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CRITICAL BRYOPHYTES FROM THE KEWEENAW PENINSULA, MICHIGAN¹

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Several moss specimens from a collection made by the writer in Keweenaw County, Michigan, in July, 1933, were found to represent unfamiliar and puzzling species, and were put aside for study after further field work had made more material available. Opportunity for further study in the Keweenaw area did not come until 1935, when the first two weeks of September were spent in the field in northern Houghton County and in the more accessible parts of Keweenaw County. Most of the coast line of Lake Superior from Eagle Harbor to a point beyond Horseshoe Harbor was traversed, as well as much of the inland region. The dense forest north of Fort Wilkins was most thoroughly studied. The eastern shore of the peninsula was visited at Jacobsville, and again in the vicinity of Bête Gris.

Professor Fernald² has published an important report upon the vascular plants which he collected in Keweenaw County in the summer of 1934. He has pointed out that parts of the Keweenaw Peninsula possess, in addition to the usual floristic elements normally present in northern Michigan, a well-marked element of isolated Rocky Mountain and west coast species of ferns and flowering plants. As a result of his discovery, Fernald includes the higher parts of Keweenaw County among the driftless or unglaciated areas which he has previous-

¹ Papers from the Department of Botany and the Herbarium of the University of Michigan, No. 595.

² Fernald, M. L., Critical plants of the upper Great Lakes region of Ontario and Michigan, Rhodora 37: 197-222, 238-262, 272-301, 324-341, plates 352-379, 1935.

ly identified in eastern North America through tracing similar anomalies of plant distribution.

During the 1935 field season an especial search was made for isolated western species of bryophytes, of which two species had already

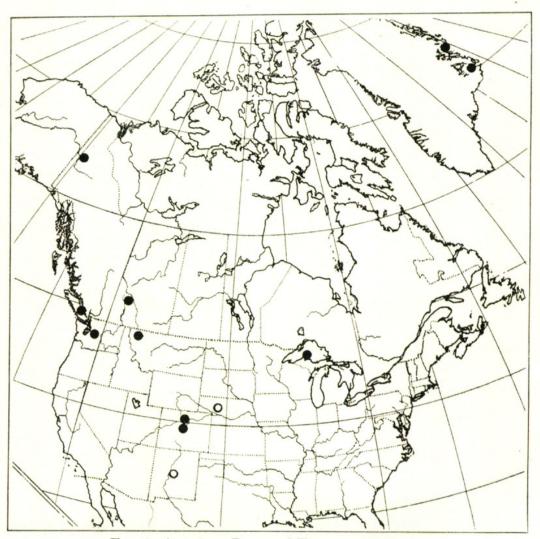


Fig. 1. American Range of Timmia Austriaca.

been collected in 1933. The search was well rewarded, and it can be established here that there is a strong element of Cordilleran, Pacific coast, and arctic species in the bryophyte flora of Keweenaw County. This situation is especially interesting because it is not generally known nor admitted that the distribution of bryophytes parallels in general that of phanerogams and pteridophytes.

From among the assemblages of arctic-alpine, trans-continentalboreal, and other interesting geographical and ecological groups of bryophytes, the following species from the Keweenaw Peninsula may be selected as being critical (in the geographical sense of Fernald); Jungermannia Schiffneri (Loitles.) Evans (Fig. 4), J. sphaerocarpa Hook., Lophozia obtusa (Lindb.) Evans, Scapania cuspiduligera (Nees) K. Müll., Frullania Bolanderi Aust. (type specimen from San Francisco) (Fig. 5), Timmia austriaca Hedw. (Fig. 1), Pseudoleskea oligoclada Kindb. (type specimen from Vancouver Island) (Fig. 3), and Hygrohypnum molle (Dicks.) Loeske. All these have been known previously on this continent only from the Rocky Mountains or the Pacific Coast, or both.

