vegetation covers a large and important part of southeast Michigan along that portion of the state bordering the St. Clair River, Lake St. Clair, the Detroit River, and Lake Erie. It occupies the glacial lake basin following the trend of the ancient beach lines in its western limits. Unpublished observations by Schaffner, Transeau, Sears, and others, make it evident that a similar distinction exists over this glacial lake basin which extends southward and eastward over northern Ohio, bordering Lake Erie. In a survey of the vegetation made by automobile they were enabled to mark the change of vegetation wherever they passed upon the basin area. Over the western morainal area, such as we observe about Ann Arbor, the hard maple and beech, in order of relative abundance, are characteristic trees. This is the climax forest, as recently given by Zon for this region. Over the eastward lake basin area occur a variety of associations, but we notice a marked absence of the hard maple-beech forest, except for a small area here and there, as in southeast Brownstown. Beech often occurs but, except for the small Plymouth-Northville district, it is associated with *Acer rubrum, A. saccharinum,* and other trees, forming a forest totally unlike that outside the basin, both in character and appearance.

CHARACTERISTIC TREES.

The great variety of species occurring in several of the forest associations of Wayne County makes it difficult, at the outset, both to recognize some of the associations, particularly in the central north-to-south belt, and to follow the boundaries formed by the meeting of two associations, each composed of over ten associated species, such as are commonly met with in the vicinity of Dearborn, Wayne, and numerous other places in the county, where it is not at all uncommon to count over twenty species of trees growing on a quarter of an acre.

The problem is greatly simplified by selecting those species which show the most marked tendency to be limited in local distribution to some given area. With this in view, ten species have been chosen as the ones most decidedly related in their local distribution in the county, to areas where certain optimum conditions exist more or less uniformly. They are believed to be the trees which are the most certainly confined to restricted areas, and it has been found that these ten trees indicate as many regions which, together, cover the county, yet do not overlap. These ten trees are assumed to be the most characteristic elements of all the forests of Wayne County, past, as well as present.

A portion of this number, like *Larix*, formed forests of pure growth or like-commensal forests; others, like sassafras, tend to form mixed forests or unlike-commensal forests; others, like hard maple, may form forests of pure growth, but also occur in forests of mixed growth. The list, therefore, falls under three headings, as indicated below:

I. *Species tending to form like-commensal forests.*

These are formed by tamarack *(Larix laricina)*, birch *(Betula alba var. papyrifera)*, and aspen *(Populus tremuloides)*, giving us respectively, the tamarack forests, paper-birch forests, and aspen forests. Yet forests of pure growth are rare in Wayne County, occurring as small island-like patches here and there.

Larix is the most strongly social species of this region and tends, more than any other species, to form stands of pure growth. While the few isolated individuals found here and there in some portions of the county, usually in the vicinity of peaty areas, in Livonia, Greenfield, and other places, would suggest that the species may have been somewhat more common in the past than at present, it is not probable that the numerous lakes and ponds existing in the past, and now all reclaimed by vegetation, ever had the *Larix* forest stage in the filling-in process, so common in the kettle hole bogs farther inland. Such lakes and ponds, while numerous in the past throughout the northeast-southwest central sand drifted belt of the county, were invariably shallow and have all been reclaimed by vegetation, and, except for Yerkes Lake, near Northville, are now represented by beds of peat. An excellent example is found in northeast Brownstown, showing the final stage in the filling-in process. The peaty areas are covered by wet prairie, formed by social grasses or sedges. There is no evidence to show that such areas were ever occupied by trees of any kind. The black oak forest meets the prairie so formed at a sharp line. The area covers nearly three square miles. Sand has so drifted as to form knolls, reaching above the level of the prairie, and there occur islands of black oak forests on these sand knolls, surrounded by prairie. The absence of all trees, even seedlings, on the prairie, indicates little or no advance of trees over the peat. This and many similar areas seem to have been treeless from the start. The peat is reported to be not over ten feet deep and in dry seasons is likely to take fire and burn to the bottom.

The aspen *(Populus tremuloides)* is social, showing a tendency to form stands of pure growth. The best example of this type begins on a swampy area, northwest of Wayne, and follows two miles northward along the Wayne-Plymouth electric line on both sides of the track. The aspen forest is totally unlike any other of the region in appearance, and is one of the most noticeable features to be seen in the vegetation along this route. It is one of the best examples of a like-commensal forest. The total area of pure aspen in the county, however, is not large, although it is larger than that of any other gregarious species. Like the birch, it commonly mixes with other species. Portions of the aspen forest north of Wayne contain red maple, pin oak, *Populus deltoides,* and other trees, evidently pioneers of other associations, which are very slowly encroaching on the aspen.

A forest of exceptional interest begins well within the city limits of Detroit and extends northwestward and north, covering about forty square miles. It is characterized by paper birch which often forms over 65 per cent of the woods, as in the S. W. ¼, S. E. ¼, Sec. 16, Greenfield. Palmer Park and the west side of the Grand Lawn Cemetery wood preserve a portion of this association. The soil is sandy, of good to fair productiveness.

II. *Species tending to form both like- and unlike-commensal forests.*

The black oak *(Quercus velutina)* forms a thin forest sometimes called oak openings, upon sand which is light and dry and is blown by the wind. It is too poor for agriculture, at least under present methods. The people should plant poplar windbreaks and forest planting should be undertaken. The Norway pine *(Pinus resinosa)* should do well here.

An intimate relation exists between the black oak forest and the people and type of agriculture which has sprung up over the extensive area from which this forest association has been cleared. Here we find the barb-wire fence, the primitive log house and small barns. The people are generally Polish and distinct socially from those who farm where maple, beech, or any of the other forest associations described, have been removed. The conditions of soil which have supported beginning stages of forest development make it difficult for the people to develop educationally or otherwise.

Another tree which occurs in forests of both mixed and pure growth is the hard maple *(Acer saccharum).* In the townships of Northville and Plymouth, this tree is so dominant in places that secondary species are nearly excluded. The "sugar bush" is common. In other places, often in the same wood lot, it is associated with the beech. Throughout this area the walnut is very abundant, also the cherry *(Prunus serotina),* but the predominating tree is hard maple. Zon considers this the climax forest, but this and one other locality, an area of about fourteen square miles in south Brownstown, are the only ones which actually fit into the scheme. A very large portion of this hard maple-beech forest has been cleared away and the land put under cultivation. Comparing now the kind of agriculture, type of farm buildings, and the people, with those of the black oak areas, we find the greatest contrast. Here are woven wire fences and large barns with silos, indicating good conditions for the keeping of stock, especially sheep. Corn and other crops requiring good soil can be raised; the people speak English; there is the atmosphere of thrift and hospitality, which we find upon the soils from which associations indicating fertility have been removed.

A third characteristic tree occurring in both mixed and pure associations, is the shag bark hickory *(Carya ovata),* south of Trenton, on Slocum's Island. There are portions of these woods which are nearly pure hickory. The wood is well preserved, easily visited, a large portion being set aside as public ground, and is of rare interest. The associated species are *Carya alba, C. glabra, C. microcarpa, Quercus alba,* and *Q. rubra* and are present in portions of the wood lot where the stand is mixed.

The oak-hickory association tends also to form a rather narrow belt of varying width, but often less than one mile wide, along the extreme eastern part of the county along and near the shore; also, along the Huron, and to a less extent, along the River Rouge. The total area occupied by this association is not large enough to allow a distinct farming community to develop.

The sycamore also tends to form stands, both of pure growth, and mixed. The pure growth stands are small, a few hundred feet at most in extent and of recent origin, as if following a clearing. Pure stands of large diameter, suggesting that such stands occurred in the original forest, were not found. The tree seems to have occurred quite generally along with silver maple, elm, and red maple, and other wet land associations, to be described later. This mixed forest affords good evidence, showing the tolerance of the sycamore. In the S. E. ¼, S. E. ¼, Sec. 22, Greenfield, the forest is composed of *Planatus occidentalis, Ulmus americana, Acer saccharinum, Fagus grandifolia, Fraxinus nigra, Quercus bicolor* and *Carpinus caroliniana,* in order of relative abundance. The stand is of typical density, the trees standing an average distance of twelve feet apart, showing a fair amount of tolerance for this species. But the tree invariably forms forests in physiologically wet habitats, on clay, loam or shallow sand, with or without humus, associated with hydrophytic species. It shows no tendency to form forests in the black oak habitat, although this forest is open and there is plenty of chance. The results do not sustain the conclusions of Griggs,* who has overlooked the fact that one of the crucial tests of a forest type is its ability to reproduce. The constant appearance of sycamore in the hydrophytic forests of the old lake bed area is one of the distinguishing features of this forest in south east Michigan. The sycamore is also abundant on the flood plains of both the Huron and Rouge Rivers.

III. *Species tending to form unlike-commensal forests.*

Under this head are included those characteristic trees which, of themselves, show little or no tendency to occur in pure growth, but occur in association with other species. These are the beech, silver maple, and sassafras, each associating with certain other species and characterizing three different portions of the county. The forests characterized by each of these trees, respectively, are at once the largest and most characteristic types east of the Defiance Moraine. Together they are estimated to cover over 70 per cent. of the county. The silver maple occurs as the characteristic tree of the mixed forest on the flat, wet, and poorly drained glacial clay, or till plains, of the extreme eastern portion of the county, forming a belt extending north and south, at or near the shore line, and spreading inland a distance of one to seven miles. The belt covers Gratiot township and most of Grosse Point, city of Detroit, Springwells, Ecorse, and a portion of Monguagon and Brownstown. Gratiot, with an average slope of eight feet per mile, and Ecorse, with a slope of four feet per mile, and part of Detroit, with a slope of three feet per mile, afford ideal conditions for the growth of this forest.

The forest is quite uniform in composition, the numerous lists taken from different wood lots throughout the belt, showing a remarkable similarity in composition and relative abundance. The silver maple often forms over 50 per cent. of the stand. One wood lot listed in 1903 had nine species on one-fourth acre, in which the silver maple formed 71 per cent. of the stand. The most common secondary species of trees are *Ulmus americana, U. fulva, Fraxinus pennsylvanica, F. pennsylvanica* var. *lan-*

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*Ohio Biological Survey, Bulletin 3, page 295.

ceolata, Quercus bicolor, Tilia americana. Westward from this belt, wood lots occur, showing an association of silver maple, elm, and ash; but these are easily distinguished as belonging to a different series. The elm is still prominent, but the silver maple becomes subordinate or almost absent. Red maple takes its place, becoming prominent. There is less red ash and more black; also it will be found that the association is seldom pure, but mixed with species clearly belonging to other types, the most common of which are the beech, soft maple, the oak-hickory, and sassafras associations.

As before mentioned, this association is one of the three largest in the county. It is composed of hydrophytic species and the forest occurs in situations too wet for agriculture. On clearing away the forest it was necessary to drain the land before it could be put under cultivation. This has been difficult to accomplish, because of the very level topography and it has been difficult to raise crops requiring early cultivation like corn. Pastures start late and conditions are not so well suited for the keeping of cattle, sheep, and other animals. The barns are of the roomy, symmetrical kind, suitable for storing hay, for this is good grass land. Wherever it has been possible to secure good drainage, cereals do well, as a rule.

A second large and fairly distinct forest association is composed of beech and red maple, in order of their relative abundance. This forms a wide, but somewhat interrupted belt, throughout the central portion of the county occurring in the east portion of Livonia, Nankin and Romulus townships, with extensions into Taylor, Dearborn and Redford. The association is entirely distinct in appearance from the hard maple-beech forest of the Northville region. The surface is level, the soil is clay, often loamy, with here and there a shallow covering of sand which interrupts the drainage, and causes local swamps.

The drainage problem has been quite generally and successfully solved and conditions are excellent for the raising of cereals; the farm buildings are of the kind best suited for the keeping of stock; the people are hospitable, interested in educational work, particularly with branches that have to do with the improvement of the soil and what it produces. It is surprising how people in the beech-red maple area, busied as they are in their daily work, actually study, and even accurately investigate, the conditions with which they have to deal. It is common to meet people here who know a good deal of plant physiology, soil-physics and chemistry, and can even talk intelligently about Mendel's Law. Conditions remind one strongly of the hard maple-beech area about Northville, but there is a difference. The hilly land in the Northville region, possibly because it interferes with the cultivation and harvesting of crops, is often reserved for sheep pasture, and flocks of sheep are numerous here. Sheep are rather uncommon in the beech-red maple area.

The third and last great forest association occurring in Wayne County is a highly mixed one occurring on rather shallow sand and characterized by sassafras. The tree is associated with two others which are not quite so abundant or so uniformly distributed throughout the area, namely: *Quercus palustris* and *Nyssa sylvatica*. These three species, while not quite commensal, are rather closely associated. A careful study of this association leads to the conclusion that these are the three most characteristic species of this highly complex association. Thus a list of a quarter-acre area from any given place in the county where this association occurs, may disclose only one of the characteristic species; most frequently this will be sassafras, but may be either pin oak or *Nyssa* instead. The sassafras association is by far the most mixed association in the county. An excellent example is found on the S. E. ¼ of the S. W. ¼ of Sec. 32 Livonia. There are here twenty-two species within a quarter of an acre.

The two aspens, swamp oak, elm, red maple, Juneberry, bitternut hickory, butternut, wild plum, pin cherry, black cherry, and the viburnums are associate species. Dearborn and Wayne are in this association. The birch association is really an ecological equivalent. The association covers an important and large area through the sandy central portion of the county, alternating with the beech-red maple areas. The soil is moist in comparison with the black oak area. In places it is peaty. The varying soil conditions meet the demands of the market gardener. The farms are not large, the barns are small, where the labor is performed by hand. The people are of German or foreign descent. The problems with which these people have to deal are comparatively few, and there is a strong tendency for the people to follow tradition. They read little and miss a good deal of what is being done outside in the way of experimental investigations.

There have thus been indicated in order, all of the forest associations of any considerable size occurring in the county at the time of settlement by man. The present wood lots are the remaining portions of such associations, and as such are now fairly representative, although fast disappearing. Trees other than those listed occur, which, while local and not abundant, are yet of exceptional interest. Southeast of Dearborn, north of Wayne, and south of Belleville occur respectively three areas, each of about two square miles in extent, in which chestnut *(Castanea dentata)*, predominates in the forest. A fourth smaller area occurs south and east of New Boston. It is confined exclusively to sand, usually in the sassafras or black oak associations, but sometimes with beech and red maple. Also about one and one-half miles east of Plymouth, on the south bank of the Rouge, we see in plain sight from the Wayne-Plymouth electric line, a lone pine towering above the deciduous trees surrounding. This is a remnant of the white pine forest lumbered 28 years ago. There are eleven stumps remaining to tell the story, indicating the trees were 127 years old when cut. There can be no question but that this was original forest.

SUMMARY AND CONCLUSIONS.

Having now completed the salient feature of the forest vegetation of the county, some of the more general interrelations existing between the associations, as a whole, and the environmental conditions may be pointed out.

Throughout the investigation it has been plainly evident, from a careful comparative study of the returns from the cultivated land in each of the several forest associations, that land from which any given forest association has been removed possesses agricultural possibilities distinct from land from which some other forest association has been removed, though the soil in the two areas, may look exactly alike. Such differences, clearly revealed by the vegetation and of extreme importance agriculturally, are as a rule, entirely overlooked by a soil survey, however carefully done. Thus the present soil maps do not distinguish between the black oak, the sassafras, and the beech-red maple association areas. They are classed together as sand on the soil map. Very numerous other instances might be mentioned.

The forest associations may be arranged in the following order: (1) Black Oak, (2) Sassafras, Birch, (3) Hickory, (4) Hard Maple, (5) Beech, (6) Silver Maple, (7) Sycamore. This gives us a gradient scale of forest associations that may serve to indicate the degree of soil fertility, being too dry at one extreme for successful agriculture, and too wet at the other. The optimum conditions for most crops occur in the maple-beech portions.

The several associations covering most of the old lake basin area are believed to be stages of forest development tending toward the hard maple-beech association as a climax. But the change is and has been exceedingly slow, due to the correspondingly slow topographic changes occurring on this area. So slow are the topographic and soil changes occurring naturally on this area that the forest has been become arrested in its development and the several associations represent the arrested stages, the succession of which will be published in the more complete account.

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NOTEWORTHY LEJEUNEAE FROM FLORIDA[1]

ALEXANDER W. EVANS

Our knowledge of the Hepaticae occurring in Florida has been materially increased during the past few years. This is due in great part to the careful collections made by Mr. Severin Rapp in the vicinity of Sanford, Orange County, although Dr. J. K. Small, Mr. N. L. T. Nelson and other collectors have made notable discoveries. In 1915 Miss Caroline C. Haynes[2] published a list of sixty-four species which Mr. Rapp had found, including twenty-four members of the Lejeuneae. In the present paper six additional Lejeuneae are noted. Four of these are apparently undescribed, although one has already been reported from Sanford under another name. One of the remaining species has been previously reported from Cuba and the other from Jamaica. Of the new species two, according to our present knowledge, are endemic to Florida. The number of Lejeuneae now known from Sanford is twenty-nine; from the entire state of Florida, forty-four; from the entire United States, forty-eight.

1. **Cololejeunea contractiloba** sp. nov.

Plants very delicate, pale green, scattered or growing in loose mats: stems prostrate, 0.03 mm. in diameter, irregularly and sometimes abundantly branched, the branches widely spreading, similar to the stem: leaves distant to subimbricated, obliquely to widely spreading, the lobe plane or slightly convex, sometimes inflexed at the apex, ovate to ovate-lanceolate, when well developed 0.2–0.3 mm. long and 0.12–0.18 mm. wide, but often considerably smaller, gradually narrowed to an acute apex tipped with a single cell, both dorsal and ventral margins rounded in the basal half and straight or nearly so in the apical half, crenulate or denticulate from projecting cells; lobule often rudimentary, when well developed broadly ovate, about 0.13 mm. long and 0.11 mm. wide, strongly inflated throughout, apical tooth consisting of a single rounded projecting cell, lying in a more ventral plane than the rest of the free margin and bearing the hyaline papilla at its dorsal base, proximal tooth scarcely evident, consisting of a rounded cell separated from the apical tooth by a single cell, sinus

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Bryologist 18: 19–22. 1915.

shallow and very short; cells of lobe averaging 10 μ along the margin, 16 x 14 μ in the median and basal portions, each bearing a conical papilla on the dorsal surface, walls slightly thickened at the tips of the papillae, otherwise thin throughout; cells of lobule plane; stylus none: inflorescence autoicous: ♀ inflorescence borne on a somewhat elongated branch, innovating on one side, the innovation short and sterile; bracts obliquely spreading, more or less complicate, the lobe ovate to ovate-lanceolate, mostly 0.35–0.45 mm. long and 0.12–0.2 mm. wide, apex, margin and cells as in the leaves, lobule ovate to obovate, mostly 0.15–0.2 x 0.1 mm., rounded to more or less pointed at the apex; perianth obovate in outline, about 0.35 mm. long and 0.25 mm. wide, terete in lower half, five-keeled above, the keels blunt below, sharper above, rounded at the apex, beak of perianth short but distinct, surface in upper part roughened as in the leaves: ♂ inflorescence terminal on a more or less abbreviated branch, not pro-

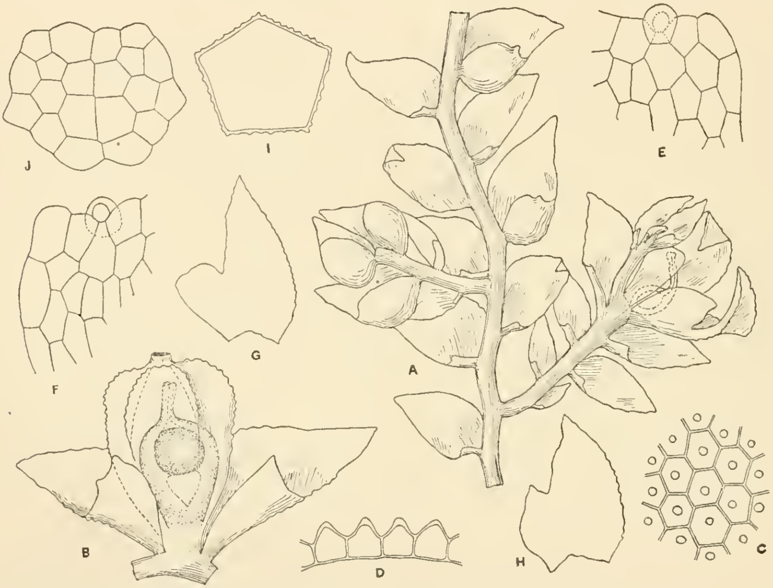

Fig. 1. Cololejeunea contractiloba Evans

A. Part of a plant with male and female inflorescences, ventral view, × 65. *B*. Perianth and bracts, base of innovation at left, ventral view, × 65. *C*. Cells from middle of lobe, × 300. *D*. Cells of keel, optical section, × 300. *E*. Apex of lobule, ventral view, × 300. *F*. Apex of lobule, dorsal view, × 300. *G*, *H*. Bracts from a single involucre, × 65. *I*. Transverse section of perianth just above middle, × 65. *J*. Gemma, × 300. The figures were all drawn from the type specimen.

liferating (so far as observed); bracts in one or two pairs, similar to the leaves but less widely spreading and with relatively shorter lobes, monandrous: capsule about 0.18 mm. in diameter: spores greenish, 12–20 μ in short diameter, minutely verruculose: gemmae abundantly produced, about 0.05 x 0.06 mm., composed (normally) of twenty cells, each apical quadrant cutting off three segments, margin crenulate from projecting cells, the youngest two segments on each side sharper, organs of attachment none. [FIG. 1.]

On bark of trees. FLORIDA: Sanford, 1913–1917, *S. Rapp*. The specimen collected in 1915 (September 28), which bears well-developed perianths, may be designated the type. The specimen collected in 1913 was at first referred by the writer to *C. Biddlecomiae* and is reported under this name by Miss Haynes.

Among the species of *Cololejeunea* known from Florida, *C. Biddlecomiae* (Aust.) Evans and *C. tuberculata* Evans agree with *C. contractiloba* in having roughened leaves and perianths. In all three cases the roughness is due to projecting cell-walls, more or less thickened at the tips of the projections. It is best marked in *C. tuberculata*, where the lobules as well as the lobes of the leaves and perichaetial bracts are usually roughened and where the projections are longer and more thickened at their tips. In the other two species the lobules are invariably smooth, and the projections are shorter and less thickened.

The lobules of the new species are especially interesting because they show the features characteristic of the genus in an abridged or reduced form. In other words the apical tooth, instead of being two cells or more long, consists of a single projecting cell, while the proximal tooth is scarcely apparent. The apical tooth is further remarkable because it lies in a more ventral plane than the rest of the free margin, the hyaline papilla lying in the same plane. In both *C. Biddlecomiae* and *C. tuberculata* the apical tooth is normally two cells long and lies in the same plane as the rest of the margin, while the proximal tooth is usually distinct.

Aside from the differences just noted *C. contractiloba* differs from *C. Biddlecomiae* in its smaller size, in its lack of a filiform stylus, and in the narrower lobes and lobules of its perichaetial bracts; it differs from *C. tuberculata* in its slightly larger size, in the entire lobules of its perichaetial bracts and in the distinct beak of its perianth. Four other speceis of *Cololejeunea* are definitely known from Florida at the present time. Since, however, the leaves of all are smooth or nearly so, there is little danger of confusing them with the present species.

2. **Lejeunea cladogyna** sp. nov.

Pale or dull green, sometimes becoming yellowish or brownish with age, growing in loose mats: stems mostly 0.08–0.1 mm. in diameter, sparingly and irregularly pinnate, the branches widely spreading and sometimes subdivided, often with smaller leaves than the stem but not microphyllous: leaves contiguous to loosely imbricated, the lobe obliquely to widely spreading, plane or slightly convex, subfalcate, broadly ovate, when well developed about 0.45 mm. long and 0.4 mm. wide, dorsal margin sometimes arching partially across the axis, sometimes not, sometimes strongly outwardly curved from the base to the broad and rounded apex, sometimes straight or slightly incurved in the basal region, ventral margin slightly outwardly curved to straight, margin entire throughout; lobule when well developed inflated, broadly ovoid, 0.09–0.12 mm. long and 0.09 mm. wide, keel straight or slightly arched, roughened from projecting cells, forming a very broad angle with the ventral margin of lobe, free margin somewhat involute to beyond the apex, sinus oblique and very shallow, apical tooth a rounded, straight, slightly projecting cell with a hyaline papilla or its proximal side; lobule usually poorly developed and reduced to a minute basal fold; cells of lobe averaging about 16 μ along the margin and 28 x 18 μ in the median and basal portions, thin-walled throughout or with minute and indistinct trigones and intermediate thickenings, cuticle smooth; ocelli none: underleaves distant, ovate to ovate-orbicular, about 0.15 mm. long and 0.12–0.15 mm. wide, bifid about one half with an acute to lunulate sinus and erect, triangular, subacute lobes, margin entire: inflorescence autoicous: ♀ inflorescence borne on a very short branch, with only one vegetative leaf and one bracteole in addition to the involucral leaves, innovating on one side, the innovation short and sterile (so far as observed); bracts obliquely spreading, the lobe oblong to obovate, when well developed about 0.3 mm. long and 0.16 mm. wide, rounded at the apex, entire, lobule about 0.2 mm. long and 0.08 mm. wide, narrowly oblong, the free portion 0.06 mm. long or less, obtuse to rounded at the apex; bracteole somewhat connate on one or both sides, oblong, about 0.3 mm. long and 0.16 mm. wide, bifid about one fourth with a narrow sinus and erect, rounded or very obtuse lobes, margin otherwise entire; perianth long-exserted, narrowly obovoid, about 0.6 mm. long, and 0.3 mm. wide, truncate at the apex and with a short beak, narrowed toward the base, sharply five-keeled above the middle, the keels indistinctly crenulate or denticulate from projecting cells, surface otherwise smooth: ♂ inflorescence occupying a short branch, not proliferating; bracts in two or three pairs, closely imbricated, strongly inflated, shortly bifid with a strongly arched, crenulate keel, and blunt divisions; antheridia in pairs; bracteole usually single at the base of the inflorescence, minute, shortly bifid: mature capsule about 0.2 mm. in diameter. [FIG. 2.]

On trees, logs, and sandy banks. FLORIDA: Caloosa, without date, *C. F. Austin;* Sanford, 1906–1913, *S. Rapp 6, 19, 64, 64a, 64b, 69;* Gainsville, 1916, *N. L. T. Nelson 104.* PORTO RICO: near Santurce, 1899, *Mr. & Mrs. A. A. Heller 616, 1365;* near Mayaguez, 1906, *E. G. Britton & D. W. Marble*, mixed with *542;* near Mayaguez, 1914, *E. G. Britton 1906.* Mr. Rapp's No. 64 may be designated the type. The specimens collected by Austin are in the Underwood Herbarium, now belonging to the New York Botanical Garden. In spite of their sterility Austin recognized their distinctness and gave them a manuscript name. Since this name has since been applied to a species from New Caledonia it is not available for the American plant.

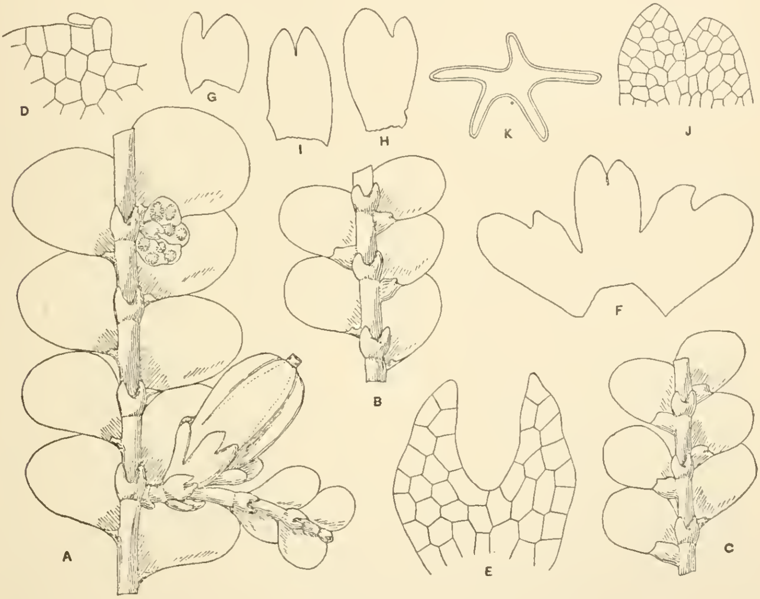

FIG. 2. LEJEUNEA CLADOGYNA Evans

A. Part of a robust plant with perianth and male inflorescence, ventral view, × 40. *B, C.* Parts of sterile plants, showing well-developed lobules, ventral view, × 40. *D.* Apex of lobule, × 225. *E.* Underleaf, × 225. *F.* Bracts and bracteole, × 50. *G–I.* Bracts and bracteole from another involucre, torn apart, × 50. *J.* Apex of bracteole shown in *F*, × 100. *K.* Transverse section of a perianth in upper third, × 50. The figures were all drawn from the type specimen.

In many species of *Lejeunea* the female branches vary greatly in length. This is strikingly true in the case of *L. minutiloba* Evans, a species of the West Indian lowlands, closely related to *L. cladogyna.* A female branch in this species is sometimes greatly elongated and sometimes so short that it bears a single vegetative leaf and a single underleaf in addition to the bracts and bracteole. Between these two extremes all intermediate conditions occur. In *L. cladogyna* the female branches, so far as observed, are always very short and conform to the second of the two extremes noted under *L. minutiloba.* It would perhaps be premature to state that this condition is absolutely constant, but it is certainly predominant, and it therefore seems justifiable to regard it as one of the distinctive characters of the species.

In size and in general habit *L. cladogyna* and *L. minutiloba* resemble each other very closely, and the inflorescence in both species is autoicous. In *L. cladogyna*, moreover, the lobule is usually reduced to a minute basal fold. While, however, this condition seems to be constant in *L. minutiloba*, inflated lobules of the usual *Lejeunea* type are occasionally produced in *L. cladogyna*, although many plants seem to lack them completely. The new species is further distinguished by its underleaves, bracts and perianths. The underleaves, even, when well developed, are only a little broader than the stem and the divisions are rarely more than four cells wide at the base; the lobules of the bracts are highly connate with the lobes and sometimes approximate them in length; the perianth is rounded at the apex, and the five keels extend to the middle or beyond. In *L. minutiloba* the underleaves are often twice as broad as the stem and the divisions may be six or more cells wide; the lobules of the bracts are less highly connate with the lobes and much shorter, appearing like small basal appendages; the perianth is truncate or slightly retuse at the apex, and the keels are restricted to the apical portion.

In *L. glaucescens* Gottsche, another West Indian species found also in Florida, the female branch seems to be constantly very short, just as in *L. cladogyna*, and the two species agree further in their autoicous inflorescence and in the fact that their lobules are often poorly developed. *L. glaucescens*, however, is a larger and more delicate species than *L. cladogyna* and has larger leaf-cells, the median cells of the lobes averaging about 33 μ in length. It is further distinguished by its sharper lobules and by the sharper divisions of its bracteoles.

Two other species of *Lejeunea*, *L. floridana* Evans and *L. flava* (Sw.)

Nees, are known from Florida. *L. floridana* agrees with *L. glaucescens* in most of its vegetative characters, but is distinguished from it by its much larger bracts and bracteole, by the short keels of its perianth (projecting slightly upward as horns), and by the fact that the female branches are often long. These features will serve to separate the species also from *L. cladogyna*. *L. flava* is distinguished by its larger size, by its much larger underleaves (which are often imbricated), by the variable length of its female branches, and by its usually well-developed lobules of the *Lejeunea* type.

3. LEJEUNEA LONGIFISSA Steph.

Lejeunea longifissa Steph. Sp. Hepat. 5: 747. 1915. [FIG. 3.]

On bark of trees. FLORIDA: Sanford, March, 1917, *S. Rapp 83*. CUBA: Monte Verde, February, 1859, *C. Wright*. The type material was collected in Cuba, no further data being given by Stephani. Since the type has not been available for comparison, the writer has been dependent upon the original description, which agrees in all essential respects with the specimens listed above.

The plants are pale green and cling closely to the substratum, forming thin irregular mats. As in so many of the Lejeuneae the best development of the leaves is found on sterile branches, rather than on those bearing sexual organs. In the latter position the lobules of the leaves are often imperfectly formed, although they rarely show the extreme reduction found in *L. cladogyna* and *L. minutiloba*. On sterile branches the leaves are loosely arranged and sometimes do not overlap at all. The lobes are plane or nearly so and spread obliquely. They are broadly ovate and slightly falcate, measuring, according to Stephani, 0.67 x 0.4 mm. The Florida specimens do not attain these dimensions, the largest lobes being about 0.4 x 0.3 mm., but the Cuban specimens have lobes 0.3–0.6 mm. in length. The apex of the lobe varies from rounded to very bluntly pointed, while the margin is entire or vaguely sinuate. The lobule, when well developed, is strongly inflated throughout, broadly ovate in outline, and measures about 0.12 x 0.1 mm. The free margin is involute as far as the apical tooth, which consists of a single, slightly projecting, blunt cell, with the usual hyaline papilla on the proximal side. The leaf-cells have thin walls with distinct trigones and frequent intermediate thickenings. According to Stephani the marginal cells measure 18 μ, the median 27 μ, and the basal cells 45 x 27 μ, these measurements agreeing with those made by the writer.

The underleaves are small and distant and show in general an orbicular outline. They are deeply bifid with an obtuse to lunulate sinus and erect or incurved lanceolate divisions, tipped with one or two cells and usually four cells wide at the base. The lateral margins are entire or vaguely and bluntly unidentate on the sides. The underleaf just below a perichaetial bracteole is usually larger than the others, with slightly broader divisions.

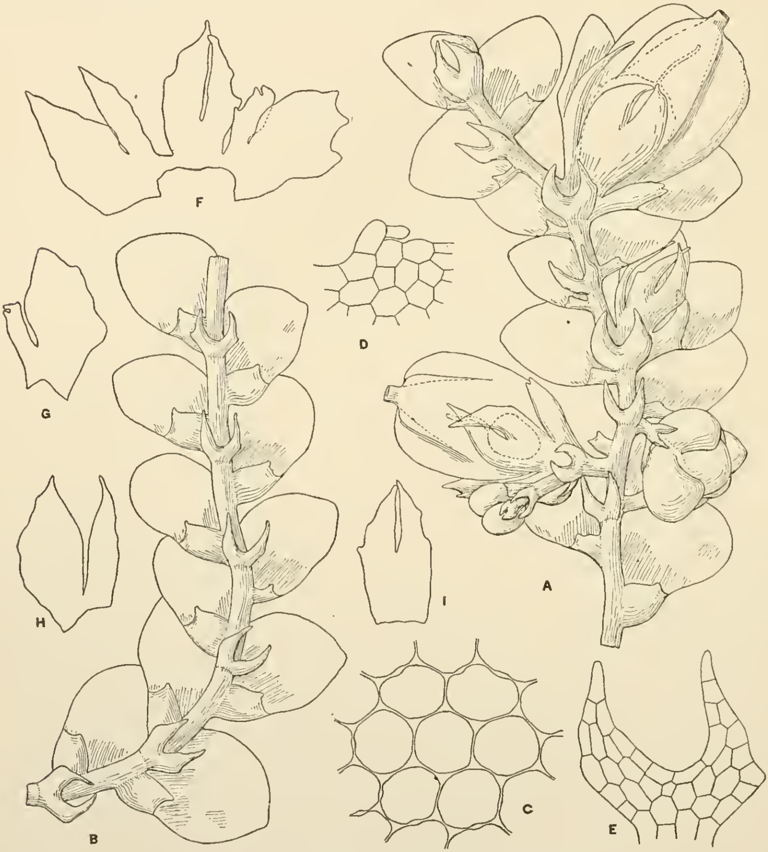

FIG. 3. LEJEUNEA LONGIFISSA Steph.

A. Part of plant with two perianths and a male inflorescence, ventral view, × 50. *B*. Part of a sterile stem, ventral view, × 50. *C*. Cells from middle of lobe, × 300. *D*. Apex of lobule, × 225. *E*. Underleaf, × 225. *F*. Bracts and bracteole, × 50. *G–I*. Bracts and bracteole from another involucre, torn apart, × 50. The figures were all drawn from Mr. Rapp's specimens, No. 83.

The inflorescence is autoicous, as in all the other species of *Lejeunea* known from the United States. The female inflorescence is sometimes borne on a short branch and sometimes on a more or less elongated branch. It innovates on one side and occasionally on both, the innovations being sometimes short and sterile, sometimes again floriferous. The bracts are exceedingly variable. The lobe of the outer bract is usually broad and blunt, the margin varying from entire to coarsely and irregularly sinuate or toothed. The lobe of the inner bract is usually narrow and sharper. The lobule of the outer bract is also blunt in most cases and often shows two indistinct teeth at the apex; the lobule of the inner bract is usually slender and long-pointed. Unfortunately these differences between the bracts are not always apparent. The bracteole is slightly connate on both sides; it is deeply bifid with a narrow sinus and slender, long-pointed divisions, and the margin is sometimes sparingly and irregularly toothed. The perianth is obovoid and distinctly five-keeled, the dorsal keel being shorter than the two ventral. The keels are crenulate and sometimes show very narrow and interrupted wings. The apex of the perianth is rounded or truncate and the beak is distinct. The measurements of the involucral leaves and perianths which Stephani gives are somewhat higher than those made by the writer. According to him the lobes of the bracts measure 0.9 x 0.45 mm. while the perianth is said to be 1.25 mm. long and 0.67 mm. wide. In the writer's experience the lobes of the bracts measure 0.35–0.7 x 0.22–0.35 mm., and the perianth 0.5–0.9 x 0.35–0.5 mm. Stephani speaks of the perianth as being "quasi pedunculata," so that his measurements were evidently made from plants which had passed maturity. In view of the great variation in size exhibited by the bracts and perianths, the discrepancies just noted hardly seem sufficient to warrant a specific separation. The male spikes vary in position and in length and apparently never proliferate. They sometimes occupy short branches and sometimes terminate long branches, and the bracts are mostly in two to six pairs. The antheridia are borne singly or in pairs.

Perhaps the most striking features of *L. longifissa* are the deeply bifid underleaves, from which it receives its specific name, and the variable perichaetial bracts, some of which at least have sharp-pointed and coarsely toothed lobes. In all the other species of *Lejeunea* known from Florida the lobes of the bracts are either rounded or very bluntly pointed, while their margins are entire or vaguely margin entire: inflorescence autoicous: ♀ inflorescence borne on a more or less abbreviated branch, sometimes with only a single vegetative leaf and a single underleaf in addition to the bracts and bracteole, innovating on one side, the innovation short and usually sterile but sometimes bearing a second ♀ inflorescence; bracts obliquely spreading, sharply or bluntly keeled, the lobe falcate, ovate to obovate, about 0.45 mm. long and 0.3 mm. wide, rounded to very bluntly pointed at the apex, margin entire or vaguely sinuate, narrowly oblong, about 0.3 mm. long and 0.09 mm. wide, the free portion scarcely 0.06 mm. long, rounded to acute; bracteole free, ovate-elliptical, about 0.4 mm. long and 0.3 mm. wide, bifid about one third with a narrow sinus and erect or connivent lobes, obtusely to acutely pointed, margin entire or vaguely crenulate; perianth about half exserted, obovoid, mostly 0.6–0.7 mm. long and 0.45 mm. wide, cuneate toward the base, rounded to truncate at the apex with a short beak, five-keeled, dorsal keel shorter and blunter than the others, extending scarcely to the middle, lateral keels sharp, ventral keels usually united into a broad two-angled keel, lateral and ventral keels sometimes very narrowly and vaguely winged, slightly roughened from projecting cells, surface of perianth otherwise smooth: ♂ inflorescence terminal on a more or less elongated branch or occupying a short branch, sometimes proliferating; bracts mostly in four to six pairs, imbricated, about as large as the vegetative leaves, strongly inflated, shortly bifid with a rounded dorsal lobe, a pointed ventral lobe, and a strongly arched keel slightly roughened from projecting cells; antheridia in pairs; bracteoles mostly two at the base of the inflorescence, similar to the underleaves: mature capsule about 0.2 mm. in diameter. [Fig. 4.]

On bark. Florida: Sanford, January, 1917, *S. Rapp 86;* Robinson's Spring, eight miles south of Sanford, May, 1917, *S. Rapp 86a* No. 86 may be designated the type.

In discussing the genus *Cheilolejeunea* several years ago the writer[3] called attention to the fact that its relationship to *Euosmolejeunea* was uncomfortably close. Typical species of *Cheilolejeunea*, to be sure, are clearly distinct from typical species of *Euosmolejeunea*, but other species occupy an intermediate position and might be placed in the one genus almost as well as in the other. The present species is a case in point. In its small size, general habit, foliar characters and small underleaves it agrees with *Cheilolejeunea* better than with *Euosmolejeunea*, but its five-keeled perianth indicates that it should be referred to the latter genus. Possibly, when the species of the two genera are more thoroughly understood, it may be advisable to include them under a single genus.

[3] Bull. Torrey Club 33: 5. 1906.

The closest known relative of *E. parvula* is *E. duriuscula* (Nees) Evans, another species on the border line between *Cheilolejeunea* and *Euosmolejeunea*. *E. duriuscula* is widely distributed in tropical and subtropical America and occurs abundantly in Florida. It is only a trifle larger than *E. parvula*, the lobes of its leaves measuring about 0.4 x 0.35 mm., the lobules in the two species are much like the apical tooth, being very short in both, the underleaves and leaves are very similar, and the perianths, except for a slight difference in size, agree closely. *E. duriuscula*, however, is a yellowish plant of a firmer texture, the leaf-cells have larger and more distinct trigones, the female

FIG. 4. EUOSMOLEJEUNEA PARVULA Evans

A. Part of a plant with perianth and male inflorescence, ventral view, × 50. *B*. Apex of lobule, showing distal hyaline papilla, × 300. *C*. Apex of another lobule, papilla not shown, × 225. *D*. Apex of an underleaf-division, × 225. *E–G*. Bracts and bracteole from a single involucre, × 50. *H, I*. Bract and bracteole from another involucre, × 50. *J*. Transverse section of a perianth in upper third, × 50. The figures were all drawn from the type specimen.

inflorescence is usually borne on a leading branch, and the lobules of the perichaetial bracts are relatively broader and separated from the lobes by deeper sinuses. An even more important difference than any of these is found in the autoicous inflorescence of the new species, *E. duriuscula* being invariably dioicous.

One other species of *Euosmolejeunea*, the widely distributed *E. clausa* (Nees & Mont.) Evans of tropical and subtropical America, is likewise known from Florida. This species agrees with *E. duriuscula* in its dioicous inflorescence but is characterized by its larger underleaves, distinctly rounded or cordate at the base, and by the fact that the female inflorescences are borne on more or less abbreviated branches. The dioicous inflorescence and the underleaves would at once separate *E. clausa* from *E. parvula*, although the short female branches might suggest a relationship. It is further distinguished by its yellowish-green color, by its larger size (the leaf-lobes measuring about 0.5 x 0.4 mm.), and by its firmer texture, the leaf-cells being provided with distinct trigones, just as in *E. duriuscula.*

Other Florida species with which *E. parvula* might perhaps be confused are *Cheilolejeunea polyantha* Evans and *Rectolejeunea phyllobola* (Nees & Mont.) Evans. In the *Cheilolejeunea* the inflorescence is dioicous, the leaves are densely imbricated, the lobes are orbicular and measure about 0.4 mm. in diameter, the underleaves are often broader than long and are rounded or cordate at the base, and the dorsal surface of the perianth is practically without a keel. All of these features would separate it from the new species. The *Rectolejeunea* agrees with *E. parvula* in its autoicous inflorescence but is a somewhat larger plant when well developed and is further distinguished by the proximal position of the hyaline papilla associated with the apical tooth of the lobule, by the lack of a dorsal keel on the perianth and by slight differences in the form of the underleaves, bracts and bracteoles.

6. **Ptychocoleus heterophyllus** sp. nov.

Yellowish or brownish green, scattered or growing in depressed mats: stems 1.5–2 mm. in diameter, sparingly pinnate, the branches obliquely to widely spreading, usually of the *Radula* type, rarely of the *Frullania* type, similar to the stem: leaves loosely to closely imbricated, squarrose when moist, the lobe falcate, ovate, 0.6–0.75 mm. long, 0.45–0.6 mm. wide, rounded at the dorsal base, then strongly outwardly curved to the rounded or very obtuse apex, margin entire; lobule broadly ovate-triangular when explanate, 0.35 mm. long, 0.3 mm. wide, the inflated portion forming a narrowly ovate water-sac, keel strongly arched near the base, then almost straight and forming a very wide angle with the slightly involute ventral margin of the lobe, free margin rounded at the base, then almost straight to junction with lobe (including the apical sinus), bearing usually from five to seven short and strongly inflexed blunt teeth, each consisting of a single projecting cell and separated from its neighbors by about two cells, apical tooth like the others, hyaline papilla proximal to the apical tooth and situated on the dorsal surface of the second cell from the margin, cells of lobe more or less convex, averaging about 13 μ at the margin, 25 x 20 μ in the middle, and 32 x 16 μ at the base, trigones distinct, triangular, mostly with two convex sides and one concave side, intermediate thickenings infrequent, oval: underleaves loosely to closely imbricated, plane, broadly orbicular, mostly 0.3–0.35 mm. long and 0.35–0.4 mm. wide, apex rounded to truncate, base shortly cuneate, rounded, or minutely and indistinctly auriculate, margin entire: inflorescence dioicous: ♂ inflorescence at first terminal, afterwards proliferating; bracts mostly in six to ten pairs, closely imbricated, similar to the leaves but the lobe relatively broader, lobule with a broader inflated portion, ovate, truncate at the outer end, the sinus forming about a right angle with the rest of the free margin, apical tooth one or two cells long, not inflexed, margin otherwise entire or nearly so; bracteoles similar to the underleaves; antheridia in pairs: vegetative reproduction by means of small caducous leaves borne on specialized upright branches with persistent squarrose underleaves: ♀ plant unknown. [FIG. 5.]

On bark of trees. FLORIDA: Sanford, March, 1911, and May, 1912, *S. Rapp;* Robinson's Spring, eight miles south of Sanford, May, 1917, *S. Rapp*. HONDURAS: in deep swamp along Highland Creek, near Puerto Sierra (Tela), at about sea-level, February, 1903, *P. Wilson 569*. The Florida plants lack both antheridia and archegonia; the Honduras specimens bear antheridia only. Mr. Rapp's specimen, collected in 1917, may be designated the type.

The close relationship existing between *Ptychocoleus* and *Brachiolejeunea* has already been emphasized by the writer in another connection.[4] In their vegetative organs the two genera are essentially alike, and the only constant difference between them is the absence of subfloral innovations in *Ptychocoleus* and their presence in *Brachiolejeunea*. Since the plants just described are wholly without archegonia it is clearly impossible to determine their generic position beyond all question. They are referred to *Ptychocoleus* largely on account of their caducous leaves, borne on specialized branches, the leaves

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[4] Bull. Torrey Club 35: 161, 162. 1908.

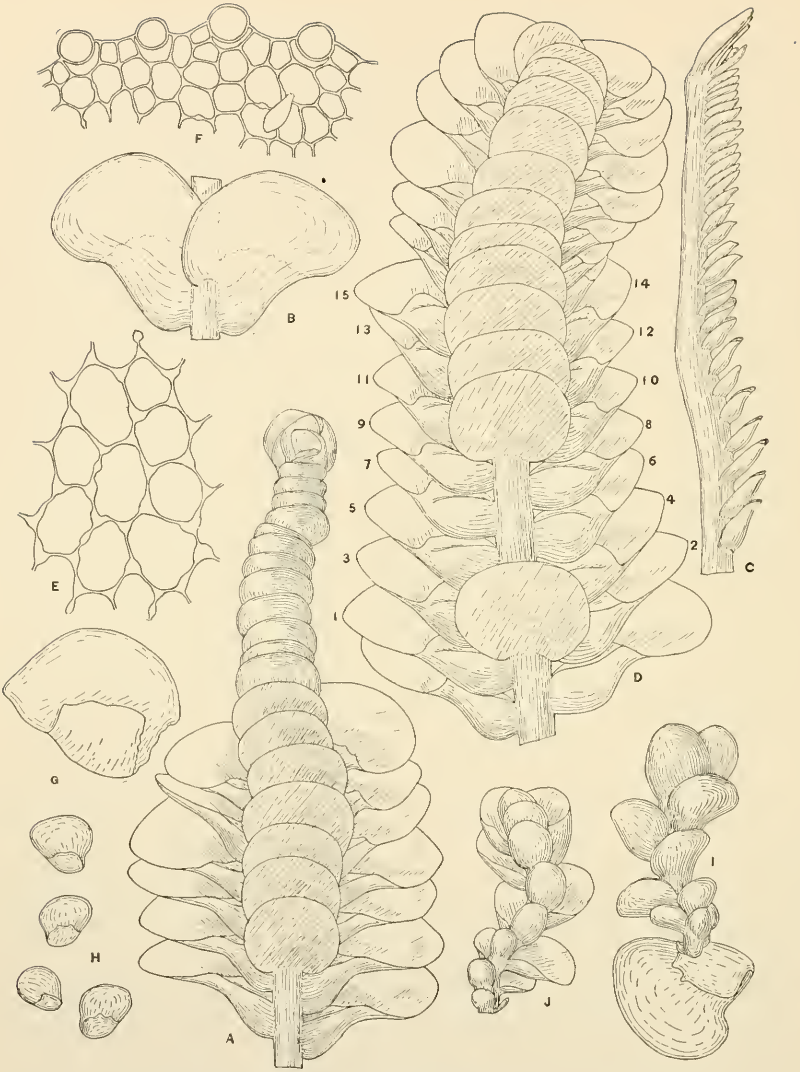

FIG. 5. PTYCHOCOLEUS HETEROPHYLLUS Evans

A. Part of a branch, the apical portion specialized, × 40. *B*. Two vegetative leaves, dorsal view, × 40. *C*. Specialized branch, lateral view, × 40. *D*. Part of plant, including a male inflorescence, the male bracts numbered 1–15, ventral view, × 40. *E*. Cells from middle of lobe, × 300. *F*. Part of lobular margin, the apical tooth at right, × 225. *G*. Male bract, × 40. *H*. Caducous leaves, × 40. *I*. Caducous leaf bearing a new shoot, × 50. *J*. Ventral view of the same shoot, × 50. *A*, *B*, *E* and *F* were drawn from the type specimen; *C*, *H*, *I* and *J*, from the specimen collected by Mr. Rapp in 1912; *D* and *G*, from the Honduras specimen.

serving as organs of vegetative reproduction. Such leaves and branches are unknown in *Brachiolejeunea* but are found in the South American *P. torulosus* (Lehm. & Lindenb.) Trevis.,[5] as understood by Spruce, although their true significance has been overlooked.

Vegetative reproduction by means of leaves which become separated and which afterwards give rise to new shoots by a process of regeneration are now known in several genera of the Hepaticae. In most cases the deciduous leaves are essentially like ordinary leaves and the line of separation is irregular. Such leaves are "Bruchblätter," according to the definition of Correns.[6] In rarer cases the leaves are distinctly modified and separate by means of a regular and definite line. Such leaves are "Brutblätter." Examples of the latter have been described by the writer in *Rectolejeunea flagelliformis* Evans and *R. Berteroana* (Gottsche) Evans,[7] and their occurrence has been noted in *Frullania Bolanderi* Aust.[8]

The caducous leaves of *Ptychocoleus heterophyllus* are likewise Brutblätter. Although they show the usual differentiation into lobe and lobule, both are greatly reduced in size, the lobe measuring about 0.25 x 0.2 mm. and the lobule 0.14 x 0.09 mm. The latter is further distinguished by bearing only one or two marginal teeth, not inflexed as on ordinary leaves. The separation takes place at the very base and no cells are torn across in the process. After separation the basal cells project as minute crenulations.

The branches which bear the caducous leaves vary greatly in length but their growth is limited sooner or later, and no evidence is at hand that they ever revert to the typical vegetative condition. In one case thirty pairs of leaves had been produced. The transition between ordinary leaves and caducous leaves is abrupt; as soon as the latter begin to be formed the branch curves away from the substratum and ceases to form rhizoids. The persistent underleaves are much like ordinary underleaves and their reduction in size is less marked than in the case of the leaves. They are very densely crowded, however, and are distinguished also by being squarrose and more or

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[5] In his Species Hepaticarum (5: 37. 1912) Stephani cites the present writer as authority for this combination with the reference, "Torr. Bot. Cl., 1908, p. 165." If this reference is consulted it will be seen that the combination is correctly assigned to Trevisan.

[6] Unters. über die Vermehrung der Laubm. 338. 1899.

[7] Bull. Torrey Club 33: 10, 13. 1906.

[8] Bryologist 18: 88. 1915.

less convex. At the apex of the branch the few leaves which are still attached bend backward almost as strongly as the underleaves. After the leaves have fallen away the surface of the branch appears irregularly roughened from projecting cells, but it is difficult to determine the actual lines of attachment. The upright leafless branches, with their persistent and crowded underleaves, present a very distinctive appearance. Aside from *P. torulosus* branches of this character have not been noted in the Lejeuneae Holostipae. They may be compared with the flagelliform branches found in *Frullania Bolanderi* and in the two species of *Rectolejeunea* noted above.

The behavior of the caducous leaves after they have fallen away was observed in but a single instance. In this case a new shoot had grown out from the lower surface of the lobule not far from the apical tooth. This shoot was leafy from the very base and had immediately formed undivided underleaves as well as leaves. The latter, although small, showed distinct lobules. In the few Lejeuneae where germination has been observed the spore first gives rise to a row of cells (sometimes very short), then to a flat thallus and finally to a leafy shoot. In certain other genera the leafy shoot at its beginning is destitute of underleaves and shows undivided leaves, even though the adult shoot bears well-developed underleaves and bilobed leaves. It is of interest to note that the shoot growing out of the caducous leaf in *P. heterophyllus* showed none of these embryonic features. At the same time it would be premature to draw any general conclusions from a single example, and it is probable that cases of more pronounced reversion may yet be discovered. It is also probable that the new shoots do not always arise from the lobule. In *Rectolejeunea flagelliformis*, where the caducous leaves lack lobules, the new shoots grow out from the margin of the lobes, and it would be natural to suppose that the *Ptychocoleus* might show the same phenomenon.

The lobular teeth in *P. heterophyllus* are usually five to seven and are remarkable for their uniform structure and regular spacing. On account of their being so strongly inflexed it is easy to overlook them, and their features can only be made out satisfactorily by careful dissection. Each tooth consists of a single projecting cell borne on a broader basal cell, and the apical tooth is indistinguishable from the others except by its position. The proximal tooth, however, is often less definite. The apical sinus, in explanate lobules, continues the line of the free margin and does not form a distinct depression. On the underleaves basal auricles are occasionally present, but they are never well developed, and are always difficult to demonstrate.

The South American *P. torulosus* is still incompletely known and it is possible that the species, as at present defined, represents an aggregate. The type specimen was collected in "Guiana," and the species has since been reported from Dutch Guiana, from Venezuela, and from Brazil. In the Hepaticae Spruceanae specimens were distributed from Obidos, Brazil, and from the vicinity of Chimborazo, Ecuador. These and a portion of the type material in the Mitten herbarium have been available for study.

In the type specimen perianths are present but neither androecia nor caducous leaves were detected. The plants are considerably larger than those of *P. heterophyllus*, and the lobes of the leaves are relatively broader, measuring 1.1–1.3 mm. in length and 0.95–1.2 mm. in width. The ventral margin of the lobe is further distinguished by being distinctly revolute. The margin of the lobule is said to be entire in the original description, but the marginal teeth were soon noted by Lindenberg and Gottsche.[9] They usually number four to six and are less strongly inflexed than those of the new species but resemble them in other respects. The underleaves measure about 0.5 mm. in length and 0.75 mm. in width; in most cases they show small basal auricles, but these are not always distinct and may be absent altogether. A leaf, an underleaf, an involucre, and a perianth in cross section have been figured by Schiffner,[10] presumably from material in the Lindenberg Herbarium at Vienna.

Spruce's specimens are scarcely larger than those of *P. heterophyllus*, but their leaves agree in shape with those of the type from Guiana, measuring about 0.75 mm. in width and scarcely more than that in length. The underleaves, too, are much broader than long and usually show distinct auricles. The free margin of the lobule, however, offers a few distinctive features, when compared with the type. Although the number of teeth is about the same, the apical tooth is longer than the others and extends outward, instead of being inflexed, a distinct sinus being thus formed between the apical tooth and the distal portion of the margin. The other teeth are inflexed, but not very strongly so. The branches with caducous leaves are

[9] Linnaea 24: 627. 1851.

[10] Hedwigia 33: *pl. 7, f. 8–10.* 1894.

probably referred to by Spruce when he speaks of "rami decurvi apice subaphyllo." They agree in all essential respects with those of *P. heterophyllus*.

Two species of *Brachiolejeunea* are known from Florida at the present time, *B. corticalis* (Lehm. & Lindenb.) Schiffn.[11] and *B. bahamensis* Evans.[12] Both usually bear perianths in abundance with the subfloral innovations characteristic of the genus. They are both somewhat darker than the new *Ptychocoleus*, and are slightly more robust, their leaf-lobes measuring about 0.9 mm. in length. Further differences in the marginal teeth of the lobules may be noted. There are usually four of these teeth in *B. corticalis* and five in *B. bahamensis*, the teeth being only slightly inflexed, so that it is possible to flatten them out. In *B. corticalis* the teeth are relatively simple, but in *B. bahamensis* they are usually three or four cells in length and show considerable irregularity.

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[11] See Evans. Mem. Torrey Club **8**: 131. *pl. 18, f. 1–11.* 1902.

[12] Evans. Bull. Torrey Club **35**: 383. *pl. 28, f. 1–4.* 1908.

[Reprint from THE BRYOLOGIST, Vol. XXI, No. 2, March, 1918.]

ADDITIONS TO THE LIST OF BRYOPHYTES FROM CAPE BRETON[1]

George E. Nichols

Two years ago the writer published an account of the bryophytes of Nova Scotia, with special reference to Cape Breton Island.[2] Since then, two more summers have been occupied in the botanical exploration of northern Cape Breton, and in this connection thirteen bryophytes heretofore unrecorded from there have been collected.[3] A list of these is given below. Except where otherwise indicated the various species apparently are unknown from the peninsula of Nova Scotia.

1. Lophocolea minor Nees. French River *1834*.

2. Scapania curta (Mart.) Dumort. Aspy Bay *2024*.

3. Anthoceros levis L. Middle River *2015*.

4. Sphagnum capillaceum (Weiss) Schrank. Mt. Smoky *1763*. This has also been recently collected near Annapolis, Nova Scotia, by Professor J. B. Porter. The var. *tenellum* (Schimp.) A. L. Andrews was reported in the previous paper.

5. Sphagnum Dusenii C. Jens. Ingonish Barrens *2001*.

6. Swartzia inclinata Ehrh. Aspy Bay *2014*.

7. Tortula mucronifolia Schwaegr. Aspy Bay *2008*. Recorded also from Nova Scotia (Macoun).

8. Tortula ruralis (L.) Ehrh. Aspy Bay *1807*.

9. Bryum fallax Milde. Barrasois *1806*.

10. Bryum inclinatum (Sw.) Br. & Sch. Aspy Bay *2012;* Cape North *1805*. Recorded also from Nova Scotia (Macoun).

11. Calliergon giganteum Schimp. French River *1815;* Aspy Bay *1837*.

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Bryologist **19**: 38–47. 1916.

[3] To the species recorded in this paper may be added *Jungermannia lanceolata, Ulota phyllantha,* and *Encalypta contorta,* not previously collected by the writer though listed by Macoun.

12. Buxbaumia aphylla L. Barrasois *1820*.

13. Polytrichum piliferum Schreb. Wreck Cove *1816*. Recorded also from Nova Scotia (Macoun).

These additions bring the number of species of bryophytes recorded as having been collected in Cape Breton up to 361: 96 liverworts and 265 mosses. The bryophyte flora of the province of Nova Scotia as a whole is now known to include 408 species: 105 liverworts and 303 mosses. The writer is indebted to Dr. A W. Evans, Dr. A. L. Andrews, and Mrs. E. G. Britton for assistance in determining various species.

Sheffield Scientific School of Yale University.

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[From Bulletin of the Torrey Botanical Club, 45: 235-251. 15 Je 1918.]

The air chambers of Grimaldia fragrans*

Alexander W. Evans

(with fourteen text figures)

Introduction

In most of the Marchantiales the thallus shows a layer of green tissue with air spaces or chambers below the dorsal epidermis. These chambers exhibit many differences when the group as a whole is considered, but it is possible to refer the majority to three distinct types. To these the names of the representative genera *Riccia*, *Reboulia* and *Marchantia* may be applied.

In the *Riccia* type the chambers occupy a single layer and are in the form of canals with their long axes approximately vertical; the canals are usually narrow and bounded by only four rows of cells, but in certain cases they are broader and bounded by a greater number of cells. In the *Reboulia* type the chambers are in two or more layers (at least in the median portion of the thallus) and are in the form of irregular polyhedrons, often tending to be isodiametric; this type is sometimes complicated by cellular outgrowths into the chambers. In the *Marchantia* type the chambers are again in a single layer (as in the *Riccia* type) but are in the form of more or less flattened polygonal prisms with their longer dimensions approximately horizontal; they are further distinguished by the presence of numerous simple or branched green filaments, extending from the floors of the chambers nearly or quite to the epidermis. In all three types the chambers communicate with the outside air by means of openings in the epidermis. In the *Riccia* type these may be nothing more than continuations of the canalicular chambers, but in the two other types the openings are usually surrounded by specialized epidermal cells and form the characteristic air pores or epidermal pores of the group.

Among North American genera the *Riccia* type is restricted to *Riccia* and *Oxymitra;* the *Reboulia* type is found in *Ricciella,*

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* Contribution from the Osborn Botanical Laboratory.

Ricciocarpus, *Peltolepis*, *Sauteria*, *Clevea*, *Plagiochasma*, *Reboulia*, *Grimaldia*, *Neesiella*, *Cryptomitrium*, *Asterella* and *Bucegia;* while the *Marchantia* type occurs in *Corsinia*, *Targionia*, *Conocephalum*, *Lunularia*, *Preissia* and *Marchantia*. The reduced air chambers of *Cyathodium* conform best perhaps to the *Marchantia* type, in spite of the absence of green filaments, while the adult thallus of *Dumortiera* lacks air chambers altogether.

The genus *Grimaldia* Raddi, as understood by most recent writers, contains about half a dozen species. The most widely distributed of these is *G. fragrans* (Balb.) Corda, which is found in Europe, Asia and North America. Other well-known species, closely related to *G. fragrans*, are the Mediterranean *G. dichotoma* Raddi and the Californian *G. californica* Gottsche. In the eastern parts of the United States *G. fragrans* is sometimes locally abundant, preferring sunny trap ridges and growing on earth among rocks, rather than on the rocks themselves. It was in such a locality as this, on West Rock Ridge, near New Haven, Connecticut, that the material used in the present study was collected. The narrow thallus is firm and compact and produces an abundance of purple ventral scales with bleached-out appendages. The upper surface is grayish green and shows no indications of the boundaries of the air chambers beneath the epidermis. The margins, as well as the ventral surface, are more or less pigmented with purple. The species is markedly xerophytic, the margins becoming involute when dry, thus covering over and protecting the upper surface.

THE AIR CHAMBERS OF THE MATURE THALLUS

The green tissue of the thallus in *Grimaldia* has been repeatedly described, most of the observations having been based on either *G. fragrans* or *G. dichotoma*. Unfortunately the descriptions show marked discrepancies. Stephani (11), for example, states that the air chambers are densely filled with erect green filaments composed of long cylindrical cells, and K. Müller (6, p. 259) notes the presence of vertical plates of cells in addition to the filaments. Schiffner (9, p. 309) criticizes these descriptions. According to his account the chambers of *Grimaldia* undergo a secondary partitioning by means of irregular green lamellae which grow upward from the floors and lateral walls of the chambers. A spongy tissue is thus formed in which narrow air spaces run, scarcely broader than the thickness of the lamellae, and the original partitions of the chambers soon become unrecognizable. He admits that in section the plates of cells one cell thick look like filaments and that marginal cells of the plates sometimes project as teeth, but he maintains that actual filaments are never present and that this fact is at once made evident by sections of the green tissue cut parallel with the surface of the thallus. Massalongo (5, p. 730), on the other hand, agrees with Stephani and states that the chambers are filled with vertical uniseriate filaments, some of them reaching the epidermis. His figures not only show filaments clearly but indicate that the boundaries of the chambers are distinct, in this respect also differing from Schiffner's account.