Although this list of Cordilleran and west-coast species is not a very extensive one, when compared numerically with the list of "critical" phanerogams and ferns given by Fernald, the discrepancy may be explained readily on at least two grounds. In the first place, the inconspicuousness of mosses and hepatics, especially in dry weather, prevents the collector from getting every species on his first inspection of an area. In the second place, when one considers the disparity in the sizes of the two groups, the list of "critical" bryophytes becomes proportionately nearly as large as that of phanerogams and ferns. The total number of species of bryophytes in any one county, even under the most favorable conditions, probably does not exceed 300, whereas there may be as many as 1500 species of flowering plants and ferns.

It is apparent, then, that the geographic distribution of vascular plants, which Fernald uses as a proof of the absence of recent glaciation, is almost exactly paralleled by the distribution of the bryophytes. It is difficult to determine just how much support is given to Fernald's thesis by this discovery. Very little is known of the exact distribution of bryophytes, and of the influence of glaciation upon them. There is no more than presumptive evidence that the bryophytes of Keweenaw County have not migrated there in post-glacial times. bryophyte floras of the various driftless areas have not been studied intensively, and we do not know, consequently, to what extent the species may be regarded as trustworthy indicators of areas which have escaped glaciation. Notwithstanding my sympathy with Fernald's ideas, I do not consider that there is enough evidence based entirely on the distribution of mosses and hepatics to enable a cautious bryologist to conclude that parts of Keweenaw County escaped glaciation. The geological evidence cited by Fernald is very sound, and easily

observed by visitors to Keweenaw County. His conclusion that parts, at least, of Keweenaw Peninsula are unglaciated, will probably prove to be justified, if one may judge by the long series of similar proposals which he has made and which have become generally accepted, although many of his propositions were as startling as this one, when first published.

The possibility that other higher areas along the south shore of Lake Superior may also have escaped glaciation is indicated by the presence there of a significant number of Cordilleran species. Thus the list of "critical" species from the Keweenaw area is well supplemented by collections from the adjoining highlands of northern Michigan. Dr. Nichols¹ has reported Grimmia patens (Hedw.) Bry. Eur. [Rhacomitrium patens (Hedw.) Hüben.] from the Huron Mountains of Marquette County. This species, according to the most recent monograph of the family,² has the following distribution: "Greenland to Alaska, British Columbia, Washington, Oregon, Idaho, and Montana." From a further exploration of the Huron Mountains in 1936 Dr. Nichols reports (personal communication) Grimmia Hartmani Schimp. var. anomala (Hampe) Mönk. Jones (l. c.) gives the known distribution of this moss as follows: "On the divide between Traille River and Independence Creek, Idaho, altitude 6,000 feet This is apparently the only record for North America."

In late August, 1935, Dr. Nichols and I, collecting together in the Porcupine Mountains, found three western bryophytes, which have also been collected by myself in Keweenaw County. These species are Frullania Bolanderi Aust., Pseudoleskea oligoclada Kindb. (Fig. 3), and Hygrohypnum molle (Dicks.) Loeske.

Since the report³ dealing with the Porcupine Mountain bryophytes went to press, Mr. Bartram has very kindly identified several additional specimens from the Porcupine Mountains which had puzzled me very much. As a result, *Tortula intermedia* (Brid.) Berk.,⁴ another

¹ Nichols, G. E., The bryophytes of Michigan with special reference to the Huron Mountain region, Bryologist 38: 11-19, 1935.

² Jones, G. N., *Grimmiaceae*, Moss Flora of North America 2 (1): 1–65, 25 pl., 1933. ³ Nichols, G. E. and W. C. Steere, *Bryophytes of the Porcupine Mountains, Ontonagon County, Michigan*, Papers Mich. Acad. Sci., Arts & Lett., 1937 (in press).