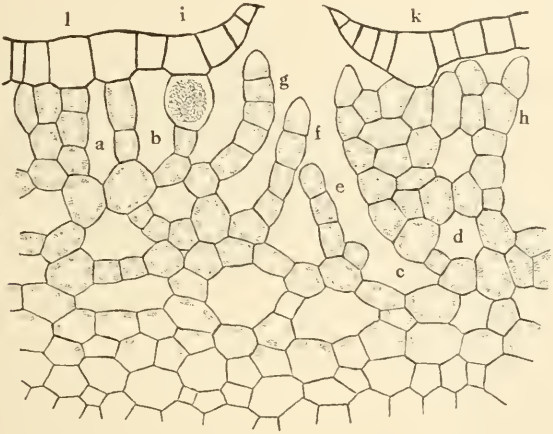


FIG. 1. Transverse section through epidermis and green tissue, × 270. *a–d*, air chambers; *e–g*, apparent filaments; *h*, plate-like outgrowth; *i*, *k*, *l*, boundaries between chambers.

The green tissue of *G. fragrans* is so compact that it is difficult to make out its true structure from ordinary hand sections. Even microtome sections are not always easy to interpret, but they give a much clearer idea of the complex arrangement of the cells and of the intricate system of aërating chambers and help to explain some of the conflicting statements in the published descriptions. In a transverse section, such as the one shown in FIG. 1, the chambers are seen to be in three or four layers in the thickened median portion of the thallus. As the margins are approached the thallus becomes thinner, and the number of layers decreases until only the uppermost layer is left. Except in this uppermost layer the chambers are usually polygonal in outline and tend to be isodiametric. In the uppermost layer they tend to be elongated vertically, as shown in the spaces *a* and *b*. That the spaces communicate with one another is also indicated in the figure. The space *c*, for example, is connected with a space nearer the epidermis, and the space *d* probably represents a passageway to a chamber in another section. The figure seems, at first sight, to confirm the statements made by Müller, that both filaments and cell plates are present. Immediately beneath the pore there are apparently three filamentous outgrowths, *e*, *f*, and *g*, and a plate-like outgrowth is clearly shown at *h*. Of course, as Schiffner intimates, apparent filaments may be nothing more than sections of cell plates. In the section drawn careful focusing does indeed show that *e* and *f* are in close contact with another apparent filament in another plane, and the same thing is true of other apparent filaments in the section. Some of the cell plates, moreover, appear to have a fluted surface, so that a section cut parallel with the surface of the plate might readily give the impression of a series of filaments. At the same time there are many apparent filaments which seem to be entirely free from one another, and it is impossible to determine their true status except by the study of other sections. It will be noted that the more deeply situated chambers are free or nearly so from outgrowths of any kind.

The figure is of further interest in showing that some of the apparent filaments and plate-like outgrowths end freely in the chamber without reaching the epidermis, this being especially true in the vicinity of the pores; others, as shown by the one between the spaces *a* and *b*, extend to the very epidermis and seem to be connected with it. It is doubtful, however, if the connection is ever anything more than a close contact, such as the free filaments in *Marchantia* and *Conocephalum* often exhibit. No instance has been observed where an outgrowth extends downward from the epidermis and ends freely in a chamber, and there is no adequate evidence that the epidermal cells themselves ever give rise to outgrowths, as Schiffner suggests may be the case. The original boundaries of the dorsal air chambers are not absolutely unrecognizable, but they are by no means as distinct as Massalongo's figure represents them. In FIG. 1 the boundaries of the chamber with the air-pore are shown at *i* and *k*, while another boundary is situated at *l*.

The longitudinal section drawn (FIG. 2) brings out the fact that many of the air chambers are more or less elongated. This is strikingly true of those most deeply situated but is also well

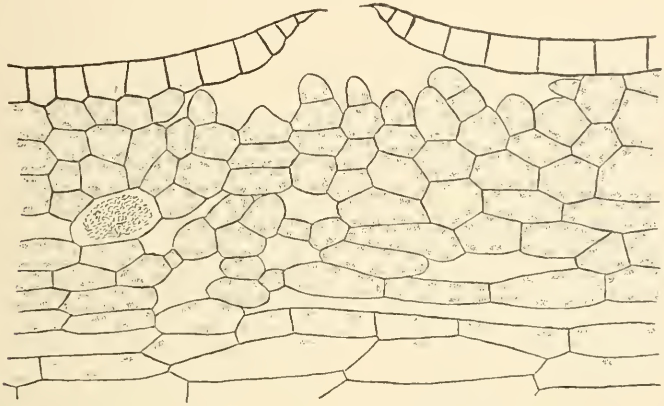
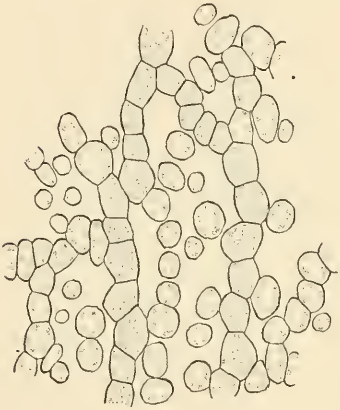


FIG. 2. Longitudinal section through epidermis and green tissue, × 270.

shown by the chamber with the air-pore, although the actual boundaries of this chamber are not definitely indicated. It will be noted that the upper margin of the cell plate represented, which extends almost longitudinally beneath the pore, is distinctly dentate, some of the teeth being over a cell in length. This accords, on the whole, with Schiffner's statement that the marginal cells of the plates may project as teeth. Although some of the teeth shown are more than projecting cells, it would be a stretch of the term to describe them as filaments. The figure, therefore, presents no evidence of the occurrence of true filaments. Other sections, however, show apparent filaments, similar to those represented in FIG. 1.

According to Schiffner, a section through the green tissue parallel with the surface of the thallus will at once show that the chambers are destitute of free filaments. FIG. 3 shows a part of such a section, cut immediately below the epidermis, and seems at first to belie his statement. The figure shows the partitions, almost complete, of an air chamber, the cells being distinguished by stippling. Only one end of the chamber is represented; the other end did not show because the section was slightly oblique in that region and passed through the epidermis instead of the green tissue beneath. That the stippled cells represent the boundaries of a chamber is evident from their close union and also from the fact that an epidermal pore was situated above the middle of the space which they enclose. It will be seen that the chamber contains a number of cells, circular in section and either entirely free or else loosely connected with one another or with the cells of the partitions. Similar cells are shown elsewhere in the figure, and a superficial examination would interpret them as the sections of filaments, especially if they were considered in connection with Fig. 1.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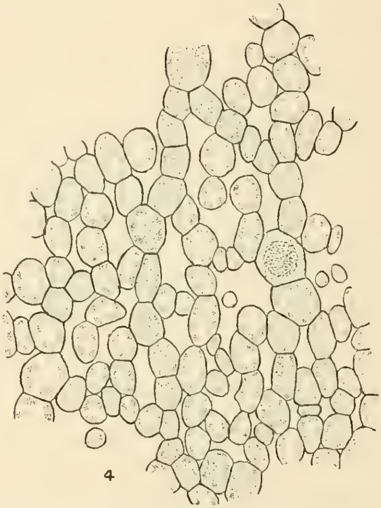
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Fig. 3. Section parallel with the surface, just below epidermis, × 270.
Fig. 4. Section a short distance below the one shown in Fig. 3, × 270.

The incorrectness of this interpretation is brought out by a comparison with Fig. 4, which shows the same chamber at a lower level, the cells of the partitions being again indicated by stippling. In this figure the complete boundaries of the chamber are shown, but the cells enclosed present a very different appearance. They are not only much more numerous but are, with a few exceptions, more or less firmly united, and the entire chamber is thus divided up into smaller chambers, some of which seem entirely cut off while others show their connections with other chambers. The seven cells shown on the right of the left-hand partition in FIG. 3 are represented in FIG. 4 by seven united cells, showing at once that these seven cells are not the cross sections of filaments but simply the cross sections of teeth, like those shown in FIG. 2. Similar conclusions would be created by comparing other apparently free cells in FIG. 3 with their representatives in FIG. 4. It thus becomes established that there are no free filaments in the chambers. It will be noted further that FIG. 4 presents a much more complicated condition than FIG. 3 and that the boundaries of the air chamber would be hardly distinguishable except through comparison with the simpler figure. It is probable that a section like the one shown in FIG. 4 was responsible for Schiffner's statements, which it certainly strongly supports.

In FIG. 5 a section from another thallus is shown, cut at a still lower level. This section shows a loose spongy tissue, two of the chambers being connected by a passageway. Cellular outgrowths are very infrequent, but a single cell, apparently free, is shown in one of the chambers, and a single short outgrowth in another. When compared with FIG. 4 the spaces are relatively larger and fewer and the tissue in consequence much less compact. Sections cut farther down show elongated spaces, similar to those represented in FIG. 2, while sections beneath these show the ventral parenchymatous tissue without spaces of any sort.

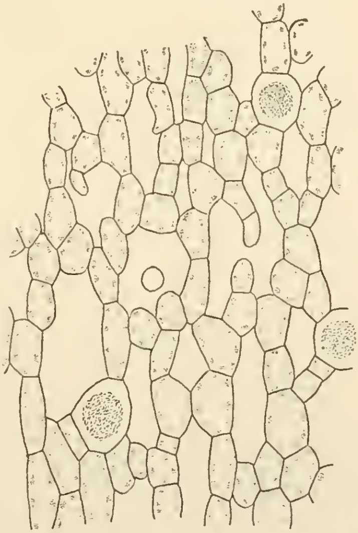


FIG. 5. Section parallel with the surface below the dorsal layer of chambers, × 270.

It is clear from a comparison of transverse, longitudinal and horizontal sections that a distinction may be made between the dorsal layer of air chambers in *Grimaldia* and the more deeply situated layers. In the dorsal layer the original chambers show a secondary partitioning by a system of more or less vertical cell plates, the free margins of which sometimes bear scattered teeth, apparently always less than two cells long. Except for these teeth the chambers lack filaments completely. In the more deeply situated layers, the chambers are much simpler and rarely show evidences of any kind of outgrowth. These conclusions show the incorrectness of certain statements made by Stephani, K. Müller, and Massalongo and the essential correctness of Schiffner's account.

The complex conditions found in the green tissue of *Grimaldia* are duplicated by *Plagiochasma* and by certain species of *Asterella*. The other genera showing the *Reboulia* type of air chamber have a much looser green tissue, the secondary partitioning being less highly developed or absent altogether.

ORIGIN AND ENLARGEMENT OF THE AIR CHAMBERS

The development of the air chambers in the Marchantiales has aroused a good deal of interest among students of the Hepaticae, and the history of the subject is fully given by Barnes and Land (1). The explanation which they advance to account for the origin of the chambers differs in certain respects from the older explanation advanced by Leitgeb and accepted by many of his successors. Leitgeb's explanation was based primarily on his study of *Riccia*, but he extended its application to the more complex genera. According to his ideas the air chambers do not originate in compact tissue, and no splitting of cell walls is involved in their formation. They arise, rather, on the surface of a young thallus and are due to a cessation of upward growth in certain limited areas, the surrounding parts growing upward vigorously. The areas where growth is supposed to cease are situated in most cases where four of the surface cells come together; they mark the lower ends of the chambers, the vertical extent of which depends upon the degree of upward growth which the surrounding parts exhibit.

According to Barnes and Land there is nothing to support Leitgeb's views. In their opinion the chambers always originate in compact tissue below the surface of the young thallus by a splitting of cell-walls and, in case the mature chamber has an epidermal pore, the splitting extends upward until the surface is reached. They based their conclusions on a study of *Ricciella* (*Riccia fluitans* L.), *Ricciocarpus* (*Riccia natans* L.), *Marchantia, Lunularia, Conocephalum, Dumortiera, Asterella* (*Fimbriaria*), and *Plagiochasma*, and assumed that they would apply as well to *Riccia* (in its restricted sense). After the chambers are once established their increase in size need not involve any further schizogenous processes. It is largely brought about by the growth of the cells surrounding the chamber, and may be wholly brought about in this way; in other words, by the surface extension of the bounding cell-walls. According to Leitgeb's ideas the increase in the size of the chambers is brought about in much the same way, except that a total absence of splitting is always assumed. It will be seen, therefore, that the most important differences between the two explanations are concerned with the very beginning of the developmental process: according to Leitgeb the chamber is superficial in origin and no splitting occurs; according to Barnes and Land the chamber is not superficial in origin and splitting does occur.

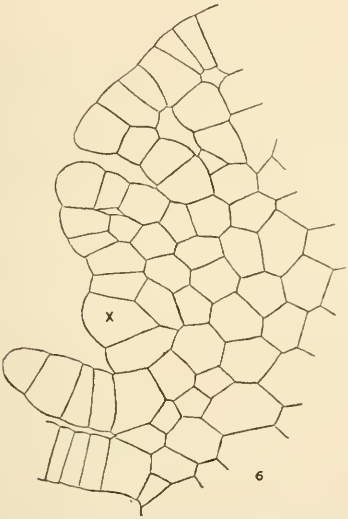
Among recent papers dealing with air chambers, those by Miss Hirsh (4), Pietsch (8), Deutsch (3), Miss O'Keeffe (7) and Miss Black (2) may be briefly noted. Miss Hirsh's work is based largely on *Ricciocarpus natans* (L.) Corda and *Riccia Frostii* Aust. She reaches the conclusion that the first of these species agrees with Barnes and Land's explanation, while the second agrees with Leitgeb's. Her figures of *R. Frostii*, however, by no means support this conclusion fully. Although they show that the chambers drawn may have been superficial in origin, they show as well that a splitting must sometimes have occurred, because some of the chambers extend below the original surface of the thallus. This is brought out clearly by her *f. 6*, upon which she lays especial emphasis. This figure, in fact, presents no convincing evidence that the chamber may not have been initiated by a schizogenous process.

Pietsch's work is remarkable for its thoroughness and accuracy. It deals with species of *Riccia* and *Ricciella*, and his account is therefore based on the group of plants from which Leitgeb drew his conclusions. Although he criticises the work done by Barnes and Land, his observations lead to similar conclusions, so far as the development of the air chambers is concerned. He finds that even in *Riccia* the chambers originate from a splitting of cell walls, the split beginning below the surface and then extending upward until the surface is reached.

Deutsch's paper, devoted to *Targionia hypophylla* L., includes an interesting observation on the development of the air chambers. He states that they arise by a splitting apart of cells close to the apical cell but maintains that the split begins on the outside and extends inward, instead of beginning below the surface and extending outward. The *f. 3*, which he cites as evidence, would be more convincing if the youngest chamber shown did not extend into the hypodermal tissues; as the figure stands it might equally well bear the opposite interpretation from the one drawn. Deutsch does not consider that his account differs in any essential respect from the explanation of Barnes and Land, in spite of the superficial origin which he assigns to the chambers. Miss O'Keeffe, who also worked on *Targionia*, fully supports Deutsch in his statements about the origin of the chambers. Fortunately, the youngest chamber which she shows (*f. 1*, *A*, *a*) seems to be conclusive; it appears in longitudinal section as a split between two superficial cells and does not extend beyond them.

Miss Black's paper deals with *Riccia Frostii*, one of the species investigated by Miss Hirsh, and the same conclusions are drawn as to the origin of the air chambers. Her *f. 6*, however, is open to the same criticism as Miss Hirsh's figures. It represents the apical region of a thallus cut longitudinally and including five young air chambers, but even the youngest of these projects below the original surface, showing that a splitting of a cell wall must have taken place. Miss Black emphasizes the fact that she observed no cases in which an intercellular space appeared below the surface and then broke through to the outside, so that her conclusion regarding the superficial origin of the chambers seems justified. At the same time her figure presents no evidence that the chambers may not have originated from splits between superficial cells, as Deutsch and Miss O'Keeffe maintain is the case in *Targionia*.

The thallus of *Grimaldia fragrans* is so complex that it is impracticable to trace the cell divisions which take place in the segments cut off from the apical cell, as Pietsch has so ably done in the case of *Riccia glauca* L. Figs. 6–8, however, give some idea of the apical region and bring out the fact that a single apical cell with four cutting faces is present. In Fig. 6, immediately above the apical cell the meristematic tissue forms a compact mass without intercellular spaces. Between the fourth and fifth cells the first indication of a chamber appears in the form of a split a short distance below the surface. Between the fifth and sixth cells an older and longer chamber is visible, which has reached the surface, apparently through the upward extension of a similar split. The elongation and widening of the chamber have been largely due, it would appear, to the growth of the bounding cells. The still older chambers shown in the figure are not cut squarely in the middle and need not be further considered.



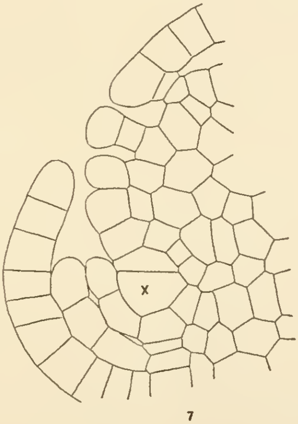


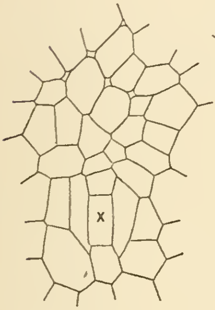
Fig. 6. Longitudinal section through a growing point, × 500. *x*, apical cell.
Fig. 7. Longitudinal section through another growing point, × 500. *x*, apical cell.

In FIG. 7, which represents the apical region of another thallus, a somewhat different condition is revealed. In this case the first indication of an air chamber appears between the third and fourth cells and is likewise in the form of a split, but this time the split evidently began on the outside and extended inward. Although the chamber is thus superficial in origin, there is no evidence that a surface area has had its upward growth arrested, as Leitgeb's explanation demands. The split clearly extends inward from the original surface. The chamber between the fourth and fifth cells is considerably deeper and broader, and it is clear that its increase in size has involved further schizogenous processes. The next chamber shown gives evidence of a further horizontal extension.

It would appear from these two figures that the air chambers in *Grimaldia fragrans* owe their origin to a splitting of cell walls, but that the place where the split first makes its appearance is not always the same. It may be below the surface and extend outward, in which case it agrees fully with the explanation advanced by Barnes and Land; it may be at the surface and extend inward, thus agreeing with Deutsch's account of *Targionia hypophylla*. In the writer's opinion the figures published by Miss Hirsh and Miss Black might be interpreted in the same way as FIG. 7, so that there still seems to be no conclusive evidence that Leitgeb's explanation ever applies.

FIGS. 8–10 yield further evidence as to the origin of the chambers; they were all drawn from a single section, cut at right angles to the long axis of the thallus, and show for the most part superficial cells. In FIG. 8 the apical cell appears in the form of a rectangle. Directly above it an air chamber reaching the surface is shown between the fourth and fifth cells, corresponding apparently with the chamber between the fourth and fifth cells of FIG. 7. The schizogenous origin of this chamber seems clear, but there is nothing to show whether the split began at or below the surface. Between the third and fourth cells no signs of a chamber can be discerned, although a superficial split may be present like the one shown in FIG. 7. The figure at any rate gives no evidence of a split beginning below the surface.

FIGS. 9 and 10 are much more conclusive. They represent a portion of the thallus to the right of the apical cell and derived from lateral segments. In drawing FIG. 9 the microscope was focused on the surface of the cells in a circumscribed area; in drawing FIG. 10 it was focused a little below the surface of the same area. FIG. 9 shows a series of cells in close union and two air chambers which have reached the surface; FIG. 10 shows the same two chambers and six additional ones. The latter clearly represent schizogenous spaces below the surface and demonstrate an origin like that of the youngest chamber in FIG. 6.



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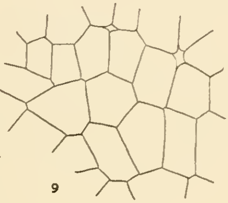

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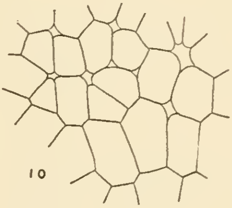

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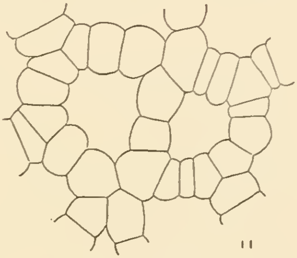

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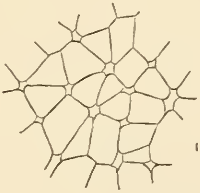

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FIG. 8. Transverse section through a growing point, × 500. *x*, apical cell.

FIG. 9. Superficial cells to the right of the apical cell shown in FIG. 8, × 500.

FIG. 10. The same region as that shown in FIG. 9, but at a slightly lower focus, more very young dorsal chambers being visible, × 500.

FIG. 11. Slightly older dorsal chambers than those shown in FIG. 10, the section parallel with the surface, × 500.

FIG. 12. Section just below the one shown in FIG. 11, the numerous intercellular spaces being the beginnings of more deeply situated chambers, × 500.

The rudimentary chambers shown in FIGS. 6–10 represent the beginnings of the complex dorsal chambers shown in FIGS. 1–4. The later stages in the development of these chambers and the origin and development of the more deeply situated chambers are exceedingly difficult to follow. For a while the dorsal chambers are distinct enough in sections cut immediately below the epidermis. Such a section is shown in FIG. 11, where two complete chambers and parts of six others are represented. The increase in size which these chambers show, when compared with the small intercellular spaces in FIG. 10, is due to the vigorous growth of the bounding cells, accompanied by rapid cell divisions. At this stage the partitions show no evidence of outgrowths. FIG. 12 represents the section just below the one shown in FIG. 11, the cells drawn, in part at least, forming the floors of the dorsal chambers. The figure shows many intercellular spaces, which are clearly schizogenous in origin; these spaces represent the beginnings of the more deeply situated chambers or, in some cases, the passageways leading from these chambers to the dorsal chambers.

A longitudinal section, representing about the same stages as those shown in FIGS. 11 and 12, may be seen in FIG. 13, the left-hand side of the figure being toward the apical cell. The very rapid development of the chambers is clearly indicated, and light is thrown on the way in which the deeper chambers originate, such chambers being indicated by the letters *a–e*. It will be seen that some of these chambers seem to be completely enclosed, showing that they may have originated by a splitting of cell walls in compact tissue, and that others already communicate with more dorsally situated chambers. Whether the connecting passageways are always formed subsequently to the chambers, or whether the formation of the passageways may sometimes precede that of the chambers is not altogether clear. If the older, right-hand side of the figure is compared with the younger, left-hand side, it becomes evident that the tissue with intercellular spaces has almost tripled in thickness and that the dorsal chambers have become distinctly deeper. The rapid growth involved in these changes has taken place in the original partitions of the dorsal chambers, in the cells which formed their irregular floors and in the cells immediately beneath. As the writer conceives the process, the growth of the partitions is both horizontal and

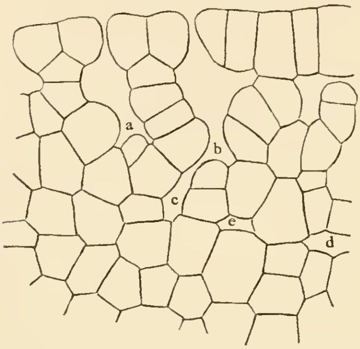

FIG. 13. Longitudinal section through young chambers, × 500. *a–e*, more deeply situated chambers.

vertical, the growth in the latter direction being often equalled by the upward growth (accompanied by cell division) of the cells forming the floors of the chambers; these in turn remain more or less united with one another and with the cells of the partitions and in this way form the system of united cell-plates in the dorsal chambers. At a later stage the margins of some of the plates which end freely in the chambers give rise to teeth as shown in FIG. 2.

It is difficult to secure direct evidence from the vegetative thallus that the partitions form surface-outgrowths. FIG. 14, however, which is drawn from a section of the young female receptacle, shows that such outgrowths are possible. The section was cut parallel with the upper surface of the receptacle, and the figure shows two complete chambers and parts of eight others; two of the latter contain sections of the tubular epidermal pores which hang down from the roofs of the chambers. The partitions are one cell thick but give the impression of being thicker when cut obliquely. The outgrowths originate as projections of cells which become cut off by walls and then continue their growth and cell-divisions. In the vegetative thallus such outgrowths evidently play a very minor part in the development of the green tissue.

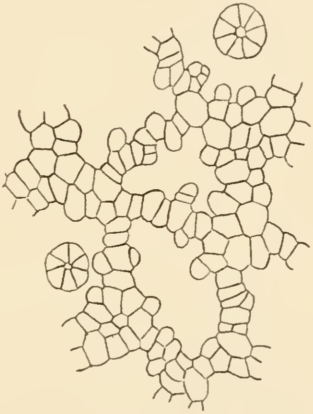

FIG. 14. Section parallel with the surface of a young female receptacle, just below the epidermis, × 270.

The chambers below the dorsal layer make their appearance very early, as seen in FIGS. 12 and 13, although they always appear later than the dorsal chambers. As the thallus becomes differentiated, these chambers increase rapidly in size through the growth of the bounding cells, but the appearance of new chambers, except in the apical region, has not been demonstrated and seems improbable. If schizogenous processes play a part in the enlargement of these chambers, it is only to a very limited extent.

The green tissue in the thallus of *Plagiochasma* bears a strong resemblance to that of *Grimaldia.* Its development has been described by Miss Starr (10), her investigation having been based on an undetermined species from Mexico. She confirms the earlier observation of Barnes and Land that the air chambers of *Plagiochasma* owe their origin to a splitting of cell walls below the surface. She notes further that the chambers are at first deep and narrow but that they soon become wide and irregular, and she ascribes the changes in size and form which they show to a "stretching and tearing of tissues between neighboring chambers." In other words she considers that schizogenous processes play a leading part in the enlargement of the chambers as well as in their origin. This conclusion is hardly supported by her *f. 11* or by the earlier figures published by Barnes and Land (1, *f. 17–22*). Although these figures indicate a schizogenous origin of the chambers, they do not disprove that the enlargement is mainly due to the growth of the surrounding cells.

SUMMARY

The air chambers of *Grimaldia fragrans* are in several layers in the thickened median portion of the thallus.

The dorsal chambers communicate with the outside by means of epidermal pores. They are subdivided by an irregular system of more or less vertical, united cell plates, enclosing narrow spaces, so that the boundaries of the chambers are difficult to distinguish. The cell plates sometimes reach the epidermis and sometimes do not; in the latter case the free margins sometimes bear scattered teeth, less than two cells in length, especially in the vicinity of the pores. Except for these teeth the chambers lack filaments completely.

The more deeply situated chambers communicate with one another and with the dorsal chambers by means of passageways; they are scarcely or not at all subdivided by cell plates.

The chambers all owe their origin to a splitting of cell walls in closely united tissue. In the case of the dorsal chambers the split sometimes begins below the surface and extends outward; sometimes at the surface and extends inward.

The dorsal chambers appear first, very close to the apical cell, but the more deeply situated chambers appear soon afterwards.

The increase in the size of the chambers is due largely to the growth of the bounding cells and only slightly to further splittings of cell walls. The system of united cell plates in the dorsal chambers and the partitions between the chambers increase in vertical height simultaneously. Direct outgrowths from the surfaces of cell plates play a very small part in the process of subdivision.

The material upon which this investigation was based was collected and prepared by Mr. John F. Logan, who expected to utilize it in his own studies. Through the pressure of other work his plans could not be realized, and his preparations were placed at the disposal of the writer for examination. The writer would therefore express his sincere thanks to Mr. Logan for his courtesy.

SHEFFIELD SCIENTIFIC SCHOOL,
YALE UNIVERSITY

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4

TRANSACTIONS OF THE
CONNECTICUT ACADEMY OF ARTS AND SCIENCES
INCORPORATED A. D. 1799

VOLUME 22, PAGES 249-467 JUNE, 1918

The Vegetation
OF
Northern Cape Breton Island, Nova Scotia

BY

GEORGE E. NICHOLS, Ph.D.,
ASSISTANT PROFESSOR OF BOTANY IN THE SHEFFIELD SCIENTIFIC SCHOOL
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INTRODUCTION

I. GENERAL PHYTOGEOGRAPHIC RELATIONS OF THE REGION

Viewed from the standpoint of ecological plant geography, the vegetation of the forested portions of eastern North America, north of southern Florida, comprises two great climatic formations: the Deciduous Forest Formation and the Northeastern Evergreen Coniferous Forest Formation. Viewed from the standpoint of floristic plant geography, it is possible to subdivide the vegetation of this area still further (in this connection see especially Transeau '05, Harshberger '11, Shreve '17), but from the ecological point of view, as will be emphasized later, the advisability of such subdivision is at least open to question.

The deciduous forest formation attains its highest and most typical development in the lower Ohio basin and the southern Appalachians, where the climax forests are made up almost wholly of deciduous trees. These include a wealth of species, prominent among which are beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*), chestnut (*Castanea dentata*) and tulip (*Liriodendron Tulipifera*), red oak (*Quercus rubra*), white oak (*Quercus alba*), hickory (especially *Carya alba*), and white ash (*Fraxinus americana*). The evergreen coniferous forest formation attains its optimum development in middle-eastern Canada. Here the climax forests are relatively poor in species, consisting mainly of balsam fir (*Abies balsamea*), white spruce (*Picea canadensis*) and black spruce[1] (*Picea mariana*), with which is associated the paper birch (*Betula alba papyrifera*).

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[1] In all the current manuals a distinction is made between the black spruce and the red spruce (*Picea rubra*). After several years of experience in the north-woods, the writer is obliged to confess his inability to differentiate with certainty between the two, an inability which he finds to be shared by many other botanists. It is his opinion that the red spruce at best should be regarded merely as a variety of the black spruce, the status which it formerly held. To be sure, the small, impoverished bog form of this tree (the typical *P. mariana* of the manuals) does appear very distinct when compared with the large, thrifty upland form (which typifies *P. rubra*); but there are all sorts of intergradations between these two

Midway between these two regions (see map, Fig. 1), is situated the Transition Forest Region, a broad zone in which, due to the overlap in the ranges of the southern and northern climax

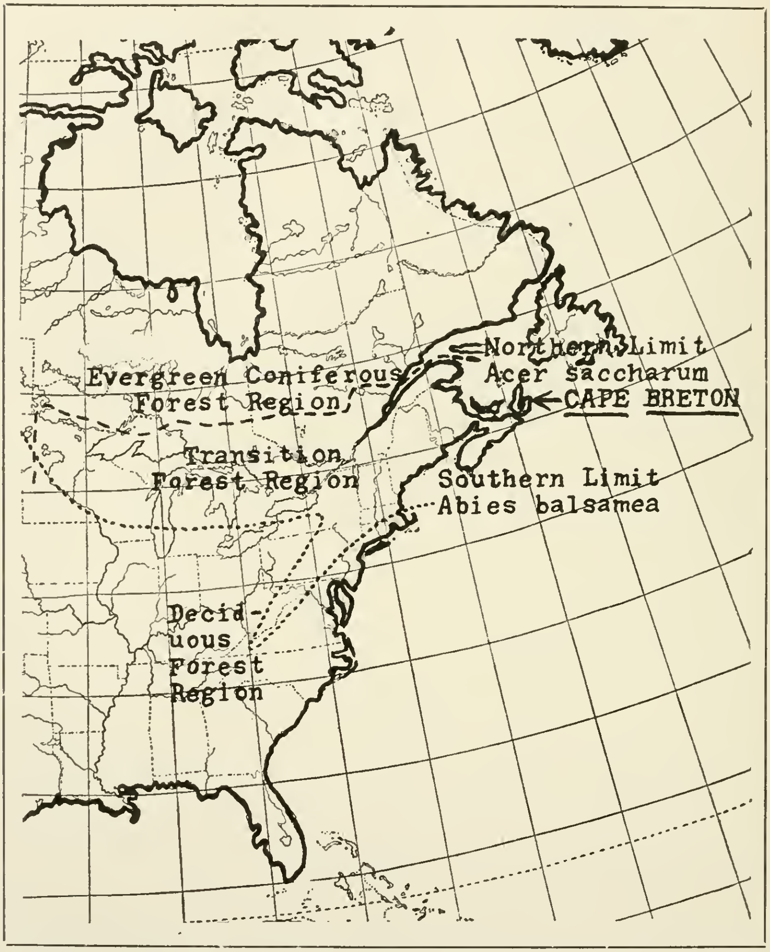

Figure 1.—Map of eastern North America, to show position of Cape Breton Island with reference to the Transition Forest Region.

extremes. Moreover, especially in these intermediate forms, the structural dissimilarities upon which the manuals lay stress in attempting to differentiate two distinct species, are far from satisfactory in their application. In the present paper no attempt is made to distinguish *P. rubra* from *P. mariana,* although it is appreciated that much of the upland spruce may perhaps well be referred to the former "species."

trees, the nature of the climax forest, taken in its entirety, is intermediate between that of the evergreen coniferous, and that of the deciduous climatic formation, as most typically developed: where, in other words, the two formations are telescoped. This region represents a great tension zone, in which competition between the northern and southern climax trees is still in active progress, and where, as a result, it is possible to study the ecological relations of the two groups of species concerned. The northern boundary of this transition region is determined by the northern outposts of the deciduous climax trees of the deciduous forest formation: it may be regarded as coinciding approximately with the northern limit of the sugar maple (see, in this connection, Cooper '13, pp. 36–39). In the same way, the southern boundary of the transition region may be said to be determined by the southern outposts of the climax trees of the evergreen coniferous forest formation, in so far as these grow on uplands: it may be regarded as coinciding roughly with the southern limit of the balsam fir. These boundaries are indicated on the map (FIG. 1), but the lines as drawn can represent little more than a rough approximation; for, owing largely to variations in topography, at higher elevations the evergreen coniferous forest formation locally extends far to the south of the northern boundary, while at lower elevations the deciduous forest formation is typically developed considerable distances north of the southern boundary of the transition region, as here represented.

From the standpoint of floristic plant geography it is significant that the geographic center of distribution for the so-called Canadian element in the flora of eastern North America lies within this transition region. Many Canadian species are practically confined to this area, prominent examples of this latter group, among the woody plants, being *Pinus Strobus* and *P. resinosa, Tsuga canadensis, Betula lutea, Acer pennsylvanicum,* and *Viburnum alnifolium.* But while, from the floristic point of view, the vegetation of this region certainly is more or less unique, from an ecological point of view it is doubtfully to be regarded as a distinct climatic formation. And while its intermediate character is generally recognized, nevertheless, largely because of the almost universal supremacy, in situations edaphically favorable to their development, of the climax trees of the deciduous forest formation over those of the northeastern evergreen conifer-

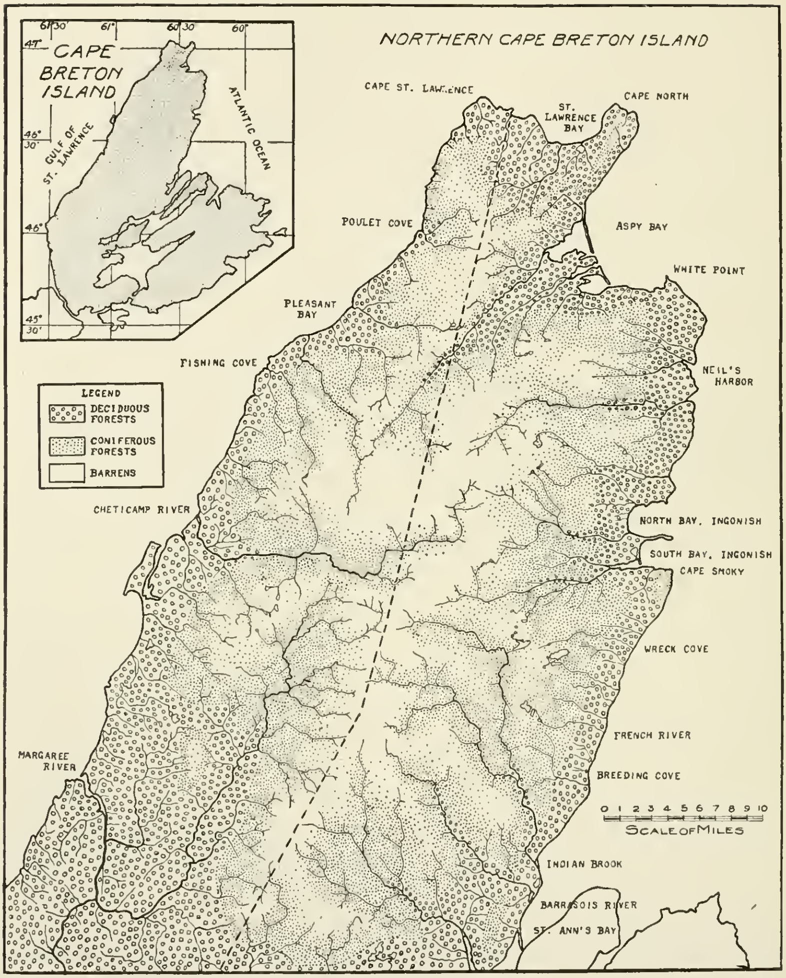

FIGURE 2.—Map of northern Cape Breton, showing approximate distribution of deciduous forest climatic formation and northeastern evergreen coniferous forest climatic formation. The unshaded areas are very largely occupied by barrens. Inserted map: Cape Breton Island, together with a small portion of the peninsula of Nova Scotia.

ous forest formation, wherever these two groups come into competition with one another, from the standpoint of ecological plant geography it seems best, on the whole, to regard the vegetation of this transition region as constituting merely the northward extension of the deciduous forest formation.

As a glance at the map (FIG. 1) will show, Cape Breton Island, located northeast of the peninsula of Nova Scotia (lat. 45° 30′–47° N.; long. 60° 15′–61° 30′ E.), and separated from the mainland only by the Gut of Canso, a narrow strait scarcely a mile wide, is situated near the northern edge of the transition forest region. In northern Cape Breton, owing chiefly to differences in climate at different elevations, both the deciduous forest formation and the northeastern evergreen coniferous forest formation are well represented: the former predominates from sea level up to an altitude of about 700 feet; the latter prevails at higher elevations. The approximate distribution in this region of these two formations is mapped in FIG. 2. The vegetation of the Barrens, which occupy the highest parts of the plateau, apparently bears much the same relationship to the evergreen coniferous forest formation on the one hand and the arctic tundra on the other that the vegetation of the transition forest region bears to the deciduous forest formation and the evergreen coniferous forest formation respectively: it seems to represent a transition between evergreen coniferous forest, as typically developed, and tundra. For various reasons the barrens have been mapped as distinct, but their vegetation is to be regarded merely as the upward extension of the evergreen coniferous forest formation.

II. PREVIOUS BOTANICAL INVESTIGATIONS, AND FIELD WORK OF THE AUTHOR

Aside from the work of Ganong ('91, '93, etc.) and Transeau ('09), practically no investigations of a purely ecological nature have been conducted in the Maritime Provinces of eastern Canada (New Brunswick and Nova Scotia). The present paper aims to portray in a general way the ecological relations of the vegetation in a portion of this area.

So far as is known to the writer, only three other botanists—John Macoun ('83–'02, '98), C. B. Robinson ('03, '04, etc.), and

J. R. Churchill—have undertaken any explorations in northern Cape Breton. Aside from the work of these three, which was almost wholly taxonomic, scattered observations of general botanical interest are recorded in the report on the geology of this region ('85) by Hugh Fletcher, the pioneer geologist whose detailed maps, constructed more than thirty years ago, have afforded the basis for all subsequent explorations; while B. E. Fernow, on the basis of a survey made for commercial purposes, has briefly described the forests here, with an accompanying map, in his account of the forest conditions of Nova Scotia ('12).

The writer's acquaintance with northern Cape Breton dates back to 1905 when about three weeks were occupied in a tramp along the coast from Baddeck to Ingonish, across the island from North River to Northeast Margaree, and thence back to Baddeck. It was on this trip that the curly grass fern (*Schizaea pusilla*) was first recorded from Cape Breton (see Nichols '05). In 1909, a month was spent in camp near the mouth of the Barrasois River, but beyond the collection and identification of mosses and liverworts no serious botanical work was attempted. The investigations embodied in the present paper were projected in 1913 and have been carried on for parts of four summers. Altogether, during this time, more than six months have been occupied by field work in northern Cape Breton. In 1914, and again in 1915, a base camp was maintained for about a month along the lower course of the Barrasois River (St. Ann's), from which point excursions were made into the surrounding country, while another month was spent at various points along the eastern coast, between St. Ann's Bay and Aspy Bay, and in the interior. During the summer of 1916 the entire length of the coast from St. Ann's Bay to Cape North was traversed on foot, and a week was spent in the interior. On this trip the writer was accompanied by Dr. L. H. Harvey, whose experience in the Mt. Ktaadn region suggested many interesting comparisons. The first draft of the present paper was prepared during the college year 1916-1917, and in the summer of 1917 another month was spent in the field, partly for the purpose of checking up previous observations, partly with the object of visiting the western coast of the area under consideration. On this trip, starting from Baddeck, the author traveled to Middle River, Northeast Margaree and Margaree Harbor, thence along the coast to Cheticamp and Pleasant Bay, across the island to Aspy Bay, and from here to Ingonish, from which point another excursion was made into the interior.

As a desirable adjunct to the ecological investigations, considerable attention has been devoted to the flora of the region: two papers on the bryophytes of Cape Breton have already been published ('16^{a}, '18), and a similar catalogue of the vascular plants is contemplated. Incidentally, in addition to the studies in northern Cape Breton, the writer has recently visited two other widely separated areas within the transition region: in the spring of 1916 a week was spent at the Yale Forest School Camp near Brandreth, in the western Adirondacks; while during the summer of 1917 nearly a month was occupied, in company with Dr. Harold St. John of the Gray Herbarium, in exploring the upper waters of the St. John River, in northwestern Maine. Also, in connection with the study of raised bogs in northern Cape Breton, a visit was made, in 1917, to one of the New Brunswick bogs described by Ganong ('91, '97).

III. ACKNOWLEDGMENTS

The writer wishes to express his indebtedness to Professor Alexander W. Evans for his continued interest in this work throughout its progress; to Mr. Albert F. Hill, Professor Merritt L. Fernald, Dr. Harold St. John, and Mr. Charles A. Weatherby, who have determined or passed judgment on the vascular plants collected; to Professors A. Le Roy Andrews and Lincoln W. Riddle, who have determined the sphagnums and lichens respectively; and to various others (see Nichols '16^{a}), who have assisted in the determination of the bryophytes.

IV. PHYSIOGRAPHY

Cape Breton Island is about 4,000 square miles in area: it is approximately four-fifths as large as the state of Connecticut. Its greatest length (from the Gut of Canso to Cape North) is about 110 miles, its greatest width (from Margaree Harbor to Cape Breton) about 75 miles. The general configuration of the island is brought out by the map (FIG. 2). It comprises two distinct peninsulas, which are united at the south by the narrow Isthmus of St. Peter (now cut by a ship canal), and which almost completely enclose the Bras d'Or Lakes, an irregularly shaped mediterranean sea fifty miles long and in places twenty miles wide. The area treated as northern Cape Breton in the present paper is about sixty miles long with a maximum width of about thirty miles.

A good idea of the general character of the country is conveyed by the accompanying series of photographs. In addition to those introduced in the present connection, attention is especially called to the following: Figs. 21, 24, 26, 28, 30, 33, 38, 41, 50, 51.

Figure 3.—View of lowland and plateau from Middle Head, Ingonish: in upper right background, Mt. Franey; to left of this, valley of Clyburn Brook; in foreground, low granitic headland, drift-covered, with second growth forests of white spruce and balsam fir.

From a topographic standpoint the outstanding feature of northern Cape Breton is the great interior plateau, which stretches in almost unbroken continuity from Cape North nearly to the Bras d'Or. This massive remnant of the ancient Atlantic Upland (Goldthwait '16), composed of granites, syenites, and other highly resistant, crystalline rocks of Laurentian age, includes the highest land in Nova Scotia. The average elevation of its surface in northern Cape Breton is between 1,000 and 1,200 feet, but in places it is considerably higher.[2] South of the area under discussion the plateau becomes greatly fragmented and its surface gradually approaches sea level. In southeastern Cape Breton the summits of the Laurentian highlands rarely attain an elevation of more than 300 feet.

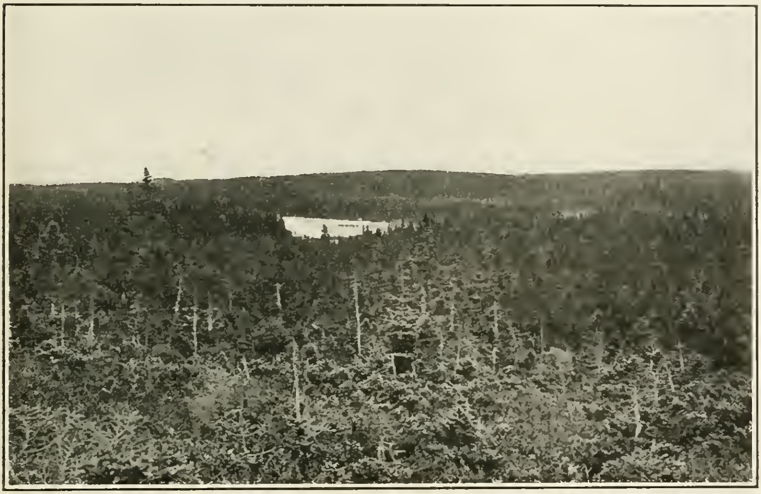

FIGURE 4.—Characteristic view on the plateau: looking westward from an eminence north of the Barrasois River; primeval forests of balsam fir, etc.

As one approaches the eastern coast of northern Cape Breton in the little coasting steamer, which affords the easiest means of travel along the shore north of Sydney, the plateau, as viewed in the distance, presents an even, unbroken skyline (see especially FIG. 30). But to one standing on the summit of Mount Franey, or some other eminence along the eastern margin of the tableland, its surface appears as a broad expanse of low, rounded hills, which stretches westward to the horizon (FIGS. 4, 51). Hidden away among these distant hills are innumerable little lakes and ponds, countless deep valleys and wild gorges.

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[2] Mount Franey (FIG. 3), the loftiest hill recorded, measures 1,370 feet in height. In the opinion of the writer there are numerous higher summits in the interior of the island.

Figure 5.—View looking southward along coast from near summit of Mt. Smoky: Carboniferous lowland in mid-distance; elsewhere the underlying rocks are crystalline.

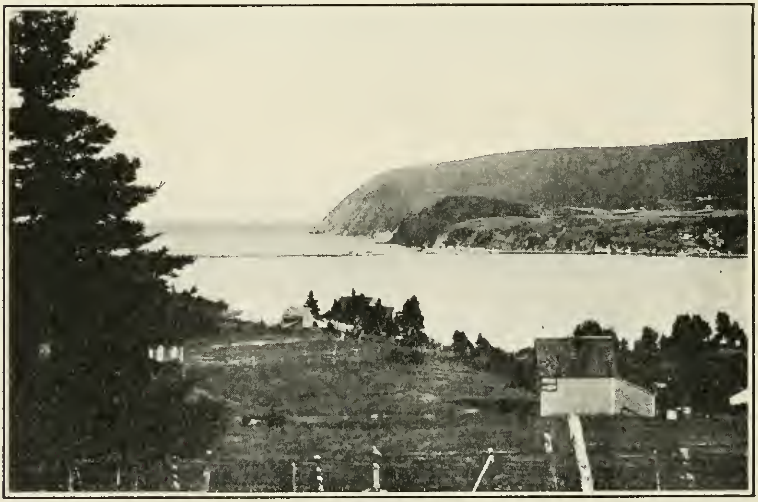

Figure 6.—Ingonish Harbor: Mt. Smoky (granitic) in distance, with lower Carboniferous hills and the shingle spit which partly encloses the harbor in mid-distance; Carboniferous lowland in foreground.

Along certain sections of the coast in northern Cape Breton the crystalline rocks extend bluffly out to the shore. In places, as between Aspy Bay and Neil's Harbor (Fig. 38), these rugged granitic shores are relatively low. Elsewhere, as at Cape North (Fig. 30) and Cape Smoky (Fig. 6), the mountains rise abruptly from the sea: at Cape Smoky and along the northwest shore are magnificent sea cliffs many hundred feet in height. But along much of the coast, a low border of Carboniferous rocks—sandstone, shale, dolomite, gypsum, etc.—intervenes between the crystalline area and the sea. On the eastern shore (Figs. 5, 26, 33), and on the western shore north of Cheticamp, this fringe of softer rocks is rarely more than a mile in width; ordinarily it is much less. At certain places even here, however, as at North River, Ingonish, Aspy Bay (Figs. 7, 20), Bay St. Lawrence, and Pleasant Bay, the Carboniferous lowland extends inland for several miles along the rivers, forming broad intervales. In the southwestern part of the area mapped (Fig. 2), in the Margaree district, the lowlands are much more extensively developed than elsewhere (Fig. 21).

Figure 7.—The Big Intervale at Aspy Bay: farms and second growth forests; *Pyrus americana* in right foreground.

It has been inferred by some geologists that Cape Breton Island escaped glaciation, and this has been assumed as a hypothesis by certain botanists (Robinson '06, p. 258; Taylor '12, p. 24), in an attempt to explain certain peculiarities of plant distribution. Such, however, is hardly the case. On the plateau, to be sure, superficial deposits of any depth are scarce, the rock surface often being bare or covered with granite boulders of apparently local origin. Soil, when present, is usually thin: commonly it consists of a coarse quartz sand or gravel derived through the decomposition of the underlying rock. But even on the plateau, as, for example, along the trail between Pleasant Bay and the Big Intervale at Aspy Bay, there may be found considerable deposits of drift. Further, the seemingly complete absence of a truly alpine flora, even on the higher summits, would point strongly toward glaciation. In the lowland, the Carboniferous formations everywhere are hidden by a mantle of glacial débris: in places along the coast, as at French River and

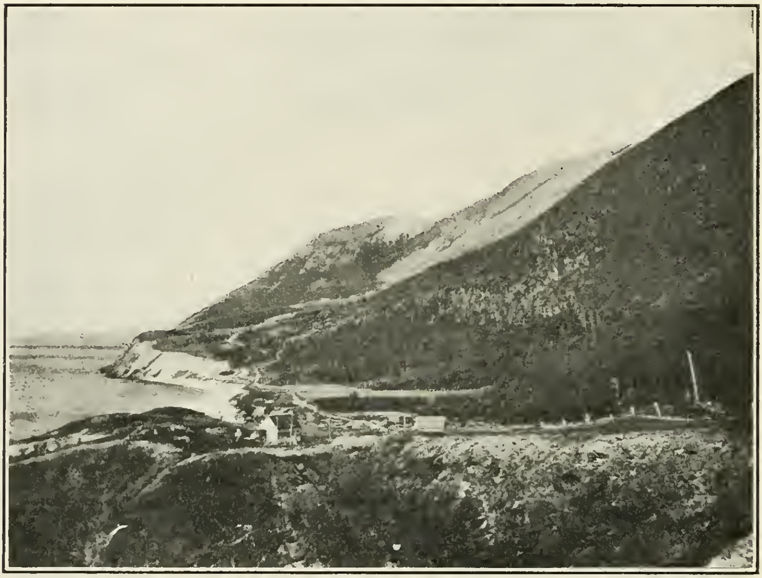

FIGURE 8.—Mountains and granitic, drift-covered lowland north of Cheticamp.

Pleasant Bay, there are sea bluffs, more than fifty feet high, composed entirely of glacial drift, while in some of the brook valleys, e. g., in that of Power Brook, there are accumulations of drift fully as deep. Glacial striae have been observed in several localities (Fletcher '85, p. 77H), but, owing to the rapidity with which most of the rocks crumble when exposed to the weather, such evidences of glaciation are rare.

The distribution of roads and settlements in northern Cape Breton has been determined largely by the character of the topography and of the soil. Along the east coast a road follows the shore from St. Ann's Bay to Cape North, with branches extending inland a short distance wherever intervales occur. From the head of the Big Intervale at Aspy Bay (FIG. 7), a rough trail crosses the plateau to Pleasant Bay, and leads thence southward over the mountains toward the mouth of the Cheticamp River, where, in conformity with the better character of the country, roads are again encountered. The southwestern part of the area mapped affords excellent farming and is well populated, but elsewhere the farms, for the most part, are confined to the intervales and to the low coastal strip. The agricultural possibilities of many of the tracts which have been brought under cultivation would scarcely have been appreciated by any save the Scotch Highlanders, whose descendants constitute the larger proportion of the population of the country. At several points along the coast, as at Cheticamp and Neil's Harbor, the fishing industry supports considerable communities. The mountainous interior of northern Cape Breton is a wilderness, uninhabited and roadless, difficult to travel and little known, seldom visited except by trappers and hunters.

V. CLIMATE

In TABLE I are given the average temperature and precipitation records for twenty years at Sidney.[3] Although there are known to be certain discrepancies, in a general way these figures doubtless represent the meteorological conditions in northern Cape Breton. For purposes of comparison, climatic data for various

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[3] Part of the climatic data here given has been supplied by Director R. F. Stupart of the Canadian Meteorological Service. The remainder has been secured from various sources.

selected stations in eastern Canada are briefly presented in TABLE II. Of the stations here listed, the first five are in the Maritime Provinces: Sidney, Halifax, and Yarmouth front on the ocean, and St. John on the Bay of Fundy; while Frederickton

TABLE I

AVERAGE TEMPERATURE AND PRECIPITATION RECORDS FOR TWENTY YEARS AT SYDNEY, N. S.

Month	Degrees of Temperature, Fahrenheit					Precipitation	
	Mean Daily	Mean Daily Maximum	Mean Daily Minimum	Monthly Extremes		Total Amount (Inches)	Number Rainy Days (0.01 inch or more)
				Maximum	Minimum		
January ...	23	31	15	57	−14	5.19	12
February ..	21	30	13	59	−15	4.39	10
March	28	36	20	58	−18	4.90	13
April	37	44	29	77	3	4.04	12
May	46	55	37	78	22	3.00	11
June	55	64	45	86	28	2.66	10
July	64	73	54	92	35	3.16	10
August ...	63	72	54	88	36	3.03	11
September.	57	66	48	88	30	3.48	11
October ...	48	56	40	77	25	4.11	13
November.	39	45	34	67	12	5.63	14
December.	30	36	24	58	0	5.92	14
Year......	42	51	33	92	−18	49.51	11

TABLE II

TEMPERATURE AND PRECIPITATION DATA FOR VARIOUS STATIONS IN EASTERN CANADA

Station	Temperature (in Degrees Fahrenheit)				Precipitation	
	Normal Mean Daily for Hottest Month	Normal Mean Daily for Coldest Month	Average Extreme Maximum for Years 1907–1914	Average Extreme Minimum for Years 1907–1914	Normal Annual Amount (inches)	Per cent. Falling in Months October–March
Sydney, N. S......	64	21	88	−10	49.51	61
Halifax, N. S......	65	24	91	−10	56.81	57
Yarmouth, N. S....	61	27	78	1	51.94	55
St. John, N. B.....	61	19	80	−13	48.08	55
Frederickton, N. B.	66	13	92	−27	46.44	56
Quebec, Que.......	66	10	90	−24	41.10	49
Montreal, Que.....	69	13	91	−18	40.32	52
Port Arthur, Ont...	62	7	91	−32	23.22	29

lies inland, about fifty miles west of St. John. Of the three remaining stations, Quebec and Montreal are situated in southern Quebec, about 200 miles from the seacoast, and Port Arthur is located in western Ontario, on the north shore of Lake Superior. This latter station is introduced, partly because it exemplifies the relatively continental as compared with the relatively maritime type of climate, and partly because of its proximity to Isle Royale, the scene of Cooper's investigations ('13).

Northern Cape Breton may be said to possess a cool-temperate, maritime climate. In the following paragraphs the general climatic features of this region are briefly summarized, and attention is called to certain differences between the climate of the plateau and that of the lowland.

a. GENERAL CLIMATIC FEATURES OF NORTHERN CAPE BRETON

Temperature.—As compared with regions which are not in close proximity to the ocean, the temperature here is more equable. Some idea of the difference is suggested by the figures in Table II. It will be seen here, for example, that the disparity between the mean temperatures for the warmest and coldest months of the year at Sydney is only 43°, as compared with 53° at Frederickton, and 55° or more at Quebec, Montreal, and Port Arthur. This same dissimilarity between coastal and interior regions is brought out by comparing the extreme maximum and minimum temperatures for the year at the various stations. The winters in northern Cape Breton are long and cold, but extremes of temperature such as prevail toward the interior of the continent are seldom experienced (see Table II). Spring is sometimes very late in arriving, owing partly to the quantity of drift ice in the adjacent waters. The summers are short and cool, but there are only three months in the year when the mean monthly minimum at Sydney is *lower* than 32°. This latter fact is in marked contrast to the conditions at Port Arthur (see Cooper '13, p. 8), where the mean monthly minimum is *higher* than 32° only during June, July, and August.

Precipitation.—In common with other regions along the Atlantic Coast the precipitation in northern Cape Breton is copious and is well distributed over the entire year. More than 60 per cent. of it comes during the period of comparative vegetative inactivity, a condition quite the reverse of what prevails in the interior of the continent (see TABLE II), and also to that which characterizes the Atlantic Coast farther south (at Charleston, S. C., for example, out of an annual precipitation of 52.07 inches, only 39 per cent. falls during the period from October to March). Snowfall in winter is usually heavy and, on account of the backward spring, the snow commonly remains on the ground for a long time. Fletcher ('85, p. 86) notes that in the middle of June, 1881, patches of snow still lingered in sheltered situations, while in 1914 and 1915 the writer observed snow-ice as late as August at the foot of an open north-facing slope along the Barrasois River.

Humidity.—Fogs are more or less prevalent at all seasons, and even in clear summer weather the humidity of the atmosphere is quite perceptible. Figures regarding the rate of evaporation throughout the growing season are not available, but during the summer of 1915, for a period of nearly three weeks, the writer operated a series of porous cup atmometers in various habitats, and the results obtained from those set up in the open near the coast are given in TABLE III. The readings in the first four columns of this table were taken near the Barrasois River. The "Shore" station was situated on an exposed, east-facing hillside, about a quarter of a mile from the seacoast. The "Intervale" station was located in a similar site about five miles from the shore, at the head of a broad open valley. The figures in the fifth column were obtained from an instrument set up on a low hill at Ingonish, within a stone's throw of the open ocean. The average daily rate of evaporation for the entire period at the shore stations was about 12.2 cc. During the period of July 22–August 3 there was considerable rain and fog, while during the

TABLE III

RATE OF EVAPORATION ALONG THE COAST OF NORTHERN CAPE BRETON DURING THE SUMMER OF 1915, AS INDICATED BY THE POROUS CUP ATMOMETER

Station	July 22–July 27	July 27–August 3	August 3–August 7	Daily Average	August 20–August 23
Shore..........	28.8 cc.	45 cc.	84.2 cc.	9.8 cc.	79.2 cc.
Intervale........	39.4 cc.	53.3 cc.	91.9 cc.	11.5 cc.	(3½ days)

periods August 3–7, 20–23, the weather was uniformly clear. For these latter periods the daily rate of evaporation at the shore stations averaged 21.7 cc. The evaporation rate at the intervale station, it will be noted, averaged slightly higher than that at the shore station.

b. CLIMATE OF THE INTERIOR PLATEAU COMPARED WITH THAT OF THE COAST

Temperature.—Aside from a few figures obtained by the writer, few accurate comparative data are available regarding climatic conditions on the plateau, although various interesting observations have been supplied by trappers. In August, 1915, two recording thermometers were set up in the open, one near the shore at Ingonish, the other in the barrens about fifteen miles west of Ingonish (elevation perhaps 1,200 feet). During the writer's stay in the barrens daily readings were made from these instruments, and subsequently readings were taken at intervals of a few days by a competent guide, who made trips into the barrens for this purpose. The readings were continued at each station until a temperature of 32° or lower had been recorded. The figures given in Table IV and covering part of this period are suggestive, if nothing more. It is of interest to note that the daily maximum temperature in summer is frequently higher, and the daily minimum invariably lower, while the average daily range of temperature is perceptibly greater on the plateau than along the coast. Observations recorded for nine days show the average daily minimum to range from six to ten degrees lower on the plateau than along the coast, and the average daily maximum about one degree lower. For the barrens station the first freezing temperature was recorded on

TABLE IV

Maximum and Minimum Temperatures (°F.) in the Interior and Along the Coast of Northern Cape Breton; August 18–23, 1915

	Mean Daily Maximum	Mean Daily Minimum	Mean Daily Range	Extreme Maximum	Extreme Minimum
Barrens........	74°	48°	26°	80°	43°
Ingonish........	71°	56°	15°	75°	52°

September 8 (30°), eighteen days earlier than at the Ingonish station (September 26: 31°). There is little doubt that on the plateau, during some seasons, the temperature falls below freezing during every month of the year. And not only are the daily minimum temperatures here during the growing season lower than in the lowland, but the growing season is considerably (probably from six weeks to two months) shorter here than there.

Precipitation, Evaporation and Wind.—No exact observations have been made regarding precipitation on the plateau, but from the writer's experience and from numerous inquiries it can be stated with certainty that during summer the rainfall is somewhat heavier here than along the coast. The evaporating power of the air in *clear* weather, at least during the summer, is apparently greater than along the coast. This observation is deduced from atmometer readings, taken for the brief period of three and a half clear days in August, when an instrument on the barrens indicated a daily evaporation rate of 28.4 cc., as compared with 22.6 cc. near the shore at Ingonish. But, on the whole, the humidity of the atmosphere is greater on the plateau than on the lowland. This is due to the prevalence here of fogs. During dull weather the clouds hang low, covering the slopes and summits of the mountains above an elevation of seven or eight hundred feet, sometimes for days at a time. Even though it may not actually rain, everything is saturated with moisture. The higher rate of evaporation during clear weather is correlated with the heavy winds which sweep across the plateau at all seasons. So effective are these that a wet, spongy bed of cladonias may become dry and brittle within a few hours. The effect of wind on the vegetation, as seen in the barrens, is even more pronounced in winter than during the growing season. This will be discussed later in connection with the vegetation of the barrens.

VI. ECOLOGICAL CLASSIFICATION OF MATERIAL; NOMENCLATURE

The ecological classification adopted in the present paper has already been described in considerable detail elsewhere (Nichols '17), and need be only briefly outlined here. The fundamental unit of vegetation from the standpoint of physiographic ecology is the *plant association:* any group or community of plants, taken in its entirety, which occupies a common habitat. Associations which are correlated with a common type of habitat and which are ecologically equivalent to one another may be referred to a common *association-type.* The culminating member of any specific successional series is termed an *edaphic climax association.* In favorable situations this edaphic climax coincides with the *regional climax association-type:* the most mesophytic type of vegetation of which the climate of the region permits the development on ordinary uplands. But, in unfavorable situations, the edaphic climax may be represented by an association which is less mesophytic than the regional climax type.

Parenthetically, it may be remarked that while emphasis is usually placed, as above, on the relatively high degree of *mesophytism* which characterizes the regional climax association-type, it is quite likely that this conception, while in general doubtless holding true, should be altered somewhat. In the lowland of northern Cape Breton, for example, a coniferous forest association on ordinary uplands represents either a temporary stage, destined to give way to deciduous forest, or else an edaphic climax (see definition below); yet not infrequently, in so far as their relative mesophytism is concerned, such forests seem quite on a par with forests of the regional climax type. The differentiating factors concerned in this particular case are suggested in the writer's discussion of the ecological relations of the balsam fir (p. 285).

In any unit area where more than one association is represented, the associations, taken collectively, constitute an *association-complex.* Within any specific geographic region the associations are grouped naturally into a series of more or less definite complexes with reference to the physiographic features of the region, i. e., with reference to topography and soil. Any association-complex which is thus related to a specific physiographic unit area constitutes an *edaphic formation.* Edaphic formations which are correlated with a common type of physiographic unit area may be referred to a common *edaphic formation-type.* The edaphic formations of any unit area, where more than one is present, taken collectively, constitute an *edaphic formation-complex.* The edaphic formation-complex of any climatic region constitutes a *climatic formation.* To sum up: the association is a unit determined by habitat; the edaphic formation is a unit determined by physiography—a unit of a higher order than the association; while the climatic formation similarly is a unit determined by climate—a unit of a still higher rank than either of the preceding.

In the account of the ecological relations of the vegetation of northern Cape Breton which follows, the two climatic formations here represented are discussed separately. The scheme followed in classifying the innumerable associations which, taken collectively, comprise the vegetation of the respective regions concerned is partially outlined in the table of contents, which may be looked upon as in the nature of an analytical key. For the benefit of readers to whom the writer's paper on classification may not be available, a few further remarks regarding the system on which this synopsis is built up may be added.

First of all, taking into account their successful relations to one another and their distribution with reference to specific physiographic unit areas, the various individual units of vegetation, the associations, have been assembled into definite association-complexes. An individual association-complex, as thus defined, constitutes an edaphic formation. For obvious reasons, however, the various individual associations have been treated collectively, as association-types, and, similarly, emphasis has been laid on the edaphic formation-types rather than on the individual formations (see definitions above). Proceeding further, the edaphic formations (and formation-types) of the region have been divided primarily with reference to the water relations of the areas which they occupy into two successional series: formations of the xerarch series, and formations of the hydrarch series.[4] Under each of these two heads, in the case of the region of deciduous forests, it has seemed desirable to distinguish between primary and secondary formations, the latter embracing formations in which the vegetation has been modified

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[4] The term xerarch, to quote Cooper ('13, p. 11), "is applied to those successions which, having their origin in xerophytic habitats, such as rock shores, beaches, and cliffs, become more and more mesophytic in their successive stages; . . . [the term hydrarch] to those which, originating in hydrophytic habitats, such as lakes and ponds, also progress toward mesophytism."

by cultivation, lumbering, or fire. The formations of the xerarch and hydrarch series respectively are further subdivided with reference to the general topographic features of the region, these being considered from the standpoint of their relationship to one another through physiographic development. Thus, among the formations of the xerarch series, three groups of formation-types are distinguished: the formation-types, respectively, of ordinary uplands, of uplands along streams, and of uplands along the seacoast. In the same way, the formation-types of the hydrarch series fall more or less naturally into three groups: the formation-types of lakes, ponds and swamps inland, the formation-types in and along rivers and streams, and the formation-types along the seacoast. The classification of formation-types primarily on the basis of water supply is open to certain objections, but so also is their classification primarily on the basis of physiography, a method which might perhaps equally well have been followed.

In discussing the vegetation of each region, the regional climax association-type is taken up first, since an understanding of this, representing as it does the highest degree of mesophytism permitted by the climate—the climatic indicator, so to speak, is prerequisite to an adequate interpretation of subordinate association-types and of successional relations. The edaphic formation-complex of the region, which of course includes all the edaphic formations and formation-types, with the associations and association-types which comprise them, including the regional climax association-type, is then considered, after the manner outlined in the preceding paragraph.

In matters of nomenclature the author, in general, has followed the seventh edition of Gray's Manual ('08), with the emendations of Robinson and Fernald ('09), for the vascular plants, his own papers on the bryophytes of Cape Breton ('16^{a}, '18) for the mosses and liverworts, and Fink's Lichens of Minnesota ('10) for the lichens. In the case of the vascular plants, changes in nomenclature since the publication of the Manual for the most part have been neglected. Only in exceptional cases are authorities cited for the names used. In cases where a plant is referred to by its common name, the scientific name is usually given only in connection with its first mention in the text.

THE DECIDUOUS FOREST CLIMATIC FORMATION IN NORTHERN CAPE BRETON

I. THE REGIONAL CLIMAX ASSOCIATION-TYPE: THE CLIMAX FOREST

Present and past distribution of the climax forest.—To one visiting northern Cape Breton at the present day the prevailing aspect of the lowland forests (FIGS. 9, 39, 42, etc.) appears to be coniferous: white spruce and balsam fir predominate on every side. But practically all of these forests are secondary in their origin. Although settlements in this region for the most part date back scarcely one hundred years, during this short period the greater part of the country has been either cut or burned over, and much of it, at one time or another, has been cultivated or used for pasturage. In view of the widespread destruction or modification of the original vegetation, the nature of the primeval forests must be judged very largely from the

FIGURE 9.—Second growth woodlands of balsam fir and white spruce; Barrasois.

scattered vestiges which for one reason or another have remained intact. From the study of many such fragments, together with certain little modified tracts of second growth forest, it has become unmistakably evident that in former times a very large portion of this area was clothed with forests in which the predominant trees were deciduous. It is certain (and this conclusion is confirmed by statements of many of the older settlers) that forests of this sort were developed in practically all edaphically favorable situations; they were by no means local in their occurrence, but rather of very general distribution. The

FIGURE 10.—Primeval forest of the regional climax type, on lower slopes of mountains along Northeast Margaree River; mostly beech and maple; balsam fir well represented in undergrowth and to some extent in mature stand.

structure of these regional climax forests is considered in brief detail in the following paragraphs. Their general aspect is illustrated by Figs. 10–12.

The trees of the climax forest.—The nature of the individual associations which comprise the climax association-complex of the lowland varies considerably. In some places the forest is made up wholly of deciduous trees, but more commonly it consists of a mixture of deciduous and evergreen species. The various trees which may enter into the composition of the forest are named below, together with remarks as to their frequency and ecological importance. (1) Deciduous Species:—Beech (*Fagus grandifolia*) is almost invariably the predominant species, in some cases including fully 65 per cent. of the mature trees. Sugar Maple (*Acer saccharum*) is always present and usually ranks second in abundance to the beech. Yellow Birch (*Betula lutea*) is likewise omnipresent and sometimes outnumbers the sugar maple. Red Maple (*Acer rubrum*) is rarely absent, and frequently occupies a prominent position in the forest. Paper Birch (*Betula alba papyrifera*) ordinarily grows scattered through the forest. In some stands these five species are the only large-sized trees represented in the mature growth. The northern Red Oak (*Quercus rubra ambigua*) is widely distributed, and in some localities, as at Pleasant Bay and in the vicinity of Cape North, is an important constituent; but in most places it is only sparingly represented, and often it is absent. White Ash (*Fraxinus americana*) is not uncommon in many low intervale forests, but elsewhere it is comparatively rare. Balsam Poplar (*Populus balsamifera*) is occasionally encountered in virgin forests. (2) Evergreen Species (conifers):—Balsam fir (*Abies balsamea*), in the majority of cases, is a conspicuous, though not necessarily abundant, member of the forest, growing intermixed with the various deciduous species. Hemlock (*Tsuga canadensis*) is locally abundant and sometimes is the predominant tree; but often it is absent or represented only by scattered trees. White Pine (*Pinus Strobus*) is also an important constituent, locally, at any rate. It is particularly characteristic of the steep, well-drained, rocky slopes and ridges which flank many of the larger streams; but repeated cutting has thinned out this tree to a greater extent than any other single species. White Spruce (*Picea canadensis*) grows sprinkled here and there through the forest, though seldom present in quantity. Black Spruce (*Picea mariana*) also is frequently represented by scattered specimens.

In the account which follows, for the sake of convenience, forests of the usual climax type, predominantly deciduous but with a more or less pronounced admixture of evergreen trees, are frequently referred to simply as "deciduous forests."

FIGURE 11.—Primeval forest of the regional climax type, along Indian Brook; mostly beech, maple, and hemlock, with some yellow birch and balsam fir; dense undergrowth of yew.

Size of trees in climax forest.— The relatively large size attained by some of the trees in the primeval forests of northern Cape Breton is suggested by the following diameter measurements[5] which were noted for various species: beech, 25 inches; sugar maple, 36 inches; yellow birch, 42 inches; red maple, 18 inches; paper birch, about 3 feet; red oak, 35 inches; white ash, 24 inches; balsam poplar, about 2 feet; balsam fir, 16 inches; hemlock, 30 inches; white pine, about 30 inches; white spruce, 26 inches; black spruce, about 12 inches.

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[5] Diameter measurements of trees were taken at breast height.

Woody undergrowth in the climax forest.—Two small trees, the mountain maple (*Acer spicatum*) and the moosewood (*Acer pennsylvanicum*), are usually conspicuous in the undergrowth. The latter species sometimes attains a diameter of nearly a foot, but, in the forest, both are usually little more than shrubs. The mountain ash (*Pyrus americana*) is not infrequent, but is more characteristic of the evergreen coniferous climax forest of the highland. Of the shrubs, the yew (*Taxus canadensis*) is the most characteristic species: usually this is common, and frequently it forms a dense tangle which excludes other plants in much the same way that the mountain laurel (*Kalmia latifolia*) does in the woods of southern New England. Sometimes, however, the yew is entirely absent over considerable areas. The northern hazel-nut (*Corylus rostrata*) occupies a position in the forest here somewhat parallel to that held by the witch hazel in woods farther south. A few other shrubs are ordinarily represented by scattered specimens, namely: fly honeysuckle

Figure 12.—Primeval forest of the regional climax type, at Tarbet, along the Barrasois; mostly beech, maple, and yellow birch; balsam fir abundant in undergrowth but absent from mature stand.

(*Lonicera canadensis*), withe-rod (*Viburnum cassinoides*), gooseberry (*Ribes lacustre*), dogberry (*Cornus alternifolia*), and red-berried elder (*Sambucus racemosa*). The hobble bush (*Viburnum alnifolium*), one of the most representative shrubs of the climax forest throughout much of the transition region, is very local in northern Cape Breton.

The herbaceous vascular plants of the climax forest.—The following list includes the more characteristic ferns and herbaceous seed plants of the regional climax forest.[6]

Phegopteris polypodioides	*cc*
Polystichum acrostichoides	*fc*
Polystichum Braunii	*lf*
Aspidium noveboracense	*fc*
Aspidium Filix-mas	*lc*
Aspidium marginale	*lc*
Aspidium spinulosum var.	*cc*
Botrychium virginianum	*of*
Lycopodium lucidulum	*cc*
Carex arctata	*fo*
Clintonia borealis	*cc*
Smilacina racemosa	*ff*
Maianthemum canadense	*cc*
Streptopus roseus	*cc*
Medeola virginiana	*ff*
Trillium cernuum	*of*
Habenaria orbiculata	*co*
Epipactis decipiens	*co*
Epipactis tesselata	*co*
Coralorrhiza maculata	*co*
Actaea rubra	*cf*
Actaea alba	*lr*
Oxalis Acetosella	*cf*
Viola canadensis	*of*
Viola incognita	*cf*
Aralia nudicaulis	*cc*
Sanicula marilandica	*of*
Pyrola elliptica	*cf*
Monotropa uniflora	*cf*
Monotropa Hypopitys	*fo*
Trientalis americana	*cc*
Epifagus virginiana	*lf*
Mitchella repens	*cf*
Linnaea borealis americana	*of*
Aster acuminatus	*cc*

Several species have been omitted from this list which are characteristic of low-lying intervale forests, but not of climax forests in general. These will be noted later.

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[6] In this and in several subsequent lists of the plants characteristic of the climax association-type, an attempt has been made to indicate both their general prevalence and their relative abundance when present. The following symbols are used: *c = common; f = frequent; o = occasional; r = rare; l = local.* In each case two symbols are given, the first indicating merely the frequentness with which the species is represented (i. e., is either present or absent) in associations of the climax type, the second indicating its relative abundance, when present, in the individual association. For various reasons it has not seemed feasible to carry out this scheme in connection with other association-types.

The bryophytes and lichens of the climax forest.—Corticolous mosses and liverworts form a striking feature of these forests. Loose mats of *Neckera* and *Leucodon, Porella* and *Frullania* often literally plaster the trunks of maple and other trees; *Ulota* grows in scattered, compact tufts, particularly on trunks of beech; while two lichens, *Sticta pulmonaria* and *Parmelia saxatilis,* are of very common occurrence. Tree bases, logs and rocks also are usually hidden by masses of *Bazzania, Anomodon* and various Hypnaceae. A list of some of the more conspicuous species follows:

Bazzania trilobata	*cc*	*Thuidium delicatulum*	*cf*
Ptilidium ciliare	*cf*	*Brachythecium reflexum*	*cf*
Porella platyphylloidea	*cc*	*Rhytidiadelphus loreus*	*fc*
Frullania Tamarisci	*cc*	*Rhytidiadelphus triquetrus*	*fo*
Dicranum longifolium	*ff*	*Hylocomium splendens*	*cf*
Dicranum scoparium	*cc*	*Hylocomium umbratum*	*cf*
Ulota ulophylla	*cc*	*Ptilium crista-castrensis*	*co*
Mnium cuspidatum	*cc*	*Stereodon cupressiformis*	*cf*
Leucodon sciuroides	*cf*	*Heterophyllon Haldanianum*	*cf*
Neckera pennata	*cc*	*Hypnum Schreberi*	*cf*
Heterocladium squarrosulum	*cf*	*Webera sessilis*	*fo*
Anomodon attenuatus	*ff*	*Polytrichum ohioense*	*cf*
Leskeella nervosa	*co*		

But while mosses and liverworts are present in profusion in these deciduous climax forests, it is important to note that they develop luxuriantly for the most part only on substrata which are elevated above the general level of the forest floor. On the forest floor itself the bryophytes usually are sparsely represented and they may be totally absent over considerable areas. This is in striking contrast to the conditions which prevail in the evergreen coniferous climax forests of the highland, where the ground is almost always carpeted by a rich growth of bryophytes. Various explanations for this dissimilarity have been considered by the author. At first it seemed that it might be due to differences in soil acidity, but all the forest soils tested were found to be more or less acid to litmus. Similarly, differences in light fail to afford an adequate explanation. The conclusion has finally been reached that the scarcity of mosses and liverworts on the forest floor in deciduous forests is correlated in large measure with the deciduous habit. Every year the ground is covered with a more or less continuous blanket of fallen leaves; mosses and liverworts may be buried alive, so to speak, and repeated instances have been observed where without question they have been partially or wholly exterminated in this way. In a general way it may be stated that in the climax forests of northern Cape Breton the abundance of bryophytes is inversely proportional to the abundance of deciduous trees.

Reproduction of the climax trees.—In the normal course of events, the future character of any forest is determined in large measure by the present character of the immature trees. The nature of the rising generation may be said to furnish a criterion of permanency. A permanent forest is one which is able to perpetuate itself. It is therefore a significant fact that in the primeval forests of this region the composition of the younger generation of trees, at least so far as the dominant species are concerned, is essentially the same as that of the mature stand. Beech, sugar maple, birch, and red maple almost everywhere exhibit good reproduction underneath the forest canopy. The same is true, more locally, of the oak and hemlock, and to a less extent of the ash and white pine. Reproduction in the balsam fir is discussed in subsequent paragraphs. Young trees of paper birch and white spruce are seldom found, and it seems probable that, in general, they either represent relicts of a more primitive type of forest, or that they are able to establish themselves only under the more favorable light relations which are occasionally created by gaps in the forest canopy overhead.

The ecological relations of the balsam fir in the climax forest.—The balsam fir may be regarded as the character tree of the northeastern evergreen coniferous climatic forest formation (in this connection, see especially Cooper '13, pp. 36–39). In parts of Cape Breton where this climax formation holds sway, the balsam far outnumbers all other trees. In the competition for supremacy between the deciduous and the evergreen coniferous climax forest-types, the balsam fir, in this region at any rate, is the last element of the more northern type of forest to disappear. For this reason, the ecological relations of this tree in the climax forests of the lowland have been given considerable attention, although it must be admitted that the observations have not been wholly conclusive.

Seldom, if ever, is a tract of climax forest encountered from which the balsam fir is wholly absent. Frequently, however, it is represented only in the younger growth. This latter condition is well brought out by TABLE V, which shows the relative abundance of various trees on two quadrats in a hardwood forest along the Barrasois River (FIG. 12). The most interesting facts to be deduced from this table are: (1) that, of the trees less than five inches in diameter and more than one foot high, balsam fir includes 18.5 per cent. (as compared with beech, 50 per cent.; sugar maple, 26.6 per cent.; yellow birch, 2.4 per cent.; red maple, 2.4 per cent.); while (2), of the trees more than five inches in diameter, none at all are balsam (as compared with beech, 55.5 per cent.; sugar maple, 22.2 per cent.; yellow birch, 16.6 per cent.; red maple, 5.5 per cent.). In the mature stand, taken as a whole, it was estimated that beech includes fully 65 per cent. of the trees, sugar maple and yellow birch each about 15 per cent., red maple and paper birch together about 5 per cent. So far as observations extended, no mature balsam fir whatever is present, the largest living specimen noted being about fifteen feet high; but several dead, standing or fallen, trunks having a diameter of about eight inches were found. The larger living specimens average six or eight feet in height, and are greatly suppressed, many of them showing twenty-five or more annual rings.

TABLE V

RELATIVE ABUNDANCE OF VARIOUS TREES IN TWO QUADRATS IN A HARDWOOD FOREST ALONG THE BARRASOIS RIVER[7]

Name of Species	Diameter Less than 2 Inches	Diameter 2–5 Inches	Diameter 5–10 Inches	Diameter More than 10 Inches
Fagus grandifolia......	55	5	7	3
Acer saccharum........	33	0	2	2
Betula lutea...........	2	1	1	2
Acer rubrum..........	3	0	0	1
Abies balsamea.........	23	0	0	0

The conditions noted in this tract of forest are essentially similar to those which prevail in many other areas: balsam fir

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[7] Quadrat 32.8 feet (ten meters) square. Figures for the two quadrats are added. No trees less than one foot high counted.

is abundantly represented in the younger generation, but is virtually absent from among the mature trees. The absence of mature balsam, however, is far from being the rule. In the majority of cases it grows along with the more southern climax trees, forming an important constituent of the stand, and contributing to the formation of the mixed deciduous-evergreen forest which is the prevailing climax type throughout the lowlands. In competition with the deciduous climax trees, however, the balsam seldom retains a position of dominance, and occasional tracts of primeval forest are encountered in which not only all the mature trees, but practically all the younger ones as well, are hardwoods or hemlock. Forests of this sort are essentially similar to the type which formerly prevailed in many parts of southern New England (see Nichols '13).

In view of the facts set forth above, the query naturally arises: Assuming the climatic conditions to be equally favorable to all the species concerned, why is it that, in competition with maple, beech, hemlock, and the other species which characterize the deciduous climax forest, the balsam fir is unable to hold its own? For obvious reasons this is an important question, and one to which various answers may be suggested.

(1) The relative tolerance of shade exhibited by the various species concerned, at first thought, seems to afford the most likely explanation. Beech, sugar maple, and hemlock are notably tolerant species: they are capable of successful reproduction in their own shade. Regarding the tolerance of the balsam fir there seems to be a discrepancy of opinion. According to Cooper ('13, pp. 17–22, 42, 43), the balsam demands abundant light for successful reproduction: "Later in life the young trees can endure severe shading, but for a successful start abundant light seems to be a necessity." Zon ('14, p. 39), on the other hand, states that, "For the first five or six years of its life, balsam will grow in dense shade, but as it develops it demands more and more light." In northern Cape Breton, the sparsity of balsam seedlings and young trees in many hardwood tracts might well harmonize with Cooper's conclusions, were it not for the fact that in other equally shady forests the young balsam growth is quite abundant. In this connection the observation of Moore ('17, p. 157), made on Mount Desert Island, that, "Under many spruce stands which have reached about middle

age, the fir reproduction is nearly all composed of large seedlings approximately 1–3 feet in height; young seedlings are scarce," is of interest. As indicated above, parallel conditions have frequently been observed in the lowland climax forests of northern Cape Breton. Moore suggests that, "In these cases it appears that the fir came in profusely under a set of environmental conditions different from the present ones . . . . One of them may have been stronger light than at present. Indications of this were found in the fact that some of these cases of fir reproduction occur in stands which were formerly more open than they are now." In one striking case of this sort, observed by the writer, the abundance of young balsam in a primeval hardwood forest is certainly correlated with the occurrence, about fifteen years ago, of a fire which, while it was not sufficiently severe to seriously injure the larger trees, must have resulted temporarily in a considerably increased illumination of the forest floor. Certain it is that the balsam reproduces best and grows most vigorously in well-lighted situations, and there seems to be little question that it is less tolerant of shade than sugar maple, beech, and hemlock. Nevertheless, repeated observations have led to the conclusion that at any rate tolerance alone, even in the broadest interpretation of the term (see Burns '16, pp. 3, 4, 22), cannot be regarded as the cause for the elimination of the balsam.

(2) It has been suggested by Murphy ('17) that the burial of the seeds of the spruce by a mulch of hardwood leaves may be a very important factor in the suppression of this tree in competition with deciduous trees. That the yearly accumulation of leaf litter on the floor of a deciduous forest is, in a somewhat similar manner, responsible for the poor development of the bryophytic ground cover, was a conclusion already arrived at by the writer (see page 284); and it seems not impossible that this may also be a factor of some significance as affecting the reproduction of the balsam fir.

(3) In the opinion of the writer, however, *longevity*, in the last analysis, is the critical factor which enables the maple, beech, hemlock and the associated climax trees of the deciduous forest climatic formation of eastern North America to win out in competition with the balsam fir. In this connection, the behavior of the hemlock, as studied in the primeval forests of north-

western Connecticut (see Nichols, '13), is enlightening. The hemlock is capable of growing in a suppressed condition under the shade of other trees for more than a century. A tree which has been thus suppressed may have attained at the end of a hundred years a diameter of perhaps six or eight inches and may have grown well up into the forest canopy overhead. With the improvement of light conditions, which may be accomplished either through its own upward growth or through the downfall of contiguous trees, such a tree grows vigorously, and may attain an age of more than 300 years, with a diameter of more than four and a height of more than a hundred feet, before its death is brought about through disease, wind, or other agency. What is said of the hemlock applies also to the sugar maple and beech, although these trees are perhaps more susceptible to disease than the hemlock. The behavior of the balsam fir is in marked contrast. Although, like the hemlock, the balsam is able to grow for many years in fairly dense shade, it is handicapped by its susceptibility to fungus diseases, largely in consequence of which its lease on life is limited. At the age of a hundred years, a hemlock, even if it has been growing suppressed all this time, will usually have a sound, healthy trunk. In northern Cape Breton, at any rate, the balsam fir, even under favorable conditions, seldom reaches the age of seventy years without having become infected by heart rot,[8] and by the time it has rounded the century mark its trunk usually has become badly rotted within. In addition to the "ground rot," which, in conjunction with the brittleness of the wood, renders the tree liable to windfall (FIG. 13), the balsam fir, when growing in a suppressed condition under hardwoods, is likely to be affected by "top rot," which may cause it to die back from the top. Like the hemlock, however, a balsam may ultimately find an opening in the forest canopy overhead. But by

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[8] According to Zon ('14), two species of fungi are concerned: *Trametes Pini* (Brot.) Fr. and *Polyporus Schweinitzii* Fr., which may cause either "ground rot" or "top rot." According to the observations of Dr. G. P. Clinton in the western Adirondacks, and of the writer in northwestern Maine and northern Cape Breton, in these regions heart-rot in the balsam fir seems to be attributable to still another fungus, *Fomes pinicola* Fr., a species which Duggar ('09, p. 467) has also mentioned as one which causes disease in the balsam.

this time it is an old tree. For, while the hemlock at a hundred years is still comparatively young, the balsam is already a veteran, since (at least in northern Cape Breton) it seldom lives to be more than 125 years old.

To sum up, if it is assumed that the climatic conditions are equally favorable to all the species concerned, the apparent inability of the balsam fir to compete successfully with the species which characterize the deciduous climax forest formation can be attributed in large part to its shorter tenure of life, coupled with which are its greater susceptibility to fungus diseases and its less pronounced tolerance of shade. That the climate in this region is favorable to the deciduous climax trees is attested by their vigorous growth and the large size which they commonly attain. That it is favorable to the balsam fir is manifest from the manner in which this tree thrives wherever there is freedom from competition. It should be added that, considering the transition region in its entirety, account must also be taken of climate. Climatic factors without doubt have been

FIGURE 13.—Wind-felled balsam fir; Adirondack Mountains, New York. The specimen in the background shows the manner in which the trunk commonly splinters.

of great importance during the northward migration of the deciduous climax trees which has ensued in post-glacial time (see especially Adams '02), and there is little question that in parts of the transition region farther south, where balsam is absent or restricted in its distribution, such factors are still of large significance.

General features of transition climax forests in northern Cape Breton and elsewhere.—The trees which characterize forests of the climax type in the lowland of northern Cape Breton may be divided into four groups, as follows: (*A*) Deciduous species, such as the beech and sugar maple, whose center of distribution lies south of the transition region; (*B*) Deciduous species, notably the yellow birch, whose center of distribution lies within the transition region; (*C*) Evergreen species, notably the hemlock, whose center of distribution lies within the transition region; and (*D*) Evergreen species, such as the balsam fir and white spruce, whose center of distribution lies north of the transition region. To these might perhaps be added a fifth group: (*E*) Deciduous species, such as the paper birch and the balsam poplar, whose center of distribution lies north of the transition region.

It has been intimated in earlier paragraphs that the relative abundance of the different climax trees is subject to considerable local variation. By way of summary, it may be stated that in forests of the regional climax type the trees of group *A* commonly predominate, though sometimes they are outnumbered by those of group *C*. The yellow birch, representing group *B*, is practically always present, varying greatly in abundance, usually common though seldom predominant (but see in this connection p. 387). The trees of group *D* are seldom completely absent: usually they occupy a prominent, but rarely a predominant, position in the forest. The trees of group *E* are commonly represented, but always as a minor element in the forest: frequently they are missing altogether.

While the above observations are made primarily with reference to conditions in northern Cape Breton, they are capable of much wider application. Throughout much of the vast expanse in eastern North America which is embraced by the transition region, the five groups of trees specified in the preceding paragraph are represented. Broadly speaking, throughout this area the nature of the regional climax forests is essentially similar, in so far as their ecological aspect is concerned; but, just as in Cape Breton, there is considerable local variation in their composition—in the presence or absence of certain species and in their relative abundance when present. Leaving out of consideration the species of the fifth group, which occupy a relatively insignificant position here, it is possible to distinguish, with reference to the presence or absence in the forest of members of the first four groups outlined above, eleven different group-combinations of trees which may comprise an equal number of floristically different types of climax forest. Indicating the respective groups by letter, these various group-combinations are as follows: (1) *A-B;* (2) *A-B-C;* (3) *A-B-C-D;* (4) *A-B-D;* (5) *A-C;* (6) *A-C-D;* (7) *A-D;* (8) *B-C;* (9) *B-C-D;* (10) *B-D;* (11) *C-D.*

In sections of the country where all four groups of climax trees (*A, B, C, D*) are well represented, forests comprising any and each of these group-combinations may be encountered. As might be expected, however, while the trees of groups *B* and *C* are about equally well represented in forests throughout the transition region, those of group *A* are most generally represented southward, those of group *D* northward. It is along the southern borders of the transition region, in that part of the area where climatic conditions presumably are most favorable to the trees of group *A* (and least so for those of group *D*), and which these have occupied for the longest time that the first group-combination (*A-B:* the "northern hardwood" type of forest) is most extensively developed. Here the trees of group *D* tend to be localized in situations which are edaphically favorable: they develop best in areas which are somewhat swampy. Conversely, along the northern borders of the transition region, in that part of the area where climatic conditions presumably are less favorable for the deciduous species of group *A* (but more so for those of group *D*), or which, it may be, these species in their post-glacial migration have reached only in comparatively recent time, the trees of group *D* are commonly a conspicuous and even the predominant element in forests of the regional climax type. Here the trees of group *A* tend to be restricted to the better drained soils. It is important to note in this connection, however, that even along the northern border of the transition region, as in Cape Breton, purely deciduous forests are by no means lacking, and that the trees of group *A* growing here compare quite favorably in size, vigor and ability to reproduce themselves with those growing in forests farther south. It is of further interest that along the southern border of the transition region the trees of group *D* may occupy a prominent position in climax forests: in one locality in northwestern Connecticut, for example, at an elevation of less than 2,000 feet, the black spruce is thriving on uplands, reproducing well, attaining a large size, and growing in association, not only with beech and maple, birch and hemlock, but with such species as chestnut (*Castanea dentata*) and mountain laurel.

Considerable interest attaches itself to the relative importance, in transition forests where the trees of group *D* are represented, of the balsam fir and black spruce. In northern Michigan (Whitford '01), Ontario (Howe & White '13), and elsewhere the balsam fir, as in Cape Breton, seems to be the predominant northern conifer. But in other localities the black spruce occupies the position of relative predominance. This seems to be true, to cite localities with which the author is personally familiar, in the western Adirondacks and in northwestern Maine. In the primeval forests about Big Moose (elevation about 2,000 feet), in the Adirondacks, for example, where it grows abundantly, in company with beech, sugar maple, yellow birch, and hemlock, the black spruce attains a diameter of more than three, and a height of more than 125 feet. Here, as in Maine, the balsam fir is present in the forest, but it is more characteristic of the "flats" and moister sites. As noted earlier, the black spruce is represented in the climax forests of the lowland in northern Cape Breton, but here it is infrequent and never reaches the size exhibited by the spruce in the Adirondacks.

In proceeding northward from the region of deciduous forests to that of coniferous forests (Fig. 1) there is a gradual transition from one type of forest to the other. Broadly speaking, however, due largely to the predominating influence of the deciduous element, forests of the regional climax type are essentially similar in their ecological aspect throughout the transition region. Various attempts have been made to define subdivisions of this region on the basis of vegetational dissimilarities, but while such subdivisions may be of floristic importance, their significance from the standpoint of ecological plant geography is at least open to question. Thus, it is doubtful whether the "Northern Mesophytic Evergreen Forest" region (characterized in the east by the presence, as the most common species, of white pine, hemlock, jack pine [*Pinus Banksiana*] and balsam fir), which Shreve ('17) maps as distinct from the "Northeastern Evergreen-Deciduous Transition Forest" region, should be so separated, since throughout this area, as elsewhere in the transition region, climax forests of the deciduous type are commonly encountered in situations which are edaphically suited to their development. Similarly, the "White Pine Region" of New England, as mapped by Hawley and Hawes ('12), while distinct from the standpoint of the forester, does not seem to be so from the standpoint of ecological plant geography. White pine is a frequent constituent of the climatic climax forest throughout the transition region; but, when growing in pure stands, it probably represents either a temporary association or else an edaphic climax. Not only does it appear unwarranted, from the standpoint of ecological plant geography, to recognize such subdivisions as distinct, but, as elsewhere suggested (p. 261), from this point of view the vegetation of the transition region itself is best regarded merely as a part of the great deciduous forest climatic formation of eastern North America.

II. THE EDAPHIC FORMATION-COMPLEX OF THE REGION

A. Primary Formations of the Xerarch Series

1. **The Formation-types of Ordinary Uplands**

a. INTRODUCTORY

In attempting to formulate the successful series which lead toward and, under favorable circumstances, culminate in the climax association-type of the region, there are three possible sources of evidence: (*1*) areas in which succession is actually taking place at the present time (or has taken place within comparatively recent times), as indicated more particularly by the presence of (*a*) relicts of more primitive associations, or (*b*) pioneers of more advanced associations than the present ones;

(*2*) areas in which, owing to the limiting influence of certain local factors, the succession has culminated in an edaphic climax which is less mesophytic than the regional climax association-type; and (*3*) areas which have been denuded of their original vegetation, and where secondary succession is taking place. Secondary successions are discussed in a separate section, but they obviously possess many points in common with primary successions.

Aside from the views of the regional climax forest (FIGS. 10–11), the primary formation-types of ordinary uplands are pictured only by FIGS. 14–16; but see in this connection the figures illustrating secondary formations (FIGS. 33–40).

b. THE ASSOCIATION-COMPLEXES OF ROCK OUTCROPS

Rock surface association-types.—The first forms of life to grow on a bare rock surface are usually the lichens. Commonly the crustose lichens appear first: species of *Buellia, Lecanora, Lecidia, Rhizocarpon,* etc. These are closely followed and often accompanied by foliose lichens: species of *Parmelia, Gyrophora,* etc. Associated with these may be the fruticose lichen, *Stereocaulon* sp., and certain lithophytic mosses, such as *Hedwigia ciliata* and *Grimmia apocarpa*. Where the rock slopes steeply, other plants may be entirely absent, owing to their inability to secure a foothold on the bare rock surface, and the succession may become arrested at this early stage.

But on gentle slopes the conditions are different, for here plants are able to maintain their positions even when entirely unattached to the substratum. Situations of this sort are favorable to the development of the fruticose lichens, notably species of *Cladonia* (e. g., *C. rangiferina, C. sylvatica*). These usually establish themselves first in shallow depressions of the rock surface, where moisture conditions are relatively favorable, and from here they may spread laterally in all directions until the surface of the rock becomes completely covered with a loose, essentially unattached mat of vegetation. In company here with the fruticose lichens very commonly grow certain mosses: these may include any of the species mentioned below as characteristic of crevices, but particularly *Racomitrium canescens* and species of *Polytrichum*.

Crevice association-types.—Contemporaneously with the rock surface "subsuccession" (Cooper '13, p. 118) occurs the crevice "subsuccession." In the crevices, and also, to some extent, in hollows of the rock surface, a soil is usually present, and this enables plants to grow which are unable to secure a foothold on a rock surface or to maintain themselves in such an environment. The pioneer crevice vegetation may include the fruticose lichens already mentioned as growing on rock surfaces. It may also include various mosses, such as *Ceratodon purpureus, Leucobryum glaucum, Dicranum scoparium* and *D. Bonjeanii,* and *Polytrichum piliferum.* But more important than these, in the light of subsequent events, are the ferns and seed plants. Of the ferns, *Pteris aquilina* is the most frequent crevice form, although *Polypodium vulgare* often grows here, in sheltered situations. Among the more important herbaceous seed plants which inhabit crevices may be cited *Potentilla tridentata,* which seldom grows anywhere else, *Deschampsia flexuosa* and *Danthonia spicata, Cornus canadensis,* and *Solidago bicolor.* Of the shrubby and semi-shrubby seed plants, *Vaccinium pennsylvanicum, V. canadense,* and *Gaultheria procumbens* are rarely absent, while *Vaccinium Vitis-Idaea* is especially characteristic of such habitats. Almost any of the trees to be mentioned presently as occurring on the heath mat may be found in crevices. In a sense there may appear to be a succession of growth forms in crevices, herbs preceding shrubs, etc., but succession of this sort, on the whole, is probably more apparent than real.

The heath association-type.—Up to a certain point, the rock surface and the crevice "subsuccessions" are distinct from one another. But with the formation of the lichen–moss mat over the rock surface, and the gradual accumulation of soil which accompanies the process, the two tend to merge into one. The various seed plants, particularly the shrubs, which hitherto have been largely confined to the crevices, become increasingly abundant over the rock surface, and ultimately there may arise what Cooper has aptly termed a "heath mat" ('13, p. 125). Here the ground is still covered by a mat of fruticose lichens and mosses, but these are no longer the dominant plants. As such they have been superseded by ferns and seed plants, whose roots tend to bind together the hitherto loose mat and to consolidate it into a more or less compact turf. The predominant plants of the heath association-type are low shrubs, particularly Ericaceae. A list of species characteristic of this phase in the succession is given below.

Herbaceous Plants

Pteris aquilina
Deschampsia flexuosa
Danthonia spicata
Cornus canadensis
Melampyrum lineare
Solidago bicolor

Shrubby and Semi-shrubby Plants

Juniperus communis depressa
Juniperus horizontalis
Salix humilis
Alnus crispa
Amelanchier sp.
Empetrum nigrum
Nemopanthus mucronata
Rhododendron canadense
Kalmia angustifolia
Gaultheria procumbens
Epigaea repens
Gaylussacia baccata
Vaccinium pennsylvanicum
Vaccinium canadense
Vaccinium Vitis-Idaea
Viburnum cassinoides

Trees

Pinus Strobus
Abies balsamea
Picea canadensis
Picea mariana
Betula alba papyrifera
Pyrus americana
Prunus pennsylvanica
Acer rubrum

As a rule the dominant shrub of the heath mat is *Vaccinium pennsylvanicum.* But *Vaccinium canadense* may be equally abundant; while in some places the *Kalmia* forms an almost pure growth, or may grow mixed with *Rhododendron. Gaultheria* and *Epigaea* usually form a lower story of vegetation; and the same, locally, is true of *Vaccinium Vitis-Idaea. Empetrum* is particularly characteristic of exposed bluffs along the seacoast, and will be referred to again in that connection. Occasionally the grasses, *Danthonia spicata* and *Deschampsia flexuosa,* are dominant forms.

The coniferous forest association-type.—As already pointed out, trees may inhabit the crevices at an early stage in the succession. With the improvement of soil relations which results from the mantling of the rock surface by a mat of vegetation, they cease to be confined to crevices and invade the areas between. At first few and scattered, they gradually increase in number and size and come to occupy the ground more completely. In the course of time, groups of trees in the more favorable situations form patches of embryonic woodland, and, as these spread and unite with one another, a more or less continuous forest may be evolved. Not infrequently trees come in so rapidly and in such force at the outset that the heath stage in the succession is virtually eliminated. The succession does not proceed with equal rapidity everywhere, even within a given physiographic unit area. For, owing to locally unfavorable edaphic conditions, succession in some situations lags behind that in others, with the result that there commonly arises a complex of associations, in which various stages in the developmental series are represented. This promiscuous intermingling of primitive and advanced associations becomes less pronounced as time goes on, but even in the midst of a climax forest there may be situations in which succession has never progressed beyond the rock face–crevice stage.

During the early phases of forest development, the white spruce commonly stands out as the predominant tree: the balsam fir, as a rule, is second in importance. Common associates in the rising forest are the paper birch, conspicuous by reason of its light color and large size; the black spruce, red maple, and mountain ash; and, less commonly, the white pine. As the forest matures, the relative importance of the two dominant trees undergoes certain changes, due very largely to the differing degree to which the two are tolerant of shade. The white spruce is a relatively intolerant species. Its seedlings thrive only in situations where there is abundant light. While it reproduces prolifically in the open, young trees are rarely encountered in the forest. The balsam fir, on the other hand, is relatively tolerant of shade. Like the white spruce, it reproduces best in well lighted situations, but unlike the white spruce its seedlings are also capable of thriving in moderate shade. The result is obvious. With the diminished illumination of the forest floor which accompanies the growth of the forest, there is a marked decrease in the rate of reproduction of the white spruce, while the balsam fir is much less affected. It follows that, as the forest matures, the white spruce tends to become relatively less abundant, the balsam fir relatively more so.

Contemporaneously with the ever-increasing amount of shade produced by the canopy of foliage overhead, the vegetation of the forest floor also changes. The cladonias of the heath stage are largely superseded by bryophytes. Of the mosses, *Hypnum Schreberi* is the pioneer forest species and often appears on the heath mat well in advance of the forest itself. Along with this, but much less common, may grow *Rhytidiadelphus triquetrus.* As the shade and moisture conditions on the forest floor become more favorable, two relatively mesophytic mosses, *Hylocomium splendens* and *Ptilium crista-castrensis,* together with the liverwort, *Bazzania trilobata,* come to play an important part in the formation of the moss carpet, by which the ground sooner or later becomes almost completely covered over.[9] Of the shrubs and herbaceous vascular plants which are characteristic of the heath mat, certain species, such as *Pteris aquilina, Cornus canadensis, Epigaea repens, Vaccinium pennsylvanicum* and *V. canadense,* are equally characteristic of the coniferous forest, particularly during the early phases of its development. Coincident with the formation of the moss carpet, however, other species begin to appear which, while they may have been represented to some extent in the earlier stages of the succession, are more typical of the forest. The forerunners include *Maianthemum canadense, Aralia nudicaulis, Pyrola secunda, Trientalis americana, Chiogenes hispidula,* and *Linnaea borealis americana.* Later on, as the forest matures, these relatively xero-mesophytic forms are followed by other species which are more truly mesophytic, such as *Clintonia borealis, Coptis trifolia, Oxalis Acetosella, Moneses uniflora, Pyrola minor,* and *Aster acuminatus.*

Very often, during the early development of a coniferous forest there is a considerable period when the ground underneath the trees is almost barren of a plant cover. The probable explanation of this frequently observed phenomenon is suggested later in connection with the discussion of succession in abandoned pastures.

The edaphic climax association-type.—Theoretically, at least,

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[9] Cooper ('11) has described a similar succession of lichens and mosses as accompanying the development of the climax forest on Isle Royale.

it is conceivable that even on a bare rock surface, through the gradual amelioration of the habitat by biotic factors, the succession of plant associations might progress still further, and that the vegetation here might ultimately attain the condition which characterizes the climax association-type of the region. But, as a matter of fact, on bare rock outcrops the succession seldom proceeds further than the coniferous forest stage. In other words, the coniferous forest can be regarded as representing the edaphic climax association-type of the rock outcrop successional series: it is a permanent association-type, though ordinarily less mesophytic than the regional climax association-type (in this connection, see Nichols '17, pp. 310-317). In its optimum development, the coniferous forest association-type of the rock outcrop series in the lowland may resemble very closely the climatic climax of the mountains, and indeed it may be quite as mesophytic as the regional climax type. Balsam fir is the predominant tree, while white spruce, paper birch, black spruce, white pine, red maple, yellow birch, and mountain ash are more or less abundantly represented. But, as has already been suggested, such may be the effect of the limiting edaphic factors that in many places the succession halts at a much earlier stage than this.

c. THE ASSOCIATION COMPLEXES OF GLACIAL DRIFT

Extensive outcrops of bare rock are seldom encountered in the lowland. The most widespread type of substratum here is glacial drift. The drift, to perhaps a greater degree than any other type of substratum, is well adapted to rapid colonization by plants. So favorable, indeed, were the original conditions here, and so rapidly has the succession of plant associations ensued, that the drift everywhere has long since become covered by forests. It is only where the original plant cover has been destroyed, either through the agency of stream or wave erosion, or else as the result of human activity or fire, that the earlier phases of the succession become apparent. The early stages of primary successional series on drift can be reconstructed by analogy, after a fashion, from the study of primary successions on other substrata and of secondary successions on the drift.

Coniferous forest locally an edaphic climax.—Disregarding for the present the earlier phases of the succession, suffice it to state that eventually there may arise on the drift a type of forest essentially similar to what has been described above as constituting the ultimate phase in the rock outcrop series: a forest of balsam fir, white spruce, paper birch, etc. And it is of interest to note that, locally, such a forest may also constitute an edaphic climax, even on the drift. In the vicinity of Baddeck, for example, over most of the country succession has never progressed beyond the coniferous forest stage. This circumstance, without much question, is correlated with the heavy, clayey nature of the drift here, which has acted as a limiting factor to prevent the attainment of the regional climax. It is of further interest in this connection that around Baddeck, and in certain other localities where the soil is heavy, the tamarack (*Larix laricina*) is an important arborescent pioneer and a constituent of the coniferous forest. Throughout much of northern Cape Breton the tamarack is a rarity. Its ecological status will be referred to again in another connection (p. 412).

Development of the regional climax.—The yellow birch may be regarded as the forerunner of the deciduous trees which characterize the regional climax forests. This tree is usually represented in coniferous forests in the lowland, but there it occupies a position of prominence only in forests which are well advanced in their development. As the pioneer among the deciduous climax trees, it seems not unlikely that this tree, together with the red maple and paper birch, may help to pave the way for the beech and sugar maple. The effect on the moss carpet of the periodic accumulation of fallen leaves has been referred to elsewhere; and it is at least conceivable that the deciduous advance-guard in the coniferous forest, through the medium of leaf-fall, may in some way exert an ameliorating influence on the substratum, which facilitates the invasion of the forest by beech and sugar maple.

At any rate, wherever the soil conditions are favorable, coniferous forests are superseded by forests of the regional climax type. The trees of the coniferous forest stage in the succession may persist in varying degree, as earlier suggested, but they relinquish their position of dominance. All stages of transition may be found between forests of the coniferous type and those which are purely deciduous. During the transition from one type to another the undergrowth undergoes various changes. Certain species of the coniferous forest stage, such as *Coptis* *trifolia* and *Chiogenes hispidula,* vanish almost completely; others, such as *Pteris aquilina, Cornus canadensis, Epigaea repens,* and *Moneses uniflora,* become much less common; while still other species, such as *Polystichum acrostichoides, Smilacina racemosa,* and *Sanicula marilandica,* which were poorly or not at all represented in the coniferous forest stage, come to occupy a more or less prominent position.

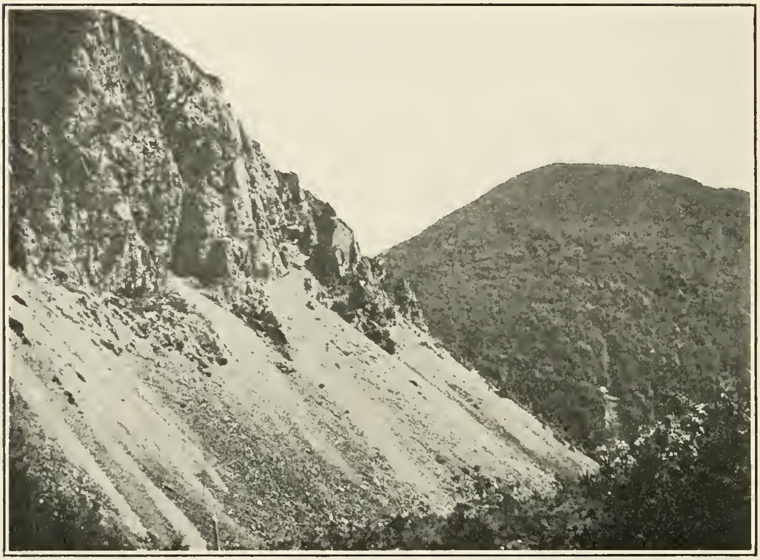

FIGURE 14.—Granitic talus of the prevailing type; north of Cheticamp.

d. THE ASSOCIATION-COMPLEXES OF TALUS

With reference to the size of the component rock fragments and the consequent degree of stability of the rock mass, talus slopes (FIG. 14) vary greatly. Two extreme types may be distinguished: the *Boulder Talus* and the *Gravel Slide.* Boulder talus consists essentially of large rock fragments (sometimes many feet in diameter), which tend to lodge together and interlock with one another on the slope in such a way as to produce a relatively stable rock mass. A gravel slide, on the other hand, consists primarily of fine, loose rock débris, which is not held together in any way but is constantly tending to slip further down the slope, and thus produces a very unstable rock mass. Between the two extremes are all degrees of intergradation.

The association-types of boulder talus.—As in the rock outcrop series, two types of habitat are available to plants here, the rock surfaces and the crannies between the fragments. The surfaces of the boulders are usually overgrown with crustose and foliose lichens. Any of the rock face species previously cited may grow here. These, however, play little or no active part in the talus succession as a whole: the latter is instituted almost entirely by the plants which grow in the crannies. Here, through the further disintegration of the larger rock fragments, and also to some extent from other sources, a soil accumulates. Toward the base of a talus slope soil gathers faster and soil moisture is more abundant than higher up, so that as a rule succession progresses much more rapidly here than elsewhere on the slope. Very commonly the base of a talus slope will be clothed by a mesophytic forest while above there are only scattered trees and shrubs.

The shade and protection from exposure afforded by the blocks which surround the crannies create here conditions which are congenial to mesophytes as well as to many xerophytes. The pioneer plants may include various species of *Cladonia* and any of the bryophytes which have been cited as characteristic of crevices in the rock outcrop series. It also commonly includes certain more mesophytic species, such as *Ptilidium ciliare, Hypnum Schreberi,* and *Hylocomium splendens.* The lichen-bryophyte element may perform an important function in the succession by forming cushions and mats which often spread away from the crannies over the adjoining rock surfaces, creating a substratum favorable for the germination of the spores and seeds of higher plants. The presence in the crannies of a soil, however, permits the growth at the outset, not only of lichens and bryophytes, but of vascular plants as well. Herbaceous plants are sparingly represented by *Polypodium vulgare* and a few other species, while the two shrubs, *Sambucus racemosa* and *Rubus idaeus canadensis,* usually occupy a prominent position. But both herbs and shrubs are subordinate in importance to trees. These gain a foothold early and may predominate the succession from start to finish. For a long time, at least as long as the intermittent bombardment of the slope continues by rocks dislodged from above, the trees remain scattered, and, at this stage, paper birch commonly is the most conspicuous tree. The reason for this frequently observed predominance of paper birch over conifers at this time, as pointed out by Cooper ('13, pp. 218, 219), is undoubtedly due to the ability of the former to sprout from the stump and thereby recover from the injuries inflicted by falling boulders. Ultimately, a coniferous forest of the type already described may become established, in which the predominant trees include the balsam fir and white spruce, the paper birch and yellow birch, the white pine, the black spruce and mountain ash. On north-facing slopes, coniferous forests, while attaining a high degree of mesophytism, frequently represent the culminating phase of the succession: in other words, they constitute an edaphic climax. But, under favorable conditions, the regional climax association-type is capable of attainment on boulder talus, as on the glacial drift.

The association-types of gravel slides.—In extreme cases, as, for example, on gypsum slides[10] (FIG. 15), the instability of the rock mass may be so great that plant life is almost excluded. Largely on account of this instability, lichens and mosses usually play but little part in gravel slide successions: only plants with roots are capable of maintaining a foothold here. The most important pioneers are xerophytic ferns and seed plants, especially herbaceous forms which perennate by means of roots and rhizomes: such species, for example, as *Pteris aquilina, Dicksonia punctilobula, Danthonia spicata, Campanula rotundi-*

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[10] In this connection it is worthy of note that floristically the vegetation of gypsum outcrops commonly differs to a marked degree from that of other rock outcrops which may be physically similar. On the gypsum the vegetation includes a pronounced calciphilous element which elsewhere is mostly absent. Prominent among the seed plants are *Carex eburnea, Shepherdia canadensis, Cornus circinata,* and *Erigeron hyssopifolius.* The bryophytes include *Swartzia inclinata, Gymnostomum rupestre, Tortula mucronifolia, Encalypta contorta, Myurella Careyana,* and *Thuidium abietinum.* Generally speaking, however, while there are frequent other evidences throughout this region of a similar correlation between the chemical nature of the underlying rock and the character of the vegetation, the writer has been unable to distinguish any broad relationships of general ecological significance. Aside from the influence of topography, the general aspect of the vegetation appears to be correlated more with the physical character of the substratum than with its chemical character.

folia, Anaphalis margaritacea, and *Solidago bicolor.* Most of the weeds found in pastures and along roadsides thrive on gravel slides. Of the herbaceous plants, the grasses, particularly *Danthonia spicata,* commonly play an essential rôle, contributing to bring about increased stability in the substratum through the formation of a more or less continuous sod. Shrubs, notably *Rubus idaeus canadensis,* and trees, especially the white spruce, are also important in this respect.

FIGURE 15.—Gypsum ("plaster") outcrop along shore of Ingonish Harbor.

Sometimes a xerophytic weed stage in the succession, in which the plants are scattered and the vegetation open, is followed by a definite grass stage, in which the ground is completely carpeted by vegetation. But more commonly trees are present from the outset, and the first continuous plant cover is dominated by trees, which form an open grove, the ground between the trees being grassed over or else occupied by colonial herbaceous species, such as *Dicksonia* and *Anaphalis,* or by *Rubus.* The white spruce invariably stands preëminent among the trees, but there is a scattered representation of balsam fir, paper birch, balsam poplar, bird cherry (*Prunus pennsylvanica*), etc. In the course of time a closed coniferous forest may be developed, and, under favorable conditions, this may be superseded eventually by a forest of the regional climax type.

One of the commonest types of talus in northern Cape Breton is shown in Fig. 16. The rock fragments are relatively small and the rock mass is much less stable than the large-bouldered talus, though more so than the gravel slide. The common pioneers here are the white spruce, the raspberry, *Dicksonia*, and *Anaphalis*.

Figure 16.—Pioneer association of white spruce, etc., on granitic talus; Barrasois.

2. The Formation-types of Uplands along Streams

a. INTRODUCTORY

In a general way, two topographic features are intimately associated with streams: valleys and flood plains. In northern Cape Breton the valleys range from deep, narrow ravines and gorges in which the stream occupies entirely the narrow floor, on the one hand, to wide, open valleys with broad, flat floor, on the other. All of the larger streams, in their passage from the interior toward the coast, flow during at least part of their course through deep valleys (FIG. 17), while on a lesser scale ravines are well developed along many of the small brooks. In general, so far as the larger streams are concerned, narrow ravines (FIG. 19) are more characteristic of the higher, crystalline areas, broad valleys of the lower Carboniferous regions. Broad, open valleys (FIGS. 7, 20) are especially well developed in the zone of contact between the lowland and the highland, where very frequently the Carboniferous lowland extends as a finger-like depression for several miles into the heart of the higher crystalline formation. The floor of such a valley, as a rule, is relatively flat and is referred to locally as an *Intervale*.

FIGURE 17.—Valley of Barrasois River, just above contact between crystalline and Carboniferous areas; *Pinus Strobus* in right and left foreground. Compare with FIG. 18, photographed but a short distance downstream.

The glacial débris, which at one time must have buried the floor of every valley to a considerable depth, has been very largely scoured out from the narrow-floored ravines through stream activity; but in the broad-floored valleys, as throughout the Carboniferous lowland in general, it may still form, at least locally, deposits many feet thick. Wherever these heterogeneous deposits are exposed to the erosive action of the current, the finer materials tend to be carried away, the coarser constituents being left behind and forming what are here designated as *Boulder Plains*—areas covered with stones, mostly rounded, but of all shapes and sizes (Figs. 18, 21). Where the stones are uniformly small, they may well be referred to as *Cobble Plains*. These stony plains commonly border the larger streams wherever they flow through deposits of glacial drift. In flood time they are submerged, but ordinarily, except for the small channel permanently occupied by the stream, they are uncovered.

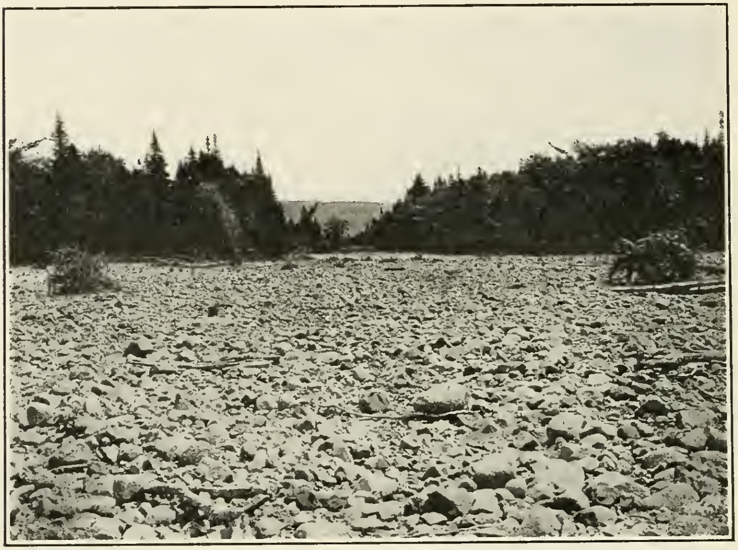

Figure 18.—Boulder plain along lower course of Barrasois River.

In contrast to boulder plains, which are a result of degradation, flood plains are a product of aggradation. They are best developed along sluggish, old-age rivers, and at first thought might not be expected to occur at all along swift, young streams, like the majority of those in northern Cape Breton. But, on the contrary, even in narrow ravines incipient flood plains may be commonly observed in situations which in some way are protected from the swift current (foreground in FIG. 17), while in wider valleys (FIG. 20) the stream is usually bordered by an interrupted series of low, terrace-like flood plains, which have been built up along the less exposed banks. The flood plains of rapid streams, however, not only in Cape Breton, but elsewhere as well, differ markedly from the familiar type of sluggish streams. There the alluvial deposits consist largely of fine-grained sediments. Flood plains of this latter sort, in northern Cape Breton, have been developed to a considerable extent locally, particularly toward the mouths of some of the larger rivers. Along rapid water courses, however, the deposits are much coarser, the swiftness of the current in times of flood being so great that most of the finer material is washed away. Even where the conditions for deposit are most favorable, the alluvial material along a rapid stream is made up largely of coarse sand and gravel, while miniature flood plains built up almost wholly of cobbles and pebbles are frequent in less favorable situations. Incidentally, it should be remarked that while, in a sense, a boulder plain might be regarded as a flood plain, for obvious reasons it is best treated separately. Typical flood plains commonly overlie former boulder plains.

b. THE ASSOCIATION-COMPLEXES OF ROCK RAVINES

This is the only type of ravine which need be considered. The associations here may be divided roughly into four groups, as follows. (*1*) The stream bed association-types: comprising the vegetation in areas where the bottom is submerged at all seasons. (*2*) The stream bank association-types: comprising the vegetation of areas, mostly along the margin of the stream, which are flooded at times of high water but at other times, of variable duration, are exposed to the air. (*3*) The association-types of cliffs: comprising the vegetation of areas above the flood zone which are too steep or unstable to support a forest. (*4*) The ravine forest. With reference to their water relations, some of these association-types are naturally classed under the xerarch series, others under the hydrarch series, but this classification is not always easy to apply. In the hydrarch category should of course be classed the stream bed association-types, and here also it seems most appropriate to include those stream bank and cliff association-types whose ecological aspect is obviously correlated with the more or less constant presence of an abundant water supply. Similarly, in the xerarch category should be classed the ravine forest and such of the association-types of stream banks and cliffs as are exposed for considerable periods of time to more or less xerophytic conditions. In the present connection attention is directed primarily to ravine associations of the xerarch series. Apropos, it may be remarked that, for reasons which the author has pointed out elsewhere ('16^{b}, pp. 237, 249, 250), in considering the vegetation of rock ravines from the dynamic point of view, the question of an actual succession of plant associations, in so far as it is correlated with the physiographic development of the ravine itself, may be virtually disregarded.

FIGURE 19.—Gorge along Indian Brook; the upper edge of the flood zone is indicated by the lower margin of the forest.

Stream bank association-types.—Largely owing to the narrowness of the channel to which the rushing flood water ordinarily is confined, the character of the vegetation within the flood zone in ravines is influenced to a marked degree by the abrading action of the current at times of high water. Particularly is this true along the larger streams (FIGS. 17, 19), to which the following remarks primarily apply. Woody plants, for the most part, are either absent or sparsely developed and even the herbaceous plants are scattered. The characteristic vascular plants of rocky banks between high and low water levels are herbaceous perennials, and these are mostly restricted to crevices and similar situations where their perennating roots and rhizomes can maintain a foothold. Common species are *Equisetum sylvaticum, Deschampsia flexuosa, Sagina procumbens, Campanula rotundifolia, Erigeron hyssopifolius,* and *Solidago bicolor,* together with various weeds, such as *Prunella vulgaris, Achillea Millefolium,* and *Chrysanthemum Leucanthemum.* In addition to these, a prominent position is frequently occupied by various bryophytes, such species as *Preissia quadrata, Fossombronia foveolata, Marsupella emarginata, Nardia obovata, Hygrobiella laxifolia, Grimmia apocarpa, G. conferta,* and *Racomitrium aciculare.* Toward the upper margin of the flood zone, skirting the lower edge of the ravine forest, there is commonly a narrow fringe of shrubs which constitutes a more or less distinct association-type. The characteristic species here is *Alnus mollis,* with which may be associated *Salix humilis, Rubus pubescens, Acer spicatum, Diervilla Lonicera,* and other shrubs, together with such herbaceous mesophytes as *Osmunda Claytoniana, Phegopteris polypodioides, Streptopus amplexifolius,* and *Solidago latifolia.*

Conditions similar to those just outlined may prevail in ravines along small streams, but here the stream bank vegetation commonly is such that it has seemed best to treat it under the hydrarch series (see p. 368).

Cliff association-types.—Certain pteridophytes are especially characteristic of crevices in cliffs, well above the level of the stream, notably *Polypodium vulgare, Aspidium fragrans, Cystopteris fragilis, Woodsia ilvensis,* and *Lycopodium Selago.* With the exception of perhaps the last-named species, these grow best in moist, somewhat shaded habitats. Various of the herbaceous perennials of the flood zone are equally common here, particularly *Deschampsia* and *Campanula,* while the crevice plants mentioned earlier in connection with the rock outcrop series of ordinary uplands may likewise be well represented. Of special interest, however, is the conspicuous position commonly occupied by the mosses and liverworts, which, in favorable situations, may develop luxuriantly, growing either in crevices or on sloping or perpendicular rock surfaces. Representative species are listed below, and, in addition to these, various of the species of wet cliffs (p. 370) may grow here.

Bazzania tricrenata
Diplophyllum taxifolium
Porella platyphylloidea
Radula complanata
Lejeunea cavifolia
Andreaea petrophila
Swartzia montana
Fissidens osmundoides
Tortella tortuosa
Racomitrium fasciculare
Ulota americana
Pohlia cruda
Bartramia pomiformis
Hedwigia albicans
Drepanocladus aduncus
Polytrichum alpinum

The ravine forest.—Nowhere in the lowland of northern Cape Breton are forests of the coniferous type more luxuriantly developed than in ravines. In general, these forests conform closely with the regional climax type of the mountains, and need not be described in detail at this point. Such forests here represent an edaphic climax association-type, and as such their development is correlated very largely with local peculiarities of temperature and soil moisture. They are best developed on north-facing slopes, where the failure of the succession to proceed beyond the coniferous forest stage may be attributed to the slowness with which the snow melts and the ground thaws out in spring and to the relatively low temperatures which obtain throughout the season. Quite commonly the north-facing slope of a ravine supports a coniferous forest while the opposite, south-facing slope is clad with a forest of the regional climax type. On north-facing slopes, coniferous climax forests are by no means confined to ravines: one of the most distinctly boreal examples of upland forest which has come to the writer's attention in the lowland is situated along the lower slopes of a steep mountain side, where ice frequently lingers as late as August, notwithstanding the fact that it faces an open intervale which was formerly occupied by a deciduous forest. In ravines which run north-and-south, and where both flanks are thus equally well exposed to the sun, on the other hand, the ravine forest may be wholly of the deciduous type.

One feature of coniferous ravine forests worthy of special mention is their great mesophytism, as evinced more particularly by the wonderful development of the bryophytic ground cover. Commonly the ground beneath the trees is literally buried beneath a thick bed of liverworts and mosses. The sphagnums in particular—such species as *Sphagnum capillaceum tenellum, S. Girgensohnii, S. quinquefarium,* and *S. subsecundum*—commonly form wide, deep cushions, flourishing here as in no other upland habitat in this region.

The summer evaporating power of the air in coniferous ravine forests, as compared with other habitats.—During the summer of 1915 a series of porous cup atmometers was operated, for a period of a little more than two weeks, in various habitats, with the object, primarily, of ascertaining the relative evaporating power of the air in coniferous ravine forests as compared with the deciduous climax forests. The habitats selected were as follows:

Station 1 ("Open—Shore"): Open hillside, east exposure, half a mile from seacoast.

Station 2 ("Open—Intervale"): Open hillside, east exposure, four miles from coast at head of intervale.

Stations 3 and *4* ("Hardwood"): Hardwood (climax) virgin forest; east exposure; near station *2*.

Station 5 ("Ravine Conifer—High"): Coniferous forest; steep north-facing slope of ravine, about 250 feet above river; near station *1*.

Station 6 ("Ravine Conifer—Low"): Dense coniferous forest; steep north-facing slope of ravine, about 150 feet above river; near station *1*.

Station 7 ("Ravine—Bed"): Gravel bar in bed of stream; exposed to sun about six hours daily; stream bed about 75 feet wide at this point; near station *1*.

The readings obtained are given in TABLE VI. During much of the period that the cups were in operation the weather was intermittently rainy, foggy, and clear. From August 3 to August 7, however, it was uninterruptedly clear, so that for pur-

TABLE VI

Rate of Evaporation in Various Habitats, as Indicated by the Porous Cup Atmometer

	July 22–July 27	July 27–August 3	August 3–August 7	Total
Station 1: Open—shore	28.8 cc.	45.0 cc.	84.2 cc.	158.0 cc.
Station 2: Open—intervale	39.4 cc.	53.3 cc.	91.9 cc.	184.6 cc.
Station 3: Hardwood A	16.0 cc.	19.6 cc.	42.1 cc.	77.7 cc.
Station 4: Hardwood B	15.3 cc.	16.3 cc.	37.8 cc.	69.4 cc.
Station 5: Ravine Conifer—high	14.4 cc.	20.6 cc.	52.5 cc.	87.5 cc.
Station 6: Ravine Conifer—low	11.0 cc.	14.0 cc.	43.3 cc.	68.3 cc.
Station 7: Ravine—bed	24.1 cc.	31.1 cc.	63.0 cc.	118.2 cc.

pose of comparison the third column of figures is the most reliable. From an examination of these figures various facts are obvious, but only one of these need be emphasized, namely, that the evaporating power of the air in the coniferous ravine forest differs little from that in the climax deciduous forest. Greater humidity, then, will not explain the luxuriant development of the moss carpet in a ravine forest. Other explanations have already been suggested.

c. THE ASSOCIATION-COMPLEXES OF OPEN VALLEYS

Chiefly by reason of the protection which they afford from cold winds in spring and fall, open valleys (Fig. 20), in general, present edaphic conditions which are more congenial to plants of southward distribution than those of any other type of habitat-complex. Robinson ('03) has already called attention to the relative abundance in the intervales of eastern Nova Scotia of early spring-flowering plants, and the writer (16^b, pp. 252, 253) has commented on parallel conditions in Connecticut. Nowhere in northern Cape Breton are forests of the deciduous-hemlock climax type more luxuriantly developed than on the floors of broad, sunny valleys, i. e., in the intervales. Here, more abundantly than anywhere else, grow the hemlock, red oak, white ash, and elm (*Ulmus americana*), among the trees, together with various herbaceous plants of pronounced southward range. Of the latter, many forms, such as *Anemone virginiana, Sanguinaria canadensis,* and *Dicentra Cucullaria* (*fide* Robinson '03), *Actaea alba, Epifagus virginiana,* and *Triosteum aurantiacum,* are practically restricted to the intervales or to the adjoining slopes. From the standpoint of their physiographic origin, the intervales are largely the result of stream activity, and their vegetation in part is that of the boulder plains and flood plains which are still in the course of formation. But in large part, so far as the vegetation is concerned, the influence of the stream is of merely historical significance. In the case of boulder plains and flood plains, local soil as well as local atmospheric factors have to be taken into account.

FIGURE 20.—The Big Intervale along North Aspy River: floor of valley at this point largely under cultivation; in background, talus slopes in various stages of forestation; view taken toward upper end of intervale; compare FIG. 7.

d. THE ASSOCIATION-COMPLEXES OF BOULDER PLAINS

In extreme cases, vegetation may be almost wholly lacking on boulder plains (FIG. 18). But such cases are not common. While from a distance the lower and more frequently flooded portions of a boulder plain may have almost the aspect of a desert, closer inspection usually reveals, even here, a goodly representation of shrubs and herbaceous plants, which maintain a precarious foothold in the interstices between the cobbles and boulders, rooting in the sand and gravel which have accumulated in the shelter afforded by the larger rocks. The pioneers are preëminently herbaceous perennials: species which are able to tide over the unfavorable periods by means of underground organs. Except for shrubby willows (such species as *Salix cordata, S. lucida,* and *S. humilis*), which are able to survive considerable battering and locally may form dense, low thickets (FIG. 21), woody plants are scarce.

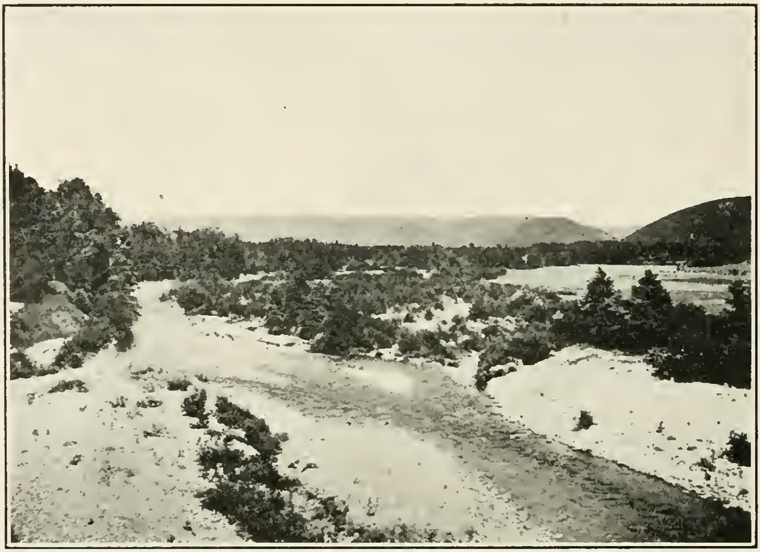

FIGURE 21.—View along Middle River, showing boulder plain with scrubby willows, etc. (left foreground), young flood plain with pioneer tree stage (center, mid-distance), and mature flood plain, now under cultivation (right, mid-distance).

On the higher parts of a boulder plain, the vegetation is much more abundant, but always open. In addition to the willows, species of alder, particularly *Alnus incana,* are ordinarily conspicuous here, together with such other woody plants as *Rubus idaeus canadensis, R. pubescens,* and *Spiraea latifolia.* A list of some of the more characteristic herbaceous plants of boulder plains is given below. This list does not include weeds, many of which occupy a very prominent position here.

Equisetum arvense
Calamagrostis canadensis
Agropyron repens
Poa pratensis
Carex torta
Ranunculus repens
Fragaria virginiana
Viola cucullata
Viola pallens
Epilobium angustifolium
Epilobium adenocaulon
Apocynum cannabinum
Eupatorium purpureum
Solidago canadensis
Aster radula
Aster puniceus

e. THE ASSOCIATION-COMPLEXES OF FLOOD PLAINS

Transition from boulder plain to flood plain.—It commonly happens, sooner or later, that the stream shifts its course or that the current is deflected by some sort of an obstruction, so that an area occupied by a boulder plain becomes protected in a measure from the erosive activity of the stream. If the protection is sufficient, degradation may become largely superseded by aggradation, and a flood plain may gradually be built up on top of the former boulder plain (FIG. 21). Eventually, even along swift stretches of the stream, such flood plains may attain a height of five or six feet above low water level. At first composed of coarse gravel and cobbles, as the surface is raised higher the successive deposits become finer, and finally the soil comes to consist of coarse sand. Only in exceptionally favorable situations, however, does the soil approximate the fine alluvium of old-age rivers.

The succession of plant associations outlined.—In the familiar type of flood-plain succession (to be discussed later), the pioneer stages of the series are usually hydrophytic: in other words, the succession is hydrarch. In the boulder plain–flood plain succession, on the other hand, the pioneer stages, as a rule, are relatively xerophytic: that is, the succession is xerarch. Three more or less distinct stages in the succession may be distinguished: the gravel bar stage, the pioneer tree stage, and the edaphic climax forest.

The gravel bar association-type.—The pioneer association-type of gravel bars consists largely of the shrubs and herbaceous perennials listed as characteristic of boulder plains, most of which grow in greater profusion here than there. It also may include many species which are not prominent on boulder plains: such, for example, as *Alnus mollis* and *Diervilla Lonicera; Campanula* *rotundifolia, Anaphalis margaritacea,* and *Centaurea nigra.* The mosses, *Racomitrium canescens* and *Polytrichum piliferum,* frequently form a loose, discontinuous ground cover in protected spots; while species of *Cladonia* may also be present. Locally, wherever the soil is fairly moist, the early vegetation may include mesophytic species, such as *Clematis virginiana, Thalictrum polygamum,* and *Heracleum lanatum*—forerunners of subsequent stages in the succession.

The pioneer tree association-type.—Although the vegetation in the gravel bar stage of the succession is predominated by shrubby and herbaceous species, trees may be present from the outset. The balsam poplar, more than any other species, is preëminently the distinctive pioneer tree of gravelly or sandy flood plains, although it often shares this honor with the paper birch and white spruce (FIG. 21). The balsam poplar owes its prominence to its copious root system and exceptional ability to maintain itself on shifting alluvial soils, its tendency to reproduce and spread by means of root suckers, and its rapid rate of growth, which enables it to outstrip any chance competitors. In these respects it resembles its southern relative, the cottonwood (*Populus deltoides*), of which it may be regarded as an ecological counterpart. One frequently encounters on flood plains groves of good-sized balsam poplars, beneath which the more characteristic trees of the climax forest apparently are just beginning to establish themselves. But any of the climax trees may appear simultaneously with the poplar. On one small, treeless stretch of gravelly flood plain, for example, the writer noted seedlings of nearly every tree (all except white pine, hemlock, and red oak), which has been cited earlier as growing in the climax forest; also seedlings of bird cherry and choke cherry (*Prunus virginiana*). For the reasons suggested above, however, the poplar usually gains a temporary ascendancy over its competitors, thereby giving rise to a more or less distinct phase in the succession.

The edaphic climax forest.—Flood plain forests of the sort ordinarily associated with old-age rivers have been developed along some of the larger lowland streams, and in some cases the physiographic history of the areas which these occupy has probably been similar to that of flood plains as described in the preceding paragraphs. But in the most typical instances observed, such forests represent the culmination of hydrarch rather than xerarch successional series, and they will therefore be discussed later (p. 371), in connection with hydrarch successions.

The average climax forest of sandy flood plains along swift streams approximates closely the climatic climax forest-type of the region, differing from this chiefly in the presence, or more luxuriant development, of such species as *Ulmus americana* and *Fraxinus americana,* among the trees, and of various herbaceous plants, such as the following:

Osmunda Claytoniana
Polystichum Braunii
Cinna latifolia
Trillium cernuum
Smilacina racemosa
Listera convallarioides
Streptopus amplexifolius
Thalictrum polygamum
Sanicula marilandica
Osmorhiza divaricata
Pyrola asarifolia
Solidago latifolia

3. The Formation-types of Uplands along the Seacoast

a. INTRODUCTORY

Under this heading are included only those upland associations which are peculiar to habitats in the immediate proximity of the shore and whose ecological aspect is obviously correlated with this fact. The character of vegetation along the seacoast is influenced to a greater or less degree by wind, salt water, and physiographic agencies. The plant associations are best classified with reference to physiographic factors, as (*1*) Associations along Eroding Shores, and (*2*) Associations along Depositing Shores. As eroding shores are classed the sea bluffs and headlands which form such a striking topographic feature along much of the coastline. Depositing shores include the commonly encountered shingle beaches and the less frequently encountered sandy beaches and dunes.

In addition to the figures that accompany the description which follows, attention may be called in this connection to Figs. 3, 6, 8, 15, 33, 38, 41.

b. THE ASSOCIATION-COMPLEXES OF SEA BLUFFS AND HEADLANDS

Association-types of rocky sea bluffs.—The application of the term sea bluff is here restricted to the more or less precipitous slopes which face directly on the shore and therefore are most exposed to the action of waves and spray (FIG. 3). Along such bluffs there is usually a pronounced zonational arrangement of plant associations. Between low and high tide levels, wherever the base of the bluffs is submerged, the rocks are usually plastered with sea-weeds, prominent among which are species of *Fucus* and *Ascophyllum*. Above high tide level is a zone of varying width in which, owing largely to the mechanical action of waves and ice, vegetation is absent. Higher up, and sometimes reaching to a height of thirty-five or forty feet, is a zone in which the vegetation consists largely of scattered halophytic crevice plants. The upper limits of this zone are presumably determined by the height of the waves in winter storms. The most abundant plant here is *Plantago decipiens,* along with which commonly grow *Solidago sempervirens* and *Sagina procumbens*—the latter, of course, hardly to be considered a typical halophyte. Other halophytic species which may inhabit crevices or ledges toward the upper edge of this zone and which, like the preceding, may also occur on low headlands far beyond the actual reach of the waves, are *Potentilla pacifica, Atriplex patula hastata,* and *Lathyrus maritimus.* The most characteristic plant on that part

FIGURE 22.—*Juniperus horizontalis* on sea bluff; Middle Head, Ingonish.

of a bluff which lies beyond the usual reach of the waves is the trailing juniper (*Juniperus horizontalis*), which commonly sprawls out here in great profusion (FIG. 22), and is only occasionally found in any other habitat. Commonly associated with this shrub is the crowberry (*Empetrum nigrum*) and frequently the low juniper (*Juniperus communis depressa*), while any of the other species to be cited presently as occurring on headlands may also grow in the crevices of precipitous, rocky sea bluffs.

FIGURE 23.—*Alnus mollis* and *Picea canadensis* on sea bluff of clayey drift; Cape North.

Association-types of sea bluffs in uncompacted rock.—So long as a sea bluff of clay or glacial drift continues to be acted on, from time to time, by the waves, vegetation is scantily developed. Just as along the shores of the Great Lakes (see Cowles '01, pp. 164–167), about the only plants present here are xerophytic annuals and "slump plants" (i. e., plants which have slid down from the crest of the bluff). As soon, however, as there is a cessation or diminution in the erosive activity of the waves, which may be brought about by the formation of a shingle beach between the bluff and the sea or through the accumulation along the base of the bluff of boulders derived by erosion from the bluff itself, a plant cover is rapidly developed. *Equisetum arvense* and *Agrostis alba maritima* frequently, and *Elymus arenarius* occasionally are conspicuous pioneers, but for the most part the pioneer species here are largely weeds and slump plants. Sometimes a grassy sod is formed, but more commonly *Alnus mollis* (Fig. 23) comes in along with the grasses and forms a dense thicket. Sooner or later, trees appear, mostly white spruce and paper birch, and these may supersede the alders, forming a low, scrubby forest along the bluff. The trees often exhibit the same one-sided habit as those on headlands.

Figure 24.—Exposed rocky headland at White Point; scrubby forests, mostly white spruce; in right foreground a characteristically one-sided spruce. Photograph by Dr. L. H. Harvey.

Owing to the abundance of seepage water, soil conditions locally, especially along clay bluffs, may be unusually favorable for plants, and in such places it is a common thing to find the vegetation made up in large part of species which are ordinarily associated with swamps or flood plains: such, for example, as *Alnus incana, Calamagrostis canadensis, Juncus effusus* and various sedges, *Heracleum lanatum, Eupatorum purpureum,* and *Aster puniceus.* Associations of this sort, though mentioned here for convenience, should naturally be classed under the hydrarch series.

Association-types of exposed headlands.—Bleak headlands like the one pictured in Fig. 24 are a prominent feature of the coast, especially northward. In the vicinity of Cape North and in other very exposed situations the mountain sides in some places are devoid of forest from sea level to a height of fully a thousand feet. Without doubt many of these areas were formerly wooded and their barren aspect has been induced primarily through the action of fire or human activity; but the continuance of this condition is attributable very largely to the retarding effect on succession of exposure to strong winds, frequently laden with salt spray. Wherever, on headlands of the sort pictured, there is a depression which affords shelter, scrubby forests are encountered, while scattered trees are commonly present in the barren area itself. These latter, as well as many of the trees which fringe the lower margin of the forest farther up the slope, are usually unsymmetrical in shape and dwarfed in size. Frequently the living part of the crown is wholly on the landward side of the tree.

FIGURE 25.—Detail view of vegetation on exposed headland shown in FIG. 24; see text. Photograph by Dr. L. H. Harvey.

In some cases the predominant type of vegetation on these headlands is grass: species such as *Danthonia spicata*, *Festuca rubra*, and *Deschampsia flexuosa*. But more often (FIG. 25) the ground is covered very largely with a dense tangle of low, sprawling shrubs which are seldom more than a foot high. Perhaps the most characteristic, and commonly the predominant shrub is the crowberry, but associated with this and often equally abundant may be *Juniperus communis depressa, Vaccinium Vitis-Idaea, V. pennsylvanicum,* and occasionally *Juniperus horizontalis.* Other species commonly encountered on bleak, exposed headlands, but not yet mentioned in this connection, are listed below.

Botrychium ramosum
Smilacina stellata
Iris setosa canadensis
Myrica carolinensis
Arenaria lateriflora
Fragaria virginiana
Potentilla tridentata
Lathyrus palustris
Ligusticum scothicum
Cornus canadensis
Gaultheria procumbens
Halenia deflexa
Euphrasia Randii
Euphrasia Randii Farlowii
Campanula rotundifolia
Solidago puberula
Aster novi-belgii

To these should be added *Cladonia* sp., *Polytrichum piliferum,* and *Polytrichum juniperinum,* which frequently carpet the bare soil where other vegetation is absent.

c. THE ASSOCIATION-COMPLEXES OF BEACHES AND DUNES

Association-types of shingle beaches.—Even along parts of the coast which are exposed to active erosion, at least where the eroding land mass consists of glacial drift, a rocky, beach-like strip commonly intervenes between the foot of the bluff and the water's edge. Such deposits may be composed in part of wave-washed material, but as a rule they are largely made up of boulders and cobbles of all sizes which have been washed out of the bluff itself. The analogy with the boulder plain is obvious. All degrees of transition exist between such deposits, which may be virtually destitute of vegetation, and the typical shingle beaches, which constitute a familiar feature along the shore. These latter commonly form a narrow fringe along the seaward edge of the land, but wherever there are reëntrants in the coast line, barriers and spits tend to be developed. St. Ann's Bay and Ingonish Harbor are nearly closed in by narrow, rocky spits, and there are similar spits at the mouth of the Barrasois River and Indian Brook. Near the Barrasois and at South Bay, Ingonish (Fig. 42), lakes of considerable size have been cut off from the sea by barriers, the one at the latter place being fresh and several feet higher than high tide level. Small ponds and lagoons, cut off by barriers, are of frequent occurrence (Fig. 26).

In a general way, a shingle beach, like a sandy beach, is subdivided into three more or less distinct zones which, following the classification of Cowles ('01, p. 170), may be termed respectively the lower, middle, and upper beaches (Fig. 27). The lower beach is the part submerged by ordinary high tides. It ranges in width from a few yards to more than a hundred feet. The deposit here (at least in summer) is usually gravelly or sandy toward its lower limit, becoming pebbly above and gradually merging with the shingle. Except for the occasional presence near low tide level of *Zostera marina* and brown algae such as *Fucus,* vegetation is absent. The middle beach comprises that part of the beach immediately above the lower beach which is swept by the waves of winter storms or is covered over by ice in winter. Like the lower beach, it varies greatly in width. The deposit here consists almost wholly of water-rounded cobbles

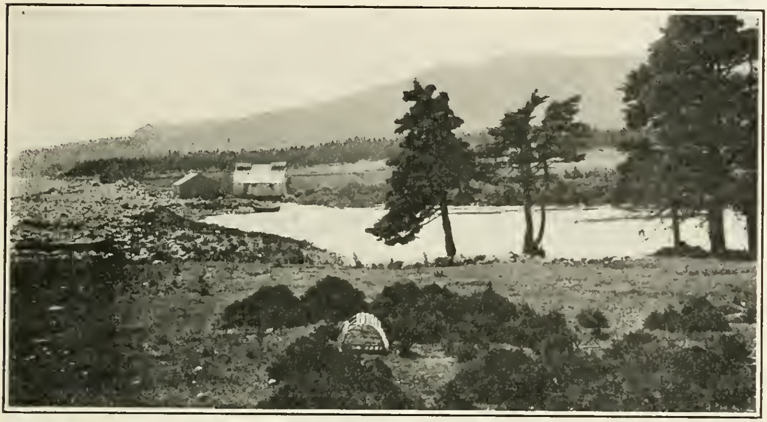

Figure 26.—Shingle beach enclosing small fresh pond; scrubby spruces, etc. in foreground, habit largely the result of grazing; in background, second growth spruce, etc.; Wreck Cove. Photograph by Dr. L. H. Harvey.

and pebbles, ranging from the size of hens' eggs up to six inches or more in diameter—the type of accumulation commonly referred to as *Shingle*. Vegetation is sparse and xerophytic, practically the only plants ordinarily present being the annual, *Cakile edentula,* and the herbaceous perennials, *Lathyrus maritimus* and *Mertensia maritima.* The last-named species, the so-called sea lungwort, with its glaucous foliage and rose-pink or blue flowers, and growing in depressed, circular patches two or three feet in diameter, is by far the most striking of the beach plants. The upper beach includes that part of the beach which, except during unusual storms, when parts or all of it may be wave swept, lies beyond the reach of the waves at all seasons of the year. Its crest is commonly more than three and occasionally as much as six or eight feet higher than ordinary high tide level. Stones are cast up on these higher beaches only by exceptionally severe storms, perhaps years apart. Like the middle beach, the upper beach, especially in its more exposed parts, may be little more than a great stone heap on which, except for a frequently

Figure 27.—Shingle beach near mouth of Barrasois River; forest of white spruce, etc. along landward edge.

luxuriant growth of lithophytic lichens, vegetation is scantily developed. Common lichens on the shingle are *Rhizocarpon geographicum* (crustose), a form which is very conspicuous by reason of its bright, greenish yellow color, and *Lecidea tenebrosa* Flot. (crustose) and *Gyrophora hyperborea* (foliose), both of which are blackish in color. As a rule, however, even in such places, there is more or less gravel and coarse sand underneath the stony surface layer, while in the older parts of the upper beach the shingle in some cases (Fig. 28) has been covered over by sand to such an extent as to produce conditions approximating those to be described presently as characteristic of sandy beaches. All intergradations may be found on lea slopes between rocky shingle at one extreme and sandy beach at the other.

Figure 28.—Spit near mouth of Barrasois River; to right, a typical shingle beach; to left, a mixture of sand and shingle, overgrown with *Ammophila*, white spruce, etc.

On the upper beach, soil conditions usually favor the development of vegetation, and there may be a succession of plant associations leading to the formation of a scrubby forest. The pioneer plants here are predominantly herbaceous, and various introduced weeds figure prominently. Indeed, almost no other natural habitat supports a greater variety of weeds than shingle beaches. In this connection it may perhaps be remarked that there seems little question that in former days, in so far as they were then represented in this region, the majority of the plants popularly classed as weeds, and which to-day thrive in a variety of open situations created by man's activity, were restricted to situations such as gravel slides; boulder plains, sandy flood plains and rocky banks along streams; and sea beaches. Excluded through competition from situations edaphically more favorable to them, the weeds, which as a group are essentially pioneers, have always flourished in these open situations.

In addition to the weeds, the grasses are well represented on the upper beach by such species as *Ammophila arenaria, Danthonia spicata, Poa compressa, Poa pratensis, Festuca rubra,* and occasionally *Elymus arenarius,* while the sedge, *Carex silicea,* is seldom absent. Other common herbaceous species here are *Fragaria virginiana, Potentilla tridentata, Geranium Robertianum, Oenothera muricata, Ligusticum scothicum, Campanula rotundifolia,* and *Anaphalis margaritacea.* Various xerophytic mosses, notably *Ceratodon purpureus, Racomitrium canescens, Brachythecium albicans, Polytrichum juniperinum,* and *Polytrichum piliferum,* thrive in open, gravelly soils, while the foliose lichens, *Cladonia rangiferina, C. sylvatica,* and *Stereocaulon coralloides* may also be represented. But the vascular vegetation is by no means restricted to herbaceous forms, for even on rocky and quite exposed parts of the beach there usually are scattered shrubs and trees. In stony situations the plants may secure a foothold in patches of gravel between the cobbles, but very frequently a favorable substratum is created by the decomposition of logs which have been cast up by storms. Of the shrubs, *Juniperus communis depressa, Myrica carolinensis, Rubus idaeus canadensis, Empetrum nigrum, Gaylussacia baccata,* and *Vaccinium pennsylvanicum* are quite characteristic of shingle beaches, and *Vaccinium Vitis-Idaea* grows well in grassy, gravelly or sandy areas. The commonest tree is the white spruce, though the balsam fir is scarcely less frequent. Both of these trees often exhibit a weather-beaten aspect, but this is especially true of the balsam fir. On the beach at Englishtown (Fig. 29) grow specimens of the latter which measure less than two feet in height but sprawl out on the ground over a radius of more than six feet. Their low stature is due to the repeated killing off of the leader, and this in turn is probably attributable to the erosive effect of wind-driven snow in winter, a phenomenon which will be referred to again in connection with the vegetation of the barrens.

Wherever a shingle beach borders on the mainland, there is a tendency for the forests of the adjoining upland to encroach on the beach (Fig. 27), and even on barriers and spits scrubby forests are frequently developed on the older parts of the upper beach (Fig. 29), usually on lea slopes where there is optimum protection from wind and wave. Such forests are quite open, and are composed almost wholly of white spruce and balsam fir, which seldom reach here a height of more than twenty-five feet. In the open spaces between the trees grow in more or less profusion various of the shrubs and herbaceous plants which have been listed as occurring on the upper beach, while certain less xerophytic species, which have been cited earlier as characteristic of the pioneer forest stage in the ordinary upland series, are found here also. Common bryophytes in the shade of the trees are *Ptilidium ciliare, Dicranum Bonjeanii, Dicranum undulatum,*

Figure 29.—Stunted balsam firs (foreground) and scrubby forest (left background) on shingle beach; St. Ann's Bay; compare Fig. 33.

and *Hypnum Schreberi.* On the whole, the aspect of such a forest is quite xerophytic.

Association-types of sandy beaches and dunes.—Aside from their frequent association with shingle beaches, to which reference has been made above, broad strips of sandy beach fringe the mainland here and there in somewhat protected situations along the coast, as at North Bay and South Bay, Ingonish. Frequently such beaches overlie deposits of shingle and during heavy storms the sand may be completely swept away from the more exposed parts of the beach. The finest display of sandy beach along the coast of northern Cape Breton is seen at Aspy Bay, where North Pond is nearly cut off from the ocean by a sand spit (FIG. 30), which is fully three miles long and averages perhaps a hundred yards in width. South Pond similarly is almost shut in by a shorter but much broader spit, on which have been built up a fine series of sand dunes.

FIGURE 30.—Sand spit at North Pond, Aspy Bay; *Ammophila,* etc.; in the distance, Cape North.

As in the case of shingle beaches, the lower beach here is practically plantless, while the middle beach is populated by a scattered growth of annual and perennial herbaceous plants which maintain a precarious foothold on the shifting sand. The number of species in this latter zone is small, the only forms noted here being *Ammophila arenaria, Salsola Kali, Arenaria peploides, Cakile edentula, Lathyrus maritimus, Euphorbia polygonifolia,* and *Mertensia maritima.* The lower and middle beaches vary in width. On the South Pond spit, each is about 150 feet wide; but ordinarily they are much narrower. The upper beach likewise varies in width; at South Pond it is fully 250 feet wide, but this is exceptional. At both North and South Ponds the crest of the beach proper is perhaps four feet above high water mark. At North Pond the upper beach is covered by a broad, low dune which in places rises to a height of eight or ten feet above high water mark. The plant cover here consists mainly of a rank, open growth of *Ammophila,* with which are associated *Lathyrus maritimus* and, locally, *Elymus arenarius.* Over limited areas on the lea slope, the shrubs, *Myrica carolinensis* and *Rosa virginiana,* have replaced the *Ammophila* association. In one place a scrubby forest has been

FIGURE 31.—Sand dunes with forest of white spruce, etc.; South Pond, Aspy Bay.

buried by the sand, but at the present time trees are scarce and of merely sporadic occurrence.

The South Bay spit with its dunes (Fig. 31), from the standpoint of physiographic ecology, affords in itself a study of exceptional interest, and has already been written up in some detail by Dr. Harvey ('18). In crossing the spit from the seaward margin on the east to the "pond," which is between one and two miles wide, one encounters in order (*1*) the lower beach, (*2*) the middle beach, (*3*) the upper beach, and (*4*) the salt meadows and marshes which border the spit on its western side. Along the seaward edge of the broad upper beach is a row, sometimes double but mainly single, of sand-dunes, mostly less than six feet in height, but in one locality rising to fully fifteen feet. Some at least of the dunes have originated in moist depressions, or "pans," in which grow *Juncus balticus littoralis* and *Iris versicolor*. On many of the lower dunes, as might be expected, the sand-reed (*Ammophila*) is the predominant plant, fulfilling in connection with dune-formation the twofold function of (*1*) breaking the force of the wind and causing it to drop part of its burden of sand, and (*2*) binding together and holding, by means of its copious, slender roots, the sand which thus accumulates. More often than not, however (Fig. 32), the sand-reed is absent and in its place occurs a luxuriant growth of wire-grass (*Poa compressa*), which seems fully competent to carry out the functions elsewhere performed by the sand-reed.

Figure 32.—Low dunes at South Pond, Aspy Bay; in foreground, *Poa compressa* acting as a sand-binder.

On the lea slopes of these low dunes, trees germinate, predominantly white spruce, but some balsam fir. The reciprocal relation between these trees and the dunes is rather striking. Germinating in the first place in the shelter of the low dunes, as the trees increase in size they afford an effective wind-break, which in turn is largely responsible for the further increase in the height of the dunes. The bases of the trees may be covered to a depth of six feet or more by sand, but both the spruce and the balsam are able to accommodate themselves to the changed conditions through the development of adventitious roots from the buried part of the trunk. The highest dunes are covered at the crest with good-sized trees which have thus been partially buried.

The dunes very likely would attain a greater height here, were it not for the fact that they are exposed to winds from two directions; the westerly winds which sweep across the pond tend to check the growth of the dunes, which is due mainly to the easterly winds from off the ocean.

In the lea of the dunes, between them and the salt meadows, is a broad stretch of low, sandy "back beach," the surface of which is rolling, and is covered partly by an open coniferous forest, partly by grassy areas with scattered trees. Below is given a list of the vascular plants, exclusive of certain weeds, which occur more or less abundantly in these open tracts.

Juniperus communis depressa
Panicum implicatum
Agrostis alba maritima
Danthonia spicata
Festuca rubra
Arenaria lateriflora
Fragaria virginiana
Potentilla tridentata
Lechea intermedia juniperina
Vaccinium Vitis-Idaea
Campanula rotundifolia
Leontodon autumnalis

The grassy sward is nowhere very close, but the sand is nearly everywhere hidden by the two mosses, *Tortula ruralis* and *Dicranum spurium,* and species of *Cladonia.* In among the trees occur a number of species which were not noted in the more open situations, or only rarely so, such as *Maianthemum canadense, Trientalis americana, Rhus Toxicodendron, Ribes lacustre,* and the mosses, *Dicranum undulatum* and *Hypnum Schreberi.* The branches of some of the white spruces support the most luxuriant growth of the dwarf mistletoe (*Arceuthobium pusillum*) that the writer has ever seen.

B. SECONDARY FORMATIONS OF THE XERARCH SERIES

Formation-types Resulting Primarily from Human Activity

a. ASSOCIATION-COMPLEXES DUE TO CULTIVATION

Notwithstanding the comparative recency with which this country was settled, deserted farms are a familiar sight, and abandoned farmlands in all stages of revegetation are encountered. It is only through constant grazing and cutting, or repeated mowing, that pastures and meadows can be kept open, for the rapidity with which a neglected field reverts to woodland is even greater here than in southern New England. The association-types which arise in the course of secondary successions subsequent upon cultivation may be considered under two heads: (*1*) the association-types of fallow fields, and (*2*) the association-types of abandoned pastures.

FIGURE 33.—Cultivated fields, abandoned pastures, and coniferous second growth forests along St. Ann's Bay; in the left background, the shingle beach which nearly encloses St. Ann's Harbor (compare FIG. 29).

The following figures, in addition to those introduced herewith, illustrate secondary formations: FIGS. 3, 9, 15, 24, 41, 42, 46.

The association-types of fallow fields.—For several years after a plowed field has been abandoned its vegetation may consist largely of weeds. Common species in such a habitat are:

Rumex Acetosella
Spergula arvensis
Raphanus Raphanistrum
Prunella vulgaris
Galeopsis Tetrahit
Plantago major
Solidago graminifolia
Achillea Millefolium
Chrysanthemum Leucanthemum
Leontodon autumnalis
Taraxacum officinale
Cirsium arvense

In the early stages of reclamation, so long as the plants are scattered and the vegetation relatively open, both annual and perennial species may be about equally well represented. But as the ground comes to be more densely populated, most of the annuals are crowded out and the plant cover comes to consist almost entirely of species which are perennial. Various grasses, especially *Danthonia spicata* and *Poa pratensis,* appear rather early in the succession, and as time goes on these come to comprise a more and more important element. Sooner or later a continuous mat of vegetation is developed, in which the grasses are usually the predominant plants, and the formerly bare soil becomes covered over by a thin turf. Species of *Cladonia* and *Polytrichum* also commonly play an important part in the development of the turf. With the formation of a grassy sward, the conditions come to approximate those of pastures. A few shrubs and trees may have appeared, but on the whole the succession beyond this point is essentially the same as that in abandoned fields, which is discussed in the following paragraphs.

The association-types of abandoned fields.—The predominant plants in open fields are the grasses. In dry pastures *Danthonia spicata* and *Poa pratensis* are ordinarily the most abundant species, but growing along with these and contributing to the formation of the thin sward may be various perennial weeds, particularly any of those mentioned in the second column of the preceding list as characteristic of fallow fields, together with other herbaceous perennials such as *Fragaria virginiana, Trifolium repens,* and *Antennaria neodioica.* Species of *Cladonia* and *Polytrichum* also are usually present here; sometimes the ground cover consists almost wholly of *Polytrichum* and *Leontodon.*

The general aspect of the vegetation, as just described, is xerophytic. Under favorable edaphic conditions, however, it may be much more mesophytic. In moist meadows the grass forms a denser growth and is made up largely of species such as *Poa pratensis, Agrostis alba,* and *Anthoxanthum odoratum.* Common associates of the grasses here are *Euphrasia purpurea* Reeks and *Rhinanthus Crista-galli.* The *Euphrasia* occupies much the same ecological position in the fields of northern Cape Breton as does *Houstonia caerulea* in those of southern New England. Any of the perennial herbs referred to above may grow in moist meadows, but here, in addition, pronounced mesophytes, such as the orchids, *Habenaria clavellata, H. lacera,* and *H. psycodes,* are also frequent.

FIGURE 34.—Abandoned field with white spruce and *Dicksonia;* Barrasois.

Whenever a field is permitted to run wild, *Dicksonia punctilobula* (FIG. 34), *Pteris aquilina, Anaphalis margaritacea,* and other herbaceous perennials which grazing or haying have held in check tend to assert themselves, while various shrubs may also become conspicuous. Among the latter, *Juniperus communis depressa, Rubus idaeus canadensis* and *Vaccinium pennsyl-*

vanicum are common in neglected pastures, while *Salix humilis, Alnus mollis* and *Spiraea latifolia* are frequently prominent. But while *Dicksonia* and other herbs often develop luxuriantly, and while shrubs may sometimes come to predominate over considerable areas, on the whole there is no sharply defined intermediate successional stage between grassland and coniferous forest. As a matter of fact, trees are present from the outset.

FIGURE 35.—Reproduction of balsam fir and spruce in abandoned field, Barrasois.

A close examination of almost any grassy field will usually reveal the presence of numerous young seedling coniferous trees (FIG. 35). In the face of repeated mowing these trees will persist for several years and are ready, whenever the opportunity offers, to grow up and to more or less completely occupy the ground. Grazing may check tree reproduction but seldom prohibits it entirely. In one field where sheep are pastured much of the year, the writer counted as many as twelve seedling white spruces to the square yard. The browsing of cattle may check their growth and is responsible for various grotesque tree shapes, but only frequent cutting will prevent trees from eventually gaining supremacy. The speed with which grassland may become superseded by woodland is suggested by the conditions observed in two quadrats (10 meters, 32.8 feet square), which were located in fields that had been neglected for twelve or fifteen years. In one case, counting only specimens which were more than a foot high, there were ninety trees in the quadrat, ranging up to twelve feet in height and thirteen years in age. Of these trees, thirty-four were white spruce, twenty-seven balsam fir, twenty-seven paper birch, and two white pine. In another similar quadrat there were fully five hundred trees, dead or alive, ranging up to fifteen feet in height and averaging between eight and fifteen years in age. In this case, the trees without exception were white spruce. These quadrats illustrate the varying composition which an old field woodland may possess. In some cases there will be nearly pure stands of white spruce, in others intimate admixtures of this tree with black spruce, balsam fir, and paper birch. In the vicinity of Baddeck, and in a few other localities noted, the tamarack, in many cases, rivals the white spruce for the position of prominence in abandoned pastures. The local frequency of the tamarack, as already suggested, is attributable, without much question, to soil conditions: indeed, it seems quite possible that the local distribution of this tree might prove of value as an indicator of the capabilities of land for crop production. It seems quite probable that variations in the composition of old field woodlands can be correlated still further with local differences in soil, etc., although, so far as the observations of the writer have extended, the variations might well be explained, in large measure at any rate, by the proximity of seed trees and the fortuitous distribution of seed.

The changes which accompany the development of woodlands in old fields can best be brought out by a specific illustration: a series of pastures along the Barrasois River which have been abandoned at different dates. The vegetation of the pastures themselves is essentially as described above. The pioneer trees are mostly white spruce. These germinate prolifically, especially in places where there is a carpet of *Polytrichum*. The moss carpet apparently furnishes an ideal seed bed, since in situations where it is absent reproduction is noticeably sparser. As the spruces mature, forming first a rather open grove (Fig. 36) and later a closed forest, a sequence of changes may ensue similar to what has been described in connection with the later phases of the rock outcrop succession. By the time the grove phase has been attained, much of the pasture vegetation has vanished. In its place, in the semi-shaded, narrow lanes (or spaces) between the trees (or groups of trees), is a more or less continuous bed of moss, growing on which may be found the pioneer representatives of various woodland species of plants. The moss carpet at first may consist of *Polytrichum commune,* but soon this is largely superseded by *Hypnum Schreberi.* Among the herbaceous woodland pioneers noted here are *Lycopodium complanatum, L. clavatum, Maianthemum canadense, Cornus canadensis, Viola incognita, Epigaea repens, Linnaea borealis americana,* and *Trientalis americana.* Small white spruce seedlings grow scattered over the moss carpet, but, practically speaking, white spruce reproduction has come to a standstill, for few of these seedlings are destined to mature.

FIGURE 36.—Grove of white spruce in former pasture; Barrasois. Photograph by Dr. L. H. Harvey.

In this connection, there is one feature of a young spruce forest that demands special comment. On the ground beneath the trees in such a forest there may be no vegetation whatever, but only a dry layer of dead spruce needles, comprising what the forester familiarly refers to as "duff." The absence here of plants does not seem to be attributable directly to insufficient light. In remarking recently on this same phenomenon, Moore ('17, pp. 156, 157) has concluded that the lack of vegetation is due to the dryness of the soil which results from the interception of the precipitation by the crowns of the trees. The writer had already arrived at a conclusion somewhat as follows. During the development of a group of young spruces in the open, at first there is ample light for all. But later on, in the competition for light which ensues as they become larger, many of the trees are killed. The accumulation on the ground beneath, both of the needles which fall from these dead trees and of needles derived from the shaded branches of the living trees, may take place so rapidly that the ground vegetation is buried. The formation of this thick, loose layer of dry needles not only wipes out the original ground cover, but, because of its dryness, prevents any new vegetation from getting a start. This process, initiated while the tree growth is still open, continues during the transition from the grove to the forest stage in the succession. A layer of needles several inches thick may collect on the forest floor, and all the mosses and herbaceous plants, as well as the seedling trees described in the preceding paragraph, may be exterminated. The extreme paucity of vegetation on the forest floor which results in this manner is a very characteristic feature of young coniferous forests. Later on, as the forest matures, the trees becoming greatly decreased in number by the constant competition for light, and in consequence becoming more widely spaced, the rate of leaf-fall gradually slackens so that a certain degree of equilibrium is brought about on the forest floor. It then becomes possible for a new ground cover to establish itself: *Polytrichum commune* and *Hypnum Schreberi* reappear, followed shortly by *Hylocomium splendens,* and a moss carpet is gradually reëstablished, on which woodland herbs and shrubs, together with seedlings of balsam fir and other trees of the coniferous forest association-type become increasingly abundant. The history of the forest beyond the grove stage of the succession is practically identical with what has been described in connection with primary successions.

b. ASSOCIATION-COMPLEXES DUE TO FIRE

Fire, like cultivation, destroys the original vegetation and causes the institution of new successional series. According to the completeness of the devastation, particularly as it affects the humus layer with its subterranean plant organs and its micro-organisms, broadly speaking, two lines of succession may be distinguished: one where the humus has escaped serious injury, the other where the humus has been destroyed. Between these there of course are intermediate possibilities.

Humus little injured.—Let it be assumed that previous to the conflagration a burned area has supported a forest of the climax type. Aside from the annihilation of much of the antecedent vegetation, the most obvious immediate effect of fire is the removal of the forest cover and the consequent increased illumination of the forest floor. The revegetation of such an area is destined to be accomplished partly through the agency of plants which in various ways have survived the fire, partly through the invasion of plants from other sources. Almost the first aftereffect of the fire is seen in the rapid spread of certain herbaceous species which were only sparingly represented in the original forest, but which are able to flourish in the new environment. *Cornus canadensis* perhaps nowhere develops more luxuriantly than in burned areas, while *Linnaea borealis americana* and *Maianthemum canadense* also thrive here. Of the shrubs and small trees in the burned forest, *Corylus rostrata, Acer spicatum* and *Viburnum cassinoides* frequently survive. The local herbaceous element in the flora may predominate for a longer or shorter period, but it is soon augmented by an extraneous element in which the following species are usually conspicuous: *Lycopodium clavatum* and *Gaultheria procumbens; Solidago bicolor* and *S. macrophylla; Pteris aquilina* and the "fire-weeds," *Epilobium angustifolium* and *Anaphalis margaritacea,* which frequently form a rank growth; and *Rubus idaeus canadensis,* which within a few years may produce an almost impenetrable tangle over the entire area.

In the reëstablishment of forests in burned areas of this sort, the paper birch, as elsewhere in the northwoods, is everywhere the conspicuous pioneer. This tree, it will be recalled, is sparingly represented in the regional climax forest. After a burn it reproduces rapidly, partly by means of coppice shoots from stumps which have survived the fire, partly from seed, and with its rapid rate of growth it quickly gains the ascendancy over other trees in the rising forest. Red maple also frequently plays an active rôle in reforestation, reproducing in much the same manner as the birch; while the bird cherry and any of the poplars may be present in greater or less abundance. A point of interest, to be emphasized in this connection, is that the balsam fir, with the spruces, may appear at a very early stage in the succession: in fact, their seedlings may be present from the outset. But, on account of their relatively slow growth in the shade cast by the birch canopy, the conifers continue to occupy a position of subordinate importance for many years (Fig. 37). By the time a hundred years has elapsed, however, a marked change in the character of the forest has taken place; for by this time the balsam fir has usually become the predominant tree. This latter phase in the succession is well illustrated by an old burn forest near Indian Brook. Here the bulk of the mature stand consists of balsam fir intermixed with

Figure 37.—Succession after a burn; balsam fir coming in under paper birch; northwestern Maine.

frequent white spruces, scarcely any of the balsams being more than ten inches in diameter. Paper birch is rarely present in the younger growth, but is represented abundantly by scattered older specimens ranging up to a foot and a half in diameter, while the ground beneath is strewn with the remains of fallen trees. Large red maples are frequent and one large hemlock with a healed fire scar was noted, obviously a relict of the former forest.

The ultimate association-type of the burn succession is a forest of the regional climax type, provided edaphic conditions are favorable to its development. Indeed, very often the beech and others of the climax trees beside those already mentioned may appear early in the series, arising either from coppice sprouts or from seed. It seems hardly necessary to describe the changes in the undergrowth which accompany the development of the forest.

FIGURE 38.—View along coast north of Neil's Harbor: barrens and second growth forest, mostly white spruce; aspect largely the result of repeated burning. Photograph by Dr. L. H. Harvey.

Humus destroyed.—There are extensive tracts of land along the eastern coast of northern Cape Breton, particularly between North Bay, Ingonish and Aspy Bay (FIG. 38), which it is presumed were formerly covered, very largely at any rate, with deciduous forests, but which have suffered so severely from fires that at one time or another not only the greater part of the vegetation, but most of the humus as well has been consumed. In areas of this sort succession must start all over again from near the bottom and a sequence of stages similar to what has been described in primary successional series may be observed. To be sure, succession in an area which has been denuded by fire differs in certain respects from a primary succession, owing chiefly to the fact that even repeated fires fail to completely annihilate all the previously existing humus and plant life, and that the relicts which have thus survived may play an important part in the succession. But it is hardly worth while to attempt to depict the stages in detail. In general it may be stated that, just as in the case of primary successions, there is a marked variation in the nature of the primitive associations, due to local differences in the nature of the substratum, etc., but that all successional series tend to merge in the formation of forest.

FIGURE 39.—White spruce reproduction in an area which has been repeatedly cut and burned; South Bay, Ingonish.

Abundance of white spruce the result of fire and cultivation.—At the present day, throughout the region of deciduous forests, wherever tracts of land have been cultivated and then abandoned or have been ravaged by repeated fires, white spruce, with local exceptions, is everywhere the most abundant tree of second growth forests. The explanation of this fact is obvious. The white spruce is essentially a pioneer. It seeds prolifically and rapidly colonizes open grounds of almost any description (Fig. 39). The effect of cultivation and fire in destroying the seedlings of balsam fir and other trees, which otherwise might have dominated, enables the spruce, with its capacity for rapid reproduction in the open, to establish itself and to make headway which otherwise would be impossible. The common practice of burning over woodlots in order to keep them open for pasturage or for some other reason, naturally favors the spruce. In brief, the combined effect of cultivation and fire is to arrest the succession, so that it rarely progresses beyond the pioneer forest stage.

Figure 40.—Blueberry barren near Frizzleton.

Blueberry barrens.—Among the most unique features of the interior plateau of northern Cape Breton are the Barrens. These natural barrens, which will be described later, should not be confused with the barrens of the lowlands (Fig. 40), which are the result of repeated fires, usually set intentionally every few years in the interest of the blueberry crop. Extensive blueberry barrens of this sort are found in the Margaree district, where they may occupy hundreds of acres. The predominant plants in such tracts are the blueberries, *Vaccinium pennsylvanicum* and *V. canadense,* with which, though far less abundant, are associated other ericaceous shrubs, such as *Kalmia angustifolia, Vaccinium Vitis-Idaea, Gaultheria procumbens,* and *Ledum groenlandicum.* Various herbaceous plants occupy a prominent position, notably *Pteris aquilina, Danthonia spicata* and *Aster multiflorus,* while *Cladonia rangiferina* and the mosses, *Polytrichum commune, P. juniperinum,* and *Hypnum Schreberi,* are common. The ecological aspect is that of a heath, though there are scattered trees, mainly tamarack and white spruce. The balsam fir is virtually absent.

Left to itself, such an area becomes forested within a few years. The process of reclamation is graphically illustrated by one area examined, which adjoins a large heath, but is separated from it by a highway that has acted as a "fire line." This area is now occupied by an open forest of tamarack and white spruce. The balsam fir is absent from among the larger trees, but is abundantly represented in the young growth. The heaths are present in greatly reduced abundance, as compared with the barren area across the road, and the moss carpet has become correspondingly more luxuriant.

c. ASSOCIATION-COMPLEXES DUE TO LOGGING

The indiscriminate removal of the merchantable timber in a climax forest by logging usually has little effect on the future composition of the forest, provided the area escapes being burned over. Some trees, notably the paper birch and balsam fir, tend to become somewhat more abundant here, and frequently pioneer species such as the aspens are able to establish themselves temporarily in cut-over tracts. But, on the whole, the forest may be said to regenerate itself through the younger generation of trees which was present in the original forest. Where a forest is lumbered *discriminately,* as is frequently done for fir and spruce alone, it is of course obvious that the detailed physiognomy of the forest may be quite appreciably altered. Where the removal of the timber is followed by burning, most of the younger trees are destroyed and complete regeneration is impossible. This latter point is well illustrated by conditions near an old settlement along Indian Brook, which has been deserted for many years. The climax forest was cut over in two adjoining tracts, one of which was afterward burned over, the other not. To-day, perhaps forty years after cutting, the unburned area is covered by a forest of yellow birch, sugar maple, and other climax trees, with scattered specimens of paper birch and large-toothed aspen (*Populus grandidentata*). The burned area, on the other hand, supports an almost pure forest of paper birch. In both forests the balsam fir is the most conspicuous undertree.

C. PRIMARY FORMATIONS OF THE HYDRARCH SERIES

1. The Formation-types of Lakes and Ponds Inland

a. INTRODUCTORY

The ecological relationship of lakes and swamps.—For purposes of convenience, lakes and swamps are here treated under separate headings, but, broadly speaking, they belong to the same family and there is no sharp dividing line between them. Through the activity of various agencies a lake or pond may become filled in and converted into a swamp. The manner in which this transformation may be accomplished by plants, together with the changes in vegetation which accompany the process, is outlined in the following paragraphs, quoted, with slight alterations, from an earlier paper by the writer ('15, pp. 175–178):

> The important rôle commonly played by plants in the conversion of lakes into swamps has long been recognized. When the plants in a lake die, their remains sink to the bottom where, because of insufficient oxidation, the vegetable débris is only partially decomposed. In this way there collects on the floor of the lake a layer of vegetable muck, or peat; and through the continued addition of fresh layers the deposit is gradually thickened and built upward. This constructive process may go on until ultimately the surface of the deposit reaches the level of the water, when the lake gives way to a swamp. But the rate at which the substratum is built up and the length of time which elapses before it reaches the water level varies greatly in different parts of a lake. Plants grow most luxuriantly in shallow water; they may be practically absent from the deeper areas. It follows, therefore, that the accumulation of muck or peat proceeds much more rapidly in shallow than in deep water—so

> much so, in fact, that the shoreward parts of a lake may have become completely filled in before any appreciable accumulation has taken place in the deeper areas. The filling in of deep lakes usually proceeds centripetally. This is due to the fact that the shoreward zones of vegetation, in consequence of their more vigorous growth, exhibit a tendency to push outward into deeper water. Where this tendency is pronounced, the shoal water zones may completely override the deeper water zones, at the same time causing the lakeward slope of the deposit to become much steeper. The filling in of the deeper parts of a lake may also be effected to a varying degree by the accumulation of loose débris from the adjoining shallows or by the deposition of sediment in flood time, while various plankton forms may contribute in a small measure to the deposit.
>
> Coincident with the upbuilding of the substratum through the deposition of muck or peat, as outlined in the preceding paragraph, transformations occur in the character of the vegetation growing on the lake's bottom. For, as the depth of the water diminishes, it becomes possible for plants to develop which were unable to grow in the deeper water. And as these shallow water plants increase in number and abundance, they may crowd out and eventually replace the deeper water species. Thus there may follow one another a series of plant associations, each one of which, by helping to raise the bottom of the lake to a higher level, prepares the way for less hydrophytic associations, but at the same time, by so doing, brings about its own extermination.
>
> It is a familiar fact that the plants which fringe the edges of so many lakes are commonly massed in more or less definite bands or zones that tend to be concentric with respect to the deeper parts of the lake. The floristic composition of these zones in any given lake is determined largely by the ecological requirements of the various species of plants which happen to be present, in relation to the depth and clearness of the water . . . Reference has already been made to the succession of plant associations which accompanies the building up of the lake bottom. It has been found that this dynamic Vertical Succession corresponds closely with the apparently static Horizontal Zonation just outlined . . . . . This general coördination between the contemporaneous horizontal sequence of zones and the historical or vertical order of succession has been verified repeatedly by the stratification of plant remains observed in peat deposits, and is of great assistance in reconstructing the past or predicting the future course of events in any specific locality.

Of course, not all swamps have originated in the manner just described (see further under head of swamps) ; neither, on the other hand, do all lakes exhibit any pronounced tendency to become converted into swamps. For reasons which are not always clear, there is the greatest variation in the speed at which the transformation is brought about, and in many lakes, not only does there seem to be scarcely any tendency toward swamp formation, but little change would appear to have taken place at any time since their formation.

Geological and other factors influencing the distribution and vegetation of inland lakes.—The majority of the lakes and ponds in the lowland of northern Cape Breton are glacial: they occupy depressions which have resulted from glacial activity (see further discussion in Nichols '15, pp. 170–171). In calcareous districts, however, particularly in localities where there are extensive deposits of gypsum, "sink holes" due to subterranean erosion are common, and these frequently are occupied by ponds. Still a third type of water basin, due entirely to vegetative activity, is encountered on the plateau, and will be described in some detail later.

FIGURE 41.—Freshwater Lake, South Bay, Ingonish; cut off from ocean by a shingle beach; in distance, Middle Head, mostly granitic; in right foreground, a gypsum outcrop; second growth forests of white spruce and balsam fir. Photograph by Dr. L. H. Harvey.

In their influence on the vegetation of lakes and ponds, drainage and permanency are factors of considerable significance. The effect of drainage will be discussed presently in connection with the formation-types of swamps. The effect of permanency is seen in comparing the vegetation of permanent, with that of periodic, lakes or swamps. Permanent and periodic lakes and swamps, as related to topography and ground water level, have been fully discussed in the writer's paper referred to above ('15, pp. 172–175).

b. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED LAKES AND PONDS

The association-types of permanent lakes.—Freshwater Lake (FIG. 41) and Warren Lake, at Ingonish, may be taken as representative examples of fairly large, well-drained lakes. Except for *Chara* and various algae there is little vegetation below a depth of six feet. The majority of aquatic plants grow best in water less than three feet deep. Along sandy shores, which are the prevailing type in both ponds, the following aquatic species are more or less abundant.

Chara sp.
Fontinalis sp.
Isoëtes echinospora Braunii
Sparganium angustifolium
Potamogeton Oakesianus
Potamogeton heterophyllus
Potamogeton bupleuroides
Glyceria borealis
Scirpus subterminalis
Eleocharis palustris vigens
Scirpus americanus
Juncus militaris
Nymphaea advena
Ranunculus Flammula reptans
Myriophyllum humilis
Nymphoides lacunosum
Eriocaulon septangulare
Lobelia Dortmanna

Nymphaea and *Nymphoides* are the commoner forms in the deeper shallows. *Eriocaulon* often forms a bright green carpet on the bottom in water three or more feet deep, but seldom flowers where it is more than a foot deep: *Ranunculus* forms similar carpets in shallow water, but flowers only on the shore. In places *Juncus* and *Isoëtes* grow in profusion. But for the most part the sandy bottom is only sparsely covered by vegetation. It might be added that *Carex aquatilis,* not noted in either of these lakes, is a frequent form along the shores of lowland lakes, locally giving rise to marshy marginal swamps similar to those to be described later in connection with lakes in the highlands.

The narrow sandy beach, between high and low water marks, supports a scanty growth of herbaceous species, among them

Equisetum arvense, Juncus articulatus, and *Ranunculus Flammula reptans.* Above high water mark there is ordinarily a fringe of *Myrica Gale* (nearest the water) and *Alnus incana.*

Muddy shores are developed to some extent in sheltered situations. Here the aquatic vegetation includes most of the species already listed, and in addition *Utricularia intermedia* and *U. vulgaris.* Certain other species, mostly amphibious, grow in shallow water or on the mucky shore, which is swampy at low water. These latter include: *Sphagnum* sp., *Drepanocladus fluitans, Dulichium arundinaceum, Iris versicolor, Potentilla palustris, Hypericum virginicum, Sium cicutaefolium,* and *Lysimachia terrestris.* As along sandy shores, the sweet gale and alder fringe the shore at high water mark. Along sandy shores there is little evidence of succession, but along muddy shores there is a tendency for swamps to develop.

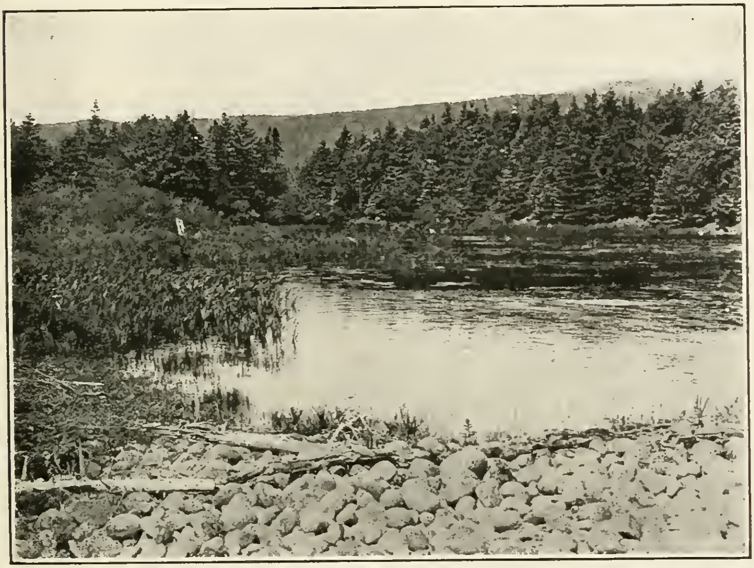

FIGURE 42.—Fresh pond behind shingle beach, well drained by seepage through barrier; *Typha latifolia* in left foreground; Barrasois.

The association-types of permanent ponds.—Small ponds (FIGS. 26, 42) may differ little from lakes in the character of their vegetation. But, on the whole, aquatic plants are apt to be relatively more abundant here by reason of the lesser depth of the water, its comparative quietness, etc. Largely because of the absence of any appreciable amount of wave action, the shores of small ponds tend to be more muddy than those of the larger bodies of water. The vegetation of sandy shores is similar to what has been described above, and the same is true in general of muddy shores. Here, however, there is often a rank growth of cat-tails (*Typha latifolia*) and bulrushes (*Scirpus occidentalis, S. cyperinus, S. atrocinctus,* etc.), through the activity of which the pond tends to become filled in and converted into a swamp.

Sink-hole ponds frequently exhibit the phenomenon of marl-formation (see Nichols '15, pp. 194–196). In such ponds there is usually a luxuriant growth of *Chara,* one of the most important marl-forming plants, and of various algae. Among the prominent aquatic seed plants here may be *Potamogeton pectinatus* and *P. pusillus.* Leaves and stems of all submersed forms are usually incrusted with a thin, whitish, flaky deposit of marl.

The association-types of periodic ponds.—Periodic ponds are not sharply delimited from permanent ponds on the one hand or from periodic swamps on the other. Very shallow depressions, which during the growing season contain water for only a brief period, are commonly occupied by a rank growth of such species as *Scirpus cyperinus* and *S. atrocinctus, Juncus effusus* and *J. brevicaudatus,* and *Iris versicolor.* In the case of ponds which disappear completely only for a short period during the summer, there may be a striking concentric zonation of plant associations. In one instance, for example, the wetter central area is largely occupied by the moss, *Amblystegium riparium.* Proceeding from here toward high water level there are encountered (*1*) a zone of more or less amphibious species such as *Sparganium americanum, Juncus effusus, Ranunculus Flammula reptans, Hypericum canadense, Lysimachia terrestris,* and *Sium cicutaefolium;* (*2*) a zone of *Iris versicolor;* (3) a zone of *Alnus incana.* Elsewhere *Eleocharis palustris* and the species cited earlier in this paragraph may be prominent as marginal plants, while in some cases the liverwort, *Marchantia polymorpha,* develops profusely on the muddy shores of periodic ponds.

c. THE ASSOCIATION-COMPLEXES OF UNDRAINED LAKES AND PONDS

The association-types of permanent ponds.—Sink-hole ponds commonly have no visible outlet and are practically undrained. Aquatic vegetation as a rule is luxuriantly developed here, but varies greatly in its floristic composition, even in neighboring ponds. In one small pond, for example, *Potamogeton natans* is practically the only species present; in another, *Chara;* in another, *Fontinalis gigantea;* while in still another, *Chara, Fontinalis gigantea,* and *Potamageton pusillus* grow intermixed. Such ponds fluctuate more or less in level from season to season and the marginal vegetation resembles that of periodic ponds.

Of particular interest, in view of their subsequent history, are the undrained ponds in which originate peat bogs. The water in these fluctuates very little in level from season to season, and while the ponds may be small in area they are usually fifteen or more feet in depth. Depressions of this sort are by no means common near the coast, and most of those which were discovered had already attained the bog stage in their development. It is of interest to note, however, that the pioneer vegetation in and about these ponds is similar in most respects to that of other ponds. The aquatic vegetation includes *Nymphaea advena,* species of *Potamogeton,* and various aquatic mosses and algae. *Chara,* however, seems to be rare or absent. In the shallow water near the margin may grow *Sparganium americanum, Eriocaulon septangulare, Carex Pseudo-Cyperus, Potentilla palustris,* and *Lobelia Dortmanna.* Along the more or less mucky shores may occur herbaceous species, such as *Onoclea sensibilis,* various sedges, *Iris versicolor, Lysimachia terrestris, Hypericum virginicum,* and *Lycopus americanus;* and shrubs, such as *Myrica Gale, Alnus incana, Rosa nitida,* and *Ilex verticillata.* The most striking difference between these and ordinary ponds is seen in the frequently luxuriant development of various species of *Sphagnum,* the significance of which will be pointed out later. The marginal shrubs here also commonly include *Chamaedaphne calyculata* and *Kalmia angustifolia,* both of which are typical bog forms.

The association-types of periodic ponds.—Periodic undrained ponds scarcely differ in their vegetation from periodic well-drained ponds, since essentially the same end is accomplished through the periodic drying up of the pond as might be attained through drainage. They therefore require no special comment.

2. The Formation-types of Lake- and Spring-swamps Inland

a. INTRODUCTORY

Lake-, spring-, and precipitation-swamps.—Swamps which have originated in the manner described earlier, through the filling in of lakes by vegetation, may be designated *Lake-swamps.* Many swamps, however, probably the majority of those in the lowland, owe their existence to the relation between topography and ground water level, i. e., to the presence of spring or seepage water. Such swamps may be designated *Spring-swamps* (see Nichols '15, pp. 184, 192). Lake- and spring-swamps are widespread in their distribution throughout most regions. In regions like the one under consideration, where precipitation is high and the evaporating power of the air low, there is still a third type of swamp whose existence is dependent very largely on direct atmospheric precipitation. Swamps of this sort, well exemplified by the raised bogs of the high interior plateau, may be designated *Precipitation-swamps.*

The ecological significance of drainage.—In his study of the geographical distribution and ecological relations of bog associations in eastern North America, Transeau ('03, p. 420) arrived at the conclusion that "the 'drained swamp' and 'undrained swamp' classification will not hold over any great area." Drainage, however, has been employed as a basis of classification by Cowles ('01, pp. 145–156) and others, and it is the conviction of the writer that, from the standpoint of physiographic ecology, this factor affords by far the most fundamental criterion yet conceived, at least for the classification of the lakes and swamps in the inland group. The relationship between cause and effect may often be obscure, since the influence of drainage is commonly expressed indirectly through other, more direct factors; but, in the last analysis, drainage, more than any other single factor or set of factors, seems to have a vital influence on the vegetation, through its effect on the aeration of the soil and on the accumulation therein or removal therefrom of various deleterious substances, as well as on other peculiarities of the substratum with which the character of the vegetation may be more directly correlated (in this connection, see Rigg '16; also Harper '18, pp. 27–31).

Drainage as a basis of classification.—In treating the lakes and swamps of the inland group in northern Cape Breton, drainage has been selected as the most fundamental basis of classification. On this basis the lakes and ponds have been divided into two groups, well-drained and undrained, and the swamps into three, well-drained, poorly drained, and undrained. The practical application of any scheme of classification of course has its limits, owing to the difficulty, if not the impossibility, of adequately correlating cause and effect, and whatever factors are selected as criteria, all sorts of intergrading conditions are encountered. Particularly in the case of swamps is the complexity of the situation enhanced in a cool, humid region such as this by the fact that atmospheric factors may react on the vegetation in such a manner as to neutralize to a greater or less degree the influence of dissimilar edaphic conditions.

During the course of the present investigations in northern Cape Breton, the writer has examined several hundred different lakes and swamps. In a number of the swamps, in addition to observations on the surface conditions, soundings were taken with a fifteen foot iron rod (summer of 1915). By this means it was possible (*1*) to ascertain the depth of the underlying vegetable deposit; (*2*) by the attachment of a Davis peat-sampler (see Bastin & Davis '09, p. 61), to determine the character of the deposit at different depths; and (*3*) with the aid of a hand-level, to figure out the topography of the underlying terrain, with particular reference to its bearing on the drainage problem and also its general relation to the surface of the swamp.

Well-drained and undrained swamps compared.—In their typical development, well-drained and undrained swamps differ from one another in several important respects. (*1*) Well-drained swamps are best developed on springy slopes, where the gradiant is sufficiently steep to insure adequate drainage. They also commonly occur along the banks of streams (many such swamps, more especially along small brooks, are better included with the swamps of the inland group than with those of the river group). Undrained swamps, as exemplified by bogs, ordinarily are best developed in relatively deep, undrained or poorly drained, water filled depressions. For reasons which will be apparent later, however, in humid regions, like the one under discussion, swamps of the undrained type are by no means confined to depressions. (*2*) Both well-drained and undrained swamps may be underlain by peat; but in the former the deposit usually is quite shallow and sometimes it is entirely absent. Moreover, in well-drained swamps the peat as a rule is mucky, the plant remains being pretty thoroughly decomposed. Undrained swamps invariably are underlain by peat deposits, which often exceed fifteen feet in thickness; the peat is more or less spongy, and the plant remains for the most part are well preserved. (*3*) The soil in practically all swamps in northern Cape Breton is acid to litmus, but it is appreciably more so in swamps of the undrained type than in others. (*4*) The vegetation of well-drained swamps is characterized by the moderate abundance of the sphagnums; by the great variety of herbaceous seed-plants, which in large part are hydrophytes; by the scarcity of ericaceous shrubs; and by the presence of several deciduous trees of southward distribution. The vegetation of undrained swamps, on the other hand, is characterized by the luxuriant development of the sphagnums; by the comparatively small number of species of herbaceous seed-plants, which in large part are bog xerophytes; by the abundance of ericaceous shrubs; and by the absence of practically all trees except the black spruce and tamarack.

b. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED SWAMPS

Pioneer association-types.—Among the important pioneers in the development of vegetation on springy or wet slopes are the bryophytes, notably the following species:

*Marchantia polymorpha**
*Pellia epiphylla**
*Pallavicinia Lyellii**
*Scapania nemorosa**
Sphagnum squarrosum
*Philonotis fontana**
*Mnium punctatum**
Brachythecium novae-angliae

Of the herbaceous vascular plants, almost any of the species to be listed later as characteristic of wet meadows may appear at a very early stage in the succession, but the following list includes the forms which, on the whole, are more prominent as pioneers:

*Onoclea sensibilis**
Equisetum sylvaticum
Glyceria canadensis
Glyceria laxa
Scirpus atrocinctus
Scirpus rubrotinctus
Carex crinita
*Carex scabrata**
Carex stipata
*Juncus articulatus**
Juncus brevicaudatus
Juncus effusus
*Iris versicolor**
*Sagina procumbens**
*Cardamine pennsylvanica**
Drosera rotundifolia
*Chrysosplenium americanum**
Hypericum canadense
Epilobium palustre
Lysimachia terrestris
Lycopus americanus
*Mentha arvensis**

Association-types of open swamps.—The luxuriant growth of the grasses, sedges, and rushes may result in the development of a wet meadow association-type, characterized by the predominance of grass-like growth-forms and the relative absence of woody plants. During the evolution of the wet meadow, the plant cover gradually becomes denser, while the nature of the substratum may become modified through the formation of a layer of mucky peat. Contemporaneously with these changes, many of the pioneer species (notably those starred [*] in the above lists), either disappear or else become restricted in their distribution to the more open, wetter habitats. Others become more abundant, and at the same time still other species not before represented may make their appearance. The following list includes various herbaceous plants, which, in addition to those already mentioned, and together, less frequently, with those to be given in a subsequent list, commonly are more or less abundantly represented in open, well-drained swamps.

Aspidium Thelypteris
Aspidium cristatum
Osmunda cinnamomea
Osmunda regalis
Agrostis hyemalis
Calamagrostis canadensis
Eriophorum virginicum
Carex canescens disjuncta
Habenaria dilatata
Habenaria psycodes
Thalictrum polygamum
Fragaria virginiana
Geum rivale
Sanguisorba canadensis
Chelone glabra
Galium palustre

Carex flava
Carex intumescens
Carex pallescens
Carex paupercula
Carex stellulata
Habenaria clavellata
Eupatorum purpureum
Aster nemoralis
Aster puniceus
Aster radula
Aster umbellatus

The bryophytes, as a rule, are well represented in open swamps, usually forming a more or less conspicuous understory of vegetation. The following additional species may be mentioned as characteristic:

Sphagnum palustre
Sphagnum imbricatum
Sphagnum magellanicum
Sphagnum Girgensohnii
Camptothecium nitens
Rhytidiadelphus squarrosus
Chrysohypnum stellatum
Acrocladium cuspidatum

More often than not, shrubs put in their appearance so early that the wet-meadow stage in the succession is of very brief duration. Frequently it is eliminated as a distinct phase. Instead, there may arise a mixed growth of shrubs and herbaceous plants: these with scattered trees constitute the most familiar type of vegetation in open swamps. The common pioneer shrub is the alder (*Alnus incana*). Associated with this may grow any (or all) of the following species:

Salix humilis
Myrica Gale
Ribes hirtellum
Spiraea latifolia
Rubus pubescens
Rubus canadensis
Rosa nitida
Ilex verticillata
Viburnum Opulus americanum
Viburnum cassinoides

On the whole, ericaceous shrubs (or semi-shrubs) are scarce in well-drained swamps, but *Chiogenes hispidula* commonly, *Kalmia angustifolia* frequently, and *Chamaedaphne calyculata* and *Vaccinium macrocarpon* occasionally are present.

The edaphic climax association-type.—Ultimately the entire swamp may become wooded, but, as a rule, much of it remains fairly open, with trees scattered, but more abundant toward the margin, and with the shrubs and herbaceous plants of open swamps occupying the spaces between them. The predominant trees, as a rule, are balsam fir, black spruce, white spruce, and red maple; but associated with these, in varying abundance, may grow paper birch and yellow birch, white ash and black ash (*Fraxinus nigra*), and occasionally white pine.

The vegetation of wooded swamps may include various of the herbaceous and shrubby species already listed, but in addition to these a number of forms occur here which have not yet been mentioned, although some of them may likewise grow in open swamps. Such, for example, are the following:

Phegopteris polypodioides
Aspidium noveboracense
Osmunda Claytoniana
Taxus canadensis
Carex trisperma
Carex tenella
Carex leptalea
Carex folliculata
Clintonia borealis
Maianthemum canadense
Coptis trifolia
Mitella nuda
Oxalis Acetosella
Viola renifolia
Circaea alpina
Cornus canadensis
Linnaea borealis americana
Aster acuminatus

c. THE ASSOCIATION-COMPLEXES OF UNDRAINED SWAMPS

Occurrence of bogs along the coast.—In the vicinity of Baddeck and in other localities where the clayey nature of the soil retards drainage, bogs may develop in shallow depressions of any description. They develop best, however, here as in regions farther south, in fairly deep, closed, water-filled depressions. Raised bogs, such as occur along the coast in New Brunswick (see Ganong '98), and which are extensively developed on the interior plateau in northern Cape Breton, are apparently absent along the coast. The finest series of bogs discovered in the lowland is situated near the mouth of the Barrasois River, where in a tract of woodland less than a square mile in area there are six or eight fine examples. All of these occupy closed basins, presumably kettle holes in the drift, but possibly drift-covered sink holes, range in size from less than one to more than three acres, and bear a remarkable resemblance to certain Connecticut bogs (see Nichols '15, pp. 202–217). The following observations relate more particularly to this collection of bogs, which can be regarded as representative.

The floating mat and its association-types.—The early stages of bog development are best exhibited in the largest of these bogs, where, at the south end, there still remains a pond some sixty feet long by twenty-five feet wide (Fig. 43). The filling in of such a pond is accomplished through the intervention of a floating mat, and the general features of mat formation are quite similar to what the writer has described for Connecticut bogs ('15, pp. 196–202). Its formation is brought about through the combined activity of shrubs, sedges, and sphagnums. Very commonly the forerunner of mat formation is the cassandra (*Chamaedaphne calyculata*). This shrub occurs both along the shore and along the edge of the advancing mat and frequently grows out several feet into the open water. Its relation to the mat is similar to that of the steel framework to a concrete building: it forms a skeleton upon which the sphagnum may be supported. The necessity for such support will be pointed out in the next section. Where, as is commonly the case, the cassandra is followed by a dense growth of sphagnum, a mat is

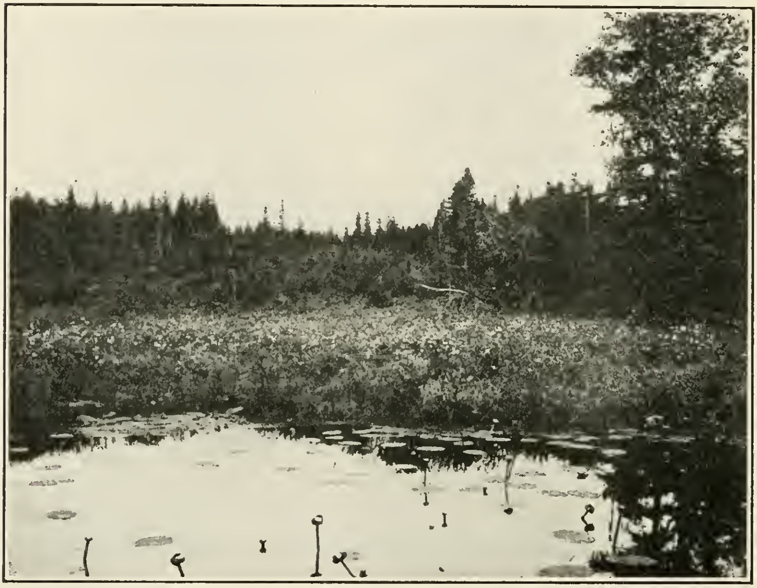

Figure 43.—Bog near mouth of Barrasois River; *Nymphaea* in foreground; sedge-shrub-sphagnum mat in middle distance; bog forest in center background.

developed. Where, however, as along the south shores of several of these bogs, shade conditions preclude the growth of the sphagnums, no mat is developed (see further on p. 363). So luxuriant, as a rule, is the development of the sphagnums that the important rôle played by the cassandra is liable to be overlooked; but if a newly formed "sphagnum mat" be dug into, the woody ribs formed by this shrub will usually be found.

In some instances, certain sedges play a rôle similar to that just ascribed to the cassandra. Certain of these, e. g., *Carex filiformis,* in contrast to the shrubs, are quite capable of forming a mat themselves, independently of any assistance from the sphagnums. But, as a rule, the sphagnums make their appearance at an early stage in the history of the mat and thereafter play an important part in its development: ordinarily they spread so rapidly and grow with such luxuriance as to quickly become the predominant element of the plant cover. Various features associated with the formation and growth of floating mats are discussed further in the following paragraphs and in later pages, in connection with the swamps of the highland.

On the "sphagnum mat" thus formed, in greater or less abundance, grow various sedges and shrubs which, by their roots, rhizomes and trailing stems, tend to bind together and consolidate the otherwise loose structure. Characteristic species are the following:

Eriophorum callitrix
Eriophorum virginicum
Rynchospora alba
Carex canescens disjuncta
Carex paupercula irrigua
Carex stellulata
Kalmia polifolia
Ledum groenlandicum
Vaccinium macrocarpon
Vaccinium Oxycoccus
Menyanthes trifoliolata

Along the wet margin of the mat, where it borders on the marginal ditch (see further below), and in the ditch itself where this is swampy, commonly grow various forms which one ordinarily associates with well-drained swamps; among them: *Sparganium americanum, Iris versicolor, Alnus incana, Myrica Gale, Rosa nitida, Ilex verticillata, Hypericum virginicum, Lysimachia terrestris,* and *Lycopus americanus.* These plants seldom occur in the older parts of the bog.

The sphagnums in relation to the formation of floating mats.—The relatively subordinate rôle played by the sphagnums in initiating the formation of floating mats was suggested by Ganong ('03, pp. 440–441) and Transeau ('05-'06, p. 363), and has been emphasized by Davis ('07), Cooper ('13) and others. From these and the writer's observations it seems certain that in general the appearance of the sphagnum is subsequent rather than antecedent with reference to that of the vascular plants. The inability of the sphagnums of themselves to form a mat may be attributed largely to the lack of coherence and buoyancy in the mass of floating vegetation which they sometimes form. But added to this is the fact that comparatively few species of sphagnum are capable of flourishing with their foliage completely submerged. Of course there are certain sphagnums which are distinctly aquatic in their mode of growth, but among the twenty species which have been recorded from Cape Breton, only two definitely belong in this category, namely, *S. Pylaisei* and *S. cuspidatum* (see in this connection the ecological classification of bog sphagnums on p. 422). In many mountain ponds these two species grow in great profusion, floating at or just below the surface of the water, and their ecological relations there will be discussed in some detail later (see especially pp. 424, 429), Neither of these two species, however, occurs in any abundance along the coast: in fact, the writer has never seen *S. Pylaisei* except in the mountains, while *S. cuspidatum,* though frequently represented in lowland ponds by the var. *Torreyi,* is seldom of ecological importance here. The important mat pioneers among the sphagnums in the Barrasois bogs, which may be regarded as representative of lowland bogs in general, are *S. papillosum, S. magellanicum,* and *S. recurvum.* These three species grow best in very wet situations, but they will flourish only where the nature of the substratum is such that, at least throughout most of the growing season, their shoots remain partially raised above water level. The maintenance of this position they are not sufficiently buoyant to accomplish themselves, so that the preexistence of some sort of a support to prevent their sinking below the surface is essential. Hence the importance of shrubs and sedges as pioneers in the development of a "sphagnum mat."

The marginal ditch and its significance.—The formerly water-filled depressions now occupied by the Barrasois bogs have become almost completely filled in through the activity of vegetation. All that remains in most cases to remind one of the pond stage in the succession is a moat-like marginal ditch or fosse, which averages perhaps ten feet in width and up to two or more feet in depth, which may be open and filled with water or occupied by a wet sphagnous swamp, and which, as a rule, more or less completely encircles the area occupied by the bog proper. The significance of this marginal ditch is not wholly clear. Elsewhere ('15, pp. 207, 208), the writer has been inclined to uphold the explanation first suggested by Davis ('07, pp. 150, 151), which attempts to correlate it with fluctuations in water level. But conditions here in northern Cape Breton are even better explained by Atkinson's theory ('05, pp. 615, 616) that the formation of the ditch is due to the shade produced by the forest along the shore, which hinders or prevents the growth of the mat-forming plants. In several of the forest-encircled Barrasois bogs the ditch is open along the southern shore, i. e., along the shore where the effect of the shade produced by the fringing forest naturally would be most pronounced, while along the northern, least shaded shore it has become completely filled in by vegetation. This condition obviously cannot be explained by the fluctuation theory; and for that matter, as already mentioned, there is very little seasonal fluctuation in water level in these basins.

Development of the edaphic climax association-type.—Beyond the wet bog stage, further development is largely dependent on two species of *Sphagnum* which have not as yet been mentioned: *S. fuscum* and *S. capillaceum tenellum,* particularly the former. Where the hydrophytic (or relatively mesophytic) pioneer sphagnums are superseded by these relatively xerophytic forms, the surface of the bog may become built up a foot or more above water level. In a mature bog the sphagnums almost everywhere are the predominant plants underfoot. They cover the ground with a continuous, hummocky, mattress-like carpet, which consists for the most part of the russet-green *S. fuscum,* interspersed with occasional more or less extensive patches of the reddish *S. capillaceum tenellum.* Commonly growing along with the sphagnums, in the older parts of the bog, are two mosses: *Polytrichum commune* and *P. juniperinum,* while in some of the higher, drier areas the sphagnums may have become superseded by cladonias or by such bryophytes as *Ptilidium ciliare* and

Hypnum Schreberi. Here and there, even in an old bog, there are moist or wet depressions in which may occur the more hydrophytic species of *Sphagnum,* together with liverworts such as *Cephalozia fluitans* and *Mylia anomala* and mosses such as *Calliergon stramineum* and *Drepanocladus fluitans.*

Scattered about over the sphagnum substratum, and varying greatly in abundance locally, are diverse trees, shrubs, and herbaceous plants. The characteristic and omnipresent tree of bogs is the black spruce. Invariably dwarfed in size, it commonly forms low, scraggly clumps, the result of layering followed by the death of the parent tree or of the original trunk.[11]

The predominant bog shrubs are ericads: *Chamaedaphne calyculata, Gaylussacia baccata, Kalmia angustifolia, K. polifolia,* and *Ledum groenlandicum,* to which should be added the semi-shrubby forms, *Chiogenes hispidula* and *Vaccinium Oxycoccus.* Three non-ericaceous shrubs also are usually well represented: *Amelanchier* sp., *Nemopanthus mucronata,* and *Viburnum cassinoides.* The most important herbaceous species are *Osmunda cinnamomea, Eriophorum callitrix, E. virginicum, Rynchospora alba, Carex trisperma Billingsii,* and *Cornus canadensis.* Three orchids, *Habenaria blephariglottis, Pogonia ophioglossoides,* and *Calopogon pulchellus,* are conspicuous when in flower; *Drosera rotundifolia* is common, and *Lycopodium inundatum* occasional in moist depressions; *Smilacina trifolia* occurs locally in wet places; *Empetrum nigrum* grows abundantly in the drier portions of one bog; while *Arceuthobium pusillum* is a frequent parasite on the black spruce.

d. THE ASSOCIATION-COMPLEXES OF POORLY DRAINED SWAMPS

Under the head of poorly-drained swamps are classed swamps of an intermediate character: swamps whose vegetation resembles in some respects that of well-drained swamps, in other respects that of undrained swamps. Boggy swamps of this character are of far more general occurrence than are those of the more extreme types, such as have been described in the foregoing paragraphs.

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[11] Ganong ('97: see quotation on p. 447 of the present paper) has called attention to layering as a means of reproduction in *Picea mariana,* and the phenomenon has been discussed in some detail by Cooper ('11) and Fuller ('13).

Illustrative examples.—The general situation in poorly drained swamps is unusually well illustrated by a group of small swamps on Broadcove Mountain, which were studied in some detail. These swamps occupy a series of very shallow, trough-like depressions, which cross approximately at right angles the road from Ingonish to Neil's Harbor. Three of them, which may be designated respectively as swamps *A, B,* and *C,* are roughly represented in longitudinal section in FIG. 44. The surface slope, depth of peat, etc., were determined by means of sounding-rod and level. All three swamps have outlets at the lower end, and swamp *A* has a small brooklet traversing perhaps half its length. At the time they were studied (August, 1916), the outlets in swamps *B* and *C* were dry, but a small amount of water was trickling out of *A*.

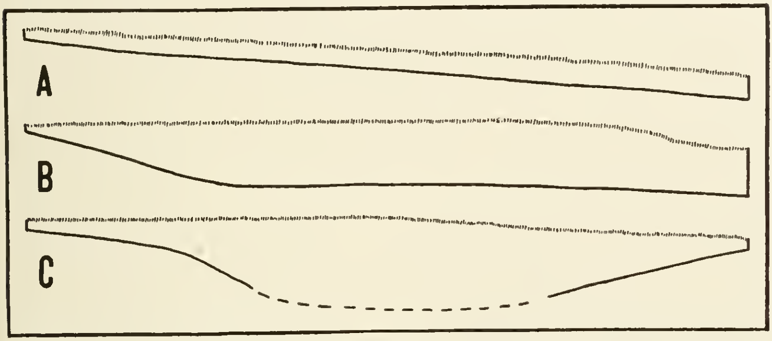

FIGURE 44.—Diagrammatic longi-sections of poorly drained swamps on Broadcove Mountain, north of Ingonish: see text.

Swamp *A*.—This swamp is the least boggy of the three. Genetically it represents a condition which presumably obtained at an earlier period in the development of swamp *B*. In area it is about 300 feet long by 100 feet wide. In proceeding from its upper to its lower end, the ground slopes gently, dropping at the rate of about 1 : 50. Over almost the entire tract a layer of peat from two to two and a half feet in thickness has been formed. The aspect of the vegetation over much of the area is that of a meadow: *Scirpus hudsonianus* and *S. caespitosus* with species of *Sphagnum* form the bulk of the plant cover. Scattered over the meadow are various herbaceous plants, shrubs, and trees, *Osmunda regalis* in particular of the herbs forming considerable patches locally. Along the margin of the swamp is a fringe of swamp forest. Floristically the vegetation of this swamp resembles in many respects that of an ordinary well-drained swamp. The majority of the vascular plants present there are also represented here, but they are relatively much less abundant. *Myrica Gale* is perhaps the commonest shrub in the open part of the swamp, and there are present here three shrubs not previously listed: *Pyrus arbutifolia atropurpurea, Rhamnus alnifolia,* and *Lonicera caerulea.* The boggy nature of the swamp is suggested by the presence of such plants as the two species of *Scirpus* mentioned, *Rynchospora alba, Smilacina trifolia, Sarracenia purpurea, Vaccinium Oxycoccus,* and *Lobelia Kalmii,* as well as by the luxuriant growth of the sphagnums. The dissimilarity between this swamp and a bog is emphasized, among other things, by the presence among the marginal woody forms of *Taxus canadensis, Acer rubrum, Fraxinus americana* and *F. nigra.*

Viewed from a genetic standpoint, it seems apparent that the area formerly occupied by the swamp vegetation was much more restricted than that which it occupies to-day. Originally long and narrow, as the surface has become built up through the accumulation of peat the swamp has spread out laterally, encroaching on the adjoining forested areas. Evidences of quite recent encroachment were noted just above where the swamp crosses the road. Among the pioneer seed plants, to judge from a relict colony near the lower end of the swamp, were *Calamagrostis canadensis, Juncus brevicaudatus,* and *Iris versicolor;* but the upbuilding of the surface and the lateral expansion of the swamp have been largely attributable to the luxuriant growth of the sphagnums and of the two sedges, *Scirpus hudsonianus* and *S. caespitosus.* It may well be said that the nature, and indeed the very existence, of the swamp as it is to-day is closely correlated with the activity of the compact mass of peat thus formed and of the superimposed plant cover in obstructing the drainage and thereby conserving the water supply.

Swamps *B* and *C.*—Swamp *B,* from a genetic standpoint, may be regarded as representing a later stage in the developmental series than swamp *A.* Conditions in swamp *B* have been more favorable to peat accumulation than in swamp *A,* owing to the more level nature of the terrain, and over much of the area the deposit of peat is more than six feet thick. It will be noted (toward the right in Fig. 44) that where the rock floor is slightly inclined the layer of peat becomes thinner. Swamp *C* differs from both swamps *A* and *B* in having originated in and around a shallow, poorly drained pond, the extreme depth of which was not ascertained. In its larger aspects, the vegetation in both these swamps is similar to that of swamp *A:* the two species of *Scirpus* and the *Sphagna* predominate, and various species characteristic of both well-drained and undrained swamps are represented. But the still more boggy nature of the habitat is evidenced particularly by the frequency here of the ericaceous shrubs, *Chamaedaphne calyculata* and *Ledum groenlandicum,* neither of which occur in swamp *A*. The relatively xerophytic nature of the habitat is further suggested by the presence of *Pteris aquilina* and *Juniperus communis depressa.*

The following list of species characteristic of one or all of the Broadcove Mountain swamps, but mostly not heretofore mentioned in any connection, is of interest.

Selaginella selaginoides
Larix laricina
Muhlenbergia racemosa
Eriophorum tenellum
Eriophorum viride-carinatum
Carex Michauxiana
Carex oligosperma
Spiranthes Romanzoffiana
Potentilla fruticosa
Viola conspersa
Conioselinum chinense
Solidago rugosa
Solidago uliginosa
Cirsium muticum

General observations.—In general, bogginess seems to be correlated with poor drainage; and this may be either occasioned by the nature of the terrain or brought about through the influence of vegetation. Topography favors the development of boggy swamps where the surface is flat, fairly level, and so situated that the ground becomes covered with a thin sheet of water in wet weather. Boggy swamps are frequently encountered, for example, on low, flat areas, bordering lakes and ponds, which are subject to periodic inundation (see in this connection p. 419). A heavy soil which dries out slowly favors the development of boggy swamps. But many of the tracts, which in northern Cape Breton are occupied by swamps of this type, in a warmer, less humid climate would be merely periodic swamps of the ordinary, well-drained type. The general prevalence here of boggy swamps may be attributed in large measure, indirectly, to the influence of the cool, humid climate of the region. The climate favors the luxuriant development of the sphagnums and other peat-forming plants, and it seems to be very largely through the direct influence of the layer of peat to which these give rise, in retaining the water and thereby extending the swampy condition throughout the season, that the boggy condition is brought about. Very often, in this way, through the obstruction of the drainage which results from the activity of the vegetation, a swamp which, during the early stages of its development, would be classed as well-drained, in the course of time becomes increasingly boggy. This is well illustrated by the examples just described.

It has been mentioned earlier that peat accumulation may occur in connection with well-drained swamps; but there, as already suggested, the deposit is mucky and invariably shallow. Again, the bog has been cited as the characteristic swamp-type of undrained depressions; but not infrequently shallow, undrained depressions are occupied by swamps of the poorly drained type. Sink hole swamps are often of this character. Fluctuations in water level, underground drainage, alkalinity of the soil water, or some such factors may perhaps explain the discrepancy here. But, after all, the whole swamp situation is an extremely complex one, and it is candidly admitted that there are any number of questions which must be left unanswered.

4. The formation-types in and along Rivers and Streams

a. INTRODUCTORY

Under this head are included fundamentally those association-complexes of hydrarch origin whose ecological aspect manifestly is correlated with the activity of rivers and streams. In so far as it affects associations of the hydrarch series, the influence of a stream on the vegetation in and along its course is expressed primarily at times of high water, and then in two ways: first, through the deposition of sediment, which leads to the development of flood plains; second, through the erosive activity of the current, which may affect the vegetation directly, particularly through the abrading action of ice, or indirectly, as seen in the formation of oxbows. Under this head have also been included the association-complexes of wet or dripping rock outcrops, since these are especially characteristic of, though by no means confined to, ravines.

b. THE ASSOCIATION-COMPLEXES OF RAVINES

The stream bed association-types.—The predominant plants in the rocky stream beds which prevail in ravines, and to a large extent elsewhere, are bryophytes. Characteristic species are the following:

Marsupella aquatica
Jungermannia cordifolia
Scapania undulata
Porella pinnata
Fontinalis dalecarlica
Oxyrrhynchium rusciforme
Hygrohypnum dilatatum
Hygrophynum eugyrium
Hygrophynum ochraceum

The degree of luxuriance exhibited by the submersed bryophytic vegetation varies greatly in different streams. The aquatic mosses and liverworts are best developed in small brooks; in large streams they may be conspicuous by their absence. This latter fact may be explained somewhat as follows. The instability of the substratum might account for their absence on small boulders and cobbles, but even where there is a firm rock substratum, bryophytes are scarce. There seems little question that, in general, the scarcity is attributable to mechanical factors—to the erosive action of the sediment-laden water in flood time, or, more likely, of ice-laden water in spring. Were the phenomenon restricted to northern Cape Breton, one might feel tempted to correlate it with the acidity of the water, which in most streams commonly contains so much organic matter that it is colored yellow or brownish (see, in this connection, Ganong '98); but the same conditions can be observed in other regions, e. g., in Connecticut streams, where the water is clear and colorless. Often the rocky bottom in swift streams is utterly devoid of plants of any description, but sometimes, in the absence of mosses, there may be a considerable growth of *Nitella* sp.

Stream bank association-types.—Along small ravine brooks the banks, as a rule, are well shaded by overhanging foliage, the air is always cool and moist, and the substratum continuously damp or wet. It is doubtful whether the plant cover in many such habitats ever has been xerophytic, and for this reason it has seemed best to treat it under the head of hydrarch successions. The outstanding feature of such a ravine is the intense mesophytism, commonly verging on hydrophytism, of its vegetation. In the periodically inundated zone along the edge of the stream there is a profuse development of mosses and liverworts, which commonly include, among others, the following species:

Conocephalum conicum
Plagiochila asplenioides
Sphagnum squarrosum
Fissidens adiantoides
Mnium hornum
Mnium punctatum
Philonotis fontana
Thuidium delicatulum
Brachythecium rivulare
Hylocomium brevirostre
Climacium dendroides
Catharinaea undulata

Vascular plants are more or less numerous, particularly toward the upper limit of the flood zone. Here the ferns are represented by a wealth of species, among which *Polystichum Braunii* is especially characteristic, while the seed plants include some of the most pronounced shade- and moisture-loving mesophytes. A list of some of the more representative ferns and seed plants follows:

Phegopteris polypodioides
Phegopteris Dryopteris
Asplenium Filix-femina
Polystichum acrostichoides
Polystichum Braunii
Aspidium noveboracense
Aspidium spinulosum var.
Streptopus amplexifolius
Geum macrophyllum
Circaea alpina
Galium kamtschaticum
Aster acuminatus

Along the larger ravine streams the banks are more exposed to sun and wind than along the smaller ones, and the vegetation tends to be less mesophytic, with shade plants in particular much less prominent. The character of the vegetation between low and high water levels is influenced to a more marked degree by the abrading action of the current in flood time. Even here, however, associations of the sort just described are frequently encountered.

Cliff association-types.—Many cliffs and steep rock outcrops are kept wet to such a degree with dripping water that their vegetation differs quite perceptibly from that of the drier cliffs described earlier under the xerarch series. It is of course difficult to draw sharp lines, since there are all degrees of intergradation. Here, as there, the most distinctive plants are the bryophytes, which thrive in crevices and frequently plaster over even precipitous rock surfaces. But in addition to various of the species cited earlier as characteristic of relatively dry cliffs, there occur here, usually as the predominant forms, various more or less hydrophytic species. Prominent among these are the sphagnums, the species mainly those mentioned elsewhere in connection with the ravine forest, and the liverworts and mosses enumerated in the subjoined list.

Marsupella emarginata
Sphenolobus Michauxii
Mylia Taylori
Plagiochila asplenioides
Diplophyllum albicans
Scapania nemorosa
Blindia acuta
Didymodon rubellus
Hymenostylium curvirostre
Anoectangium Mougeotii
Plagiothecium denticulatum
Hylocomium brevirostre
Plagiopus Oederi

c. THE ASSOCIATION-COMPLEXES OF FLOOD PLAINS

Here should be included the strips of swale which not infrequently border even rapid streams and which obviously represent incipient flood plains. In valleys, for example, and locally even in ravines, a narrow, marshy strip frequently intervenes between ordinary summer water level and the lower edge of the upland forest. The vegetation in such a tract is essentially that of a well-drained swamp, with sedges, such species as *Carex torta* and *C. aquatilis,* and the grass, *Calamagrostis canadensis,* usually the predominant forms. Swampy flood plains of this particular sort are much more extensively developed on the plateau (see p. 456) than in the lowland, where they are of minor consequence.

Of much more importance here, though somewhat restricted in their occurrence, are the flood plain formations which have been developed in particular at the mouths of some of the larger streams, as at the heads of Ingonish Harbor, Middle Harbor (Aspy Bay), and Margaree Harbor. The earlier phases of the hydrarch series of association-types, which reaches its culmination in the flood plain forests that have been developed on the higher portions of flood plains, are well illustrated by the conditions about the head of Margaree Harbor, which will be briefly described.

Pioneer association-types.—Owing to the intermittent backing up of the outflowing river water by the inflowing tide water, the depth of the water over the submerged portion of the flood plain here fluctuates daily. On parts which are permanently submerged, vegetation, where present, consists largely of submersed aquatics, notably *Potamogeton bupleuroides*. Areas which are bared at low tide, but which may be inundated to a depth of from perhaps six inches to two feet at high tide, are occupied by a wet marsh association-type, in which the following are the more prominent species:

Equisetum fluviatile
Scirpus occidentalis
Dulichium arundinaceum
Typha latifolia
Sagittaria latifolia
Acorus Calamus
Castalia odorata
Nymphaea advena
Cicuta bulbifera
Sium cicutaefolium

Fringing the shoreward margin of this marshy area is a more or less well defined transition zone, in which the predominant plants are species of generally recognized amphibious proclivities. Here, to a greater extent than in the areas of deeper water, grow, among others, the following species:

Leersia oryzoides
Juncus brevicaudatus
Iris versicolor
Caltha palustris
Rumex Britannica
Potentilla palustris
Proserpinaca palustris
Lysimachia terrestris
Menyanthes trifoliolata
Myosotis laxa
Mentha arvensis

On portions of the flood plain where the water at high tide ordinarily is very shallow, or which are flooded only in time of spring tides, the general aspect of the association-type is that of wet meadow, although various of the marsh species may grow here also. Below is a list of some of the species noted as characteristic:

Acrocladium cuspidatum
Onoclea sensibilis
Aspidium Thelypteris
Glyceria grandis
Calamagrostis canadensis
Carex crinita
Habenaria dilatata
Sanguisorba canadensis
Impatiens fulva
Viola cucullata
Scutellaria galericulata
Chelone glabra
Eupatorium purpureum
Aster novi-belgii

The edaphic climax association-type.—The condition of the vegetation on parts of flood plains which lie above ordinary high tide level has been greatly modified by human activity, owing to the suitability of such areas for raising hay, and the original character of the vegetation here must be judged from the fragmentary evidence which has survived.

In wet meadows of the sort above described, the common occurrence of scattered shrubs, such as *Alnus incana* and *Myrica Gale,* suggests that the present day meadow association-type is of secondary origin; and it is certain, from the conditions observed at Margaree Harbor, Ingonish, and Aspy Bay, that in former days the higher parts of flood-plains of the sort under consideration were occupied by forests made up largely of elm, white ash, black ash, and white spruce. Specimens of elm more than six feet in diameter are occasionally encountered on flood plains. The characteristic shrubs here include *Salix* sp., *Alnus incana, Cornus stolonifera, Viburnum Opulus americanum,* and *Sambucus canadensis.* Below is a list of the more distinctive herbaceous species of the higher parts of flood plains, most of them being noted in all three localities cited.

Onoclea Struthiopteris
Onoclea sensibilis
Asplenium Filix-femina
Calamagrostis canadensis
Laportea canadensis
Thalictrum polygamum
Clematis virginiana
Agrimonia striata
Sanguisorba canadensis
Impatiens biflora
Circaea intermedia
Heracleum lanatum
Galium asprellum
Eupatorium purpureum
Solidago canadensis
Solidago rugosa
Aster novi-belgii
Aster puniceus
Aster umbellatus

The association-types of oxbow ponds.—Oxbow ponds have been observed in a few places, as at Margaree Harbor and Pleasant Bay. Such ponds usually support a luxuriant aquatic vegetation, notably such species as the following:

Sparganium angustifolium
Potamogeton bupleuroides
Potamogeton epihydrus
Scirpus subterminalis
Nymphaea advena
Nymphaea microphylla
Castalia odorata
Ranunculus aquatilis capillaceus
Callitriche palustris
Ludvigia palustris
Myriophyllum verticillatum
Utricularia intermedia
Utricularia vulgaris

The marginal vegetation here requires no particular comment. It may include any of the wet marsh species of the flood plain series, in addition to various of the herbaceous plants and shrubs elsewhere listed as characteristic of well-drained swamps.

4. The Formation-types along the Seacoast

a. INTRODUCTORY

In this group may be included all association-complexes of hydrarch origin whose ecological aspect is influenced directly by the proximity of the sea. This influence is seen most obviously in the effect of salt water on the character of the vegetation. But beside this, from the standpoint of physiographic ecology, the dynamic agencies which are associated with the activity of waves and currents are of prime importance, either directly or indirectly: the formation and destruction of barrier beaches, which may result in the development of coastal ponds of all degrees of salinity—from completely salt to completely fresh; the deposition of sediment, which under favorable conditions may lead to the development of coastal swamps, etc. With reference to these physiographic agencies, just as was pointed out in discussing the vegetation of uplands along the seacoast, it is possible to divide the associations of lakes and swamps here into two groups: associations along eroding shores, and associations along depositing shores. Little attention has been given, however, to the associations of the first group, which comprise primarily the formation (or formation-complex) of seaweeds concerning which brief mention has already been made in discussing the vegetation of rocky sea bluffs. In the remarks which follow, attention is restricted to the associations along depositing shores. These are conveniently treated under three heads: the association-complexes of salt and brackish lakes and ponds, the association-complexes of salt marshes, and the association-complexes of brackish marshes.

b. THE ASSOCIATION-COMPLEXES OF SALT AND BRACKISH LAKES AND PONDS

The most prominent constituent of the aquatic flora in salt lakes and ponds is the eel grass (*Zostera marina*) which commonly grows in great luxuriance, covering large areas of bottom between approximately mean low water mark and a depth of several feet below. Ecologically the eel grass fulfils an important function in that, by its interference with tidal currents, it stimulates the deposition of silt and the consequent upbuilding of the bottom. Associated with the eel grass, but seldom attaining any great prominence, usually grow the sea lettuce (*Ulva* sp.) and other algae, which may either form a loose covering over the sandy or muddy bottom or grow attached to the eel grass. Another seed plant found here is *Ruppia maritima*. In Middle Harbor (Aspy Bay), to select a concrete example, this plant is not at all conspicuous toward the outlet, but in the shallow water about the head of the harbor, in company with *Potamogeton pectinatus,* it completely covers the muddy bottom with a prolific growth. The presence here at the head of a sizeable stream may account for the abundance of the *Ruppia* in this vicinity, although this plant is by no means confined to brackish water. In Cold Spring Harbor, Johnson ('15, p. 26) says that *Ruppia* is most abundant in areas of "soft bottom, bare of *Ulva,* and usually protected from currents and waves." It is worthy of note, however, that in brackish ponds, in northern Cape Breton, the bulk of the aquatic vegetation consists of *Ruppia* and *Potamogeton pectinatus.*

The shores of salt and brackish ponds may be occupied by the salt or brackish marshes which will be described presently, or they may be merely muddy or gravelly. Gravelly shores ordinarily occur in more exposed situations than muddy shores. The conditions which prevail on gravelly shores may be illustrated by a specific example, a spot just inside the entrance of a salt pond. A luxuriant growth of *Plantago decipiens, Spergularia leiosperma,* and *Salicornia europaea* covers much of the shore between mean high and low water levels. Attached to scattered cobbles in this zone are *Fucus, Ascophyllum,* and other algae. In the vicinity of high water mark grow *Puccinellia maritima, Suaeda maritima, Solidago sempervirens* and other halophytes. Such a shore may be regarded as an incipient marsh.

The vegetation of muddy shores is essentially that of the marshes. The conditions here are well exemplified by a small brackish pond near the Barrasois, which has become completely barricaded off from the ocean but is still influenced by tide water filtering through the barrier. The pond itself is densely populated by *Ruppia* and *Potamogeton pectinatus,* together with various algae. Surrounding the pond is a low, muddy border from two to five feet wide, which is ordinarily submerged at high tide. The predominant plant here is *Scirpus nanus,* which forms a low, soft sward. Associated with it grow *Triglochin maritima, Ranunculus Cymbalaria, Spergularia canadensis,* and *Salicornia.* At a slightly higher level, barely covered at ordinary high water, is a narrow zone of *Spartina patens,* together with *Agrostis alba maritima, Carex norvegica,* and *Triglochin;* while at a still higher level, not submerged by ordinary tides, is a zone occupied almost exclusively by *Juncus balticus littoralis.* Such an association-complex, like the preceding, might equally well, if not better, be considered in connection with salt and brackish marshes.

c. THE ASSOCIATION-COMPLEXES OF SALT MARSHES

As might be anticipated, in view of its exposed coastline, coastal swamps are nowhere extensively developed in northern Cape Breton. The finest area of this sort which has come to the writer's attention is situated along the oceanward shore of South Pond (Aspy Bay), bordering the pondward side of the sand-spit elsewhere described, and extending out into the salt pond nearly a quarter of a mile (Fig. 45). This particular salt marsh is of unique interest because of the presence here *in situ* of a number of large white pine stumps. These occur scattered throughout the landward half of the marsh and their roots are well exposed above its surface. The explanation for this unusual condition seems to be this. The pines formerly grew on a low, sandy, pondward extension of the present spit. Through some shifting in the tidal currents the sand was eroded away from around the bases of the trees, and subsequently, presumably as the result of further shifting in the current, deposition has succeeded erosion and the salt marsh has been built up. The active erosion of the sand spit which is now taking place along certain other sections of the shore upholds the plausibility of the explanation just given, and excavation of the muddy deposit about the stumps shows beach-sand at a depth of scarcely a foot below mean low tide level (in this connection, see also Harvey '18).

FIGURE 45.—Salt marsh at South Pond, Aspy Bay; scattered stumps in marsh; see text.

The pioneer association-type.—The mechanics of salt marsh formation need not be detailed here: suffice it to say that it is accomplished through the combined activity of plants and physiographic agencies (see in this connection, Davis '10). In northern Cape Breton, as in salt marshes along the New England coast, the pioneer stage in the salt marsh successional series is dominated by the rank-smelling salt thatch (*Spartina glabra alterniflora*). In typical cases this grass forms a fringe along the outer edge of the marsh. It predominates from about a foot above mean low tide level upward to within a few inches of mean high water mark, its actual vertical range being scarcely two feet. Except for *Vaucheria* and certain other filamentous algae, which commonly thrive on the muddy substratum, the salt thatch is ordinarily the only plant present in this outermost zone (*Spartina glabra* association-type).

The salt meadow association-types.—By the time the surface of a marsh has been built up to such a height that it is submerged for only a few hours daily, the pioneer association-type has given way to salt meadow: the rank, but open growth of tall, coarse salt-thatch has become superseded by a sward of lower, finer grasses, predominantly the salt meadow grass (*Spartina patens*). Along with the salt meadow grass in this association (*Spartina patens* association-type) commonly grow in greater or less abundance: *Distichlis spicata, Triglochin maritima, Plantago decipiens*, and *Limonium carolinianum.*

At this point there is one feature which is almost universally associated with salt marsh building and which demands a few words of comment. During the elevation of the substratum there may arise in various ways, which will not be discussed in detail here (but see in this connection, Yapp and Johns '17; Johnson and York '15, pp. 22, 25, etc.; Harshberger '16), sloughs and depressions which become generally distributed throughout the higher parts of the marsh. Here the depressions may be deep or shallow; they may be filled much of the time with more or less stagnant water or may be merely muddy. In the majority of these so-called "pans" the difference in level between their bottoms and the higher surfaces of the surrounding meadow is but a matter of inches or even fractions of an inch, yet they present an environment for plants which is quite different from that afforded by the higher, better drained areas. The pans may be quite barren of vegetation or they may be well populated, but their plant cover is usually in marked contrast with that of the surrounding meadow. Especially characteristic of such situations are *Salicornia europaea* and *Spergularia canadensis,* which, one or both, may be the only forms present or which may grow in association with such species as *Scirpus* *nanus, Glaux maritima obtusifolia* and *Puccinellia maritima.* Again, the pans may be colonized almost exclusively by the salt thatch, which in such situations forms a dense but usually depauperate growth, while *Distichlis* frequently skirts the edges.

In proceeding from the outer margin of a salt marsh toward the mainland, the general level of the surface becomes slightly higher and the general character of the vegetation changes correspondingly. But even in the older, higher parts, owing to the local variations in elevation and drainage, the surface vegetation is far from being uniform. The predominant plant on the higher, shoreward reaches of the salt meadow is *Juncus balticus littoralis* (*Juncus balticus* association-type), which in the salt marshes of northern Cape Breton occupies an ecological position quite similar to that held by *Juncus Gerardi* in regions farther south. The latter species is seldom met with here. Associated with the *Juncus,* and locally dominant, may be *Agrostis alba maritima, Hierochloë odorata, Scirpus campestris paludosus,* and *Eleocharis palustris.* The two latter species are especially well developed in the wetter situations, where also *Ranunculus Cymbalaria* and *Potentilla pacifica* are commonly present. Other species characteristic of the shoreward reaches of the salt meadows are *Triglochin palustris, Stellaria humifusa, Atriplex patula hastata, Solidago sempervirens,* and *Aster novi-belgii.* In addition to these, the salt thatch and most of the species of the *Spartina patens* association-type are represented here: *Spartina glabra, Scirpus nanus, Spergularia,* and *Salicornia* in poorly drained depressions; *Spartina patens* and *Plantago decipiens* in low but fairly well-drained situations. *Limonium,* however, apparently is confined to the outermost meadows.

c. THE ASSOCIATION-COMPLEXES OF BRACKISH MARSHES

Brackish marshes are of far more general occurrence than salt marshes. To some extent they are developed toward the mouths of many of the larger streams (Fig. 46), but the finest examples observed are situated at the heads of Ingonish Harbor and of Middle Harbor (Aspy Bay). The vegetation of brackish marshes includes many of the plants which have been listed as characteristic of salt marshes, but it also includes other species which are rarely represented there. The wetter parts of a brackish marsh ordinarily support a rank growth of coarse sedges, notably *Scirpus occidentalis, S. campestris paludosus, Carex maritima,* and *C. salina.* These, singly or collectively, may constitute the pioneer association-type. On the higher parts of the marsh the predominant forms usually are *Juncus balticus littoralis* and *Agrostis alba maritima.* Other forms which may be more or less abundantly represented in brackish marshes are listed below.

FIGURE 46.—Brackish marsh near mouth of Barrasois.

Triglochin maritima
Triglochin palustris
Hierochloë odorata
Spartina Michauxiana
Eleocharis palustris
Scirpus americanus
Scirpus rufus
Eleocharis palustris
Carex Oederi pumila
Juncus pelocarpus
Atriplex patula hastata
Spergularia canadensis
Potentilla pacifica
Plantago decipiens
Solidago sempervirens
Aster novi-belgii

Transitions from salt to brackish, from brackish to fresh swamps, etc.—It is impossible to draw a sharp line between brackish and salt swamps, on the one hand, and between brackish and fresh swamps, on the other. In the character of the predominant plants, the vegetation of the higher, shoreward reaches of a well developed salt marsh almost invariably resembles that of a brackish meadow, and it commonly includes various species characteristic of fresh water swamps. Along the shoreward edge of a salt marsh, for example, in places where unquestionably they are subject to partial submergence in salt water, at least by the high, semi-monthly "spring-tides," commonly grow such non-halophytic swamp species as *Iris versicolor, Sanguisorba canadensis,* and *Lysimachia terrestris; Vaccinium macrocarpon, Alnus incana, Myrica Gale,* and *Spiraea latifolia.* By way of further illustration, two specific transitional series will be briefly described.

MacDonald's Pond, near the mouth of the Barrasois, affords an unusually interesting illustration of this sort. At the present time the pond, which is perhaps half a mile long, is completely shut in by a barrier beach and its water is brackish; but within twelve years it communicated with the sea by a narrow outlet. Around much of the margin the vegetation is similar to that described in preceding paragraphs. The area of particular interest is a sheltered cove, connected with the main pond by a shallow open channel a dozen feet wide, presumably fed by springs, and occasionally (probably every spring) the recipient of the flood waters of the Barrasois, which reach it through a channel ordinarily dry. This cove has been for the most part filled in to a depth of more than a dozen feet with a mixture of peat and silt. From a small but deep pool near the center of the swamp thus formed to the outlet of the cove runs the open channel already referred to. Toward the outlet of the swamp, the vegetation is predominantly that of a slightly brackish marsh, consisting largely of *Spartina Michauxiana, Agrostis alba maritima, Scirpus americanus,* and *Eleocharis palustris,* together with *Potentilla pacifica, Triglochin palustris,* and *Carex maritima.* In the open water of the channel grow *Ruppia maritima* and *Potamogeton pectinatus.* Bordering the pool is a zone of *Typha latifolia,* followed by a zone of *Juncus balticus littoralis.* But throughout the remainder of the area the vegetation is predominantly that of a fresh swamp, the more prominent herbs including *Calamagrostis canadensis, Scirpus cyperinus, S.*

rubrotinctus, Carex canescens disjuncta, C. crinita, C. paupercula irrigua, Juncus filiformis, Sium cicutaefolium and *Galium palustre.* Considerable patches have been preëmpted by *Myrica Gale,* while *Sphagnum imbricatum* is locally abundant. From a superficial study it would appear that at the present time the fresh swamp, presumably as a result of the comparatively recent complete cutting off of MacDonald Pond from the sea and the consequently decreased salinity of the water, is gradually encroaching on a former brackish marsh whose vegetation over most of the swamp is now represented only by scattered relicts. But, as a matter of fact, the situation is much more complicated. This is merely suggested here, without attempt at explanation, by the facts (*1*) that while there are no living trees in the swamp there are numerous dead spruces, and (*2*) that a sample of the peat taken near the margin of the central pond showed abundant sphagnum remains at a depth of twelve feet below the surface.

Another interesting transitional series, in this case from salt pond to boggy swamp, was observed along the shores of North Pond, Aspy Bay. Here, starting from low water mark and proceeding inland, within a distance horizontally of scarcely a hundred feet one passes through the following associations: (*a*) *Sparitina glabra alterniflora* and *Spergularia canadensis;* (*b*) *Spartina patens;* (*c*) *Juncus balticus littoralis, Agrostis alba maritima,* and *Ranunculus Cymbalaria;* (*d*) *Scirpus occidentalis;* (*e*) various species of *Carex, Alnus incana, Myrica Gale, Vaccinium macrocarpon, Chrysophynum stellatum,* etc.; (*f*) boggy swamp with *Carex trisperma, Rynchospora alba, Sarracenia, Drosera rotundifolia, Vaccinium Oxycoccus, Chamaedaphne, Ledum,* various *Sphagna,* etc. Area *a-c* are below mean high tide level, area *d* is partly above and partly below, area *e* is barely out of reach of ordinary high tides, and area *f* extends down to within less than a foot (vertically) of mean high water mark.

In discussing the occurrence along the shore of Cold Spring Harbor of non-halophytic vascular plants, in places where the soil is often covered by salt water, sometimes for as much as three or four hours daily, Johnson ('15, p. 110, etc) explains the situation somewhat as follows. The ground in such places is usually springy, and the soil is saturated with fresh water, the abundance of which "prevents the salt water from really penetrating it." In such situations, therefore, many upland and fresh swamp plants which can stand more or less inundation of their shoots with salt water but which cannot endure salt water around their roots are enabled to push down to much lower levels than usual, even growing below mean high tide level. This explanation is doubtless the correct one, and the line of demarcation between halophytic and non-halophytic associations is always sharper along dry than along wet shores, although even here non-halophytic plants frequently invade areas which are subject to tidal overflow.

Of peculiar interest in this connection is the occurrence of bryophytes in situations where they must necessarily be more or less exposed to the influence of salt water. In northern Cape Breton, for example, *Chrysohypnum stellatum* commonly grows quite abundantly on the wet soil of brackish meadows, in company with such vascular species as *Triglochin palustris* and *Ranunculus Cymbalaria,* and the sphagnums sometimes occur in similar situations. *Sphagnum palustre* and *Bryum inclinatum* have been collected on exposed sea cliffs well within reach of storm waves, while *Bryum fallax* thrives around the edges of salt ponds. From these and similar observations elsewhere, there seems little question that while as a class the bryophytes may be regarded as halophobous, many of them are capable of existence in habitats where, periodically at any rate, they are bathed in brackish or salt water.

D. SECONDARY FORMATIONS OF THE HYDRARCH SERIES

Formation-types resulting primarily from Human Activity

ASSOCIATION-COMPLEXES DUE TO VARIOUS AGENCIES

In so far as the association-types of lakes and ponds are concerned, the effect of human activity has been negligible. The vegetation of swamps has been variously modified, but it is only occasionally that it has suffered as severely as that of uplands. This state of affairs, in the main, is easily explained by the fact that in this climate, with its abundant atmospheric precipitation, the swamps, for the most part, are of comparatively little value from the cultural standpoint. Instances of a more or less pronounced change in swamp vegetation from its original character are afforded by well-drained swampy areas which have been converted into meadow-land. Here sedges and grasses predominate and the vegetation approximates more or less closely that elsewhere described as characteristic of open, well-drained swamps. Grazing cattle and sheep may bring about the introduction into a swampy area of plants not previously present and they may appreciably retard succession, but otherwise they do not seriously modify the conditions. Aside from instances such as those just outlined, any changes in the vegetation and succession in the swamps which are attributable to human activity have been largely due to logging and fire. The former agency may have resulted in the removal of the original forest cover, where one was present, but beyond this has had little retrogressive effect on the vegetation in the areas concerned. The influence of fire is much less in swamps than on uplands, since the very wetness of the substratum may prevent the complete destruction of subterranean plant organs. In general, the association-types of secondary hydrarch series appear to differ little from those of the primary series as described elsewhere.

THE NORTHEASTERN EVERGREEN CONIFEROUS FOREST CLIMATIC FORMATION IN NORTHERN CAPE BRETON

I. GENERAL CONSIDERATIONS

Distribution and general character.—By far the greater part of northern Cape Breton, indeed nearly all the country above an elevation of approximately seven hundred feet, is occupied by this formation. With reference to the general ecological aspect of the vegetation, however, the area thus defined can be subdivided into two regions: (*1*) the forest region proper, which hereafter will be referred to simply as the Forested Region; and (*2*) the Barrens. The extent of these regions is roughly indicated on the map (Fig. 2). In a general way, the forested region can be said to include the upper mountain slopes, together with the outer and lower, less exposed parts of the plateau. Here the country is covered by an almost unbroken forest of balsam fir, spruce, and paper birch (Figs. 4, 47, 49). The barrens (Figs. 48, 51, etc.) include primarily the higher, more exposed portions of the plateau, being especially well developed toward the interior, and occupying altogether an area estimated by Fernow ('12, p. 20) at about 375 square miles. Here forests of the usual description are largely confined to the "gulches," while the country at large is covered mainly by heath and scrubby forests, swamps and bogs ("muskeag").

Evergreen coniferous forest in the highlands a climatic, not an edaphic climax.—In a brief summary report of field work in Cape Breton, Macoun ('98, p. 199A), records the following observations: "Before going to Cape Breton, I had, like many others, a very mistaken notion of the 'barrens'[12] in the northern part of the island. After spending some time in the north and on the plateau, the conditions producing these barrens became evident. Along the base of the escarpment bordering the plateau, the subsoil is generally impervious, and here spruce and fir occupy the ground. The broken face of the escarpment is

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[12] Macoun here seems to use this term in a much more comprehensive sense than that in which it is employed by the writer.

usually covered with broad-leaved trees, such as maple, beech and birch, because it is well drained." In other words, Macoun would seem to intimate that in the mountains, as the writer has shown to be locally the case in the lowland, the evergreen coniferous forest is to be regarded as an edaphic rather than a climatic climax association-type. With this opinion the writer emphatically disagrees for reasons which are briefly outlined below.

Figure 47.—Primeval coniferous forest of the regional climax type; mountains near Cape North.

In ascending the mountain slopes which flank the plateau, there is a gradual transition from the forests of the lowland climax type to those of the highland, a transition which has been repeatedly traced out and verified. In passing upward, the character trees of the deciduous climax formation disappear in approximately the following order: beech; hemlock; oak and sugar maple; white pine; red maple; yellow birch. Except for the two species last named, none of these are represented in the evergreen coniferous climax forests of the highland. The yellow birch, however, is frequently encountered here in edaphically favorable situations, while the red maple is commonly represented by shrubby specimens, which, however, seldom attain the dignity of trees. It is also significant that for some distance above the level where it ceases to occupy a prominent position in the forest, the sugar maple still maintains an important place in the undergrowth, being represented here by more or less abundant, scraggly, shrubby specimens, which exhibit unmistakable evidence of having been repeatedly killed back. It is further significant that there is a marked correlation between the vertical distribution of most of these trees in northern Cape Breton and their north-and-south geographic range; and it is of interest to observe that toward its upper limits the deciduous-mixed forest commonly is dominated by the yellow birch.

The facts just presented, and particularly the complete absence on the plateau, even in the many situations which are edaphically favorable, of beech, sugar maple and oak, hemlock and white pine, would seem to indicate conclusively that the factors responsible for the character of the climax association-type here are climatic and not edaphic. The controlling factor in determining the upward extension of the deciduous forest climatic formation is probably temperature (see discussion elsewhere under head of climate). But atmospheric humidity may also be a decisive factor, since the upper limit of the deciduous climax forest coincides approximately with the lower limit of the low-lying cloud belt in dull weather, a feature which has been commented on earlier (p. 274).

The status of the barrens, from the standpoint of ecological plant geography.—The barrens are of peculiar interest, since they present essentially the same type of vegetation that prevails over vast areas on the Labrador Peninsula and throughout northern Canada, regions concerning which almost nothing is known ecologically. So distinct in its general aspect from that of the forest region proper is the vegetation of the barrens that it was at first thought to constitute a distinct climatic formation.

Further investigations, however, have indicated beyond question that this remarkable formation-complex, in northern Cape Breton, is the result of edaphic rather than climatic factors. The climax association-type of uplands in the barrens bears much the same relation to the coniferous forest climax of the highlands that the climax association-type of exposed headlands along the seacoast bears to the deciduous forest climax of the lowland. The relation between the edaphic formation-complex here and that of the highlands as a whole is somewhat analogous to the relation between the edaphic formation-complex of the New Jersey pine barrens and that of the whole state of New Jersey. The character of the vegetation in the barrens is attributable very largely, directly or indirectly, to conditions of exposure, topography, and soil. Along the streams the climax forests of the forested area extend into the heart of the barrens, while, conversely, in high, exposed situations the vegetation of the barrens reaches well toward the coast.

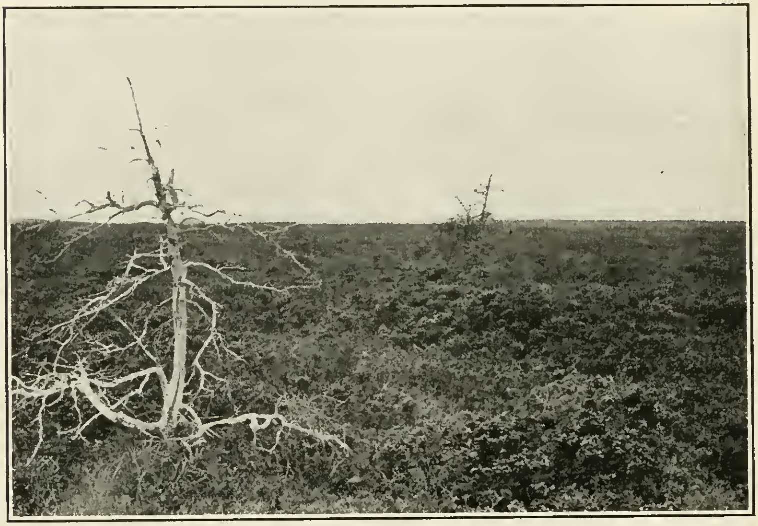

Figure 48.—Barrens in mountains north of Barrasois River (Scotchman's Barren); vegetation closely approximating heath; tamaracks in left foreground and mid-distance.

Forest resources of the region.—In summing up the results of a timber survey of this region, made a number of years ago, Fernow ('12, pp. 20, 24) estimated the commercially productive forest area of the "1200 square miles of plateau" at about 780 square miles, the unproductive area being largely occupied by barrens. He describes the forest as "an almost unbroken pure balsam fir forest, with only 15 per cent. to 25 per cent. of spruce, except in the black spruce swamps, and about three per cent. of birch," in which "the trees run from 6 to 14 inches in diameter, occasionally up to 18 inches, with 36 feet log length, and ten trees to the cord." Among the sample plots measured in connection with this survey, some 180 in all, many ran from fifty to sixty cords per acre, with an average of at least twenty. The forest is of value chiefly for pulpwood; saw timber is scarce. On a basis of the figures obtained, Fernow estimates that the area contains twelve million cords of pulpwood, or an amount equal to that which is computed to be present in the entire province of Nova Scotia outside of northern Cape Breton, an area more than sixteen times as large. And while these facts are primarily of economic import, they are also of ecological interest, since they serve to emphasize the dissimilarity between the forests of this region and those in other parts of Nova Scotia.

Apropos, it may well be suggested here that while, as has been shown in preceding pages, conditions over much of the lowland are favorable to the development of forests of the deciduous climax type, they are even more so to the growth of coniferous forests. It is only through their inability, in the long run and under natural conditions, to cope successfully with their southern competitors that the northern conifers do not today constitute the predominating element in the primeval, as well as in the second growth forests of this region. Both climate and soil are more favorable here than in the highland. It is the conviction of the writer that the commercial production of spruce and balsam fir in the lowland of northern Cape Breton offers large possibilities for the future.

II. THE REGIONAL CLIMAX ASSOCIATION-TYPE: THE CLIMAX FOREST

The trees of the climax forest.—The general aspect of these forests is well portrayed by Figs. 47, 49. The balsam fir is by far the most abundant species, comprising ordinarily more than

75 per cent. and sometimes fully 85 per cent. of the stand. Individual trees may attain a trunk diameter in excess of sixteen inches with a height approaching seventy feet, but such specimens are exceptional: the bulk of the balsams which go to make up the mature forest run from eight to twelve inches in diameter, mostly about ten, and range around fifty feet in height. The average age of such trees, as ascertained in many cases with the aid of an increment borer, would scarcely exceed seventy years. Occasional specimens are encountered which must be 125 or more years of age, but the exact age of these larger specimens it is seldom possible to determine accurately, owing

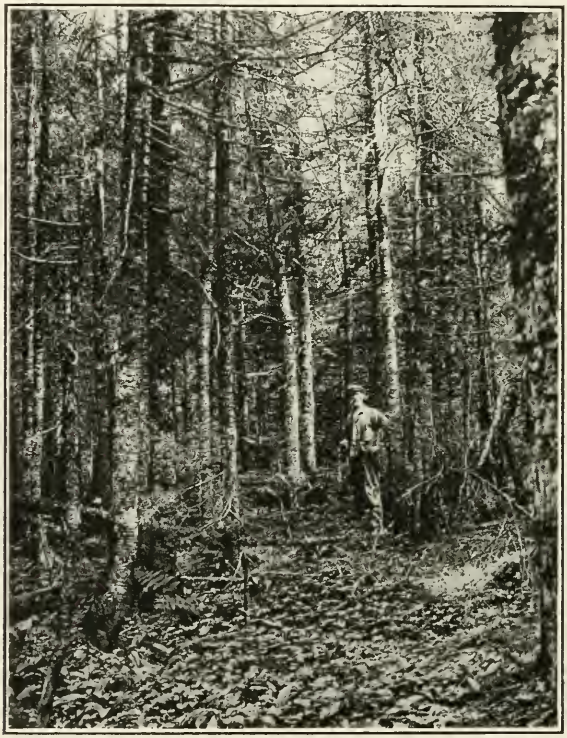

Figure 49.—Primeval coniferous forest of the regional climax type; mainly balsam fir; mountains north of Barrasois River.

to the fact that almost invariably they are heart rotted. It is a noteworthy fact, as Cooper ('13, pp. 17–21) has pointed out, that while the balsam fir far outnumbers all other trees in the forest, yet, owing to its susceptibility to fungus attack and consequent liability to windfall, its relative abundance decreases greatly with age. In other words, "its high birth-rate is balanced by a high rate of mortality."

Second in importance to the balsam fir in the climax forest is the white spruce, which is well distributed throughout, common, yet nowhere approaching the balsam in abundance, and conspicuous by reason of its relatively large size. It ordinarily attains a diameter of sixteen inches, sometimes of more than two feet, and as a rule is correspondingly taller than the balsam. Black spruce is also an important constituent, locally quite common, and in size about equal to the balsam. It never attains here the proportions which it exhibits in the Adirondacks where, in virgin forests, trees three feet in diameter and more than a hundred feet high are frequent. These three trees comprise the evergreen coniferous element in the climax forest. The deciduous element is represented primarily by two species, the paper birch and the mountain ash. The paper birch is well scattered through the forest, somewhat less abundant, perhaps, than the white spruce, but prominent by reason of its showy bark and spreading, broad-leaved crown. In height it seldom exceeds the average for the forest as a whole, and its trunk is rarely as much as a foot in diameter. The mountain ash is a very characteristic and omnipresent constituent, usually a small undertree, but sometimes fully fifty feet high with a trunk a foot in diameter. The yellow birch, though frequently represented in favorable situations, never reaches anywhere near the size which it attains in the lowland. Red maple is more or less scattered throughout, but as a rule is little more than an undershrub. The small-toothed aspen (*Populus tremuloides*) also is occasionally present.

The undergrowth in the climax forest.—Below is given a list of the characteristic shrubs and herbaceous vascular plants in the coniferous climax forest. Their general occurrence and local abundance when present is indicated by symbols, as explained elsewhere (p. 283).

Shrubs

Taxus canadensis	*cc*	*Acer spicatum*	*cc*
Corylus rostrata	*cf*	*Acer pennsylvanicum*	*cf*
Ribes prostratum	*cf*	*Lonicera canadensis*	*cf*
Amelanchier sp.	*co*	*Viburnum cassinoides*	*cf*
Nemopanthus mucronata	*cf*	*Viburnum pauciflorum*	*fo*

Herbaceous Vascular Plants

Phegopteris Dryopteris	*fl*	*Oxalis Acetosella*	*cc*
Phegopteris polypodioides	*cf*	*Aralia nudicaulis*	*cc*
Pteris aquilina	*cf*	*Cornus canadensis*	*cc*
Aspidium spinulosum var.	*fo*	*Moneses uniflora*	*cf*
Osmunda cinnamomea	*cf*	*Pyrola secunda*	*co*
Osmunda Claytoniana	*ff*	*Monotropa uniflora*	*co*
Clintonia borealis	*cc*	*Monotropa Hypopitys*	*co*
Maianthemum canadense	*cc*	*Epigaea repens*	*cf*
Streptopus roseus	*co*	*Chiogenes hispidula*	*cc*
Habenaria obtusata	*cf*	*Trientalis americana*	*cc*
Epipactis sp.	*co*	*Linnaea borealis americana*	*cc*
Listera cordata	*fo*	*Solidago macrophylla*	*ff*
Coptis trifolia	*cc*	*Aster acuminatus*	*cl*
Mitella nuda	*cl*		

Except for occasional colonies of the yew, the shrubs and herbaceous vascular plants in the undergrowth seldom form dense masses of vegetation. The ground is usually occupied by a continuous but rather open growth of the various species mentioned above. As on Isle Royale, the most conspicuous element in the herbaceous ground-cover is the bryophyte contingent, whose profuse development here in these coniferous forests is in striking contrast to its paucity in the deciduous climax forests of the lowland. Almost everywhere the ground is overlain by a soft, verdant carpet of *Bazzania trilobata, Hypnum Schreberi,* and *Hylocomium splendens,* with which are associated *Dicranum undulatum, Rhytidiadelphus loreus, R. triquetrus, Ptilium crista-castrensis* and species of *Sphagnum.* In the drier places the hypnum alone may predominate, in moist situations the sphagnums. Ordinarily all the species mentioned, except perhaps the sphagnums, are well represented. The ecological significance of this bryophyte ground cover in hindering evaporation and impeding drainage, thereby influencing not only the moisture of the substratum, but also its temperature, aeration, and toxicity, can hardly be questioned. Usually the surface layer of living plants is underlain by a more or less spongy mass of incompletely decomposed vegetable remains (the duff), which commonly is six inches or more in thickness. Corticolous liverworts and mosses in general are much more poorly developed in coniferous than in deciduous climax forests, although the lichens occupy a prominent position, particularly the beard lichen (*Usnea barbata*), which in well-lighted situations commonly drapes itself in graceful festoons from the branches of the trees.

Reproduction of the climax trees.—In his ecological investigation of the northeastern evergreen-coniferous climax forest, as developed on Isle Royale, Cooper ('13, pp. 42, 43) arrived at the following conclusions, which were based in large part on the intensive study of carefully selected quadrats. For successful reproduction the balsam fir requires abundant light, given which it will germinate and thrive in any sort of situation. In the forest, reproduction is practically confined to the openings caused by windfall. "The forest is a complex of windfall areas of differing ages, the youngest made up of dense clumps of small trees, and the oldest containing a few mature trees with little young growth beneath. The history of a windfall area is as follows. After the débris has disintegrated sufficiently to allow abundant light to reach the ground, a new generation of trees springs up, approximately even-aged, composed of the three dominant species [balsam fir, white spruce, and paper birch], *Abies* always greatly preponderant. During the continued development of this group most of the individuals are at various times eliminated, . . . Because of the dense shade no new individuals can start beneath them and the final outcome is a group composed of a few large trees, approximately even-aged, in which *Abies* has nearly or quite lost its position of dominance to *Betula*." The resultant forest is thus "a mosaic or patchwork which is in a state of continual change." Yet "the forest as a whole remains the same, the changes in various parts balancing each other."

Turning now to northern Cape Breton, it would seem that the ecological relations of the balsam fir here are somewhat different from those just described for Isle Royale. Here, as there, openings due to windfall are a characteristic feature of the forest; and the immediate sequel to windfall is a commonly prolific crop of balsam. Some of the young trees may originate from seeds shed previously to the windfall, but which have been lain dormant on the ground for want of conditions suitable to germination. Others doubtless arise from seeds shed only a short time before the windfall, or else contemporaneously with or subsequent to it. But many of the young trees represent specimens which were already present in the forest previous to the windfall. For while the reproduction of the balsam is most prolific in the windfall areas, it is by no means confined to them. It is seldom that the shade on the forest floor is sufficiently dense to prevent reproduction, and almost everywhere the undergrowth in a forest of the climax type includes numerous small, scattered balsams, mostly suppressed but ready to take advantage of any chance opening which may occur in the canopy overhead. Such openings, to be sure, are commonly due to windfall, since except in protected situations the balsam seldom dies a natural death. It is a not infrequent occurrence for groups of trees to be overthrown by the wind, thus giving rise to openings of considerable extent, but more commonly it is only scattered individuals which are blown down at one time. The influence of the openings thus created is probably twofold: (*1*) more light is introduced into the lower layers of vegetation, and (*2*) wherever sunlight reaches the forest floor the moss carpet, together with the more or less spongy underlying layers of duff and humus, tend to become somewhat dried out and in consequence warmer and better aerated. This latter indirect influence, the possible significance of which is suggested by Cooper ('13, p. 20), it seems to the writer, is of fully as great importance here in northern Cape Breton, at least so far as the balsam is concerned, as is the direct influence of increased illumination. The understory of balsams in a deciduous forest is much more thrifty than that in a coniferous forest, a circumstance which might be explained by the more favorable soil conditions there: so far as shade is concerned, this is generally greater in a deciduous than in a coniferous forest, at least during the growing season. But without question increased illumination is a very important direct factor, and perhaps the most important one, affecting the growth of the balsam. In this connection attention may be called to earlier remarks (p. 285) regarding the ecological relations of the balsam.

The white spruce and paper birch are much more dependent on an adequate light supply for successful reproduction than is the balsam fir. This is demonstrated by the relative abundance of the young growth of these two species in a windfall area or clearing, as contrasted with the great scarcity of any but large trees in the forest. In the case of the paper birch, to quote Cooper ('13, p. 22), "low birth-rate is compensated by a very low mortality and it is thus able to maintain itself in making a good proportion of the mature stand." The same observation may apply equally well to the white spruce, which apparently is relatively more abundant here than on Isle Royale. The black spruce grows best in well lighted situations, but, like the balsam, it is capable of maintaining itself for years in moderate shade.

With reference to their tolerance of shade in this climate, the writer would arrange the climax trees of the northeastern coniferous forest climatic formation in northern Cape Breton in about the following order: paper birch and aspen (very intolerant), white spruce (intolerant), balsam fir, black spruce, and mountain ash (tolerant), and yellow birch (very tolerant).

III. THE EDAPHIC FORMATION-COMPLEX OF THE REGION

A. Preliminary Observations

One of the most perplexing features of this region, when it comes to the exact analysis and delimitation of the various formation-types, is the manner in which these overlap and intergrade. This condition is attributable primarily to the abundance of atmospheric moisture. In less humid climates soil moisture plays an all important rôle in determining the character and distribution of vegetation, and as a result differences in soil and topography are associated with corresponding differences in plant cover. In general it can be stated that the influence of soil and topography on the character and distribution of plant associations is least pronounced in humid climates; most pronounced in arid climates: or, in other words, that this influence is inversely proportional to the dryness of the climate. This tendency toward uniformity in a humid region is of course due in part to the fact that here many soils, which in a less humid region would be too dry to permit the development of the types of association which characterize the better soils, are kept constantly moist. It may also be due to the fact that bare rock outcrops, which in themselves are unable to retain water except in crevices, become rapidly overgrown, except where they are too steep, by a layer of lichens and bryophytes which create a water-retaining substratum and thus tend to produce ground conditions similar to those found in soils which naturally would be more favorable to plant growth. In the coniferous forest region of northern Cape Breton, and probably in other similar regions as well, this tendency toward uniformity is accentuated by the fact that in the upland forests, owing largely to the prolific development of mosses and liverworts and the copious accumulation of humus, not only is the substratum kept constantly moist, but it is invariably acid to litmus, thus approximating the conditions which prevail in bogs and in the majority of the swamps. In less humid climates, many of the species which here are characteristic of uplands, or which grow both on uplands and in bogs and swamps, are restricted to situations of the latter sort. The tendency for different edaphic formation-types to merge into one another is exhibited to some degree in the lowland region of northern Cape Breton; it is quite pronounced in the forested portion of the highlands; but it reaches its culmination in the barrens, where it is almost impossible to draw a sharp line between the vegetation of uplands and that of the swamps.

B. Formations of the Xerarch Series

1. The Formation-types of Ordinary Uplands in the Forested Region

a. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED UPLANDS

In comparing xerarch successions on ordinary, well-drained uplands here with those of the lowland, the most striking difference is seen in the character of the climax association-type. There, a balsam fir–spruce–paper birch forest may represent merely a passing stage in the succession: in all edaphically favorable situations it is a temporary association-type, destined in the course of time to be superseded by a forest of the deciduous type. Here, however, a forest of this sort represents the culminating stage in the succession: it is a permanent association-type. Throughout most of the forested region in the highland this coniferous forest climax has been attained, and it is only in edaphically unfavorable situations or in places where the original forest has been destroyed by fire that the more primitive stages in the succession are encountered. The association-types of exposed hilltops may resemble those of similar situations in the barrens, but, on the whole, the sequence and general character of the preliminary successional stages in the highland is essentially similar to what has been described for the lowland and therefore need not be discussed further. As a rule the succession takes place rapidly, the trees of the climax forest being present from the outset, and the various stages are more or less telescoped.

FIGURE 50.—Low coniferous woodland on plateau west of Ingonish.

b. THE ASSOCIATION-COMPLEXES OF POORLY DRAINED UPLANDS

Forests of the regional climax type attain their optimum development on well-drained slopes. But over a considerable portion of the forested region the country is flat or rolling, with a tendency to be poorly drained, and the prevailing type of vegetation here is low, more or less swampy woodland (FIG. 50). No sharp line can be drawn between woodlands of this description, which constitute an edaphic climax association-type, and forests of the regional climax type. Essentially the same species may be present in both cases. Here, however, the trees average scarcely twenty-five feet in height, and black spruce may be quite as abundant as balsam, while swamp species, notably *Osmunda cinnamomea* and the sphagnums, commonly predominate in the undergrowth. Associations of this sort may originate through a hydrarch successional series, but more commonly the pioneer stages are xerophytic, the swampy condition being induced very largely through the activity of vegetation in retarding drainage. Parts of the plateau occupied by barrens are commonly skirted on all sides by low woodland, which forms a transition zone between these areas and those congenial to forests of a more mesophytic character. Raised bogs have been developed locally on uplands in the forested region, but these are especially characteristic of the barrens and will be discussed under that head.

Figure 51.—Summit of low hill in barrens; mountains west of Ingonish; vegetation in immediate foreground, dwarf shrub heath; in mid-distance (vicinity of figure and beyond), mainly dwarf shrub-spruce heath. The low, bushy spruce in center foreground was about 150 years old.

2. The Formation-types of Ordinary Uplands in the Barrens

a. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED UPLANDS

The rock face–crevice complex.—Over most of the plateau the bed rock is covered by a thin soil which may be residual or extraneous in its origin. Here and there, however, rounded knolls or blocks of granite and syenite rise conspicuously, and on these may be found rock-face and crevice associations essentially similar to those which have been described as characteristic of rock outcrops in the lowland.

But the prevailing pioneer type of vegetation on uplands in the barrens is some sort of a heath. In the heath the lichens, notably the cladonias, are invariably conspicuous, while sedges and grasses, shrubs and scrubby trees occupy a position of varying importance.

The dwarf shrub heath association-type.—This is characteristically developed on exposed hill tops, where the soil may support only the scantiest kind of a plant cover (foreground of FIG. 51). In such situations the ground in places is bare; elsewhere it is overlain by a sparse mat of cladonias and *Racomitrium lanuginosum,* or maintains a stubby growth of *Polytrichum juniperinum, P. piliferum,* and *Ceratodon purpureus.* Of the seed plants peculiar to such habitats, *Potentilla tridentata* is worthy of note, but particularly characteristic are the four shrubs: *Empetrum nigrum,* which forms low, sprawling mats; *Vaccinium uliginosum,* which occurs in depressed circular patches; *Vaccinium Vitis-Idaea,* which scrambles over the ground and frequently is intricately interwoven in the lichen mat; and *Vaccinium pennsylvanicum angustifolium,* a form of blueberry only a few inches high. In addition to these, there is usually a scattering of other plants, particularly ericaceous shrubs, all of which are noticeably impoverished.

Typical dwarf shrub heath occurs locally throughout the barrens, but in a pure state is nowhere extensively developed. In exposed situations it may constitute a permanent association-type, i. e., an edaphic climax. But more commonly it seems to represent a temporary stage, destined to be superseded by dwarf shrub–spruce heath, into which it nearly everywhere merges. In places dwarf shrub heath very evidently is a retrogressive type which has arisen subsequent to the destruction of dwarf shrub–

spruce heath; but more commonly it represents a primitive phase. Characteristic plants here, in addition to those already specifically mentioned, are the following:

Lichens

Cladonia alpestris
Cladonia coccifera
Cladonia crispata
Cladonia pyxidata
Cladonia rangifernia
Cladonia sylvatica
Cetraria islandica
Sphaeophorus coralloides Pers.

Seed Plants

Juniperus communis montana
Ledum groenlandicum
Rhododendron canadense
Kalmia angustifolia
Kalmia polifolia
Melampyrum lineare

The sedge–grass heath association-type.—This occurs in somewhat moister, less exposed situations than the dwarf shrub heath, as for example, or rather dry slopes. The ground is usually covered by a luxuriant growth of cladonias, which may be replaced locally by *Racomitrium lanuginosum* or occasionally by xerophytic species of *Sphagnum,* such as *S. capillaceum tenellum* and *S. tenerum.* The predominant vascular plants are the sedge, *Scirpus caespitosus,* and the grass, *Calamagrostis Pickeringii.* Other herbaceous plants generally present are as follows:

Lycopodium sitchense
Lycopodium annotinum pungens
Deschampsia flexuosa
Melampyrum lineare
Cornus canadensis
Prenanthes trifoliolata
Solidago uliginosa
Aster nemoralis

In addition to these, the woody species characteristic of the dwarf shrub–spruce heath are well represented, but for the most part by small specimens, scattered and relatively inconspicuous. Like the preceding association-type, the sedge–grass heath is nowhere extensively developed, and it displays a constant tendency to pass over into dwarf shrub–spruce heath.

The dwarf shrub–spruce heath association-type.—This is one of the most widely distributed and most distinctive types of vegetation in the barrens. It commonly occupies the upper slopes of hills (FIGS. 51, 52), and in general prevails on well-drained uplands wherever the conditions of exposure are such as to prevent the development of a more mesophytic type of vegetation. At first sight an area occupied by this association-type appears as a crowded, labyrinthine series of low mounds or hummocks, irregular in size and shape, but averaging perhaps from three to ten feet in diameter by from one to two feet in height. The hummocks are densely overgrown with cladonias and support a thick growth of low shrubs, mostly ericads. Depressed, bushy trees, mainly black spruce, scarcely two feet high but spreading out laterally over a radius of several feet, constitute an important element in the vegetation, growing on or alongside the hummocks. Here and there, scattered tamaracks may be conspicuous by reason of the fact that they project somewhat above the general surface level of the surrounding vegetation, which otherwise maintains a nearly uniform height at from two to two and a half feet above the floor of the depressions which separate the hummocks. In typical dwarf shrub–spruce heath, the depressions between the hummocks are open and, aside from the cladonia mat which nearly everywhere covers the ground, their vegetation is scanty.

FIGURE 52.—Dwarf shrub–spruce heath; barrens in mountains west of Ingonish.

The following list includes the more characteristic plants of dwarf shrub–spruce heath:

Lichens

Cladonia alpestris
Cladonia sylvatica
Cladonia rangiferina
Cetraria islandica

Bryophytes

Sphagnum capillaceum tenellum
Sphagnum tenerum
Ptilidium ciliare
Leucobryum glaucum
Racomitrium lanuginosum
Hypnum Schreberi

Vascular Plants

Pteris aquilina
Abies balsamea
Picea mariana
Larix laricina
Juniperus communis montana
Maianthemum canadense
Myrica Gale
Pyrus melanocarpa
Amelanchier sp.
Empetrum nigrum
Nemopanthus mucronata
Cornus canadensis
Andromeda glaucophylla
Chamaedaphne calyculata
Epigaea repens
Kalmia angustifolia
Kalmia polifolia
Ledum groenlandicum
Rhododendron canadense
Vaccinium canadense
Vaccinium pennsylvanicum
Viburnum cassinoides

Any of the other species mentioned earlier as characteristic of sedge–grass heath may grow here also, but these, for the most part, are confined to the depressions between the hummocks.

The structure of the hummocks (Fig. 53) is extremely interesting. Examination shows them to be due entirely to plant activity. Internally they consist of an intricate mass of incompletely decomposed vegetable débris: the sort of structure commonly referred to as "raw humus." Ordinarily the bulk of the material has been derived from the lichens and from the leaves of the various shrubs which inhabit the surface of the hummock, the whole being bound together by the stems and roots of the surface vegetation. In some cases the sphagnum has contributed very largely to the formation of the hummocks: in one instance the excavation of a hummock two feet high, whose surface vegetation, aside from various shrubs, consisted entirely of *Sphagnum capillaceum tenellum,* showed the whole hummock to have been built up by this moss, whose remains, still in a fine state of preservation, extended nearly to the bottom, where, at the very base of the hummock and overlying the gravelly substratum, was a thin layer of *Leucobryum* remains. It is evident that for the most part the formation of these hummocks is a result of the combined activity of the lichens, particularly the cladonias, and the ericaceous shrubs. They have arisen somewhat as follows. Previous to their formation the ground was covered by a thin mat of mosses and lichens in which grew various herbaceous plants and shrubs: essentially the same condition which prevails in sedge–grass heath and which still persists in the open depressions between the hummocks. Where edaphic conditions are favorable the cladonias exhibit a marked tendency to grow upward, but they are unable to do so to any extent without some sort of support. The needed support is furnished by the shrubs which, where they grow close enough together, afford a sort of scaffolding upon or around which the lichens are able to push upward. As the shrubs gradually become buried

FIGURE 53.—Detail view of hummock in dwarf shrub heath association-type; *Cladonia alpestris, Chamaedaphne, Ledum,* etc.; barrens in mountains west of Ingonish.

below they grow above, at the same time branching more or less profusely. And as the branches become covered over they produce copious adventitious roots, with the result that the original number of physiologically independent individuals, as viewed at the surface of the hummock, becomes multiplied many times. The shrubs, therefore, which cover the surface of a hummock have been derived directly, in large part at least, from preexisting shrubs: they antedate the hummock itself.[13]

The genetic relationship between dwarf shrub and sedge–grass heath, on the one hand, and dwarf shrub–spruce heath, on the other, has already been suggested. During the evolution of the present association-type, various of the herbaceous vascular plants characteristic of the more primitive stages either disappear or else become in large part or wholly confined to the depressions: to situations where there is no great depth of humus and where the soil relations presumably are more favorable than on the hummocks. This is true, for example, of both *Scirpus* and *Calamagrostis,* and of such forms as *Lycopodium, Potentilla, Solidago,* and *Aster.* At the same time, scrubby trees become increasingly conspicuous.

In its ecological aspect, an association of the sort just depicted certainly approximates very closely dwarf shrub heath, as defined by Warming ('09, pp. 210–214). It agrees in the nature of the underlying soil, in the dominance of lichens and ericaceous shrubs, in the low stature of the vegetation, and in the copious production of raw humus: this latter a phenomenon which, according to Warming, "must be regarded as the most characteristic peculiarity of heath." It would seem to differ from typical heath primarily in the presence of various arborescent species which, in more favorable situations, attain much larger dimensions than here. But while any of the trees of the climax coniferous forest (with the exception of yellow birch and red maple) may be represented here, it is significant that black spruce is invariably predominant; that tamarack, which is practically absent from the climax forest, is usually a prominent constituent; and that, on the other hand, balsam fir, the predominant tree in forests of the regional climax type, is of very subordinate

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[13] In this connection, see observations by Ganong, quoted on p. 447.

importance. In its typical development, then, the writer would regard this type of association as a true heath.[14]

Transition from heath to Krummholz.—All intergradations are found between typical dwarf shrub–spruce heath and *Krummholz,* the association-type to be treated next, and in this connection the behavior and ecological relations of the spruce and other evergreen conifers has an important bearing. As the principal species concerned, the black spruce will serve to illustrate the points in question. Like the ericaceous shrubs, this species appears at an early stage in the development of the heath: it is antecedent with reference to the hummocks. Through the death of the primary leader, the extensive development and copious branching of the lateral shoots, and commonly also through vegetative reproduction by layering, it characteristically assumes a low, compact, rounded, shrub-like habit. So closely may one of these bushy spruces conform with the contour of the hummock alongside which it grows that on superficial examination it appears to be growing on the hummock itself; but ordinarily the relationship is very different. For the shade produced by these clumps of spruce has an important local effect on the nature of the vegetation, in that it inhibits the growth of lichens and thereby prevents or checks hummock formation. In some areas the depressions between adjacent hummocks are completely filled in by a dense snarl of scrubby spruces which rise to about the same general level as the low vegetation which tops the hummocks. From a distance the surface contour of

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[14] Warming ('09, p. 210) defines heath as "A treeless tract that is mainly occupied by evergreen, slow-growing, small-leaved dwarf-shrubs and creeping shrubs which are largely Ericaceae." But the use of the term is not wholly restricted to such areas. Warming himself recognizes lichen-heath and moss-heath (op. c., pp. 205, 208), and Graebner ('01, pp. 26, 27), while distinguishing as most representative areas of the sort specified by Warming, extends the term to include "not only areas dominated by ericaceous shrubs, but open tracts in which there is neither a good tree growth nor a close grass turf; [in which] ligneous plants dominate, especially low shrubs. [Thus,] what we call pine or oak barrens would probably be included in Graebner's heath" (quotation from Cowles' review of Graebner's book). Applying the term in this latter sense, Harshberger ('11, pp. 165-168) regards the "plains" of the New Jersey pine-barrens as heath. Rübel ('14, p. 237) would restrict the use of the term heath to "ericoid-leaved bushland."

such an area appears quite flat and easy to travel, but one soon learns to steer clear of these "tanglefoot" barrens, as an old trapper who served as guide for the writer aptly termed them, whenever possible. Barrens of this sort obviously represent a transition stage between the dwarf shrub–spruce heath association-type and the *Krummholz* association-type. Not only is the arborescent element in the vegetation present in increased abundance, but the character of the undergrowth is different. For the presence of the spruce not only causes the exclusion of certain species, but favors the introduction of others. Underneath these dwarf evergreen trees, wherever they occur, may be found any or all of the liverworts and mosses characteristic of the climax forest of the region (e. g., *Bazzania, Dicranum undulatum, Hylocomium splendens, Ptilium*), together with various of the herbaceous plants (e. g., *Clintonia, Coptis, Linnaea*).

FIGURE 54.—*Krummholz* in immediate foreground, passing into low woodland or forest scrub behind the figure; barrens in mountains west of Ingonish.

The Krummholz association-type.—This differs from heath in the following important respects: (*1*) Dwarf, bushy trees

(*Krummholz*) predominate and form a relatively closed stand. (*2*) The lichens which characterize the heath (together with the hummocks which they form) are either absent or else poorly developed, while ericaceous shrubs occur here mainly as an understory and are of subordinate importance to arborescent species. (*3*) The undergrowth approximates that of the climax coniferous forests of the region, essentially the same list of bryophytes, herbaceous vascular plants, and shrubs being characteristic of each. (*4*) The ecological aspect is much more mesophytic. In typical *Krummholz* (Figs. 54, 55) the trees range around three and four feet in height and commonly produce a dense tangle through which it is exceedingly difficult to force one's way. It is a type of association characteristic of situations in the open barrens which are somewhat sheltered from wind. In the opinion of Dr. Harvey, who accompanied the writer in 1916, the *Krummholz* of the barrens in northern Cape Breton is a close ecological counterpart of the *Krummholz* on Mount Ktaadn, concerning which he has written ('03, p. 34): "It seems then that the *Krummholz* forest is almost as mesophytic as the *Picea-Abies* combination . . . . which very evidently is

Figure 55.—Low *Krummholz* association-type with scattered tamaracks, many of them dead, projecting up above general level of surrounding vegetation; barrens in mountains west of Ingonish.

the climatic mesophytic forest of this district." *Krummholz* differs from forest scrub not only in the lesser height of the trees, and in their more pronounced tendency to approximate the *Krummholz* growth form, but in the lesser abundance of the balsam fir.

Factors responsible for failure of forests to develop.—True alpine conditions are found nowhere in northern Cape Breton. This is evidenced by the complete absence of an arctic-alpine flora. On Mount Franey, the highest measured mountain in Nova Scotia, for example, no species were observed which are not equally abundant at lower elevations, while with the exception of perhaps a few forms such as *Betula pumila, Vaccinium uliginosum,* and *V. pennsylvanicum angustifolium,* the flora of the interior plateau scarcely differs in its composition from that of the upper mountain slopes. The general failure of forests to develop in the barrens can be ascribed very largely if not wholly to edaphic factors, especially to the combined influence of snow and wind during the winter months. Heavy winds prevail on the barrens intermittently at all seasons, but particularly in winter. The primary effect of the wind at this season is to sweep the snow from the more exposed sites and pile it up in the more sheltered situations. Exposed hill crests may be swept entirely bare, while in some of the ravines great drifts fully fifty feet in depth may accumulate. In general, it is apparent that the height of the trees, with the possible exception of the tamarack, is closely correlated with the depth of the snow in winter. In exposed situations any branches which project above the surface of the snow are liable to be killed by excessive transpiration or through the sand-blast-like action of the wind-driven snow. Individual shoots may survive a few mild winters, but then comes a severe winter and they too are killed. In the case of forest scrub, an association-type to be described presently, it is evident that, in spite of the apparently exposed position of the low hills on which it is commonly developed, local conditions favor the accumulation of snow drifts in much the same manner that sand dunes are built up along the seacoast.

Age of dwarf trees.—In this connection, a few observations regarding the ages of some of the dwarf trees may be of interest. The tamarack shown in Fig. 56, situated near the crest of the hill pictured in Fig. 51, was found to have more than 150 annual rings; and about the same number was counted in a cross section of the trunk of a balsam fir, scarcely three feet high, but with a trunk seven inches in diameter. Knee-high spruces more than fifty years old are common in exposed situations, one of those in the foreground of FIG. 51, scarcely a foot in height, having more than a hundred annual rings.

The forest scrub association-type.—From a distance, many of the low hills in the barrens appear to be well wooded, but closer inspection commonly reveals a most remarkable type of association. Because of the size of the trees, many of which may be as much as twenty feet high, it should be classed as forest; yet it is an abortive attempt at forest development rather than true forest. Three trees predominate: the balsam fir, the black spruce, and the tamarack, and one and all are battered and weather-beaten, betraying unmistakably the severity of the atmospheric forces to which they have been subjected. In this connection the dissimilar behavior of the three constituent trees under these adverse conditions is of much interest.

FIGURE 56.—Gnarled tamaracks, aged about 150 years, at summit of low hill shown in FIG. 51; barrens in mountains west of Ingonish.

The balsam fir commonly possesses a short, stocky trunk from three to six feet high, according to the depth of the snow blanket. This trunk ranges in diameter up to more than a foot (in one case sixteen inches), and some of the trees must be well over two hundred years old (one six inch trunk showed more than 150 annual rings), an unusual age for the balsam in northern Cape Breton. The total height of the tree may be little greater than that of its stubby trunk: the lateral branches, usually borne in profusion near its summit, spread out widely, giving rise to a dense, flat-topped crown, low but commonly ten or a dozen feet broad and drooping nearly to the ground. But as a rule, upon the death of the primary leader, a new leader is developed which tends to continue the upward growth of the trunk. After a few years, the length of the interval depending on the severity of the winters, this leader may be killed and replaced by a third, and so on. More than twenty dead leaders have frequently been counted on a single tree. Often several leaders may be active at the same time, but usually one of them soon gains a marked

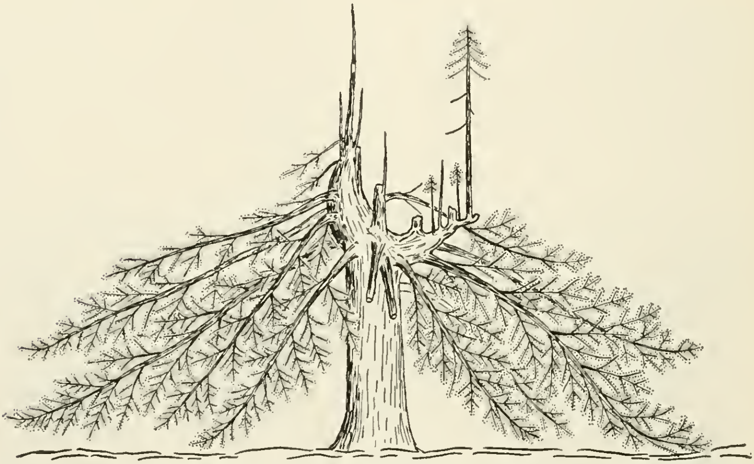

FIGURE 57.—Habit sketch of balsam fir growing in forest scrub association-type; barrens in mountains west of Ingonish. This particular tree is ten feet high (overall) and has a spread of more than a dozen feet with a trunk diameter of nearly a foot.

ascendancy over the others. Very often a leader which rises six or eight feet above the main body of the tree will have had all its foliage blasted away by the wind-driven snow except for a small, pyramidal crown at the very tip.[15] The general aspect of these trees is suggested by the accompanying sketch (Fig. 57).

Usually quite different in its behavior from the balsam fir is the black spruce. In the balsam, while the lateral branches may be capable of assuming the functions of the leader, it would appear that they are able to do so only when very young, and more often than not the leader seems to originate adventitiously from either the main axis of the tree or a lateral branch. In the spruce, on the other hand, the potential capacity for radial growth in the normally dorsiventral lateral branches is much more pronounced, and this capacity is less restricted to the younger branches. Upon the death of the primary leader, a number, often nearly all, of the lateral branches tend to assume the radial habit, thus producing a clump of leaders, all of approximately equivalent rank. As a result, while one leader may sometimes become more prominent than the rest, the spruce commonly acquires a bushy habit quite different from that of the balsam. This dissimilarity of habit in the two trees is often strikingly exhibited in the *Krummholz* association-type: the balsam here is constantly tending to send a vigorous leader up above the general level of the surrounding vegetation and invariably possesses a short, sturdy trunk (Fig. 58); while the spruce adapts itself readily to the prostrate *Krummholz* habit and is virtually devoid of a distinct trunk.

The tamarack behaves differently from either the balsam or the spruce, being apparently better able than these species to withstand the rigorous winter climate. The trees exhibit a gnarled, scraggly aspect, but seldom are killed back to any extent.

Sometimes a forest of the sort under consideration is well nigh impenetrable, and the undergrowth is essentially that of the coniferous climax forest of the region. But more often the trees occur singly or in groups, with open spaces between in which the vegetation is made up largely of the species characteristic of

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[15] A different explanation for a similar phenomenon in the spruce has been offered by Ganong ('04, pp. 188, 189).

heath. In general, this association-type is intermediate in character between heath and typical forest.

The ecological status of the tamarack in northern Cape Breton.—The status of the tamarack in the lowland has already been referred to. In the barrens it is a common tree, but throughout the forested region of the highlands it is absent or very rare in upland forests, being confined mainly to open swamps. The evident scarcity of this tree in all but open situations is correlated with the fact that it is primarily a pioneer species: it is notoriously intolerant of shade. As a result, except in barrens, swamps, or other open situations, it has almost everywhere been crowded out in competition with the more tolerant climax trees.

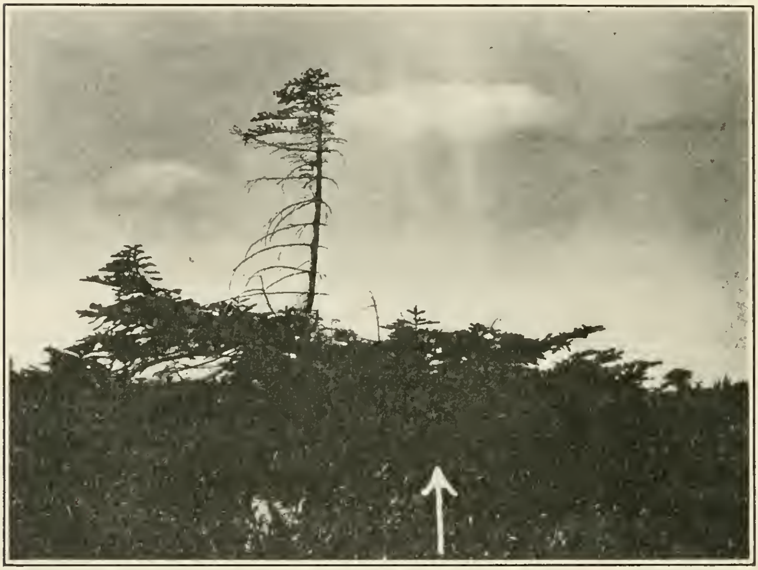

FIGURE 58.—Weather-beaten balsam fir; barrens in mountains west of Ingonish. This tree measured eight feet high (overall) and had a trunk less than three feet high (in position indicated by arrow) but seven inches in diameter and with more than 150 annual rings. The present leader, to left of trunk, shows well the effect of heavy westerly winds (from right in picture) and wind-driven snow.

The low woodland association-type.—This is essentially similar to the low woodland type of poorly drained uplands described for the forested region. It may occupy like situations in the barrens, but here it also is a frequent type on moist, fairly well drained hillsides which are protected from the wind.

Summary of successional relations.—It will be seen that in a general way the association-types of well-drained uplands in the barrens have been arranged in an ascending series; that there are all gradations between dwarf shrub heath and sedge–grass heath at the one extreme and typical forest at the other. Incident to the special discussion of the association-types, various successional relationships have been pointed out. But while it is conceivable that in the course of time the associations of relatively primitive types are everywhere destined to become superseded by associations of more advanced types, as a matter of fact this is not generally the case. For the degree of mesophytism capable of attainment in the majority of sites is limited by edaphic factors, and any of the association-types described above may constitute locally an edaphic climax.

b. THE ASSOCIATION-COMPLEXES OF POORLY DRAINED UPLANDS

Although a distinction may be made between well-drained and poorly drained uplands in the barrens, as a matter of fact, as has been intimated earlier, it is practically impossible to draw sharp lines of demarcation. Owing to the character of the vegetation, especially to the influence of the almost universally developed lichen–bryophyte ground cover in retarding drainage, an area which originally may have been well-drained rapidly becomes less so, and there are few areas in which water cannot be squeezed out of a peaty substratum at almost any time of the year.

In protected situations, wet, poorly drained uplands may support low, swampy forests of (mainly) black spruce, with an undergrowth of *Alnus incana, Osmunda cinnamomea,* and the like: forests which might almost equally well be treated under the head of hydrarch successions. Further, the occurrence of sphagnum hummocks in areas occupied by heath has already been mentioned. On flat upland areas from which the water runs off slowly or where it tends to collect locally in shallow rock basins, as well as in various other situations where drainage conditions are such as to favor, at least locally, the development of the sphagnums, bogs and boggy swamps may arise on uplands.

The discussion of these is deferred until later (see under head of raised bogs, p. 433).

3. The Formation-types of Uplands along Streams

THE ASSOCIATION-COMPLEXES OF RAVINES AND VALLEYS

The association-types of ravines.—Streams in the forested region for the most part flow through ravines or broadly V-shaped valleys. The character of the stream-bank and cliff vegetation here is essentially similar to that already described for lowland streams. Ravine forests exemplify further the general tendency of the vegetation of uplands in this region toward uniformity, since they differ scarcely, if at all, from the forests of ordinary uplands.

FIGURE 59.—Low forest in ravine, with barren hill-top above; barrens in mountains west of Ingonish.

Ravine vegetation in the barrens (FIG. 59), in general, resembles that of the forested region, and the forest-clad slopes here may afford a striking contrast to the barren aspect which prevails on adjoining exposed uplands. In shallow ravines the woodland is low, but in the deeper "gulches" the trees attain considerable size.

The association-types of open valleys.—While practically all the larger streams on their way to the sea run for long distances through deep gorges and ravines, on the plateau itself most of the streams flow through broad, shallow, characteristically flat-floored valleys, but little below the general level of the surrounding country. The slopes which flank these valleys may be covered with low woodland, or in the barrens by *Krummholz.* Their floors are commonly occupied by "hay marshes," alder thickets, and swampy woodland, which will be discussed under hydrarch successions.

C. FORMATIONS OF THE HYDRARCH SERIES

1. The Formation-types of Lakes and Ponds

a. INTRODUCTORY

Small lakes and ponds of all sizes, but mostly quite shallow, are freely interspersed among the countless low hills which go to make up the surface of the plateau and occur scattered here and there along the seaward slopes of the highland. Many of them lie at the sources or along the courses of the innumerable streams which originate in the barrens, but a large proportion are devoid of any definite outlet. Ponds of the latter type are especially common on the plateau where, owing to the abundant precipitation and the impermeable nature of the rock floor, more or less permanent bodies of water tend to collect in basins of any description. On an undulating, rock-floored table-land such as this, the number of depressions suitable to pond formation is naturally very great, but the number of ponds actually present is even greater. This is due to the fact that, in addition to those whose presence is conditioned by the character of the topography, there are numerous ponds which bear no relation whatever to the topography, whose presence is attributable primarily to the activity of vegetation. The manner in which ponds of this latter sort arise will be discussed in some detail in later paragraphs (p. 449 *et seq.*). On the highland, as in the lowland (while there are plenty of apparent exceptions, particularly in the case of well-drained water bodies) there is a general tendency for lakes and ponds to become clogged up through vegetative activity, and in this way many basins formerly occupied by ponds have become more or less completely filled in.

b. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED LAKES AND PONDS

The plants named in the subjoined list are characteristic of well-drained lakes and ponds in the highland, growing either in the deeper water or in the shallows along the shore. Extended comment seems hardly worth while, since in their local distribution and ecological relations they conform closely with what has been described for similar areas in the lowland.

FIGURE 60.—Shallow pond in mountains north of Barrasois River; aquatic vegetation and narrow marginal fringe of swamp shrubs.

Sphagnum cuspidatum Torreyi
Drepanocladus Sendtneri
Drepanocladus scorpioides
Fontinalis sp.
Isoëtes sp.
Equisetum fluviatile
Sparganium angustifolium
Potamogeton natans
Potamogeton Oakesianus
Carex aquatilis
Carex filiformis
Carex rostrata
Eriocaulon septangulare
Nymphaea variegata
Castalia odorata
Ranunculus Flammula reptans
Nymphoides lacunosum
Lobelia Dortmanna

Dulichium arundinaceum
Eleocharis palustris vigens
Scirpus subterminalis
Utricularia vulgaris
Utricularia intermedia

The character of the marginal vegetation might perhaps more appropriately be considered in connection with swamps, but two phases will be briefly mentioned at this point. Between the water's edge and the adjoining upland vegetation there may occur only a narrow fringe of swamp thicket (Fig. 60), made up of such shrubs as the following:

Myrica Gale
Alnus incana
Spiraea latifolia
Rosa nitida
Ilex verticillata
Nemopanthus mucronata
Chamaedaphne calyculata
Kalmia angustifolia
Rhododendron canadense
Viburnum cassinoides

Elsewhere, however, intervening between this thicket and ordinary summer low water mark there may be a strip of sandy or rocky beach, of varying width, which supports an open swamp association of an essentially pioneer type. Characteristic plants of such a habitat are the following:

Scapania nemorosa
Sphagnum sp.
Lycopodium inundatum
Agrostis hyemalis
Carex filiformis
Carex Michauxiana
Carex Oederi pumila
Carex stellulata
Juncus brevicaudatus
Ranunculus Flammula reptans
Drosera longifolia
Drosera rotundifolia
Hypericum canadense
Hypericum virginicum
Viola cucullata
Viola pallens
Bartonia iodandra
Vaccinium macrocarpon
Lycopus uniflorus
Utricularia cornuta
Aster nemoralis
Aster radula

Very commonly, at least locally, the lake is bordered by swamps of a more advanced type, but these are better considered under the head of swamps.

c. THE ASSOCIATION-COMPLEXES OF UNDRAINED PONDS

In the number and abundance of seed plants, the aquatic vegetation of undrained ponds as a rule is inferior to that of well-drained ponds. Of species with submerged or floating leaves the most commonly represented are *Nymphaea variegata* and *Castalia odorata, Eriocaulon septangulare, Ranunculus Flammula reptans* and *Utricularia intermedia.* In addition to these, various sedges may grow in the shallow water around the margin or elsewhere, such species as *Eleocharis palustris vigens, Carex oligosperma* and *Scheuchzeria palustris,* together with the buckbean, *Menyanthes trifoliolata.* Of particular importance, however, because of their frequently prolific growth, are the aquatic sphagnums, notably *Sphagnum Pylaisei* and *S. cuspidatum* (including the var. *Torreyi*), and certain filamentous algae. But there is the greatest variation in the vegetation even of closely adjacent and seemingly quite similar ponds. One may be quite choked up with aquatic sphagnums, while in the next there is scarcely any vegetation save a dense growth of algae on the bottom. One may contain a rank growth of *Eleocharis,* its neighbor a similar growth of *Menyanthes,* or neither of these species may be present; and so on. Practically all undrained ponds are mucky at the bottom and along the shores. The dynamics of the vegetation in lakes and ponds are discussed in later paragraphs.

2. The Formation-types of Lake-, Spring-, and Precipitation-swamps

a. THE ASSOCIATION-COMPLEXES OF WELL-DRAINED SWAMPS

As elsewhere suggested, throughout the region of coniferous forests, wherever the ground is sufficiently wet, there is a tendency for the substratum, through the influence of vegetation in obstructing the drainage, to become boggy. In view of this fact, it would not have been at all surprising to find that swamps similar to the undrained type of the lowlands were entirely lacking here. But this is not the case. While the majority of the swamps belong to the undrained or poorly drained types, swamps are frequently encountered which unmistakably are of the well-drained type. The following list of plants, from an open swamp situated on a fairly steep, springy hillside in the forested region, scarcely a mile from the edge of the barrens, is quite characteristic of well-drained swamps in this region: it has been practically duplicated in other similar areas.

Taxus canadensis
Calamagrostis canadensis
Cinna latifolia
Glyceria canadensis
Scirpus caespitosus
Scirpus hudsonianus
Eriophorum virginicum
Rynchospora alba
Carex crinita
Carex flava
Carex stellulata
Juncus brevicaudatus
Smilacina trifolia
Iris versicolor
Habenaria clavellata
Habenaria dilatata
Spiranthes Romanzoffiana
Myrica Gale
Alnus incana
Thalictrum dioicum
Drosera rotundifolia
Spiraea latifolia
Amelanchier sp.
Sanguisorba canadensis
Rosa nitida
Viola blanda
Viola cucullata
Chamaedaphne calyculata
Lonicera caerulea
Viburnum cassinoides
Eupatorium purpureum
Solidago rugosa
Aster acuminatus
Aster nemoralis
Aster puniceus
Aster radula
Aster umbellatus
Cirsium muticum

Aside from relatively steep, springy slopes, swamps of the well-drained type are commonly developed along streams, in places where the ground is subject to occasional inundation (see further under head: formation-types along streams, p. 456). The vegetation in swamps of the well-drained type is apt to include more or less admixture of bog species, as shown by the above list, but these occupy a subordinate position and sometimes even the omnipresent ericad, *Chamaedaphne,* is absent. The only occurrence of *Typha latifolia* noted on the plateau was in a swamp of this description. Well-drained swamps are far less frequent in the barrens than in the forested region, but even here they are by no means absent, particularly along the larger streams.

b. THE ASSOCIATION-COMPLEXES OF POORLY DRAINED SWAMPS

Under this head, here as in the lowland, may be included a large number of swampy areas which, in the character and ecological relations of their vegetation, appear to be intermediate between the well-drained and the undrained types. There is one group of swamps in particular which seems to fit in under this head better than under any other, swamps which are quite commonly encountered along the shores of well-drained lakes. Locally along the margins of these lakes (Fig. 61) there have been formed broad, nearly level beaches, sometimes twenty-five or fifty feet in width, which lie somewhat above the level of the lake in summer, but are submerged during winter and early spring, at times when the outlet is blocked up by the ice.

At an early period in its development the vegetation in such an area is essentially as described for the beach in connection with the vegetation of well-drained lakes and ponds (p. 417): an open swamp association of a pioneer type. In the course of time, under favorable conditions, the more or less discontinuous plant cover characteristic of this early stage may become continuous. Largely through the activity of the sedges, *Carex filiformis, Carex oligosperma,* and *Rynchospora alba,* a shallow layer of peat is formed and the level of the swamp's surface is gradually raised higher. It is worthy of special note that the sphagnums play a relatively insignificant part in the building up process: the cushion-forming species so conspicuous in bog

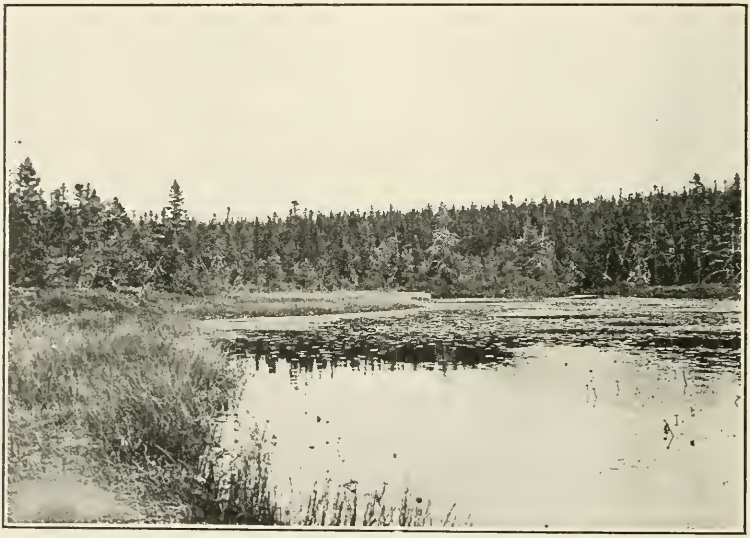

Figure 61.—Small, well-drained lake with border of marshy swamp; mountains north of Barrasois River.

formation are usually absent or poorly developed. About the only form at all abundant is *S. Pylaisei,* a rather delicate species which, with the liverwort, *Cephalozia fluitans,* commonly covers the peaty substratum in among the sedges with a thin, felty mat. At an early stage in its development, in addition to the sedges already mentioned, the vegetation of such an association-type includes, among others, the following species:

Schizaea pusilla
Lycopodium inundatum
Scheuchzeria palustris
Scirpus caespitosus
Rynchospora alba
Rynchospora fusca
Bartonia iodandra
Drosera longifolia
Vaccinium macrocarpon
Utricularia cornuta

As time goes on, *Scirpus caespitosus,* at first scattered, comes to occupy the ground more and more completely, forming a rather dense sward and crowding out most of the species listed above, except such as are able to persist in local depressions. The *Scirpus* is responsible for a still further elevation of the substratum, but the peat in such a swamp is almost invariably shallow, seldom exceeding two feet in thickness. Commonly associated with the *Scirpus* in this association-type are the following:

Calamagrostis canadensis
Carex Michauxiana
Carex pauciflora
Habenaria blephariglottis
Epilobium palustre
Drosera rotundifolia
Sarracenia purpurea
Aster nemoralis

The vegetation is predominantly herbaceous, with *Scirpus* as the character plant. As a rule, however, there is a scattering of low shrubs, such forms as *Myrica, Spiraea, Andromeda, Chamaedaphne, Kalmia polifolia, Rhododendron,* and *Lonicera caerulea,* which, along the shoreward margin, commonly form a thicket. An association of this sort bears a marked resemblance to bog-meadow, as described later in connection with raised bogs. In many situations it seems without question to represent an edaphic climax. Failure for succession to proceed further is probably correlated with an inability on the part of the cushion-forming sphagnums to gain control, an inability for which the periodic inundation seems in some way to be responsible.

c. THE ASSOCIATION-COMPLEXES OF UNDRAINED SWAMPS

Ecological characteristics of the more important bog species of Sphagnum.—Emphasis has been laid earlier on the prominence in bogs of the sphagnum mosses. Allusion has also been made to differences in the ecological relations of various species, in their manner of growth, and in the rôle which they play in bog development. It seems appropriate at this point to sum up briefly, with reference primarily to their ecological relations, the essential features of the more important species of *Sphagnum* which grow in the bogs of this region. These may be divided more or less definitely into five groups, as follows.

Group 1. Plants primarily aquatic, floating at or near the surface of the water. *S. cuspidatum:* commonly yellowish green in color, limp and flaccid, with a delicate, feathery appearance; when growing emersed, stems usually prostrate and trailing or creeping. The var. *Torreyi* is very robust, more rigid than the typical form, and ordinarily a dirty brownish green in color. *S. Pylaisei:* dark purple to nearly black in color; soft and delicate, but as a rule scarcely flaccid; slender, with sparsely developed, short branches; when growing emersed, stems prostrate and trailing or semi-erect; perhaps the most easily recognized of any native sphagnum.

Group 2. Plants semi-aquatic, amphibious; occasionally completely submerged and with a habit similar to that of *S. cuspidatum,* but more commonly with the tips of the shoots projecting well above the surface of the water; quite robust, fairly rigid, erect. *S. Dusenii:* in color, usually green, more or less tinged with yellow-brown. *S. pulchrum:* in color, olive-green to brownish green; commonly grows emersed, forming dense but rather loose, soft cushions (see further under group 4).

Group 3. Plants primarily non-aquatic, commonly growing in low, wet, boggy grounds. *S. tenellum:* erect, slender, fragile, usually occurring in dense, loose masses and forming beautiful, soft, low mats; in color, ordinarily yellowish green; one of the most delicately lovely of all the sphagnums.

Group 4. Plants mainly non-aquatic, though commonly growing in very wet places and occasionally submersed; usually very robust, erect and rather rigid; when emersed, forming dense, rather compact masses and building up fairly firm cushions; submersed forms quite flaccid. *S. papillosum:* in color, generally brownish to nearly black. *S. magellanicum:* in color, pale greenish white, or usually strongly tinged with pink or purple-red. *S. pulchrum* might perhaps also be classed here. It may be noted, as of contemporaneous interest, that in the selection of sphagnums suitable for making surgical dressings the full-leaved forms of *S. papillosum* and, to a lesser extent, *S. magellanicum* have been found to furnish the best material (in this connection, see Porter '17).

Group 5. Plants strictly non-aquatic, growing in moist or relatively dry situations; erect and mostly slender; forming dense, compact masses and building up firm cushions. *S. capillaceum tenellum:* color commonly a vivid red. *S. fuscum:* color commonly russet-green. *S. tenerum:* color commonly yellowish, or more or less tinged with pink or red.

As grouped above, the species are arranged approximately in the order of decreasing hydrophytism. For purposes of convenience, the species of group 1 may be referred to as aquatic or hydrophytic; those of group 2 as semi-aquatic; those of group 4 as *mesophytic;* and those of group 5 as *xerophytic.* In view of their tendency, of exceeding importance from an ecological standpoint, to form more or less compact cushions, the species in groups 4 and 5 may be distinguished further as "cushion-forming species." The significance of the above classification will be seen presently.

Outline of methods by which bogs arise in water-filled depressions.—Bog formation in water-filled depressions is due largely, if not wholly, to plant activity. In general, as has been indicated elsewhere (see discussion of lowland swamps), there are two methods by which the conversion of a pond into a swamp may be accomplished. These may be designated: (*1*) *filling from within,* and (*2*) *encroachment from without.* By the first method the bottom of the pond is built upward toward the surface through the gradual accumulation thereon of successive layers of organic débris, derived mainly from the incompletely decomposed remains of various aquatic plants. By the second a mat of swamp vegetation, originating on the banks or in the shallow water near the shore, pushes outward over the surface of the water, roughly speaking, into the deeper parts of the pond. In typical instances these two lines of development are quite distinct from one another, and the filling in of a pond may be accomplished entirely through one or the other. But both processes may commonly be observed in one and the same pond and, as will be shown later, the filling in and obliteration of the pond may frequently be achieved through the combination of the two.

Filling from within, with particular reference to the rôle of various sphagnums.—The commonly active participation in this process of various aquatic seed plants and algae calls for no special comment. Of more interest here is the conspicuous part often taken by certain species of sphagnum. These are particularly important in the barrens where, in the small, undrained ponds which are so abundantly developed and which constitute such a characteristic feature of the plateau, various sphagnums commonly predominate the successive stages of bog evolution from start to finish. It is to the conditions observed in and about these ponds that the following remarks apply. Here, while a subordinate part may frequently be played by various other plants, the bulk of the organic débris by which the pond becomes filled in up to water level is contributed by the two aquatic sphagnums, *S. Pylaisei* and *S. cuspidatum,* associated with which, but in lesser abundance, usually grows the liverwort *Cephalozia fluitans.* During the summer months these two species of *Sphagnum,* either or both, may be present in such profusion as to completely clog the pond to a depth of several inches below the surface with a loose, floating mass of vegetation. One is tempted to regard such a structure as a true floating mat, but such is hardly the case (see, however, in this connection, p. 429). For while the "mat" does float during the growing season, so long as there is open water underneath it sinks to the bottom in winter. It is indeed extremely doubtful whether under any circumstances sphagnum of itself is capable of forming a permanent floating mat, i. e., a raft-like growth sufficiently firm and stable to permit the establishment and maintenance on its surface of a non-aquatic type of vegetation.

Eventually, however, the bottom of the pond may become built up to such a level that, except during periods of high water, the substratum is exposed to the air, and here, in addition to the bryophytes which have been largely responsible for its development and which still cover its surface with a thin, more or less continuous mat, the soft, mucky ground usually becomes populated by a very characteristic group of vascular plants, among which the following are almost invariably present:

Lycopodium inundatum
Rynchospora alba
Eriophorum angustifolium
Carex oligosperma
Ranunculus Flammula reptans
Drosera longifolia
Vaccinium macrocarpon
Vaccinium Oxycoccus
Bartonia iodandra
Utricularia cornuta

To this list might be added the curly grass fern (*Schizaea*), which sometimes, and the bog rosemary (*Andromeda*), which frequently is met with in situations of this sort. An important ecological function is fulfilled by the sedges and the cranberries, since through the medium of their roots and stems they reinforce and bind together the mucky deposit, thereby producing a semblance to floating mat formation. For convenience, a mat of this sort, formed over a soft, mucky deposit, may be referred to as a *muck mat.*

Sphagnums of the semi-aquatic group, particularly *S. pulchrum*, frequently put in an appearance while the rising substratum is still covered by some depth of water. In such cases the succession may be modified to such a degree that the muck mat stage is omitted. For these semi-aquatic species, growing in fairly dense masses, their stems erect and projecting slightly above water level, are able to eliminate, probably through the influence of shade, the lower, more truly aquatic sphagnums. Associated with the sphagnums in such a habitat may grow, locally in abundance, *Scheuchzeria, Eleocharis, Carex limosa, Smilacina trifolia* and *Menyanthes.* These may fulfill here a function similar to that performed by sedges and cranberry in the case of the muck mat, where also they are not infrequently represented.

Returning to the consideration of the muck mat: the sphagnums of the aquatic group are incapable of building up the surface to any appreciable height above ordinary summer water level, although to a limited extent this may be accomplished by the sedges. Further elevation is dependent primarily on the advent of the more mesophytic sphagnums. For some reason, the prostrate, felty tangle of aquatic sphagnums and *Cephalozia,* which commonly covers the surface of the muck mat, seems to hinder the rapid establishment of other bryophytes, and in consequence this stage may be protracted for a long time. But sooner or later other sphagnums may secure a foothold and eventually gain the upper hand.

In general, the elevation of the bog surface above water level is accomplished very largely through the activity of species of *Sphagnum* which possess to a more or less marked degree the cushion-forming habit, but the process is greatly facilitated by the concurrent activity of the vascular plants growing on the sphagnous substratum, since these, in the manner already suggested, bind together and consolidate the sphagnum cushions, and in addition may form a sort of scaffolding which expedites the upward growth of the mosses. *Sphagnum pulchrum* with its semi-aquatic habit is a common pioneer on the muck mat, and with its erect habit of growth and tendency to form loose cushions is able to build up the surface to some height. Fully as important at this stage, and subsequently much more so, are *S. papillosum* and *S. magellanicum,* species with a generally more robust habit and a tendency to form denser cushions than *S. pulchrum.* Any of these three species may act as pioneers, and frequently all of them grow intermixed.

Once the cushion-forming sphagnums have firmly established themselves, the bog surface may be built up quite rapidly. A measure of the rate at which this takes place is sometimes afforded by shrubs which have been buried by the rising substratum. To cite a specific example, in an erect stem of *Myrica Gale* which had been partially buried to a depth of eight inches a discrepancy of seven years was found in its age near the bottom of the deposit (ten years), and at the surface (three years), a fact which would seem to indicate that here the sphagnums had grown upward at the rate of about an inch a year.

As the surface rises higher, the mesophytic sphagnums (*S. papillosum, S. magellanicum*) may gradually crowd out their more hydrophytic competitor (*S. pulchrum*). The height to which these two species are able to build up the substratum varies, being apparently conditioned in part directly by soil moisture relations, but largely by competition on the part of other species. For with its increasing elevation the substratum naturally becomes somewhat drier and consequently less congenial to the mesophytic species, while at the same time conditions become more favorable for relatively xerophytic species, such as

S. fuscum and *S. capillaceum tenellum,* which, while they may frequently be present, do not thrive in the wetter situations. These xerophytic sphagnums, at first growing intermixed with the mesophytic species, gradually become more abundant, overgrowing and eventually eliminating their less xerophytic competitors. The mesophytic cushion-forming sphagnums may be largely responsible for the elevation of the bog surface to a height of a foot or two above the original water level, but any further upward growth is dependent very largely on the xerophytic cushion-forming sphagnums, which invariably are the predominant species in a mature bog.

FIGURE 62.—Margin of small undrained pond near crest of raised bog; barrens in mountains west of Ingonish; in foreground, *Andromeda* and other shrubs advancing into the pool.

Encroachment from without, with particular reference to the formation of floating mats.—In its essential features, floating mat formation in the highlands differs little from what has been described for the lowlands. The pioneers may be either shrubs or sedges. In the former case (FIG. 62), here as there, unless the framework created by the shrubs becomes overgrown by sphagnums, mat formation proceeds no farther than this incipient stage. The important sphagnums in this connection are *S. pulchrum* and the more mesophytic cushion-forming species, but particularly the latter. As a rule these are present in abundance, and so favorable are the conditions for their growth here in the highlands that they commonly give rise to a thick mat which rises steeply from the water's edge to a height of one or two feet. *Myrica Gale, Chamaedaphne,* and *Andromeda* are all important as pioneer shrubs, now one, now another playing the leading rôle.

Locally certain sedges are more important as pioneers in mat formation than are the shrubs. *Carex limosa* frequently extends out into the open water from along the shore, growing in length as much as a foot in a single season, and sometimes it is present in sufficient abundance to form the basis of a mat. More commonly *Carex filiformis* is the pioneer sedge. The behavior of this species in mat formation has been described by Ganong ('03, pp. 440–441), Transeau ('05-'06, p. 363), Davis ('07, 135–138), the writer ('15, pp. 198–199), and others. Commonly the sedges are followed by the sphagnums, which build up the surface in the manner already described. On the whole, sedges are much less prominent in the rôle of mat pioneers than are shrubs. Moreover, the latter, because of the framework afforded by their strong, woody stems, favor much more the growth of the cushion-forming sphagnums and the consequent thickening and solidifying of the mat.

As the mat grows outward into the pond, the open water beneath gradually becomes filled in, partly by the sinking of the mat as it becomes thicker and heavier through the continued upward growth at its surface, partly by the dropping down of vegetable débris from the under surface of the mat. Where the outward growth is rapid, the mat may be underlain for some distance shoreward from its outer margin by open water; where outward growth is slow the filling in beneath may keep pace with it, so that very little of the mat is actually floating. But in either case, wherever the filling in is being accomplished primarily through the intervention of a floating mat, the water in the pond is deep right up to the edge of the mat, and in cases where the mat has become "grounded" clear to its margin, in the manner indicated above, the bank usually sheers precipitously to the bottom.

A somewhat puzzling modification in floating mat formation is exhibited in particular by many of the small ponds in the barrens. Commonly the encroaching banks advance at a more or less uniform rate into the pond from one or several sides, but frequently the rate of advance varies locally, and to such an extent that the marginal bog comes to project out into the pond in triangular or tongue-shaped masses (FIG. 64). Through the continued spread or coalescence of such masses a relatively large pond may become subdivided into several smaller ones: in one case noted a group of nine small ponds had thus originated. This singular behavior is not correlated with any differences in the depth of the water, and for a long time the author was at a loss for an explanation. The solution, however, appears to be somewhat as follows. Attention has already been called to the fact that in the small, undrained ponds of the barrens, the surface during summer is commonly occupied by a floating mass of aquatic sphagnums. In winter this mass sinks to the bottom. Here the loose tangle may become intergrown with various filamentous algae to such an extent as to render it impervious to gases, and the following spring it may be floated toward the surface as a result of gas accumulation underneath or within the mass. Cases of this sort have been frequently noted. As a rule, only portions of the mass actually reach the surface, and on the substratum thus presented sedges or shrubs may gain a foothold, thus inaugurating what essentially is a floating mat. Very often, as might be expected if this explanation is correct, peninsulas and islands of bog are encountered in these ponds. In this connection, see Powers' paper on "Floating Islands" ('14).

Encroachment from without in combination with filling from within.—It commonly happens that the conversion of a pond into a swamp is accomplished through a combination of the two methods of filling just described. The filling in up to the surface level may be due largely to the activity of aquatic vegetation, and it is on the substratum thus formed that the mat advances. In this connection the conditions observed around a small, nameless lake, near the upper limits of the forested region, and studied with some care will serve as an illustration. The lake covers an area of perhaps two acres, has roughly the shape of a rounded equilateral triangle, and is drained by a small, sluggish stream.

Its original size has been reduced about one-half by the centripetal encroachment of the bogs which now surround it to a variable width on all three sides. In the still open part of the pond, the bottom seems to be completely covered by a soft, mucky deposit which in places must be many feet thick. This deposit without question has been formed almost wholly through the accumulation on the floor of the pond of vegetable débris, which in large part has been derived from the remains of aquatic seed plants, mosses, and algae. In proceeding from the middle of the lake toward the shore, the depth of the water gradually diminishes, the mucky bottom sloping gently upward until, just before the lakeward margin of the bog is reached, it nearly or actually reaches water level. On the substratum thus produced a mat has been formed, which has advanced from the shore out into the lake as rapidly as the filling in process has permitted. And in this connection considerable interest attaches itself to the divergent courses of development which have ensued on two of the three sides of the lake.

Along one side a sedge mat has pushed its way out for a distance of a dozen or fifteen feet from the original shore. For the development of this mat three plants have been primarily responsible, namely *Carex filiformis, Rynchospora alba* and *R. fusca,* and these are still the predominant forms, practically the only other species present being *Utricularia cornuta, Drosera longifolia,* and *Sphagnum Pylaisei.* The mat is flat and firm, and, although it is but a few inches above ordinary summer water level, one can walk dry-shod almost to its edge.

Along the other shore the behavior is somewhat different. The shoal water along the margin of the advancing bog is occupied by an association made up very largely of the mosses, *Sphagnum pulchrum* and *Drepanocladus Sendtneri.* These are present in sufficient abundance to form a low, wet substratum upon which the sedges, *Carex filiformis* and *Rynchospora alba,* together locally with *Andromeda,* gain a foothold. Thus there is formed a low mat which paves the way for further progress. But subsequent development is not always the same. It may follow one of two courses, and which of these it shall be seems to depend very largely on which species of *Sphagnum* gains control over the situation. Along much of the shore *S. papillosum* establishes itself and with *S. pulchrum,* which is already present, rapidly builds up the surface to a height of a foot or more above water, at which level *S. fuscum* begins to assert itself. In this way there arises a typical bog (FIG. 63), in which the cushion-forming sphagnums and their customary vascular associates prevail. Locally, however, the low mat is usurped by *Sphagnum Pylaisei.* This sphagnum, it should be remarked, while it grows profusely in many small undrained ponds, is seldom a conspicuous element of the aquatic vegetation in ponds of any size, like the present one, especially where they are well drained. But it frequently occurs in the swamps which border them. Along with *S. Pylaisei* commonly grows the liverwort, *Cephalozia fluitans.* These two bryophytes, as elsewhere suggested, tend to form a rather compact, felty growth over the substratum, which seems in some inexplicable manner to hinder the invasion of these areas by the cushion-forming sphagnums. So tenaciously, indeed, may they hold their own that, as the contiguous higher

FIGURE 63.—A characteristic bog in the mountains west of Ingonish: sedges, ericads, and sphagnums predominant, with scattered clumps of black spruce.

portions of the bog push out into the pond, these lower areas commonly become completely engulfed. The vegetation of the hollows thus formed is strikingly different from that in the surrounding bog, being essentially similar to that of the muck mat described in earlier paragraphs. In addition to the two sedges, *Carex filiformis* and *Rynchospora,* the following vascular plants are characteristic: *Schizaea pusilla, Lycopodium inundatum, Carex oligosperma, Ranunculus Flammula reptans, Drosera longifolia,* and *Utricularia cornuta.* Ultimately these depressions seem destined to become incorporated with the rest of the bog, but they may persist virtually unaltered for a long time. The usual forerunner of the typical bog vegetation is *Scirpus caespitosus,* and this sedge seems to pave the way for the cushion-forming sphagnums which ultimately gain control.

It has already been noted that in the small ponds of the barrens, where the aquatic sphagnums play such an important part in the filling process, the mucky substratum which these form, with its felty cover of *Sphagnum Pylaisei, S. cuspidatum,* and *Cephalozia,* may similarly persist virtually without further change for a very long time. It may be added here that very commonly such areas are gradually being reduced in size and seem destined to extinction through the slow centripetal encroachment of the steep, peripheral banks of sphagnum.

The method of filling which has been described in the preceding paragraphs differs from that previously described as due entirely to "filling from within" mainly in the more obvious centripetal encroachment of the marginal swamp vegetation. As a matter of fact, there is scarcely any real distinction, for, strictly speaking, as soon as the bottom of a pond has been built to the surface through the activity of the aquatic plants, any further changes are invariably due to the invasion of plants from without.

The climax association-type of bogs.—Extended comment is hardly necessary. The character of the climax association-type varies locally, but in general it is marked by the predominance of sphagnums and ericaceous shrubs, with black spruce and tamarack. In many cases the vegetation of ordinary bogs in the highland is scarcely different from that described for lowland bogs, while in others it closely approximates the conditions found in raised bogs which will be described next.

d. THE ASSOCIATION-COMPLEXES OF RAISED BOGS

Geographical distribution of raised bogs in eastern North America.—Bogs of the raised (*"Hochmoor"*) type (FIGS. 64, 66) are extensively developed in parts of northern Europe, and there are numerous published accounts dealing with them, both from an economic and a biological standpoint. But concerning their occurrence and distribution in North America little is known, and specific references to them in the literature are scarce. Ganong, more than twenty-five years ago ('91), called attention to the presence in New Brunswick of bogs of this type, and in 1898 he published a rather detailed account of the raised bogs in the southern part of this province. He has also made some brief notes ('06^b) on the raised bogs of Miscou Island, New Brunswick. In his second paper, Ganong indicates the reported occurrence of raised bogs in Nova Scotia and Anticosti, and the probability of their occurrence in Newfoundland. In a recent

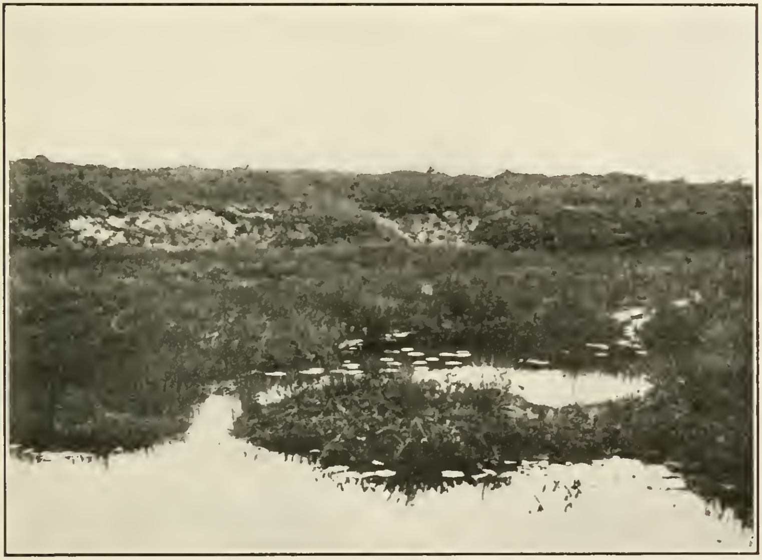

FIGURE 64.—Raised bog on Peter's Barren, in the mountains east of Frizzleton; in the foreground, pond and low, wet bog; in the background, the more elevated part of the bog, which rises more than twelve feet above the pond level.

publication ('15), the third of a series of papers on the economic aspects of peat bogs of Canada, Anrep, speaking of the Clyde Peat Bog in Nova Scotia, states (p. 55) that "this is the first 'high moor' bog encountered during the last six years of investigation" (a period during which he had studied numerous bogs in Manitoba, Ontario, and Quebec). Davis, in discussing the origin of the Maine peat deposits (Bastin & Davis, '09), gives a short description of the manner in which raised bogs are formed and of the relation between "built-up deposits" and "filled-basin deposits." The former, corresponding to the raised bog, appears to be a not infrequent type of swamp along the Maine coast as far south as the vicinity of Portland, and evidently it is of quite common occurrence northeastward. On the whole, judging from the data at hand, both published and unpublished, it would appear that in eastern North America raised bogs are largely confined to Newfoundland and to those parts of eastern Canada and Maine which are in the proximity of the sea-coast. Their limitation to this region is unquestionably correlated with the character of the climate: the abundant precipitation, relatively low atmospheric humidity, cool summers, and the absence of extreme low winter temperatures such as prevail farther inland. The paucity of literature dealing with raised bogs in this country is doubtless attributable, as Ganong suggests, to their remoteness from botanical centers and their hitherto little appreciated economic value. In Europe, "great bogs occur within easy reach of the botanists of Germany, Switzerland, and Scandinavia, and their great economic value has led to their exhaustive study both by individual workers and by government commissions" ('98, p. 131).

From the brief examination which the author was able to make of the Spruce Lake bog and two neighboring smaller bogs about a dozen miles west of St. John, New Brunswick, it may be stated that the raised bogs of this region, as described by Ganong, are essentially similar to those of northern Cape Breton.

Occurrence of raised bogs in northern Cape Breton.—In this particular region raised bogs apparently are confined to the plateau, but this is very likely due to edaphic rather than atmospheric factors, since in southeastern Cape Breton fine raised bogs occur at but little above sea-level. On the highlands in northern Cape Breton raised bogs are encountered here and there in the forested region, but their greatest display is seen in the barrens. To the study of the origin, development and ecological relations of the raised bogs here the author has devoted considerable time, and it is hoped that the facts set forth in the following pages may contribute materially to the knowledge of this fascinating swamp type, as developed on this continent.

General features of raised bogs and the influence of edaphic factors on their local distribution.—The most bizarre feature of a raised bog is the fact that it is higher toward the center than toward the margin: the surface is convex, and the entire structure frequently presents more or less the form of an inverted saucer or watch-glass. The outline of a typical raised bog, as viewed in cross section, is shown by FIG. 65, *B*. In this connection, it might be remarked that a slight convexity in the contour of the surface is perceptible in some of the lowland bogs of northern Cape Breton, and similar conditions are occasionally noted in southern New England; but in these cases the elevation of the middle portions at most is only a foot or two. In the case of typical raised bogs the difference in height between margin and center may be many feet: viewed from the surface alone, and disregarding the contour of the underlying rock floor, the higher portion may rise to a height of from fifteen to twenty or more feet above the lower marginal portions. But that the actual elevation of the bog surface above the rock substratum in reality is often much less than it appears from superficial examination will be apparent later. As shown by the cross section (FIG. 65, *C, f-h*) the surface rises rather abruptly from near the margin, then more gently, and the top of the bog may be practically flat. The angle of slope along the steeper flanks of a bog varies locally, but ordinarily the surface rises at the rate of about one foot to fifteen or twenty on the level. Sometimes, however, the slope is much steeper: in one extreme instance (foreground of FIG. 64), for example, a rise of three feet in three and six feet in twelve was noted. The bogs vary in size, but commonly they are many acres in extent, and in some cases they stretch out uninterruptedly for more than a mile. On the higher levels of the bog the ground underfoot, for the most part, is quite firm and springy, but locally, particularly in the vicinity of the small ponds which are frequently present, it may be soft and spongy. The character of the surface vegetation will be discussed in detail later: suffice it to state here that in addition to the sphagnums which form the groundwork of the mass, the most prominent plants are low, ericaceous shrubs and the sedge, *Scirpus caespitosus*.

For the development of a raised bog, the fundamental prerequisites are the presence of certain species of sphagnum and of environmental conditions congenial to their growth, since from start to finish in the evolution of such a bog these mosses play an all essential rôle. Of foremost importance is a copious water supply, and this is controlled partly by climatic, partly by edaphic conditions. Of the water which falls on the earth's surface in the form of rain and snow, part enters the ground, forming the ground water supply; part runs off over the surface into streams and lakes; the remainder is evaporated or is absorbed directly by vegetation. In so far as the development of raised bogs is concerned, it is now generally recognized that the chief source of their water supply is meteoric, rather than telluric. In other words, while locally a limited amount of the water needed may be derived from springs, on the whole their distribution and growth is independent of the ground water supply. Surface drainage from neighboring slopes may and frequently does help out, but in the large it is the water precipitated directly upon the surface of the area occupied, in the form of either rain or snow, which is most important. Swamps which thus are dependent directly upon atmospheric precipitation for their water supply have been designated precipitation-swamps, by way of distinction from spring-swamps and lake-swamps (see earlier remarks, p. 354).

The importance of edaphic factors is seen in their influence on water loss through surface runoff and downward percolation. Given a substratum sufficiently impermeable to prevent loss through percolation, a raised bog may originate under quite varied topographic conditions. In general, it may be built up either in and around a water-filled rock basin or over any essentially flat, undulating or irregular surface from which the rain and snow water tend to run off slowly or to accumulate in local depressions. Such surfaces as the latter, considered in their entirety, may be either approximately level or slightly inclined. It is probably the lack of suitable areas of impermeable substratum that is responsible for the observed absence of raised bogs in the lowland. In the highland the substratum underlying the raised bogs is practically impervious granite rock, bare, or thinly covered by a gravelly soil.

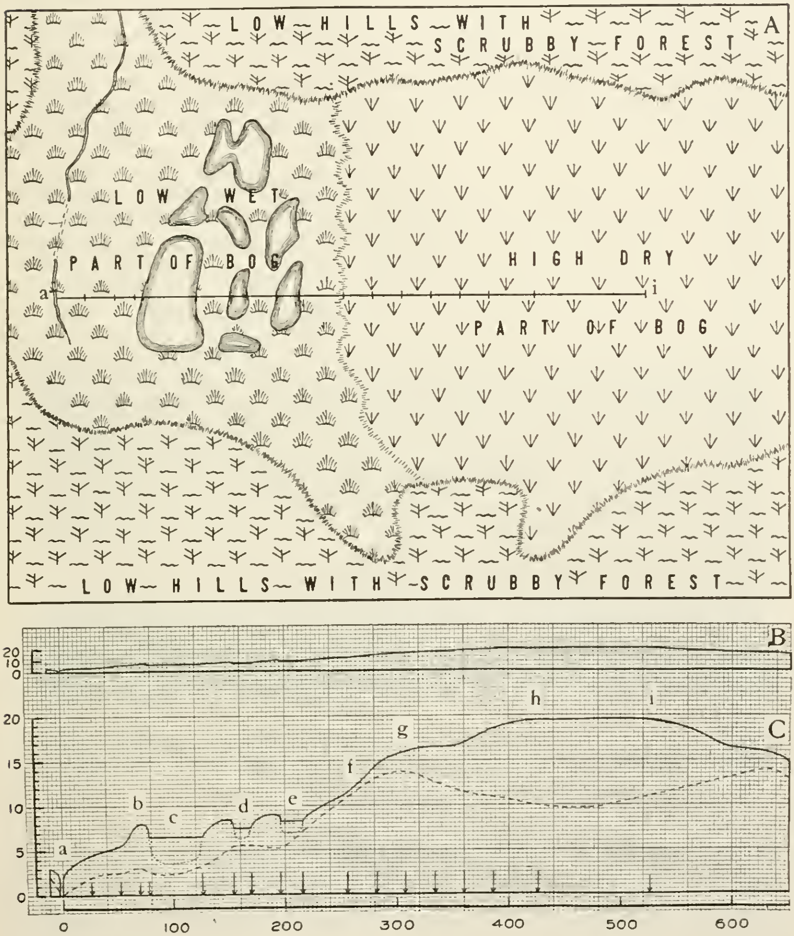

FIGURE 65.—Diagrammatic representation of a bog complex in the barrens; see text. *A.* Sketch map showing relation of area to adjoining upland. *B.* & *C.* Longi-sections along line *a–i* on map. Section *A* drawn to scale; in section *B*, vertical scale eight times the horizontal, and contour of rock floor indicated by dotted line. All measurements in feet. Arrows indicate location of soundings. Mountains west of Ingonish.

a. Development of Raised Bogs in and around Water-filled Rock Basins

An illustrative example.—In Fig. 65 is represented diagrammatically a bog-complex which was studied in some detail. Depth of peat, surface contour, and relations of the underlying topography were determined by means of sounding-rod and level. Section *B*, made along the line *a-i* in map *A*, is drawn to scale and shows the actual contour of the surface. Section *C*, identical with Section *B* but with the vertical scale eight times the horizontal, brings out the relation between the surface contour and that of the rock floor beneath. It will be seen from this diagram (*f-i*, etc.) that the upper portion of the bog-complex (the portion pictured in Fig. 66) is occupied by a typical raised bog, which has been developed in and around a shallow rock-basin. Through the accumulation of peat, the surface has been built up more than six feet above the rim of the basin and about ten feet above its bottom, and has spread out over the rim. Attention may now be given to the manner in which this bog

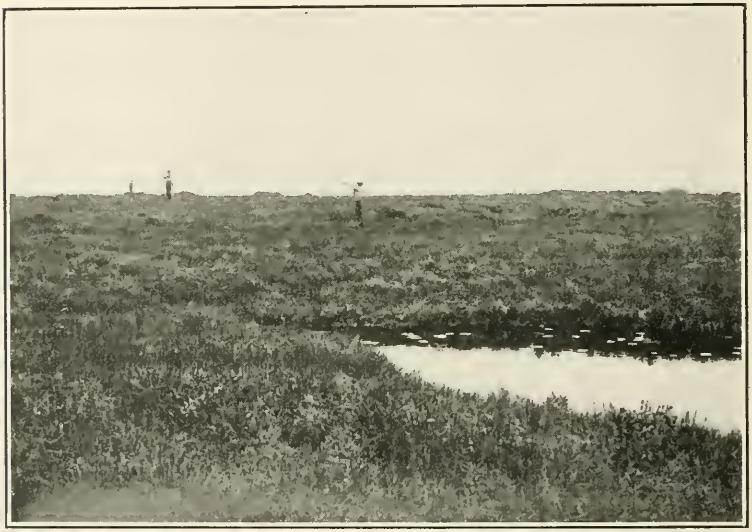

Figure 66.—Raised bog in barrens, mountains west of Ingonish; photograph taken from point between *d* and *e* in Fig. 65. In foreground, wet bog; figures standing on dry bog; see text.

has been formed, the lower portion of the complex (FIG. 65, *C, a-f*) being neglected for the moment.

The rock basin in question is situated at the summit of a low, rounded hillock which is bounded laterally by slightly higher hills. Partly as the result of direct precipitation, partly perhaps through surface drainage from the adjoining higher ground, this basin originally was kept filled with water, which spilled out over the rim at *g*. The manner in which this pond became obliterated was doubtless similar to what has been described in the general discussion of bogs a few pages back. The open water may have become filled in through the activity of the aquatic sphagnums, or through the encroachment from the margin of a floating mat, or through a combination of both these methods. Assuming the aquatic sphagnums to have been the pioneers, and that through their activity the pond had been more or less completely clogged up, the second stage in the succession was probably dominated by the mesophytic cushion-forming species (*S. papillosum, S. magellanicum, S. pulchrum*), although there may have been an intermediate stage of semi-aquatic species (*S. pulchrum, S. Dusenii*). Largely through the activity of the mesophytic cushion-forming sphagnums the surface may have been raised to a height of one or two feet above the former pond surface, at which point the xerophytic cushion-forming species (*S. fuscum, S. capillaceum tenellum, S. tenerum*) asserted themselves. It is to the species of this latter group that the further elevation of the bog surface to its present height has been largely due. Throughout this series of changes, various seed plants have occupied a more or less prominent position, and have played an important rôle by binding together and strengthening the ground-work formed by the sphagnums. The stages characterized by the predominance of the mesophytic and of the xerophytic sphagnums may be designated respectively the wet bog and the dry bog stages. The character of the surface vegetation in these two stages will be described later.

General observations.—The exact stage at which the central water body becomes obliterated in successions of the sort just described varies. In the present case, the pond has been overwhelmed so completely that there is absolutely nothing on the surface of the bog that even suggests its former presence. In other cases, however, the pond may persist for an indefinite period, and may even be present on the higher parts of the mature bog. The factors concerned may be various, but of particular importance seem to be the depth of the basin to start with and the luxuriance with which the aquatic sphagnums develop. Where these latter are absent or poorly represented, so that the filling in is dependent on encroachment from the margin, the elimination of the pond proceeds slowly. For while the mesophytic, cushion-forming sphagnums may grow luxuriantly, forming great banks of vegetation around the edge of the pond, the centripetal advance into the pond of the fringing banks is usually slow. For this latter fact the commonly sparse development of the pioneer, skeleton-forming shrubs seems primarily responsible, since wherever an adequate shrubby framework is presented the sphagnums tend to push out from the shore quite rapidly. The banks of sphagnum commonly come to form a complete circle about the pond and block up any natural outlet which may have existed. (Of course, in the case of spring-fed ponds or of any ponds with a considerable outflow, the outlet may not become completely dammed, but such ponds are rarely concerned here in the development of raised bogs.) Thereafter drainage must be accomplished entirely by slow seepage through the peaty banks. As these banks are built up higher through the growth of the sphagnums at the surface, the peat underneath becomes more and more compressed by the superimposed weight and in consequence less and less permeable. The result is obvious: as the drainage becomes impeded below, the surface of the pond is forced to a higher level, and in this way, as fast as the surface of the bog is built upward, the pond likewise is shoved higher and higher, until ultimately it may come to lie at the crest of the mature bog. Concurrently with the changes just outlined, the bottom of the pond may likewise be built up through filling from within, but only when this latter process proceeds at a more rapid rate than that at which the surface of the pond rises can it have any immediate visible effect.

Mention has been made earlier of the convex surface which is possessed to a greater or less degree by all raised bogs. This convexity is most pronounced in bogs like the one just described, where there is a central pond which acts as a reservoir and from which water seeps out in all directions. It is self-evident that the areas nearest the pond will be best watered: it is here that the sphagnums thrive most luxuriantly and grow most rapidly and that the surface of the bog tends to be built up the fastest and to the greatest height. Farther away from the pond, at least during dry spells, the water supply is less abundant, so that the rate of upward growth is slower and the height limit lower than in the more favorable central portions. The conditions, however, are not always as simple as are here suggested. Especially are complexities introduced through the development of ponds which are a result rather than a primary cause of bog development. Ponds of this "subsequent" type, as will be shown presently, are even more generally associated with raised bogs than are ponds of the "antecedent" type, like those just described.

β. Development of Raised Bogs over Flat or Irregularly Undulating Rock Surfaces

Perhaps more commonly than not, in northern Cape Breton, the rock floor which underlies a raised bog is essentially flat or else irregularly undulating: at any rate there are no rock basins capable of holding any appreciable amount of water. In the development of raised bogs in situations of this description, three more or less definite stages can frequently be distinguished, which may be designated respectively the *Bog Meadow* stage, the *Wet Bog* stage, and the *Dry Bog* stage. Owing largely to local variations in topography, the rate at which bog formation has progressed and the degree to which the raised bog climax has been approached varies greatly. All stages in the succession, which under favorable conditions culminates in the formation of the typical raised bog association-type, may be found, and, locally, any of the three types just mentioned may constitute an edaphic climax. Through the study and comparison of a large number of such areas, the general course or courses of development and the ecological relations of the association-types involved have been quite satisfactorily worked out. In the following account, attention is first directed to the chief features, vegetational and otherwise, of the respective stages, after which their relation to one another and to bog development will be discussed.

The bog meadow association-type.—As stated earlier, the surface of the tableland comprises a series of low, rounded hills, which rise to a rather uniform height and are separated by valleys of varying depth, but mostly shallow. Many of these valleys (Fig. 67) are quite broad, with a nearly flat or slightly trough-shaped floor, and lie but little below the general level of the surrounding low hills. Lengthwise the floor may be nearly level, but commonly it slopes gently in one direction or another. The ground here for the most part is well watered, not only by direct precipitation but by surface drainage from the higher slopes. It is in situations of this sort that the bog meadow association-type is best developed.

Figure 67.—Broad, shallow valley in barrens; mountains west of Ingonish; occupied mainly by wet bog, but partly by bog meadow. In the background, low hills covered with forest scrub.

The outstanding characteristics of bog meadow are as follows. The predominant vegetation is grass-like, being made up chiefly of *Scirpus caespitosus* and *Calamagrostis Pickeringii,* with *Rynchospora alba* locally prominent. These plants form a thin, more or less continuous sward. Woody plants are relatively inconspicuous, but there is always a scattered growth of low shrubs, mainly *Myrica Gale, Andromeda,* and *Chamaedaphne,* which rise scarcely higher than the sedges, while the tamarack commonly is represented by occasional small stunted specimens.

The cushion-forming species of sphagnum are usually inconspicuous, although the substratum beneath the grasses and sedges is commonly carpeted, at least locally, with *Sphagnum Pylaisei* and *S. tenellum,* together with the liverwort, *Cephalozia fluitans.* The ground is covered by a firm turf, beneath which there usually is a layer of peat from a few inches to a couple of feet in depth. The peat is quite compact, consisting very largely of the remains of sedges and grasses, but usually with a matrix of sphagnum remains. The surface of the swamp is flat or undulating; it is relatively smooth, and not hummocky. Slight depressions in the substratum are frequent, and in some of these water may accumulate temporarily to the depth of a few inches, but there are few if any ponds of the sort to be described as characteristic of wet bogs. In addition to the three shrubs named above, *Kalmia polifolia, Vaccinium macrocarpon,* and *V. Oxycoccus* are commonly present, the two latter, as well as the species starred (*) in the subjoined list, being more characteristic of the depressions, particularly where, as is commonly the case, *Sphagnum Pylaisei* and *Cephalozia* form a more or less continuous, felty ground cover. Additional herbaceous vascular plants commonly met with in bog meadows are as follows:

*Schizaea pusilla**
*Lycopodium inundatum**
Eriophorum virginicum
*Carex oligosperma**
Carex exilis
Habenaria clavellata
Sarracenia purpurea
*Drosera longifolia**
*Drosera rotundifolia**
*Bartonia iodandra**
*Utricularia cornuta**
Solidago uliginosa
Aster nemoralis
Aster radula

The vegetation of the shallow depressions just referred to should perhaps be regarded as constituting a distinct association-type, but for convenience they are included here merely as a type of society.

The wet bog association-type.—This is commonly developed in situations similar to those indicated for the preceding type, but conditions are most favorable where the surface slope is slight and where the presence of shallow depressions or approximately horizontal surfaces affords habitats which are congenial to the local growth of the mesophytic cushion-forming sphagnums. The influence of topography is suggested by diagram *C* of Fig.

65, where area *a-e* is occupied by wet bog, and area *e-f* by bog meadow. Frequently, as here, the two types of swamp alternate on the same slope, while very commonly the wet bog which occupies the floor of a shallow valley (Fig. 67) is separated from the typical upland vegetation on either flank by strips of bog meadow.

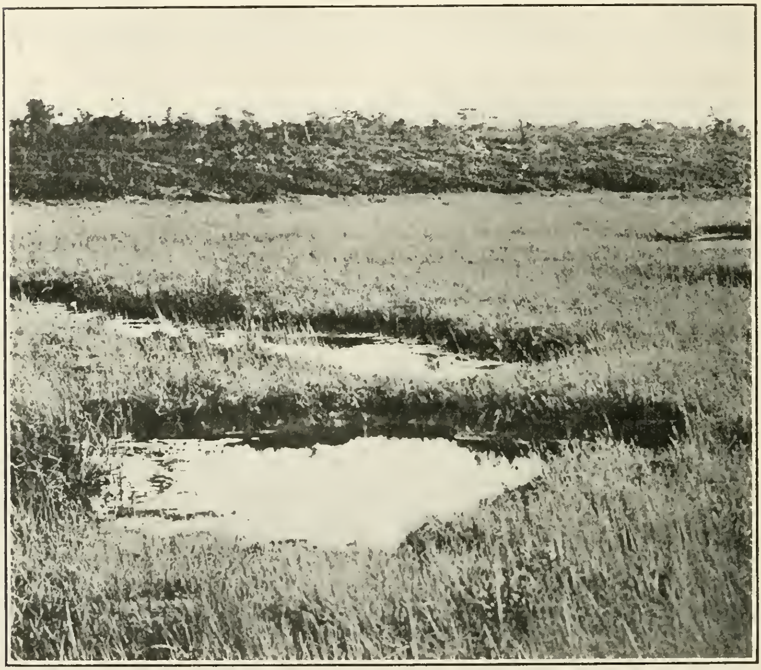

Figure 68.—In foreground, wet bog association-type (same area as that shown by Fig. 67), with pools due to activity of sphagnum (see text); in background, low hill covered with forest scrub; barrens in mountains west of Ingonish.

So far as the vascular element in the vegetation is concerned, the chief difference between this and the preceding association-type is seen in the relatively greater abundance here of the shrubs. Essentially the same list of seed plants is characteristic of each swamp type, and both shrubs (*Andromeda, Myrica, Chamaedaphne, Vaccinium Oxycoccus,* etc.) and herbaceous plants (*Scirpus, Rynchospora, Eriophorum,* etc.) are well represented here. The following additional species might be mentioned as characteristic of wet bogs, although they may also occur to some extent in bog meadows: *Eriophorum callitrix, E. angustifolium, Carex pauciflora, C. paupercula, Smilacina trifolia.* Beside these, various of the species of dry bogs, not yet mentioned, may be sparingly represented. But the vascular plants are of subordinate importance to the sphagnums, and the fundamental dissimilarity between the vegetation of wet bog and that of bog meadow lies in the predominance here of these mosses. Foremost among the sphagnums are the mesophytic cushion-forming species (*S. papillosum, S. magellanicum,* and *S. pulchrum*). Growing in rich profusion, these latter form soft, wet, cushion-like or pillow-like beds which cover the ground almost uninterruptedly over large areas. Other species of *Sphagnum,* however, are by no means absent. Hollows in the bog proper are commonly occupied by societies of *S. tenellum* and *S. Pylaisei,* species which do not form cushions, while on the higher cushions, in greater or less abundance, may grow the relatively xerophytic cushion-forming species. In addition, the small ponds or pools which commonly dot the bog surface (Figs. 62, 64, 66, 68, 69) usually contain various aquatic and semiaquatic species. These ponds constitute one of the most distinctive features of areas occupied by wet bog, but their vegetation, strictly speaking, belongs in quite a different category from that of the wet bog association-type (see further under discussion of successional relations).

The surface of a wet bog, viewed in its entirety, may be flat or slightly convex; viewed in detail it is more or less uneven and hummocky. It is commonly underlain by an accumulation of peat from two to four feet in thickness, which consists of an intimate admixture of sphagnum, sedge, and shrub remains.

The dry bog association-type.—This, the culminating association-type of the raised bog series, may develop in similar situations to the preceding but particularly or nearly level surfaces, either flat or undulating. In contrast to bog meadow and wet bog, perhaps the most striking features of a dry bog (Figs. 66, 69) are its usually convex shape, the luxuriant development of the xerophytic cushion-forming sphagnums (*S. fuscum, S. capillaceum tenellum* and *S. tenerum*), the presence of such xerophytic seed plants as *Empetrum, Gaultheria,* and *Vaccinium* *pennsylvanicum,* and the predominance among the vascular plants of ericaceous shrubs. The bake apple (*Rubus Chamaemorus*) is one of the most characteristic plants of dry bogs. The surface of such a bog is hummocky, and except in wet weather the springy substratum underfoot is quite dry. The hummocks vary from one to several feet in diameter and from a few inches to more than a foot in height.[16] The depth of peat ranges up to more than six feet over a flat rock floor, while over depressions it may be considerably greater. Pools of the sort characteristic of wet bogs are found here also, but much less abundantly. Except for these and scattered wet depressions, whose vegetation and ecological relations are quite distinct from those of the enveloping area of dry bog (see later), the surface almost everywhere is overgrown by the xerophytic cushion-forming sphagnums, associated with which, and locally predominant, are certain other mosses (such as *Dicranum Bergeri, Racomitrium lanuginosum,* and *Polytrichum juniperinum*) and fruticose lichens (notably *Cladonia alpestris, C. sylvatica,* and *Cetraria islandica*). The moist hollows between the hummocks are commonly colonized very largely by liverworts, such species as *Ptilidium ciliare, Cephalozia media, Lepidozia setacea,* and *Mylia anomala,* which constitute more or less definite societies. The characteristic vascular plants of the dry bog association-type are the following:

Picea mariana
Larix laricina
Eriophorum callitrix
Scirpus caespitosus
Carex pauciflora
Myrica Gale
Sarracenia purpurea
Drosera rotundifolia
Pyrus arbutifolia atropurpurea
Rubus Chamaemorus
Empetrum nigrum
Nemopanthus mucronata
Cornus canadensis
Andromeda glaucophylla
Chamaedaphne calyculata
Gaultheria procumbens
Gaylussacia dumosa
Kalmia angustifolia
Kalmia polifolia
Ledum groenlandicum
Rhododendron canadense
Vaccinium Oxycoccus
Vaccinium pennsylvanicum
Solidago uliginosa

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[16] Ganong remarks ('98, pp. 138, 139), that these sphagnum hummocks grow "in such rounded, radiating masses that it reminds one of the *Raoulia* or 'Vegetable Sheep,' and the resemblance is yet closer when, by drying, it assumes a grayish color."

It will be seen from the above list that nearly half the vascular species here are ericaceous shrubs or semi-shrubs, and these also comprise the greater bulk of the vascular plant cover. Herbaceous plants are subordinate in importance to shrubs, although a few forms, such as *Scirpus, Eriophorum* and *Rubus,* commonly occupy quite a prominent position. The various seed plants form a thin upper story of vegetation, but for the most part they rise less than a foot above the mossy substratum and quite commonly their shoots are buried nearly to the tip by the sphagnums. The trees are scattered and dwarfed: specimens of tamarack scarcely a foot high and an inch in trunk diameter may show more than fifty annual rings.[17]

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[17] In this connection certain further observations by Ganong ('98, p. 142), equally applicable to Cape Breton bogs, are of sufficient interest and suggestiveness to warrant quoting at length. "Most of the ericaceous plants on the bog have stems of great length running just beneath the surface, which, as Warming points out, is characteristic of bog plants. In one, *Rubus Chamaemorus,* I followed a stem over seventeen feet without finding an end, and in *Ledum* and *Cassandra* for lesser, though considerable distances, also without finding the ends. These stems run nearly horizontally, branch frequently, and send out roots at intervals. The same stem varies in thickness in different parts; is now thicker, now thinner, showing a more active growth at some times than at others. It is clear, also, that these stems are now alive only at their tips, the under-moss parts being preserved from decay by their position. When one traces what appears to be a clump of young plants of *Ledum latifolium,* he often finds that they are all branches of one plant connected beneath the surface, and he cannot find the end of any one of them; and this is true also of other species. The question now arises, when and how have such plants started, and how do they come to an end? Since the different branches can grow on continuously, and, making their own roots, become independent of one another and of the original plant, and can grow upwards continuously with the growth of the moss, there seems to be no logical limit to their growth, and no cause for death, such as brings most other woody perennials to their end in other situations. Some of them may then be as old as the bog itself, and thus would be amongst the longest lived of phanerogamic vegetation. Yet a comparison between their age and that of a tree, for example, would not be a fair one; physiologically, their longevity should be compared rather with that of those lower organisms, which grow by continuous fission. This continuous life of the bog plants, however, is pure theory; its demonstration is attended with great practical difficulties. To some extent this mode of growth is found also in the trees. In the spruces . . . one may observe how the moss is rising and burying them. As it

Successional relations.—Assuming for the purpose of illustration a nearly level or gently sloping rock floor, approximately flat as a whole but in detail with a more or less irregular surface, with slight elevations and depressions but with no basins capable of retaining any appreciable body of water, the successive steps in the evolution of a raised bog may now be outlined. On an uneven rock surface of the sort under consideration the pioneer aspect of the vegetation varies locally. In the higher, drier situations it is essentially xerophytic. Commonly the vegetation here is that of the sedge–grass heath association-type, as described in connection with xerarch successions: the ground is covered by a carpet of cladonias and *Racomitrium,* and supports a more or less luxuriant growth of *Scirpus caespitosus* and *Calamagrostis Pickeringii,* with a scattering of low shrubs. In the lower situations the vegetation may be quite similar, but here, owing to the generally more favorable moisture relations, the sphagnums commonly establish themselves, either coming in at the outset or later on replacing the cladonias and *Racomitrium.* Subsequent changes in the nature of the substratum and in the ecological aspect of the surface vegetation depend very largely on the sphagnums, not merely on their presence or absence but on the species which come to predominate. Where conditions are such that none of the sphagnums are able to establish themselves in force, any further changes will probably conform closely with what has been described earlier in connection with xerarch successions. Where conditions are such as to favor the growth of the sphagnums and these assert themselves as one of the predominating elements of the plant cover, further changes depend very largely on which particular group of sphagnums gains control over the situation.

For the sake of simplicity there will be described a hypothetical example of what may be regarded as the logical sequence of association-types: a series in which the pioneer stage gives way to a bog meadow, which becomes superseded by a wet bog, which in turn gives way to a dry bog; and, in this connection, various

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buries the lower branches, these put out new roots, turn upwards at their tips, and grow as independent stems. This growth probably, however, does not go on indefinitely, since the trees are ultimately overwhelmed and destroyed by the moss."

other possible lines of development will be pointed out. Let it be assumed, as is very commonly the case, that the low spots have become colonized by *Sphagnum tenellum* and *S. Pylaisei,* species which lack the cushion-forming habit. Under these circumstances the formation of peat and the building up of the substratum may take place very slowly, being due very largely to the accumulation of sedge remains. But, even at that, it takes place much more rapidly in these lower areas than on the higher ones. As the layer of peat in these lower areas becomes gradually thicker and the ground level is raised higher, the surface vegetation spreads out laterally and may override the higher areas; and in this way there may originate what has been described above as a bog meadow.

Further advance beyond the bog meadow stage of the succession is dependent primarily, either directly or indirectly, on the activity of various cushion-forming species of *Sphagnum.* Wherever conditions are congenial to the growth and spread of the mesophytic cushion-forming species (*S. papillosum, S. magellanicum, S. pulchrum*), bog meadow may gradually give way to wet bog. Indeed these species may have been the important ones from the very outset, so much so that the bog meadow stage in the succession may never have been developed. The factors which condition the presence or absence and the relative abundance when present of these species of *Sphagnum* doubtless have to do very largely with the amount of water available throughout the season, but it seems likely also, as suggested elsewhere, that the difficulty with which these and other species are able to invade areas already occupied by *S. Pylaisei* in particular may be a factor of considerable importance as affecting their establishment on the surface of a bog meadow.

The transformation in the character of the habitat accomplished through the agency of the mesophytic cushion-forming sphagnums and the manner in which they bring about the elimination of bog meadow or any other type of vegetation which may be present is exceedingly interesting. Heretofore, in the case of bog meadow, what water has not been absorbed by the compact, peaty substratum has been able to run off quite unobstructed over the comparatively smooth, firm surface, with the result that except during wet periods the ground at the surface may have been relatively dry. One of the essential characteristics of the cushion-forming sphagnums is their great ability to absorb and retain liquids. But while this in itself is a factor of no little significance in hindering the loss of water, even more significant is the manner in which individual clumps of these mosses run together and form banks which may obstruct the drainage to such an extent that in favorable situations, as on gentle slopes, the water may be dammed back to form ponds and pools of various dimensions. The degree to which masses of sphagnums are thus able to hold back the water is remarkable. In the boggy area diagrammatically shown by Fig. 65, *C,* for example, the level of the water in the pond at *e* is nine inches higher than that at *d,* twenty-five feet distant; and the water level in pond *d* is twelve inches above that in pond *c,* equally distant. In another instance a difference in elevation of two feet was measured between two water surfaces thirty-five feet apart; while in two other cases differences in level amounting respectively to nearly ten feet in less than a hundred, and to more than one foot in three were estimated. On the "down-hill" sides of a pond the banks of sphagnum rise steeply from the water's edge to a height of one, two, or more feet above the pond's surface. In one instance a rise of three feet within seven feet of the water's edge (or to a height of about five feet above the mucky bottom of the pond) was noted. It is obvious that these ponds, by retaining much of the water which accumulates in them during wet periods, or which drains into them from higher levels, function as storage reservoirs and insure to adjoining areas a fairly uniform water supply throughout the season.

Incipient ponds of the sort just described are frequently encountered in the bog meadow stage of the succession, but there they are usually shallow and ephemeral. It is in the wet bog stage that they first attain a position of ecological importance. The formation of ponds hastens the elimination of the bog meadow as a distinct association-type, for their spread leads naturally to the extermination of any plants which may have tenanted the areas which they now occupy, except for the few species which are able to adapt themselves to the changed conditions, either by assuming an aquatic habit (e. g., *Sphagnum Pylaisei*) or through their position above the water level (e. g., tussocks of cushion-forming sphagnums).

Sometimes these ponds appear to be distributed quite indiscriminately over the surface of a bog (e. g., see FIG. 65, *A*): particularly is this true on the higher, older bogs. But in other cases their arrangement is very definite. To cite a specific illustration of the latter sort: in one shallow, approximately flat-floored valley (similar to that pictured in FIG. 67) about a hundred feet wide, there are ten of these ponds within a distance of three hundred feet. All are more or less elliptical in outline, twenty to fifty feet long by six to twenty feet wide, and they are arranged, like a flight of steps, at right angles to the long axis of the valley floor. Between the surface of the lower pond in the series and that of the upper there is a vertical difference in elevation of five feet. It may be further noted that the rock floor beneath this bog, as determined by soundings, is quite even and that the peat is uniformly about four feet deep, except around the down-hill margins of the ponds where it is banked up higher. From the study of this and other like cases, there seems little question that a large proportion of the ponds associated not only with wet bogs but also with dry bogs have originated in the manner here described. The absence of any relationship to the character of the underlying topography is exemplified by ponds *d* and *e* in FIG. 65, *C*.

Leaving for the moment the consideration of these ponds, the further history of the bog as a whole may be briefly detailed. Largely through the activity of the mesophytic cushion-forming sphagnums, the general level of the surface has been raised and bog meadow eliminated. These mesophytic sphagnums continue to predominate and to build up the substratum for a locally variable length of time: frequently a wet bog association may represent an edaphic climax. But although the nature of the environment may be considerably modified by the influence of the ponds referred to above, it is apparent that, as a rule, sooner or later, as the surface rises higher, the conditions will become less favorable for the mesophytic sphagnums, while at the same time they will become more favorable for the xerophytic cushion-forming species (*S. fuscum, S. capillaceum tenellum, S. tenerum*). As time goes on, these latter species, which in wet bog constitute merely a subordinate element in the vegetation, gradually become the predominant forms, and wet bog becomes superseded by dry bog. Incidentally it may be remarked that, like the mesophytic forms, the xerophytic cushion-forming sphagnums sometimes predominate from the very outset, so that both the bog meadow and wet bog stages may be eliminated. On the higher, drier parts of a bog, as elsewhere indicated, the xerophytic sphagnums in turn may give way locally to various lichens and mosses, but these never become sufficiently abundant to constitute a distinct association-type.

Throughout the successive steps in bog development, as just outlined, sight must not be lost of the part played by various seed plants. These fulfill a triple rôle in that they facilitate the upward growth of the sphagnums and bind together the spongy, otherwise incoherent matrix of sphagnum remains, beside contributing in varying degree to the bulk of the deposit. Much of the springiness and comparative firmness which characterizes the surface of a mature bog is ascribable to the tangle of stems and roots with which the ground is interwoven. With regard to the rate at which the bog surface is built upward: in general, upward growth is comparatively slow at first, during the bog meadow stage, most rapid during the wet bog stage and during the early part of the dry bog stage, from which point on there is a gradual slowing down until, in the case of the older, higher bogs, growth is practically at a standstill (but see quotation from Weber on p. 456).

From the observations recorded in the preceding pages it is apparent that not only do the sphagnums as a class play an all-important part in the development of raised bogs, but that different groups of sphagnums are responsible for different phases in the development. It is also certain that the formation and upward growth of a bog is not dependent on the presence of any preëxisting water basin from which the required water is raised by capillarity. The view expressed by Ganong ('98, p. 148) that "The raised bogs are formed, as all students of them agree, by the pure Sphagnum growing upward and carrying the water by capillarity with it" has long since been exploded. To quote from Warming ('09, pp. 200–201): "It is erroneous to suppose that Sphagnum sucks up water from the soil; it raises water only for an inconsiderable distance. The movement of water in a Sphagnum-moor is essentially a descending one. The depth at which the water-table lies is dependent on the atmospheric precipitation and upon the permeability of the peat and of the substratum . . . . . [A raised bog (high-moor)] often arises on top of old low-moor; it may also take origin on wet sand, and even on rocks if these be sufficiently wet." Incidentally, it is worthy of note that although he accepted the then current conception as to the origin of raised bogs, Ganong was puzzled by, and commented at some length on, the "presence of much standing water near the surface on the higher parts" of the New Brunswick bogs which he studied ('98, p. 148).

In this connection, it is also of interest that Ganong ('98, p. 151) describes as occurring on the slopes of one of these bogs "a series of remarkable holes . . . . of various sizes, from 30 by 12 feet down to a few inches. They are a foot or two deep, have perfectly level bottoms of black muck, sometimes so dry as to crack in the sun, in others moist, in others covered with water, the latter being at the lower, the former at higher levels." Obviously these are the ponds or pond holes which have been discussed at some length by the author. In northern Cape Breton also, the water in many of them disappears during a dry season, but many of them are several feet deep and apparently always contain water. The ponds on the higher parts of a bog are usually more or less circular in outline (Fig. 69) and ordinarily have steep banks all around. They may be relatively few in number, but commonly there are several or many to the acre. In many of them, save for various algae, vegetation is sparse and any filling in is accomplished through the gradual encroachment of the banks. In others there is a luxuriant growth of aquatic sphagnums (*S. Pylaisei, S. cuspidatum*). As regards the growth of these aquatic sphagnums, the discrepancy between different ponds is hard to account for, unless, as is very likely the case, it be correlated with the abundance of algae (see next paragraph). With the exception of *Nymphaea* and *Eriocaulon,* aquatic seed plants are usually scarce. In general, the ecological relations of the vegetation here approximate what has been described earlier (see: association-complexes of undrained ponds, p. 417; also, development of raised bogs in and around water-filled rock basins, p. 438).

Weber, in his paper on the vegetation and origin of the Augstumal Hochmoor in Prussia ('02, pp. 76–78), has made some important observations regarding the origin of these ponds

(*"Hochmoorteiche"*). Previous investigators for the most part had reasoned either that they represent the remains of lakes which formerly existed in the areas now occupied by bog, or, in view of the common paucity here of sphagnums, that they represent places where springs of lime-carrying water break through, a view which was somewhat doubtfully favored by Ganong. Parenthetically it may be suggested that the luxuriance with which the sphagnums, particularly *S. Pylaisei,* not infrequently occupy such ponds in northern Cape Breton is of relevant interest in this connection. In discussing their origin, Weber points out that while undoubtedly the first explanation mentioned above is sometimes the correct one, the second one is largely based on insufficient investigation. He effectually disposes of this lime theory by making careful analyses of the water in the ponds, which he finds, like that in surrounding parts of the bog, to be extremely poor in inorganic salts. He therefore concludes that the source of water supply cannot come from the ground. He incidentally comments on the universal lack of any positive signs of springiness, an observation which the writer can con-

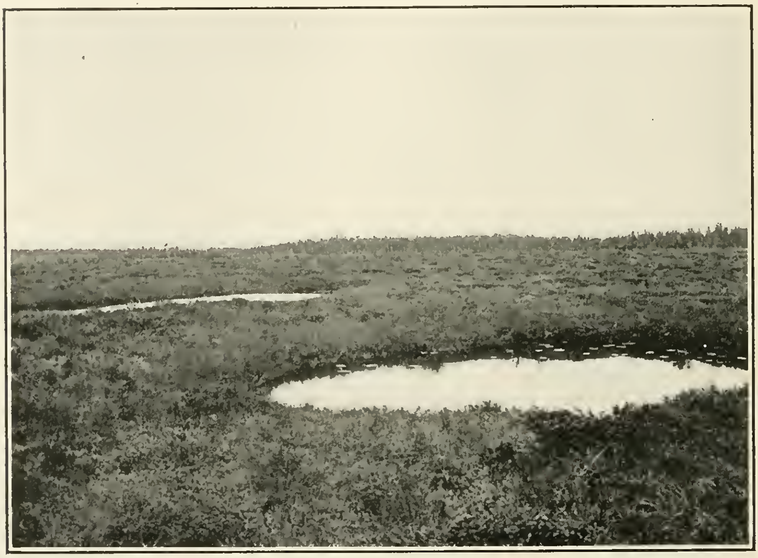

FIGURE 69.—Pools on surface of mature raised bog; Scotchman's Barren.

firm. Weber's explanation of the manner in which these ponds usually arise is somewhat as follows. They originate in the pools of water which collect in the deeper hollows between the hummocks on the surface, during wet seasons. During the dry season the water collects here only temporarily, but long enough to permit the existence of a number of low algae. The development of algae has a detrimental effect on the growth of any sphagnums which may be present, since (*op. cit.* p. 28) when the water dries up they form a thin parchment-like coat which overgrows the sphagnums and cuts off their light supply. When, in times of increased precipitation, the hollows fill up with water, wave activity brings about the enlargement of the basin, while by its mere weight, which in general is greater than that of an equal volume of water-soaked peat, the water contained in the basin causes the pond to deepen, an end which is also favored through the increasingly active circulation of oxygen through the water. He further remarks that while during subsequent dry periods numerous pools become overgrown again, in other cases the pools persist and become deeper as the surrounding surface of the bog rises higher. He consequently regards the deepest pools, in general, as the oldest ones.

Broadly speaking, Weber's explanation as to the origin of these ponds roughly approximates that arrived at independently by the writer. The essential points of both views are (*1*) the subsequent, rather than antecedent, origin of the ponds with reference to the bog; (*2*) the meteoric, rather than telluric, source of the water supply. The chief point of difference is this. According to the author's explanation, the ponds originate at a rather early stage in the bog's history and by their presence exercise an important influence on its development. Moreover, after their preliminary period of growth, there is little if any subsequent enlargement, but rather the tendency is just the reverse. According to Weber's explanation, the ponds may originate even on the surface of the mature bog. Moreover they are constantly tending to increase in size. So far as the raised bogs of northern Cape Breton are concerned, it is the opinion of the author that the majority of the ponds to be found on mature raised bogs have had a history essentially similar to what he has described. But it also seems very likely that some and quite possible that many of them may have originated in the manner suggested by Weber. At any rate, the writer agrees with Weber that even a mature raised bog is far from being in a condition of permanent equilibrium. To quote Weber (*op. cit.*, pp. 77–78): "Die Teiche sind nach alledem ebenso . . . . Symptome der beständigen Veränderung, die die Oberfläche des Hochmoores unter dem wechselnden Einflusse erfährt, den die Witterung längerer Zeiträume auf die Vegetation und den Boden ausübt. Solange die natürliche Vegetation vorhanden ist, gleicht das Hochmoor gewissermassen einem langsam pulsierenden und auf die äusseren Einflüsse in eigentümlicher Weise reagierenden Organismus."

In brief summary of the successional relations of raised bogs, as developed on essentially flat or undulating surfaces, it may be stated that, in any given area, there may ensue a sequence of stages, starting with a pioneer stage, passing progressively through bog meadow and wet bog, and culminating in dry bog, which latter constitutes the climax stage of the complete series. But the series is not always complete. In an area occupied by dry bog, either or both of the preceding stages may have been omitted; while, on the other hand, either of these two stages may constitute locally an edaphic climax. The course of events is dependent primarily on the activity of certain groups of sphagnums and is conditioned by the presence of environmental conditions suitable to their growth. In the course of a bog's development, through the activity of the cushion-forming sphagnums, ponds are formed which, by conserving the water supply, bear a vital relationship to the bog's growth. It may be added that the growth of a bog is not entirely vertical. As it grows upward it spreads out laterally. A bog originating in an edaphically favorable area may spread out in all directions, eventually covering many areas which of themselves were not favorable to bog development. In this way, as has been repeatedly pointed out, a bog may invade an area occupied by forest and bring about the destruction of the latter. Instances of this sort have been frequently observed in northern Cape Breton.

3. The Formation-types along Streams

THE ASSOCIATION-COMPLEXES OF RAVINES AND FLOOD PLAINS

The ravine associations of the hydrarch series here in the highland, like those of the xerarch series, require no special treatment, since on the whole the vegetation is essentially similar to what has already been described as characteristic of ravines in the lowland. Of special interest, however, are the association-complexes of flood plains.

Attention has elsewhere been called to the fact that on the plateau most of the streams for long distances flow through broad, shallow valleys, but little below the general level of the surrounding country. The floors of these valleys are nearly flat and gently inclined. The surface is only a couple of feet higher than the water in the stream in summer, and at times of high water it is subject to overflow. At such times a small amount of sediment is deposited, and this, together with the inundation itself, apparently has a decisive effect on the character of the vegetation. It therefore seems appropriate to regard such areas as flood plains, although they differ in a great many respects from ordinary flood plains. The mineral substratum is commonly overlain by a layer of peat one or more feet in thickness, which is rendered distinctly gritty by the fine sediment which

FIGURE 70.—Shallow, flat-floored stream valley with characteristic vegetation; barrens in mountains west of Ingonish.

is infiltrated throughout the mass. The surface vegetation is essentially that of a well-drained swamp. Over considerable areas its ecological aspect is that of a meadow, with sedges and grasses predominating. But as a rule these swales or "hay marshes" alternate with equally extensive patches of alder thicket and swampy woodland (Fig. 70). Similar associations are encountered frequently around the small lakes which lie along the courses of the streams. Here all intergradations occur between typical well-drained swamps and bogs. Along the streams themselves it is only occasionally that patches of bog are encountered, even the plants peculiar to bogs commonly being absent. In the barrens, where especially these flat-floored valleys constitute a prominent topographic feature, the flood plain vegetation here contrasts sharply with that of swamps remote from stream activity. In this connection it is worthy of note that the species of *Sphagnum* which play such an important rôle in bog development are scarce or absent here, although certain other species of *Sphagnum,* e. g., *S. Girgensohnii, S. recurvum,* and *S. palustre,* together with such mosses as *Chrysophynum stellatum* and *Drepanocladus fluitans,* are commonly represented, though never developing in any great luxuriance. A list of characteristic vascular plants follows:

Osmunda Claytoniana
Abies balsamea
Picea mariana
Picea canadensis
Larix laricina
Agrostis hyemalis
Calamagrostis canadensis
Glyceria canadensis
Scirpus caespitosus
Carex stellulata
Carex crinita
Carex aquatilis
Carex pauciflora
Carex polygama
Carex oligosperma
Carex folliculata
Juncus sp.
Iris versicolor
Habenaria dilatata
Myrica Gale
Alnus incana
Spiraea latifolia
Pyrus arbutifolia atropurpurea
Amelanchier sp.
Rosa nitida
Viola pallens
Kalmia angustifolia
Chamaedaphne calyculata
Lonicera caerulea
Viburnum cassinoides
Solidago uliginosa
Solidago rugosa
Aster radula
Aster umbellatus

SUMMARY

Cape Breton is situated northeast of the peninsula of Nova Scotia. In northern Cape Breton two topographic regions can be distinguished: the Highland and the Lowland. The highland includes primarily the lofty interior plateau, which rises to an average elevation of more than a thousand feet and is underlain by crystalline rocks of Laurentian age. In places this extends clear to the sea, but along much of the coast there is an intervening border of Carboniferous lowland, of varying width, between the highland and the shore. The entire area has been glaciated, drift being encountered on all sides in the lowland but much less frequently on the plateau.

The climate of the region as a whole may be classed as cool temperate maritime. The climate of the plateau differs from that of the lowland in the lower mean temperatures, greater daily range of temperature, shorter growing season, heavier precipitation, and generally lower humidity, this latter being attributable in large measure to the prevalence of low-lying cloud banks.

Considered from a phytogeographical point of view, Cape Breton lies near the northern border of the Transition Forest Region of eastern North America. In northern Cape Breton, owing chiefly to the differences in climate mentioned above, both the Deciduous Forest Climatic Formation and the Northeastern Evergreen Coniferous Forest Climatic Formation are well represented, the former in the lowland, the latter in the highland. These formations, as developed in northern Cape Breton, are treated separately.

The scheme adopted in classifying the plant associations of these two regions is outlined in the table of contents and has been discussed in some detail in another paper (Nichols '17).

The regional climax association-type in the lowland is a mixed deciduous-evergreen forest, comprising sometimes a dozen different trees, of which the following species are most characteristic: *Fagus grandifolia, Acer saccharum, Betula lutea, Abies balsamea, Tsuga canadensis,* and *Pinus Strobus.* All of these trees grow vigorously and to good size. The woody undergrowth in the forest includes, as the commoner species, *Acer spicatum* and *A. pennsylvanicum, Taxus canadensis* and *Corylus rostrata.*

Thirty-five herbaceous vascular plants are listed as characteristic. Bryophytes are present in profusion, but on the forest floor they are sparsely developed. This latter fact apparently is correlated with the annual accumulation on the ground of a blanket of fallen leaves which prevents the development of a moss-carpet.

The permanency of this type of forest is indicated by the composition of the younger generation of trees, which, in general, conforms with that of the mature stand. In this connection the ecological status in these forests of the balsam fir, character tree of the northeastern evergreen coniferous forest climatic formation, is considered in some detail. The conclusion is reached that the inability of this tree to compete successfully with the trees which characterize the deciduous climax forest formation can be attributed very largely to its shorter tenure of life, coupled with its greater susceptibility to fungus diseases and possibly with its less pronounced tolerance of shade.

The trees which characterize forests of the regional climax type, not only here but elsewhere in the Transition Region, can be divided into five groups: (*A*) Deciduous species whose center of distribution lies south of the transition region; (*B*) Deciduous species whose center of distribution lies within the transition region; (*C*) Evergreen species whose center of distribution lies within the transition region; (*D*) Evergreen species whose center of distribution lies north of the transition region; (*E*) Deciduous species whose center of distribution lies north of the transition region. With reference to the presence or absence of representatives of the first four groups above specified, eleven floristically different types of forest are distinguishable (see p. 292). In general, the trees of groups *B* and *C* are about equally well represented in forests throughout the transition region, those of group *A* are most generally represented southward, those of group *D* northward. In many parts of the transition region black spruce replaces balsam fir as the predominant northern conifer. Black spruce does not appear to be specifically distinct from red spruce. It is very doubtful whether the various floristic subdivisions of the transition region that have been defined should be regarded as ecologically distinct. From the standpoint of ecological plant geography the vegetation of the transition region as a whole is best treated merely as a northward extension of the deciduous forest climatic formation.

The regional climax association-type in the highland is predominantly coniferous, *Abies balsamea* being by far the most abundant tree. Associated with this in the forest, but always of subordinate importance, grow *Picea canadensis, P. mariana, Betula alba papyrifera,* and *Pyrus americana.* Ten shrubs and twenty-seven herbaceous vascular plants are listed as characteristic. Bryophytes develop luxuriantly on the forest floor, forming an almost continuous ground cover.

The permanency of this type of forest is attested by the character of the younger growth which is essentially similar to that of the mature trees. All of the climax trees grow best in the open and reproduction is most prolific in openings of the forest due to windfall. But the reproduction, at least of the balsam fir and black spruce, is by no means confined to windfall areas, which seems to be the case farther inland, as on Isle Royale.

That the coniferous forest climax of the highland is a climatic and not an edaphic climax is evidenced by the gradual transition from deciduous to coniferous forest encountered in ascending the mountains, and by the practically complete absence on the plateau, even in edaphically favorable situations, of the climax trees of the deciduous forest climatic formation.

A detailed review of the character and successional relations of the various association-types which comprise the edaphic formation-complexes of the lowland and highland respectively will not be attempted here. An outline of these is afforded by the table of contents, at the beginning of the paper, and by the paragraph headings which are scattered through the text.

By way of brief general summary it may be stated that: in the lowland, associations of the regional climax type represent the culmination of successional series in all edaphically favorable situations. Elsewhere succession stops at a stage less mesophytic than the regional climax association-type: in other words, in such situations the edaphic climax association-type does not coincide with the regional climax association-type, as it does in the more favorable situations. Due largely to human activity many areas formerly occupied by forests of the regional climax association-type are now occupied by associations of a much more primitive character, notably by forests of white spruce and balsam fir. In the lowland the regional climax forests of the highland are represented in successional series, in favorable situations being destined to give way to forests of the deciduous type but in many unfavorable situations constituting edaphic climaxes.

In the highland the same general relations hold true as in the lowland between associations of the regional climax type and those which are more primitive. But here, owing mainly to the humidity of the climate, the influence of dissimilar edaphic conditions is less pronounced than in the lowland. It can be stated in general that the influence of soil and topography on the character and distribution of plant associations is least pronounced in humid climates, most pronounced in arid climates: that this influence is universally proportional to the dryness of the climate.

The barrens represent an edaphic association-complex, the character of the vegetation being correlated with conditions of exposure, topography and soil. Of especial interest here is the extensive development of heath and of various types of scrubby forest and of raised bogs. Particular attention is called to the important part played in the development of the latter by different species of *Sphagnum.*

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The last part of Volume 18 of the Transactions has not yet been published, but Volumes 19 to 22 are now complete. The Title Pages and Tables of Contents for Volumes 21 and 22 are distributed with the present article.

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[*Reprinted from* Science, *N. S., Vol. XLVIII., No. 1227, Pages 16–18, July 5, 1918*]

SCALARIFORM PITTING A PRIMITIVE FEATURE IN ANGIOSPERMOUS SECONDARY WOOD

Professor Jeffrey, in his recent stimulating book, "The Anatomy of Woody Plants," Ch. VII., derives the vessel with the simple or porous type of perforation from the fusion of horizontal rows of circular pits in the end-wall, the scalariform pit and perforation being merely an intermediate stage in the process. Perhaps such a reversible evolution has gone on in certain groups, although it is here attempted to show that the available evidence is capable of the opposite interpretation.

Multiperforate and even uniperforate end-walls in gymnospermous vessels may arise from the fusion of circular pits with the dissolution of the closing membrane as Professor Jeffrey describes for *Ephedra;* but this fact seems inadequate to explain either the presence of scalariform pitting or the wide prevalence of scalariform perforations in the vascular elements of the less specialized angiosperms. It does not appear that all of the facts germane to the subject have been fully considered. In tracing out the development of vascular elements with uniperforated end-walls in accordance with Jeffrey's hypothesis, serious difficulty is met.

The scalariform pits in conservative regions of the secondary wood of *Liriodendron, Drimys, Asimina,* and other forms with prevailing circular pits in the less conservative regions, suggest antecedence of the scalariform condition, while a further illustration is afforded by the monocotyledonous *Dracæna.* Thus, in *Dracæna aurea,* typical secondary xylem without vessels is formed, the fibro-tracheids of which have circular pits in their lateral walls, but typical scalariform pits in the walls of the overlapping tracheid ends. There is no indication that such scalariform pits have arisen from the fusion of rows of circular pits. They are evidently a primitive feature of the tracheid and closely resemble the scalariform pits of the secondary wood tracheids of *Drimys* found in the vicinity of the pith; yet only a slight modification of the tracheids, with dissolution of the closing membranes and borders of the scalariform pits, would complete transformation into typically perforated scalariform vessels.

It is evident that, to the extent that adjacent cells become specialized, and unlike in shape, in size, and in function, as, for example, the tracheal segment and an adjacent prosenchyma cell of the angiosperms, the scalariform pit must lose its alignment as an intercommunicating structure. Conversely, the circular pit is the more adaptable, and prevails in the vascular elements of more advanced plant families as typified by the Compositæ. Just as might be hypothesized, the scalariform pit is relatively more common in the vascular elements of less specialized families included in the Ranales. Probably the scalariform pit prevailed in the early angiosperms, and is even now being slowly discarded for the smaller circular pit. It was, in case of the vessels, first discarded on the lateral sides adjacent specializing tracheids, ray-cells, wood-parenchyma, or, especially, fibro-tracheids and fibers. The close relation between a vessel and the adjacent element or elements is evident from the fact that, for example, in *Cheirodendron* (Araliaceæ) four distinct types of pits communicate respectively with prosenchyma, wood-parenchyma, ray-parenchyma, and with other vessels. However, that the end-walls should preserve the more primitive sculpture is quite in harmony with the fact that adjacent cells are, in this case, alike. Complex modification is here unnecessary, and adequate comparisons of the secondary wood of existing *primitive* and *specialized* families proves the correctness of the view advanced. It is indeed a remarkable fact that in woods with scalariform perforations in the vessels, the prosenchyma usually bears distinctly bordered pits and is thus less distinct from the tracheal segment than in case of woods in which the vessels are characterized by the simple or porous perforations.

A feature of interest not mentioned by Jeffrey is the more or less frequent occurrence of branched bars. They occur occasionally in *Liriodendron* and other genera with scalariform perforations; but in *Cheirodendron* and some other araliaceous woods this branching of the bars in the perforation may become more or less intricate.

Comparison of such types with the scalariform wood of *Cycadeoidea Dartoni* has been suggested by Dr. Wieland, and for the purpose he has placed before me recently cut sections. The preservation of this fossil is perfect. The sections show the minutest detail in the pitting of the tracheids, even under a magnification of 450 diameters. The outline of the pits, the pit-apertures, and other minute characters are preserved in every detail. The sides and ends of these tracheids, in both tangential and radial aspects, are pitted with regular scalariform bordered pits, which at once remind one of those of *Magnolia.* Along with the true scalariform pits occur a few elliptical pits, and these are inserted between the long pits in such a manner that, by the dissolution of the borders and closing membranes, occasional branched bars would result. The resemblance between the pitting of these cycadeoidean tracheids and the vascular elements of *Magnolia* on the one hand, and of *Dracæna* on the other, is perfect, and may be followed out in minute detail.

The evidence in support of the hypothesis that scalariform pitting is primitive is convincing. It is evident that the process of the breaking up of scalariform pits into circular pits was in progress in the antecedent cycads, and that this process started first in the tracheid side-walls, whereby the overlapping tracheid ends became more conservative than their truly lateral portions. The complementary relations in the wood of the cycadeoids and cycads outlined in Wieland's recent note[1] are thus anatomically reconciled. The origin of branched bars is also explained.

Excellent examples to show that perfect scalariform tracheids exist in living types occur in *Magnolia hypoleuca.* The scalariform pitting very closely approximates that of *Cycadeoidea Dartoni.* Scalariform tracheids slightly more advanced may be found in the aquifoliaceous *Byronia sandwicensis* Endl. Here the tracheids retain typical scalariform bordered pits at the overlapping ends, with the exception that occasional shorter pits are present and in a position to form branched bars should the pit membranes and pit borders be eliminated. The lateral walls show perfect transition from scalariform to circular pits. Living types, therefore, preserve all stages in the transformation of scalariform tracheids into vessels with multiseriate circular pits and simple perforations; and there is every reason to believe that modification is still going on.

Many seem to be under the impression that scalariform pitting is of rare occurrence above the cycads. A close comparison of scalariform tracheids, which Wieland's material makes possible, can leave no doubt that existing forms, in dicotyledons as well as in monocotyledons,

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[1] Wieland, G. R., Feb., 1918, "Cycadoid Wood Structure," *Science*, N. S., XLVII., pp. 141, 142.

still exhibit, in the vascular elements of their secondary wood, almost complete stages in the transformation of scalariform pitting into that of the circular multiseriate type, affording a valuable criterion by which to judge the relative primitiveness of angiosperm groups. The histologic evidence is fairly in accord with the floral evidence.

The exceptional abundance of circular pits in such forms as *Vaccinium corymbosum,* noted by Jeffrey, is accentuated by the fact that, in this type, the vessels are mostly isolated from one another and in contact with wood-prosenchyma which forms circular bordered pits in common with the vessels. Scalariform pitting occurs near the pith where, occasionally, vessels are adjacent. Here occur vessels showing perfectly the transition from scalariform pits to scalariform perforations, as well as the transition stages, noted by Thompson,[2] from scalariform to simple or porus perforations. FOREST B. H. BROWN

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[2] Thompson, W. P., Jan., 1918, "Independent Evolution of Vessels in Gnetales and Angiosperms," *Bot. Gaz.*, LXV., pp. 89-90.

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[Reprinted from The Bryologist, Vol. XXI, No. 4, July 1918.]

WAR WORK FOR BRYOLOGISTS[1]

GEORGE E. NICHOLS

Until quite recently, sphagnum has not been generally considered as possessing any particular economic value, except in connection with the formation of peat, where its importance is well recognized. To be sure, it is used quite extensively by florists and nurserymen as packing material for plants, and locally it is employed for stable litter and bedding, as well as for various other purposes. But its value in surgical work, while recognized many years ago in Germany, has been little appreciated outside of that country, and it is only recently that this phase has come into prominence. At the present time sphagnum is being used to a vast extent, particularly by the British Red Cross, in place of absorbent cotton in surgical dressings. According to Professor Hotson,[2] the present British output of sphagnum dressings amounts to a million per month. And while the sphagnum was advocated primarily as a war substitute, there is little question that it will retain a permanent position as a standard material for absorbent surgical dressings.

For use in absorbent pads, the sphagnum is not merely equal to absorbent cotton—it is superior to it. According to Professor Porter,[3] sphagnum pads surpass cotton pads in the following important particulars: (1) they absorb liquids much more rapidly: about three times as fast; (2) they take up liquids in much greater amounts: a cotton pad will absorb only five or six times its weight of water, as compared with sixteen, eighteen, and even as high as twenty-two times, for a sphagnum pad; (3) they retain liquids much better: which means, of course, that the dressings need be changed less frequently; (4) they distribute the absorbed liquids more uniformly throughout their mass; (5) they are cooler and less irritating, yet at the same time fully as soft; (6) they can be produced at much less expense.

The structural peculiarities of the sphagnum plant, which enable it to take up and retain liquids, are, of course, familiar to all moss students and require only brief comment. Suffice it to say that whereas in a cotton pad liquids for the most part are merely held within a tangle of threads, in the sphagnum we have a highly efficient absorbing system. The ability of the sphagnum in this respect can be attributed to three features: (1) the presence of the large, color-

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[1] Contribution from the Osborn Botanical Laboratory.

[2] Hotson, J. W. Sphagnum as a surgical dressing. 1–31. *f. 1–18.* Northwest Division of the American Red Cross. Seattle. 1918.

[3] Porter, J. B. Sphagnum surgical dressings. Internat. Journ. Surgery **30**: 129–135. *f. 1–8.* 1917. Distributed as a separate by the Canadian Red Cross.

less, porous cells in the leaves and frequently also in the stem and branches; (2) the close overlapping of the leaves on the branches; (3) the sponge-like matting of the pendent branches around the stem.

Sphagnum moss was officially adopted by the American Red Cross as a standard surgical dressing material early in March of this year, but the enterprise here has not yet attained the magnitude which it is reasonable to expect that it will in the near future. For one thing, the project here is comparatively new and our American army surgeons, accustomed to using absorbent cotton, seem reluctant to adopt the substitute, notwithstanding that its superiority has been conclusively demonstrated. But another very serious handicap to the sphagnum enterprise in this country is the lack of exact knowledge regarding our resources of surgical sphagnum. In the Pacific Northwest, largely through the efforts of Professor Hotson and his associates, the situation is now well in hand; but in the east, while we know in a general way that the material is here, we have all too few exact data regarding sources of supply. It is primarily with the object of eliciting information on this subject from bryologists, who of all people should be best qualified to furnish it, that the present article is written. The writer is associated with the Department of Development of the American Red Cross in the capacity of Botanical Adviser on Sphagnum and will be pleased to examine any specimens of material which may be submitted.

For the benefit of those who may be willing to coöperate, it should be emphasized that there is a great difference in different lots of sphagnum when it comes to the selection of material for use in surgical dressings. First of all, different species differ greatly in their capacity for absorption, degree of softness, etc. Thus, of the forty species of sphagnum native to North America, only those belonging to the *Inophloea* group (the group which includes *S. papillosum*, *S. palustre*, *S. imbricatum*, *S. magellanicum*, etc.) have been found wholly satisfactory. Species of the *Compactum* group (*S. compactum*, *S. strictum*) have not been tried out, but ought to furnish excellent material. *S. squarrosum* seems excellent as to foliage and probably is open to objection only on account of its usually wiry stem. The species in the remaining groups, comprising about three-quarters of our native sphagnum flora, are virtually useless for surgical purposes, although some of them may be employed to a limited extent for special purposes or in combination with material of the more suitable species.

Speaking in general, it can be said that the more robust species of sphagnum are superior to the more delicate; forms with large leaves, dense foliage and close-set branches are greatly preferable to those with small leaves, skimpy foliage and scattered branches. Harsh, stiff, or brittle forms must be avoided. In this connection it should be further pointed out that not only is there a wide range of variation in the suitability of different species of sphagnum for surgical use, but in that of the same species from different regions or from different habitats within the same region. Thus, the average quality of material from the humid districts of western Washington and Vancouver is much higher than anything that has been seen from the east. In grading his western material, Professor Hotson (*l c.*) regards *S. imbricatum* as the most desirable species for surgical work, with *S. palustre* second, and *S. papillosum* third. In the east the order of excellence appears to be exactly reversed, *S. papillosum* being regarded as by far the best species (see Porter, *l c.*). Further, the sphagnums attain their optimum growth in bogs, and, when present, the best qualities of surgical sphagnum almost invariably frequent the wettest parts of a bog. This is true even in the humid northeast, but it is even more so in regions where climatic conditions are less congenial. The same species (e. g. *S. papillosum*) may grow throughout a bog, yet it may attain the requisite degree of luxuriance only in the wettest, quakiest parts of the bog; elsewhere, not only will it be poor in quality, but the chances are that it will be more or less intimately mixed with undesirable species. In searching for surgical sphagnum, it is a good rule to avoid wooded swamps, for while sphagnums usually are present in abundance in such places, for various reasons the material generally is of too poor quality to be of surgical value. Bogs which are densely populated by heaths or other bushy growth likewise furnish unfavorable conditions, except locally, where there are wet, open depressions. The same may be said of bogs that are densely overgrown with sedges or grasses so much so as to give them the aspect of a meadow. *S. papillosum* in particular, requires plenty of sunlight as well as plenty of water. In bogs which have been flooded, as frequently happens through the damming of a lake, the better grades of sphagnum have usually been drowned out. *S. papillosum* seems especially sensitive to any change of environment. Along the coast in eastern Maine, the lumberman has thus been responsible for the extermination of much of the surgical sphagnum which formerly occupied the "flowage" swamps bordering many of the lakes and streams. During a recent trip of investigation in this region, the most ideal conditions for *S. papillosum* were found to be in low, wet, quaky bogs along the borders of well-drained ponds or small lakes, and in similar situations along slow streams. In favorable situations of this sort, this moss may comprise the bulk of the vegetation, building up broad cushions, often a foot high, and forming a more or less continuous ground cover. From a distance the most conspicuous plants in such an area are the "cranberry grasses" (*Carex filiformis, C. oligosperma*), which, on closer inspection, are usually found to form a rather scanty, open growth. Cranberries (*Vaccinium macrocarpon*) are practically always present, together with a scattering of low shrubs, such as sweet gale (*Myrica Gale*) and various heaths. Considered from the standpoint of the ecologist, it can be said that not only are bogs which have arisen through the intervention of a floating mat most favorable to surgical sphagnum, but *S. papillosum* in particular is far more likely to flourish in a bog where the mat-forming pioneers are sedges than in one where the pioneers are shrubs.

Taken as a group, the sphagnums are much more widely distributed in cool, humid regions than in warm, relatively dry regions. From a climatic point of view, the most favorable regions in the east are eastern Maine and the country lying to the northeast, along the coast: the region in which raised bogs are encountered. The best eastern material thus far collected in quantity came from Cape Breton Island, Nova Scotia. But even in the interior, good material apparently is not lacking: fine specimens of *S. papillosum* have recently been received from Michigan. Except in regions where the climate is congenial, however, it is to be expected that sphagnums of surgical value will be very local in their distribution.

In conclusion, information is particularly sought regarding the occurrence in quantity of *S. papillosum*, since this species, as already pointed out, has proven the most uniformly adapted to surgical use. *S. papillosum*, to a limited degree, of course, can be recognized by its very robust habit and its commonly yellowish brown to brown pigmentation. Information regarding *S. palustre*, *S. imbricatum*, and *S. magellanicum*, where these appear sufficiently luxuriant to be of use, will also be welcome, but these, particularly the last named, tend to be of too poor quality (too much stem in proportion to foliage, stem too stiff, etc.) to meet the requirements.

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A bunch of *Sphagnum papillosum* from a wet grassy swamp in Maine.

Prospecting for surgical sphagnum in the Maine bogs. The pool in the foreground is bordered by a luxuriant growth of *S. magellanicum.*

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THE SPHAGNUM MOSS AND ITS USE IN SURGICAL DRESSINGS*

"Are you collecting Sphagnum Moss?" Such was the question that appeared in bold type on the front cover of the London Graphic for September 2, 1916. From this journal we learn that the collecting and drying of sphagnum moss and making it up into surgical dressings "has become a national industry" in Scotland, and that "the work is being extended all over England, Ireland and Wales." Within the past two years the sphagnum industry has assumed large proportions in Canada, and in our own country it is rapidly coming to the front as an important phase of Red Cross work.

One very serious handicap to the sphagnum enterprise in this country is a lack of information regarding where to get material. Abundant supplies of good surgical moss have been located in the Pacific northwest, but the transportation of material from this region to the east presents an obvious problem. At the present time, therefore, we are scouring the east for sources of supply which can be drawn upon in case of need. What can you tell us regarding the sphagnum situation in your locality? Are there any good supplies of surgical sphagnum?

Now of course very few people are in a position to furnish offhand the sort of information that we require. To perhaps most people the very identity of the sphagnum is veiled with mystery, and of those who may know it as a kind of "bog moss" few realize that there are a large number of different kinds. Even

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* Contribution from the Osborn Botanical Laboratory.

among botanists, who of all people should know it best, there are comparatively few who can distinguish between one kind of sphagnum and another, or, what is more to the point in the present connection, who can discriminate intelligently between surgical and non-surgical material. In the account which follows, I shall discuss some of the more important facts regarding the sphagnum moss as related to surgical dressings. I shall try particularly to answer some of the many queries which are constantly being made by people who are eager to help in securing information regarding our resources of surgical sphagnum.

First of all, how did sphagnum come to be introduced into surgical practice? Who discovered its adaptability in this connection?

Along in the late seventies of the last century a workman at one of the great peat moors in northern Germany accidentally sustained a severe wound of the forearm. In the absence of anything better to use, his fellow workmen wrapped up the wound with fragments of the peat which happened to be lying near, and it was not until ten days later that the man was able to secure surgical attention. Imagine the surprise of the surgeon when, on removing the improvised dressing, it was found that the wound had almost completely healed.*

With this incident the use of sphagnum in present-day surgery may be said to have originated. As a matter of fact, however, its use in this connection is not a new thing at all: it is merely a modern and scientific revival of a very ancient practice. In parts of Great Britain, according to Professor Porter,† from time immemorial bog moss has been used by country people in the treatment of boils and discharging wounds. In Scotland and Ireland it was employed many centuries ago for exactly the same purpose that it is being used today; and moss was "at least recommended for use by army surgeons, both in the Napoleonic and the Franco-Prussian wars."

We must acknowledge our indebtedness to the Germans,

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* This incident is related by Neuber (Arch. f. klin. Chir. **27**: 757–788. 1882), a German surgeon who at that time was connected with the surgical clinic at Kiel.

† Porter, J. B. Sphagnum surgical dressings. Internat. Journ. Surgery **30**: 129–135. *8 f. in text.* 1917. This comprehensive paper has been reprinted as a separate by the Canadian Red Cross.

however, for demonstrating the value of the sphagnum in the modern, antiseptic methods of surgery. Following the incident which I have related above, investigations were set on foot as to the nature and the properties both of the sphagnum and of the peat to which it gives rise, and a number of papers were published in German medical journals, in which the sphagnum, as related to surgical practice, was discussed from various points of view. And within a very few years this moss came to be accepted in Germany as a standard material for surgical dressings, being widely used not only in private practice but in some of the largest hospitals.

During the Russian-Japanese war, the Japanese used sphagnum quite extensively as a first-aid dressing. "Many of the wounds thus dressed with sphagnum were not inspected again until the patient reached Japan, which often took ten days, but almost invariably the wound was in good condition; much better it is said than when cotton was used."* In general, however, the value of sphagnum for use in surgical dressings has not been appreciated until quite recently.

To what extent is sphagnum being utilized in war hospital practice at the present time?

Shortly after the beginning of the war it began to be feared in England that there might be a shortage of cotton, and experiments were made with various materials—oakum, wood-pulp, and even sawdust—in the hope of finding some satisfactory substitute. It was at this time that attention was directed to the neglected possibilities of the sphagnum.† In 1914, sphagnum dressings were given a thorough try-out at one of the large war hospitals in Scotland, and the results proved so satisfactory that sphagnum was at once recommended for general use. In September, 1915, sphagnum dressings were formally accepted by the British War Office. At that time the total British output of sphagnum surgical dressings was barely

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* Hotson, J. W. Sphagnum as a surgical dressing. pp. 1–31. *f. 1–18.* Separate issued by the Northwest Division of the American Red Cross. Seattle. 1918.

† See especially a paper by Cathcart, C. W., and Balfour, I. B. in the Scotsman for November 17, 1914, and one by Cathcart in Brit. Med. Journ. 38: 137–139. 1915.

250 a month. A year later it had reached 150,000, and at the present time it is nearly a million. The Canadian Red Cross alone is now putting out between two and three hundred thousand sphagnum dressings each month.

In our own country the sphagnum enterprise, so far as the National Red Cross is concerned, is still in its infancy. But we have long since passed the stage of experimentation and have reached the stage where sphagnum dressings are being produced in considerable quantities. The American Red Cross has recently turned out half a million sphagnum dressings for the Italian army, and something over twenty thousand a month are now being made for American war hospitals. But the sphagnum work of the American Red Cross is not yet being conducted on the large scale which it is anticipated that it will be in the near future. For one thing, our American army surgeons, accustomed to the use of absorbent cotton and still having plenty of this on hand, hesitate about adopting a substitute. It is inevitable, however, that sooner or later the value of sphagnum in war hospital work will be more fully appreciated in this country: for the quality of the cotton is constantly becoming poorer, while the price is soaring higher. Moreover, wherever the sphagnum dressings have been tried out in our hospitals, they have given complete satisfaction.

For just what purpose is the sphagnum used in surgical work?

Sphagnum is used to replace cotton in absorbent surgical dressings—in what are known technically as absorbent pads, or compresses.

But, so long as there is plenty of cotton, why trouble with a substitute? And, if it is desirable to use a substitute, why select sphagnum rather than something else?

For use in absorbent surgical dressings sphagnum moss is not merely a satisfactory substitute. In many respects, without question, it is superior to absorbent cotton.*

First of all, sphagnum will absorb liquids much more rapidly than absorbent cotton—about three times as fast.

In the second place, the sphagnum will take up liquids in

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* The following observations are taken mainly from Porter, *op. cit.*

much greater amount than absorbent cotton. A pad made of absorbent cotton will absorb only five or six times its weight of water. An average pad made of sphagnum will take up sixteen to eighteen times its weight of water, more than three times as much as cotton, and exceptionally good moss will absorb as much as twenty-two times its weight of water.

In the third place, the sphagnum will retain liquids much better than cotton. This means, of course, that a sphagnum dressing need not be changed as often as a cotton dressing.

In the fourth place, "the better qualities of sphagnum have the valuable property of distributing whatever liquid they absorb throughout their whole mass." An absorbent pad of sphagnum will continue to suck up fluid discharges until it is pretty uniformly saturated throughout. This is a very important feature. A cotton pad ordinarily ceases to function long before its theoretical capacity has been reached.

Now in ordinary hospital work, as Professor Porter points out, the comparative inferiority of cotton as an absorbent is not of any great consequence. Here, for the most part, the wounds are the result of operations and they are made by the surgeon himself. They are comparatively slight, and, what is particularly important, they are perfectly sterile. Discharging wounds are exceptional. But in war hospital practice every wound may be taken as infected. Discharging wounds are the rule, not the exception. Furthermore, "the methods of treatment recently so successfully developed by Carrel, Dakin, and others deliberately increase these discharges to a very great extent. For such cases . . . sphagnum is greatly preferable to any other available material."

In this connection it might be mentioned that when it is dry, the sphagnum is very light, and many varieties are very fluffy. Sphagnum of the quality insisted on for surgical dressings is quite as soft as cotton.

Finally, there is one other point in which the sphagnum is distinctly superior to cotton; and this is a matter of great practical importance. Sphagnum is cheaper than cotton. Being a product of nature, pure and simple, all that you have to do is to go and get it, and practically the only expense involved is the cost of collecting and transporting the material. As will be seen later, the process of preparing the sphagnum for use is very simple, and most of the work can be done by volunteer workers.

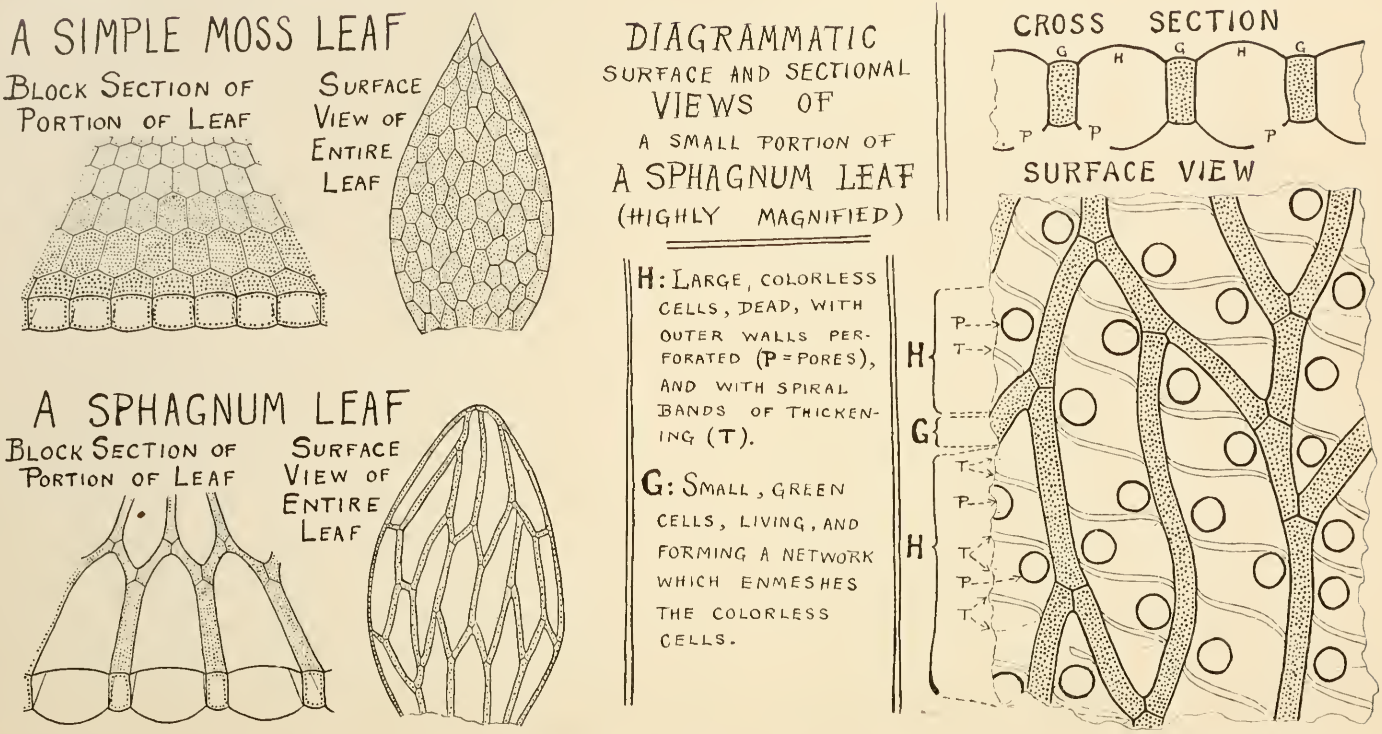
What does the sphagnum look like? How can you recognize it when you see it?

To begin with, the sphagnum is a sort of moss. But do not confuse the true mosses with the so-called "sea mosses." These are more correctly called sea-weeds: they are not mosses at all. The true mosses are comparatively small, leafy plants, seldom more than a few inches in height. They grow in all sorts of places: in dry, exposed crevices of rocks, on the bark of trees, on the ground in swamps and moist woods, and even in the water. But they never grow in salt water. To an ordinary observer, perhaps, the mosses are conspicuous chiefly on account of the great masses of vegetation which they commonly form. The sphagnums include some of our largest and most conspicuous mosses.

The sphagnum differs from other kinds of moss in a number of important respects.

First of all, a sphagnum plant seldom exhibits the deep leaf-green color of an ordinary moss. When wet, it commonly is a pale green; when dry, it may be almost white. Very frequently the green is hidden almost completely by pigments of various colors, so that the plants may be almost any shade from bright red and pink to russet green and dark brown or almost black. These colors form a very distinctive feature of many sphagnums when they are fresh. In nature, their mass effect is very striking, and they are of great help when it comes to recognizing material in the field.

But color alone is hardly a sufficient test. Other distinguishing marks are afforded by the peculiarities of the branches and of the leaves. If you examine a single sphagnum plant, you will see, first of all, that it consists of a main axis, on which are borne numerous short branches. Further, you will note that these branches are not borne singly, but in clusters of from three to six. No other moss produces its branches in clusters, after the



Diagrammatic drawings of the leaves in an ordinary moss and in the sphagnum, as seen under a microscope, to show structural peculiarities.

manner of the sphagnum. Along most of the stem these branch clusters are scattered, but toward the tip they usually grow so close together as to form a rather compact rosette which sometimes is mistaken for a flower. It might be added that the branches in each cluster are of two sorts: one kind stands out at right angles to the main axis; the other kind droops down alongside the stem and forms a sort of loose, spongy matting around it.

And not only is the arrangement of the branches on the stem distinctive. Quite as striking is the arrangement of the leaves on the branches. Every branch is completely covered over by a series of tiny, more or less spoon-shaped leaves, which closely overlap one another, somewhat after the manner of shingles on the roof of a house.

To what structural peculiarities does the sphagnum owe its efficiency as an absorbent?

To a limited degree certain of the features already described adapt the sphagnum to absorb liquids: the close overlapping of the leaves around the branches, and the sponge-like matting of the pendent branches around the stem. But the real secret of the sphagnum's efficiency as an absorbent lies in the remarkable microscopic structure of its leaves.

Before discussing the somewhat complicated sphagnum leaf, I will describe briefly the much simpler structure of an ordinary moss leaf, as it looks under the microscope. Such a leaf consists of a single layer of tiny microscopic cells. Seen in surface view the individual cells are polygonal in outline, but in reality, considered as solids, they are prismatic in shape. All of the cells in the leaf are essentially similar to one another: without exception they are green and living and they are all of approximately the same size and shape.

But in a sphagnum leaf the structure is much more complex. Here also there is just a single layer of cells, but these cells are of two totally different kinds. First, as in the ordinary moss leaf, there are the green, living cells. But these green cells, in the sphagnum leaf, are very small and very much elongated, and they are arranged to form a sort of open network which runs all through the leaf. In the meshes of this network occurs the second kind of cell. These cells are large, without color, dead, and perfectly empty. It is to the presence of these large, colorless cells and to their remarkable structure, which I shall describe next, that the sphagnum owes its wonderful power to take up liquids.

Now, to a certain extent, the cells of any moss leaf are able to absorb liquids. But the ability of the ordinary green cells in this respect is insignificant when compared with that of the large, colorless cells of the sphagnum leaf. These, because of their capacity for absorption, may well be referred to as the *absorbing cells.* There are two features in these cells which especially adapt them to the function of absorption. First, the wall of each and every one of the absorbing cells is punctured toward the outside by several minute holes or pores. It is through these pores that liquids are sucked into the cells. Each cell, acting independently, sucks in whatever liquid it comes in contact with until it is full. A sphagnum plant with its hundreds of leaves, each leaf containing hundreds of these tiny absorbing cells, represents a highly efficient absorbing system. And this absorptive ability is not confined to plants that are fresh. A dry, dead leaf is just as efficient, when it comes to taking up liquids, as a fresh one. This is due to the second structural peculiarity of the absorbing cells. For inside of each one of these cells there is a spiral, spring-like coil of thickening (or commonly a series of hoop-like ribs of thickening) which presses outward, as it were, against the walls of the cell and serves to keep it from collapsing. Even after a leaf has become completely dried out, this "framework" serves to keep the cell cavity open.

Incidentally, while it is the leaves which are most efficient in the absorption of liquids, in some varieties of sphagnum both the stem and branches are enveloped by one or more layers of absorbing cells, essentially similar to those found in the leaves.

It now becomes perfectly clear why it is that sphagnum is so much superior to cotton as an absorbent. In cotton liquids, for the most part, are merely held within a tangle of threads. In the sphagnum we find a highly specialized absorbing system, made up primarily of a vast series of absorbing cells, but supplemented to a high degree by various other structural peculiarities of the sphagnum plant.

How can surgical and non-surgical varieties of sphagnum be distinguished from one another?

Just as there are a great many different varieties of roses and chrysanthemums and dahlias, so there are a great many different kinds of sphagnum; and these different kinds are by no means of equal value for surgical purposes. Some of them, indeed, are worse than useless. A great deal of the dissatisfaction with sphagnum dressings which was expressed by army surgeons in the early days of the sphagnum enterprise can be attributed to the failure to appreciate this difference, and to the indiscriminate use of any and all species of sphagnum in making up the dressings.

In the little state of Connecticut alone there are no less than twenty-five different kinds of sphagnum; on the continent of North America there are at least forty. Of these forty species only two or three are actually used to any extent for surgical purposes. It is not enough, then, to know that a sphagnum is a sphagnum. One must be able to differentiate between suitable and unsuitable varieties.

Now, from a botanical point of view, the sphagnums are an exceedingly difficult group of plants to work with. It is a job for an expert to properly identify specimens: in fact, it is a job which very few botanists feel qualified to undertake. Fortunately, however, the recognition of material suitable or otherwise for surgical purposes is much less difficult. With a little training and experience it is well within the ability of almost anyone to at least distinguish with some degree of certainty between sphagnum which very likely will prove of surgical value and sphagnum which quite certainly will not.

Without going too much into detail, then, we will consider next just what qualities are desirable in sphagnum material which is to be used in surgical dressings.

First of all, the highest possible capacity for absorbing liquids is essential; and with reference to this qualification there is a wide range of variation between different species. In general, the more robust varieties of sphagnum are better than the more delicate; forms with large leaves, dense foliage, and close-set branches are much better than varieties with small leaves, skimpy foliage, and scattered branches. In the second place, it is essential that the material should be soft and flexible, and at the same time that it should possess a considerable degree of strength. Here again there is great variation between different species. In general, coarse or stringy forms, or forms with stiff or brittle stems or harsh texture, must be avoided.

Of all the sphagnums, there is one species which combines, to a greater degree than any other, absorbency, softness, and strength. This is *Sphagnum papillosum*. This species, at least here in the east, has been found to be much more satisfactory for use in surgical dressings than any other variety. Three other species of sphagnum have been used to a considerable extent in surgical work, namely *S. palustre*, *S. magellanicum*, and *S. imbricatum;* but while in the humid climate of western Washington and British Columbia these develop quite as luxuriantly as *S. papillosum*, and while locally, here in the east, they may compare very favorably, on the whole they tend to have too much stem in proportion to foliage or too harsh a texture to make ideal surgical material. In the field *S. papillosum* can usually be recognized by its very robust habit and brownish color: it is never red or purple. As a rule the other three species named are less robust; *S. magellanicum* commonly is pink or purplish red in color, *S. palustre* pale greenish white, and *S. imbricatum* green.

In this connection it should be emphasized not only that different varieties of sphagnum exhibit a wide range of variation when it comes to their capacity for absorbing liquids, as well as to other features which adapt them to surgical use,

PLATE 218, lower figure. 1. *Sphagnum recurvum.* 2. *S. capillaceum tenellum.* 3. *S. Girgensohnii.* These three and similar forms are mostly worthless for surgical work. 4. *S. plumulosum flavicomans.* This species is sometimes used for surgical dressings. 5, 6, 7. *S. magellanicum.* Material like No. 7, which is soft and very full-foliaged, and No. 6, which is less bushy but very soft, make excellent surgical material. These specimens grew in the water. No. 5 illustrates the usual habit of this species—very stemmy, sparsely branched, and rather harsh. Such material is useless. 8, 9. *S. papillosum.* These two specimens and Nos. 6–8 illustrate the range of variation exhibited by the same species under different conditions of environment. Moss like Nos. 7 and 9 furnishes the best surgical material.

Picking over sphagnum at McGill University, Montreal. An open sack of raw moss in left foreground. Photograph supplied by Professor John Bonsall Porter.

Forms of sphagnum suitable and otherwise for surgical dressings. For explanation see opposite page.

but also that the very same species may vary greatly in different localities. Growing under certain conditions it may acquire that soft, "bushy" habit so desirable in material which is to be used for surgical dressings, while growing under other conditions it will be harsh, stringy, and quite unfit for surgical purposes. Even *Sphagnum papillosum* exhibits considerable variation in this respect. And this brings up another question.

Where does the sphagnum grow? In what kinds of habitats does it occur, and in what sections of the country does it develop best?

When it comes to locating sources of supply for surgical sphagnum, obviously it is not enough to be able merely to recognize the sphagnum when you see it. It is not even enough to be able to distinguish surgical from non-surgical material. It is every bit as important to know in what sort of places to look for it, and also what sort of places to steer clear of.

In general, the sphagnums grow in wet places. Taken as a class they are moisture-loving plants. Considering them from a geographical point of view, it can be said that they grow best in regions where the climate is moist the year round, but especially in summer, and where the summers are not too hot. They attain their best development in cool, humid regions, such as Newfoundland, Nova Scotia and New Brunswick, Vancouver Island and western Washington. On the whole, they develop most luxuriantly near the seacoast, particularly along coasts where fogs are frequent. They are better developed northward than southward. This is especially true of *Sphagnum papillosum*, which has never been found at all south of New Jersey. In the northern regions that I have just mentioned the sphagnums are very widely distributed, occurring not only in swamps but to a considerable extent on uplands as well. Farther south, in regions where the climate is drier and the summers hotter, they are mostly confined to swamps.

Now in this connection, there is one particular type of swamp that I want to call attention to, and that is the kind of swamp known as a *bog*. It is in bogs that the sphagnums develop most luxuriantly. Let us consider first the conditions which prevail in southern New England, a region in which the bog type is in striking contrast to other types of swamp. The conditions here are essentially similar to those that prevail throughout our northern states and to a considerable extent in Canada.

The plant-population of all bogs, no matter in what section of the country they occur, is very much alike. In fact, this is so much the case that a bog can usually be recognized from the character of its vegetation alone. Especially striking is the bushy element in the vegetation. Almost invariably this is made up very largely of members of the Heath Family: such plants as the bog laurel and bog rosemary, the cassandra, the Labrador tea, and the cranberries. These are mostly absent from swamps of the ordinary description. In eastern Maine a bog is commonly referred to as a *heath*, although in Maine this word, which in Europe is commonly used with reference to similar areas, has been yankeeized to "haythe." In Europe a bog is also called a *moor*.

The characteristic tree in bogs is the black spruce. Farther north, as in Maine and the Adirondacks, this tree is by no means confined to bogs, but in southern New England it almost never grows anywhere else. Such trees as the elm and the ash, which are common in ordinary swamps, are conspicuously absent from bogs. Bogs are also the home of such bizarre forms as the pitcher plant and the sundews, plants which possess the insect-catching habit. But from our point of view the outstanding feature of a bog is the wonderful development of the sphagnums. Almost invariably they constitute one of the most prominent elements in the vegetation.

To a certain extent the sphagnums may grow in almost any wet, springy swamp, whether it is open or wooded. But in swamps which are situated along rivers, where the ground is flooded from time to time with muddy water, they are not apt to occur in any profusion. Even farther north, in regions like New Brunswick and Nova Scotia, where climatic conditions are most congenial to their development and where they are much more generally distributed than farther south, the sphagnums grow best in the bogs. So abundant as a rule are the sphagnums in this particular type of swamp that many bogs are popularly referred to as *moss bogs*.

A few words in passing regarding the nature and origin of these bogs. Bogs are perhaps most widely known on account of the deposits of *peat* by which they are commonly underlain. Peat is partly decayed vegetable matter, usually deposited under water. It represents an intermediate condition between dead plants and coal. Coal is essentially petrified peat. In parts of northern Europe peat is one of the chief sources of fuel, and our own peat deposits have been under investigation by the government for a number of years.

In our region the areas which today are occupied by bogs, almost without exception, were formerly occupied by lakes or ponds. A pond may become filled in and converted into a bog wholly through plant activity. You can find every stage between ponds in which scarcely any filling has taken place and ponds which have given way completely to bogs. Very commonly the filling in is brought about through the agency of what is known as a *floating mat.* The vegetation along the edge of the pond grows so vigorously that it spreads away from the shore, out over the open water. In this way there is developed what is commonly referred to as a *quaking bog.* This raft of vegetation, floating on the surface, rising and falling with fluctuations in the water level, may be underlain by clear water or by soft, bottomless ooze. So firm, however, may the mat become that while the surface trembles and quakes when you walk over it, nevertheless it is quite capable of supporting the weight of a man. A quaking bog is an ideal place to look for surgical sphagnum.

In most sections of the United States, bogs are rather rare in their occurrence and they are rather small in size. In cool humid regions, such as Newfoundland, Nova Scotia, and eastern New Brunswick, they are much commoner and frequently cover extensive tracts of country. In these northern regions, in addition to the ordinary type of bog, there is found a remarkable type known as a *raised bog.* Unlike our ordinary bogs, the surface of a raised bog is domed up, just like an inverted saucer. It may be fifteen or twenty feet higher toward the center than it is around the edges. Bogs of this sort are found only in regions where the climate is exceptionally favorable to the development of the sphagnums. They are built up almost wholly by the sphagnum, and they can develop only in regions where there is sufficient rain and fog to permit the sphagnum to grow up above the water level.

Now the facts regarding raised bogs that I have just pointed out have a rather important application. If, as I have said, these raised bogs are restricted to regions where climatic conditions are most favorable to sphagnum development, it follows that you ought to find your best sphagnum in regions where these raised bogs are present. In other words, you can regard the abundance of raised bogs in any region as a sort of barometer as to the degree to which the climate there is suited to the sphagnums.

I have spent a month this past summer investigating the sphagnum situation along the Maine coast. Starting in at Portland, I have visited fifteen different localities between there and Calais, which lies along the Canadian border. In the vicinity of Portland there are no raised bogs, and I was unable to find any trace of surgical sphagnum. As you travel eastward the raised bogs become more and more common, and surgical sphagnum, at first very local in its occurrence, becomes more and more general in its distribution. There seems to be little question that the coastal region of Maine, from Penobscot Bay eastward, is the most promising part of the eastern United States in which to look for supplies of surgical sphagnum. Unfortunately, however, many of the very best bogs—the ones most suited to the growth of surgical sphagnum, and the ones easiest to get at—lie along the borders of small lakes; and these lakes for years have been dammed by the lumbermen and the bogs flooded to such an extent that most of the best sphagnum has been drowned out. In other places fires have exterminated or killed back the sphagnum over large areas. *Sphagnum papillosum*, the most desirable species for surgical purposes, is extremely sensitive to any change in external conditions. In spite of these difficulties, however, I was able to locate a considerable number of sizeable tracts of good moss; and I have no doubt that others will continue to turn up.

But Maine is not the only part of the east where surgical sphagnum occurs. It may grow in almost any bog. You can only tell by looking. As I stated earlier, American army surgeons at the present time are not using sphagnum to anywhere near the extent that it is being used by surgeons in the other allied armies. But it is our business to be prepared; and to this end we want information regarding every locality which might possibly be utilized as a source of supply for surgical sphagnum. It may be that some of you know the whereabouts of a promising bog. If you do, look it over; and if you find any quantity of what looks like good material, send us a sample of it.*

In surveying any district for surgical sphagnum, there are a few practical points which it is well to bear in mind. A wooded bog may contain plenty of sphagnum, but for our purpose it is rarely of any value. The good moss almost invariably grows in open bogs. Again, an open bog all overgrown with bushes, where the sphagnum forms great soft cushions a foot or so high, is apt to afford pretty poor picking. There may be plenty of moss, but most of it will prove to be of the wrong variety; or if it is of the right variety it will be of poor quality. For that matter, it should be said that in almost any bog there is sure to be a large proportion of undesirable material. Commonly the bulk of the sphagnum will consist of species that are of no use at all for surgical purposes.

The best qualities of moss always grow in the wettest parts of a bog. A dry bog is apt to contain no material whatever of surgical value. A wet one may be full of it. The best kind of a bog for surgical moss is a wet cranberry bog: not one of the artificial variety that is so common in southern New Jersey, but one where the cranberries grow scattered over a soft carpet of moss, intermixed with more or less "cranberry grass" (*Carex filiformis* and *C. oligosperma*) and perhaps a scanty growth of low bushes. It is in bogs of this description that I have seen the best material in Maine. In exploring any bog for surgical sphagnum, always look for the wettest places: the soft, quaky spots around the edges

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* Specimens of material may be sent to the writer at Yale University, New Haven, Conn.

of ponds, the small depressions, and the wet furrows; and steer clear of the bushy places.

In this connection, there is one other important point to be borne in mind, and that is transportation facilities. Any tract of moss, to be of practical value, must be reasonably accessible. It is hardly worth while paying any attention at all to bogs that are situated away off where it will be practically impossible to get material out, even if it is there.

Finally, how is the material collected and prepared for use, and what are the sphagnum dressings themselves like?

The method of collecting and preparing sphagnum for use in surgical dressings, as outlined in Professor Porter's Instruction leaflet,* is essentially as follows. For collecting the stuff old oat or potato sacks are used. These are first thoroughly cleaned and boiled. A carefully filled sack is about as much as a man can conveniently handle, particularly where, as is usually the case, there is a considerable stretch of soft, boggy footing between the collecting ground and terra firma. Collecting the moss is not always easy work. In many places the conditions are such that only men can do it, but in other places women and even children can be employed. Under proper guidance, however, this part of the work can very well be performed by laborers. Very likely boy scouts could be used to advantage.

The detailed steps in collecting are somewhat as follows. After selecting a place where the material is as good and as clean as possible, the collector seizes a double handful of the moss, grasping it as low down as possible, and pulls it up bodily. He then squeezes the wet, spongy mass to get rid of the bulk of the water, pulls out any coarse plants that may be present, removes any muck or decayed matter from the bottom, and places the material in a sack. This operation is repeated until the collector has either exhausted the supply or obtained as much as he can handle.

The next step in the process is the drying and sorting. From the bog the sacks of moss are carted to some place where the

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* Instructions for the collection and preparation of sphagnum moss for surgical purposes. pp. 1–7. Canadian Red Cross, Montreal. 1917.

material can be spread out to dry. The drying can be accomplished by spreading out the moss on a clean lawn or on the floor of a barn or attic where there is a good circulation of air. But where large quantities of material are to be handled, it is customary to use drying racks of some sort. Drying by means of artificial heat is avoided, so far as possible, since material thus prepared is much more brittle than material that has been air-dried.

The only further treatment the moss requires before it is ready to be made up into dressings is sorting over. This is preferably done before the material has become thoroughly dried out, since the moss when dry is more or less brittle and less easy to handle than when moist. All foreign material is carefully pulled out by hand, and at the same time the moss is separated into two or more grades: first class material suitable for dressings, second class material suitable for bed pads, etc. This part of the work, indeed everything except the collection and hauling of material, is done by women. In Canada, moss sorting is one of the most popular phases of Red Cross work among the volunteer workers.

In conclusion, just a word regarding the nature of the absorbent dressings which are made from the sphagnum. The simplest type is merely a bag filled with the moss and then sewed up. This type has been extensively turned out by the Canadian and the British Red Cross and to some extent by the American Red Cross. The bag is made of light-weight muslin, this being used in preference to gauze, which is too light and of too open a texture to use in this style of dressing. This particular type of dressing has several disadvantages. The sphagnum has a tendency to slide around and to bunch up, and the dressing wets through to the back very quickly. Moreover, for various reasons the muslin is inferior to gauze or cheesecloth, such as is used in absorbent cotton pads, and it is objected to by surgeons.

This style of dressing has been greatly improved upon within the last year, and a type of pad has been devised which seems to overcome all of the objections that I have just mentioned. These pads are constructed somewhat as follows. In making the pad, first of all a layer of cheap non-absorbent cotton, the size of the dressing, is laid down. Over this is spread a layer of sphagnum. The cotton backing gives shape to the pad, and it serves to hold the sphagnum in place and to prevent it from slipping around. But in addition to this, being non-absorbent, it prevents the pad from becoming too rapidly soaked through to the back. Over the sphagnum is then spread a double layer of very thin gauze paper, the so-called Scott paper tissue. This is folded under at the edges to form a sort of envelope for the sphagnum. This gauze paper does not affect in the least the absorbing capacity of the pad, but it does serve to prevent fine particles of sphagnum from working through the cloth covering and irritating the wounds, and it therefore makes it possible to use gauze for the outer wrapping of the dressing. Pads of this type are more complicated than those composed entirely of sphagnum, and they are somewhat more expensive. But they are quite easily made, and they are cheaper and at the same time much more absorbent than the ordinary cotton pads.

Sphagnum dressings, however made, are decidedly bulky. In order to flatten them out and to economize space in packing, it is customary to run them through a clothes wringer. After this treatment the dressings are ready to be sent to the hospitals, where they are sterilized shortly before being used. Sometimes, however, for emergency use in field hospitals, etc., the dressings are sterilized before being sent out by being dipped in an antiseptic solution.

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PRESSING PLANTS WITH DOUBLE-FACED CORRUGATED PAPER BOARDS.

GEORGE E. NICHOLS AND HAROLD ST. JOHN.

THE advantages to be gained by using corrugated paper boards in plant presses was first made widely known by Collins who, in 1910,[1] described his own experience with them, together with that of several other workers who independently had developed similar methods. Briefly outlined, the scheme originally employed by Collins was as follows. In building up a press, single-faced (s. f.) corrugated boards, i. e. boards in which one face is uncovered and ridged, the other covered and smooth, were substituted for the driers customarily employed, the specimens, enclosed only by thin specimen sheets of newspaper stock, being laid directly between these. After being strapped up the press was suspended over a lamp, and around it was tied a cloth skirt, draped so as to hang nearly to the floor, and "held open by means of a stiff wire hoop sewed in at the lower edge." The effect of the continuous current of warm air from the lamp, guided by the skirt and passing upward through the corrugated ventilators, was such that, to quote Collins (*l. c.*, p. 222), "plants which formerly took a week to dry can almost invariably be perfectly dried in less than 24 hours, and commonly in less than 12 hours." Furthermore, there was the added advantage that the bother of changing driers and spreading out the wet ones to dry was entirely eliminated.

Collins experimented with various modifications of the method

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[1] Collins, J. F. The use of corrugated paper boards in drying plants. RHODORA **14:** 221–224. 1910.

just described and found that somewhat better specimens could be obtained, though not so quickly, by using ordinary driers in combination with the corrugated ventilators: a drier was placed over the ridged face of each board, so that the sheet containing the specimen lay between a drier on one side and the smooth face of a ventilator on the other. This scheme was essentially the one used in the field by Professors M. L. Fernald and K. M. Wiegand, "except that one change of driers was made in order to straighten folded leaves, etc." (*l. c.*, p. 223). It was found that such a press could be left without attention for several days, even in a humid climate. Finally, Collins suggested the practicability of using various sources of heat other than the lamp, such as an oil stove, electric heater, cook stove, steam radiator, etc.

Three years later Ricker,[1] in a government circular designed primarily to instruct novices in the preparation of presentable botanical specimens, recommended the use of corrugated boards in combination with driers for pressing, advising that the specimen sheet be separated from the ventilators on both sides by driers. He recommends double-faced (d. f.) boards, i. e. boards with both faces covered and smooth, in preference to the single-faced type, and stipulates that the corrugations should run lengthwise the board. Regarding the use of the d. f. board Collins (*l. c.*, p. 223) was of the opinion that although "it is better to handle, and can be used either side up, it appears doubtful at present if it has any particular advantages otherwise over the single-faced."

The primary object of the present paper is to proclaim the advantages of the d. f. board ventilators, and to describe briefly our experience in using them under diverse conditions, with the hope that others may profit by our results. During the summer of 1915 and again in 1916 the senior writer spent about two months in ecological investigations in northern Cape Breton.[2] As a desirable adjunct to these studies considerable attention was devoted to the flora of the region, and something over 2000 sheets of vascular plants were prepared. For pressing and drying, d. f. corrugated boards, cut with the corrugations running lengthwise, were used, driers being omitted except with occasional

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[1] Ricker, P. Z. Directions for collecting plants. U. S. Dept. Agr. Bur. Pl. Ind. Cir. 126. pp. 27–35. *f. 1–5.* 1913.

[2] See Nichols, G. E. The vegetation of northern Cape Breton Island, Nova Scotia. Connecticut Acad. of Arts & Sciences **22:** 249–467. f. 1–70. 1918.

bulky specimens. Altogether only about 75 boards were taken into the field. The general scheme followed was that described by Collins and needs little further comment. As a source of heat an ordinary kerosene lantern was used. Incidentally, in this connection, it was found that, in addition to an abundant supply of oil, a stock of extra wicks was essential, since, with the lantern running continuously day and night, the wick had to be well trimmed at least once and preferably twice a day. About a month of each summer was spent in permanent camp, and during this period the press was hung in a special shelter: the first summer in a makeshift tent, roofed with tarpaulin and walled with boughs; the second summer in a small hut constructed out of tar-paper and scantlings. The latter part of each summer was spent partly in localities where "hotel" accommodations were available, partly in trips of about a week's duration through an uninhabited wilderness where all luggage had to be packed and carried. On these latter jaunts little attempt was made to dry specimens properly, but at the hotels it was customary to run the press as usual, suspending it by means of home-made wire hooks between the backs of two chairs.

The experience gained during these two summers demonstrated conclusively the worth of d. f. driers. As a rule plants were left in the press for 24 hours, the press being reversed at the end of 12 hours to insure even drying toward both ends of the press. This length of time sufficed to completely dry ordinary specimens, and even *Mertensia*, a notoriously difficult subject, was out of the press within three days. It should be interpolated, however, in the light of more recent experience, that boards cut with the corrugations running crosswise give more satisfactory results than those with corrugations running lengthwise. With the latter there is a tendency for parts lying near the center of the press to dry slowly, a tendency which is quite obviated where the corrugations run crosswise. The specimens prepared by the method just described are all that could be desired, and are noticeably superior to those prepared with the help of s. f. driers alone. Even *Mertensia* makes a fairly presentable specimen, retaining its color at least much better than any other specimens we have seen. As might have been expected, by the end of the first summer all of the ventilators showed unmistakable signs of service, and many of those that had had the misfortune to lie next to bulky specimens were pretty much out of commission. But that they stood up well under the test is demonstrated by the fact that many of them were again used throughout the second season.

In July, 1917 we contemplated a long, hard canoe trip in northwestern Maine, with the collection of plants as our primary object. From the start nearly to the finish of our 250 mile journey we realized that it would be necessary to depend on what could be carried in two canoes, together with what could be obtained from the woods. It was obvious that botanical equipment must be reduced to a minimum and yet at the same time be absolutely dependable. In view of the satisfactory results obtained by the senior writer with d. f. ventilators, this part of the equipment was quickly settled upon. A second matter demanding attention was the source of heat. With the prospect of long, hard days of poling and dragging the canoes upstream and of at least one long portage we hesitated about loading down with a three weeks supply of oil. So, at the suggestion of the junior writer, it was decided to place our dependence on a campfire — with what success will be seen. In addition, then, to sundry press frames, straps, and specimen papers, our equipment for preparing specimens, as finally boiled down, consisted of two hundred d. f. corrugated boards, cut with the corrugations running crosswise, fifty Washington driers (the purpose of which will be pointed out presently), and an abundant supply of matches. Thus armed, we sallied forth into the wilderness.

In the preparation of specimens our general method of procedure was somewhat as follows. The freshly collected plants were placed in pressing papers and press number one was built up of these plus occasional interlarded driers. It will be seen that driers were not eliminated completely, but for the most part they were used only in connection with this first press, and here primarily to place on either side of the heaviest plants, thus protecting their neighbors from undue crushing. To a certain extent they were also used between groups of specimen sheets and to even up the press. For these purposes it was not necessary that they should be thoroughly dried out after each application. Press number one was then strapped up tightly and set aside for from twelve to twenty-four hours. Ordinarily it traveled a day in the canoe, wrapped securely in a waterproof bag. At the end of this time it would be unstrapped and the entire bale of plants carefully worked over, leaves which were crumpled or out of place being straightened or shifted, flowers or fruits being brought into due prominence, etc. From the specimens thus treated would be built up press number two, this time with a ventilator alternating with every specimen sheet. After this fashion a stack might be built up to a height of sometimes two feet or more.

In strapping up this final press, the straps were placed crosswise the press, a foot or more apart, with both buckles on the same side of the press — one of the open sides. For straps, broad, webbing trunk straps were used: these can be adjusted much more easily than leather straps and are much stronger. These straps were twelve feet in length and by tying together the free ends, a loop of any length desired could be made, by which the press could be hung up to dry.

The press was now ready for the fire. At first thought it seemed like tempting Providence to entrust our plants to an open fire, but experience showed that with due care there was little danger. Only twice during our trip, the first and the last day in camp, did any catastrophe threaten: the first time due to lack of experience, the last due to an overzealous attempt to exceed the speed limit in the drying process. On both occasions the press was rescued before any serious damage had been done.

The matter of fuel was the occasion of considerable experimentation. Coniferous wood burns too rapidly and flares up too much. Of the woods available in the region traversed, alder makes the hottest fire, but the sticks are small and a green alder fire of the sort required demands constant nursing. We finally settled on green paper birch. This was everywhere available, was easy to cut and split, and once started produced a hot fire, but without too many sparks or too much flame and smoke, a fire which could be depended on for a maximum continuous supply of heat with a minimum amount of attention, especially after it had been tamed down to a glowing bed of coals.

For holding the press in position over the fire a tripod was constructed from light saplings about ten feet long, bound together at the smaller ends with a piece of cord. The tripod was straddled over the fire and the press suspended from the projecting end of one of the saplings (one of which it was our custom to cut short for this purpose), broadside over the fire and at such an angle that the channels in the ventilators would lie in a vertical position. The height of the press above the fire was determined approximately beforehand by lengthening or shortening the loop, but both height and position could be subsequently regulated by shifting the legs of the tripod. With a slow fire the press could be left at a height of barely two feet above the coals without danger, but the "coefficient of safety" naturally varies and can be judged only by experience.

The results obtained by the method just described were fully as satisfactory as those secured when a lantern was used as a source of heat, and indeed material could be dried even more rapidly. Under favorable conditions completely dried specimens could be turned out in from three to five hours: specimens in which the natural color was retained far more perfectly than in plants prepared by the ordinary slower methods of drying, and which showed no ill effects from their hot air treatment save a slight smoky smell which soon vanished. Only in exceptional cases was the imprint of the corrugations to be detected in the finished product. Wind and rain were two of the chief enemies with which we had to contend. To avoid the former we always looked for a sheltered pocket among the evergreens where the tripod could be set up. Sometimes we rigged up a make-shift wind-break with a pack-cloth, while in wet weather a pack-cloth draped tepee-fashion around the top of the tripod served the double end of keeping the press dry and the fire alive. These, however, are two enemies against which on another trip more preparation would be made beforehand.

As with the lantern method, the d. f. ventilators stood up remarkably well. They showed some effects of their hard usage, to be sure, and after being in service for a week, with the smoke constantly rising through their pores, they began to smell like a lot of kippered herring, but what real camper would object to that! And notwithstanding that all the ventilators were in practically continuous service for twenty-four days, not one was actually rendered useless.

In conclusion, a few observations of a general nature regarding the relative merits of the current methods of drying vascular plants for herbarium specimens. The following remarks pertain more especially to field operations, but in large measure they are quite as applicable to herbarium or home practise. In the matter of driers or their "equivalents", four possibilities are open: driers, s. f. ventilators, s. f. ventilators plus driers, and d. f. ventilators. Furthermore there is the choice between various sources of artificial heat or no artificial heat at all. In deciding upon the relative efficiency of various methods, there are perhaps five principal factors to be taken into account: (1) length of time required to dry specimens and (2) quality of results; and (3) weight, (4) durability, and (5) convenience in handling of the drying equipment. Sufficient objections to driers alone are furnished by the first and third factors; to s. f. ventilators alone by the second and fourth. As to the relative merits of s. f. ventilators plus driers versus d. f. ventilators, it should be said that the results obtained with the former of these two equipments are quite equal to those obtained by the latter, but the first, third, fourth and fifth factors mentioned above are all in favor of the d. f. ventilators. Using the first equipment it takes several days to dry a load of plants, while with the second a full capacity load can be turned out each day. In this connection it should be remarked that the "Washington" drier is far superior to the ordinary type in its greater absorbent power, thinness, firmness, and strength. So far as bulk and actual weight are concerned, equal quantities of s. f. ventilators plus driers, on the one hand, and of d. f. ventilators, on the other, are about equally matched: one hundred d. f. ventilators were found to weigh 28¼ pounds, as compared with 15⅝ and 13¼ pounds for the same quantities of s. f. ventilators and Washington driers respectively. But the great saving in both bulk and weight is seen when account is taken of the speed with which results can be obtained by using the d. f. ventilators. On an extended collecting trip a given number of d. f. ventilators will turn out as many dried specimens as three or four times their number of s. f. ventilators plus driers. Add to this the greater convenience in handling and the superiority of the d. f. ventilators can hardly be questioned.

With regard to the use of artificial heat, it is our opinion, based on several years' experience, that so far as the quality of results is concerned no potent objection can be urged against it: on the contrary, as earlier indicated, the specimens dried in this way are obviously superior to those dried without heat. Moreover the saving of time and energy and, in the field, of weight and bulk are big items. As to the source of heat, for field work either a lantern or a fire is satisfactory. It must be admitted, however, that a fire does require more or less constant attention, and that on this account, where it is practicable, a lantern is to be preferred, since, while it does not produce results quite as rapidly, the lantern requires much less supervision and can be left on duty day and night.

For use in the laboratory the senior writer has found great satisfaction in the following equipment. A rectangular wooden box about three feet high and open at the top was constructed. The width of the box is slightly more than the length of a pressing frame; its length is immaterial, but is sufficient to accommodate a press about two feet thick. An inch or so below the rim of the box, lengthwise on either side, was fixed a wooden ledge. The press, instead of being suspended from above, is supported on this ledge and is girded with a canvas skirt which hangs down well below the upper edge of the box. As a source of heat a small electric stove is used, the connecting cord of which passes out through one of several holes which have been bored in the sides of the box near the base.

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[From Bulletin of the Torrey Botanical Club, 45: 391-397. 11 O 1918.]

Regeneration in Phegopteris polypodioides*

Elizabeth Wuist Brown

(with three text figures)

Introduction

The fact that plants are able to reproduce lost parts was known long before it was discovered that animals possessed this same power. It was natural that the first experimental investigation on regeneration in plants should have been carried on with the higher plants as it was a common practise to propagate many plants by means of cuttings. However, the study of regeneration has since been extended to include not only the lower groups of plants, such as the algae, fungi, liverworts, mosses and ferns, but also many groups of animals. This has resulted in the accumulation of a large amount of evidence regarding the possibilities of regeneration by most groups of organisms.

Experimental evidence has also indicated that the regenerative power of some plants is much greater in earlier than later life, while in others this power is lost completely in later life.

Goebel (2, pp. 196–203), experimenting with ferns, found that the primary leaves of the young sporophytes of some ferns, either while attached to the sporophyte or cut off and placed under moist conditions, were able to regenerate new fern plants or prothallia or intermediate forms between leaves and prothallia. Here the regenerative power seemed confined to the primary

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* Contribution from the Osborn Botanical Laboratory.

leaves of the young sporophytes, as in no case did regeneration take place with leaves of the older plants. It was thought of interest to see if the primary leaves of the young sporophytes of *Phegopteris polypodioides* Fée could regenerate in the manner indicated by Goebel, as apogamy had occurred so frequently in cultures of this fern.

EXPERIMENTAL

Spores of *Phegopteris polypodioides* were obtained from Brooklin, Maine, through the kindness of Dr. A. H. Graves. Cultures were started in the early part of October. The spores were sown on Prantl's and Knop's full nutrient solutions and modifications of these solutions. After the spores were sown the cultures were placed before an east window. In an effort to induce apogamy the prothallia were not transferred to fresh nutrient solutions from time to time, but were allowed to develop upon the same nutrient solutions upon which the spores had been sown. As a result growth and development of the prothallia was slower and fewer sporophytes formed, the majority of which were apogamous.* The primary leaves of both normal and apogamous young sporophytes were used in the regeneration experiments.

March 14, 1917, primary leaves 5–7 mm. in length were cut from the young sporophytes and placed on sand in watch glasses. In some cases the petiole of the leaf was inserted in the sand to a depth of 1–2 mm., placing the blade of the leaf in an upright position. In other cases the leaf was laid on the sand; while in still others various parts of the blades were covered with the sand. The sand in some of the watch glasses was moistened with Knop's and Prantl's full nutrient solutions, while in the others it was moistened with distilled water. All the cultures were placed in large plates and covered with bell jars. The sand was never allowed to dry and water was kept standing in the plates. In this way the air under the bell jar was always moist.

No experiments were tried to see if the leaves would regenerate while attached to the young sporophytes and no such cases were observed among either the solution or soil cultures, although frequently the leaves of this and other species of ferns, especially in

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*Wuist, Elizabeth Dorothy. Apogamy in *Phegopteris polypodioides* Fée, *Osmunda cinnamomea* L., and *O. Claytoniana* L. Bot. Gaz. 64: 435. 1917.

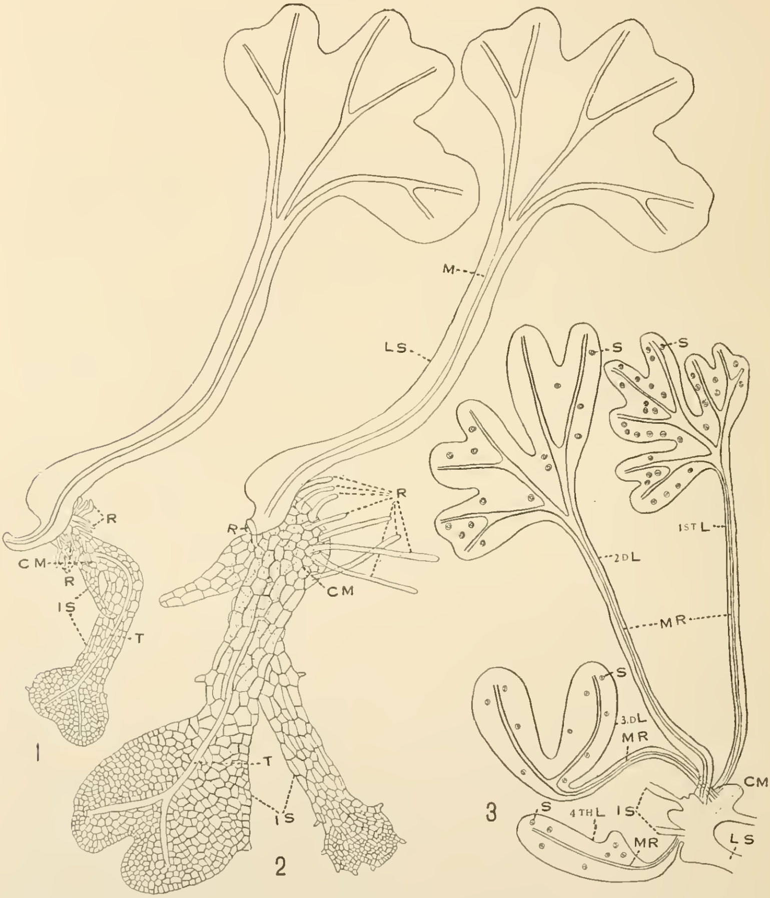
the soil cultures became appressed to the soil as a result of accidents in watering.

Only one case of regeneration was obtained, although a large number of leaves were experimented with. Regeneration began in about six weeks after the leaf had been removed from the sporophyte and laid on sand moistened with Knop's full nutrient solution. One side of the petiole, near its base, was destroyed by decay, and a short distance above this point on the opposite side of the petiole a slight swelling occurred, from which a cellular mass developed. At first it was slightly elongated, FIG. 1, afterwards it became much thickened and broadened, FIG. 2, and finally assumed the shape shown in FIG. 3. From this cellular mass there developed two intermediate structures between leaves and prothallia, then rhizoids and four normal leaves. Neither a true root nor a stem "Anlage" was formed.

The first of the intermediate structures resembled a very much elongated prothallium, one cell in thickness, with an expanded heart-shaped apex. Tracheids arranged in rows resembling a true midrib extended up through the portion of the structure corresponding to the petiole into the expanded or blade-like part. Here the rows of tracheids branched dichotomously one branch going to each lobe (FIGS. 1 and 2). The margins of both the elongated and expanded regions were for the most part smooth, with the exception of two papillae, one of which developed on the elongated and one on the expanded part.

The second intermediate structure which developed from the cellular mass was even more thalloid in form and structure than the first one. Both the elongated and broadened portions like those of the first were only one cell in thickness. The expanded portion differed somewhat in appearance as it was not so distinctly heart-shaped and its margin bore many more papillae. There were no indications of tracheids present in either of the portions representing petiole or blade.

Growth was rapid and apparently normal in both of these intermediate structures, but the second one never attained the size of the first. Neither was long-lived, death occurring soon after the normal leaves began to develop. The rhizoids resembled in every way those of a normal fern gametophyte. They formed from the cells of both the upper and lower surfaces of the cellular mass, although the majority came from the upper surface cells. Their



FIGS. 1–3. Stages in the regeneration of the young leaf of a sporophyte of *Phegopteris polypodioides* Fée, x 550. *R*, rhizoids; *LS*, leaf of sporophyte; *CM*, cellular mass; *IS*, intermediate structure; *MR*, midrib; *T*, tracheids; *S*, stomata; *1st L*, first leaf; *2d L*, second leaf; *3d L*, third leaf; *4th L*, fourth leaf.

development began at about the same time as that of the intermediate structures.

After a number of rhizoids had been formed from the surface cells of the mass, normal leaves began to develop. The first and second of the four leaves appeared almost simultaneously and their growth was very rapid. They resembled, in all respects, the leaves of a normal young sporophyte of this species of fern (FIG. 3); although the blade of the second leaf was somewhat simpler in form, having only two main divisions, each of which was lobed, instead of three main lobed divisions. However, such irregularities are to be noted in leaves of normal young sporophytes of this and other species of ferns. These two leaves attained a height of 6 mm. The third leaf, which was much slower in growth and development reached a height of only 4 mm. and was much simpler in form. The blade consisted of only two lobes, which were entire. The fourth leaf showed still greater simplicity in form and reached a height of only 3 mm. The blade was almost entire, with a slight lobe on the one side. The blades of these latter leaves, like those of the first and second ones, bore stomata.

DISCUSSION AND CONCLUSION

The various theories which account for regeneration, as advanced by the many writers on the subject, consider the following influences: (1) external influences to which the plant is subjected; (2) tendencies inherent in the plant body.

The factors considered as the possible controlling or influencing ones may be placed in the following classes: (1) nutrition disturbances; (2) wound stimuli; (3) changes in the water content; (4) the accumulation, at certain places, of definite formation substances; (5) the presence of dormant or latent rudiments; (6) correlation; (7) age and maturity of the parts; (8) form disturbance; (9) growth tension; (10) interruption of the functions of respiration, transpiration or photosynthesis; (11) isolation from the influence of the whole; (12) presence of enzymes which are responsible for the formation of the part regenerated.

The fact that regeneration was never observed in attached leaves of *Phegopteris polypodioides* and did occur in a leaf which had been separated from the plant would seem to indicate that the separation from the repressing influence of the plant body played an important part, as believed by Loeb (4, p. 153); although the fact that cases have occurred in other species of ferns when the leaves were still attached would not seem to refute this theory. Experimental evidence has shown that many species of ferns, either in the younger or older stages of their gametophytic or sporophytic life history and especially in the younger stages, does not always react in the same way to the same environmental conditions; but each has a sort of individualism which enables it to react in the way best fitted for its particular needs. It seems very probable that in this particular case regeneration is closely connected with nutrition for the reason that the severed leaf was not able to regenerate immediately another sporophyte, but could produce a cellular mass which appeared to be a reversion to a prothallus-like structure. This structure after rhizoids developed gave rise, in an apogamous manner, first to structures intermediate between leaves and prothallia; then, as the number of rhizoids increased, enlarging the absorptive surface, which in turn increased the amount of nourishment, true leaves were produced. The first of these were the ordinary type of young sporophytic leaf but later ones were much more primitive in character, due doubtless to the lowered vitality of the prothallus-like structure. This coincides with Goebel's (1, vol. 2, p. 42) views. He considers a reversion to a juvenile form as being the result of unfavorable conditions to which the plant is subjected. It is also in keeping with the results obtained by Miss Kupfer (3, p. 229) in her experiments, which indicated that at the time of cutting under normal conditions reserve food was present in sufficient quantities to initiate the first stages of regeneration. If this food was absent and its formation prevented regeneration was prohibited.

Such an explanation as this does not lose sight of the importance of the other factors so strongly emphasized by various workers, for all these factors doubtless play an important part in nutrition.

Experimental data in this particular case are not extensive enough to permit drawing conclusions as to which of the above factors or groups of factors acting separately or together, was the determining one. However, since an intimate relation exists between growth and regeneration and since growth is dependent upon nutrition, it would seem as if some phase of nutrition must be an important factor in regeneration, if not the most important factor.

SUMMARY

1. Regeneration took place near the base of the petiole of a detached leaf of a young sporophyte of *Phegopteris polypodioides*, placed upon sand moistened with Knop's solution in moist air.

2. A cellular mass, resembling a prothallium, was formed, from which rhizoids, intermediate structures between leaves and prothallia, and true leaves developed.

3. At first true leaves resembling those of normal young sporophytes were formed; then leaves of a much simpler type developed.

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