⁴ Tortula intermedia (Brid.) Berk., Handbook Brit. Mosses, p. 251, 1863 (Syntrichia intermedia Brid., Bryol. Univ., 1: 586, 1826) is much more commonly called T. montana (Nees) Lindb., Musc. Scand., p. 20, 1879 (Syntrichia montana Nees, Flora 2 (1): 301, 1819). The name in this sense is quite invalid, however, because of the existence of Tortula montana Mitt., Musc. austro-Amer., p. 156, 1869, even though it is now placed in Barbula [B. montana (Mitt.) Jaeg., Ber. St. Gall. Naturw. Ges. 1871–72: 424, 1873].

western species, may be added to the Michigan flora. It was collected along the shore of Lake Superior at the foot of the Porcupine Mountains, in Ontonagon County. Leptobarbula berica (De Not.) Schimp., an apparently very rare species, which has been reported in North America only from the northern Rocky Mountains, may be added

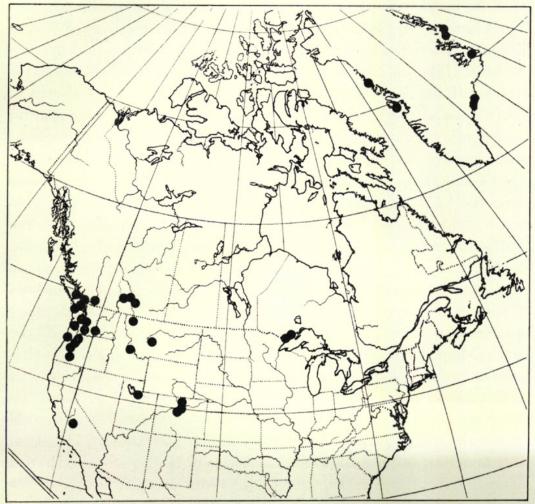


Fig. 2. American Range of Asterella Ludwigii.

tentatively, as the result of a somewhat doubtful determination of material from the Porcupine Mountains. Even the highlands on the west shore of Lake Superior yield significant species of bryophytes. Perhaps the one of most interest is Asterella Ludwigii (Schwaegr.) Underw. (Fig. 2), which in the most recent monograph¹ is given this distribution: "Greenland; Montana to British Columbia, and southward to Colorado and California." In 1927² it was reported from

¹ Evans, A. W., Rebouliaceae, North Amer. Flora, 14: 39-56, 1923.

² Conklin, G. H., Collecting hepatics along Lake Superior in northern Minnesota, Bryologist 30: 6-8, 1927.

Middle Falls, Pigeon River, Ontario, and in 1928¹ from the American side of the Pigeon River, in Cook County, Minnesota. A careful survey of the higher parts of the same region might reveal other species of significant distribution. A related species, Asterella saccata (Wahlenb.) Evans has a similar distribution (Fig. 6). In 1923 Evans² gave as its distribution: "Yukon, British Columbia, Idaho, and Washington." In 1929,³ this hepatic was reported from Winona, Minnesota, which is within the best known and unquestioned driftless area. The similar distribution of these two species of Asterella is very significant.

After seeing the remarkable parallelism of bryophyte distribution to that of vascular plants on the Keweenaw Peninsula, it is perhaps safe to predict that the converse is true, and that some of the conservative Cordilleran phanerogams will be found eventually in other areas along the Lake Superior shore. It is even possible to cite some geological evidence that other parts of northern Michigan than the northeast end of the Copper Range possibly escaped glaciation. Evidences of the last stages, at least, of the Wisconsin ice invasion are inconspicuous or even lacking in many parts of the Upper Peninsula of Michigan, especially in the areas to the south of the highlands along the shore of Lake Superior, more particularly in the shelter of the Huron Mountains and the Copper Range.⁴ Evidence that the higher parts of the Huron Mountains are driftless was presented as early as Davis⁵ says: "The conclusions reached . . . are: (1) that there exists in northern Marquette County an area of several townships' extent which is a most without glaciation. This land rises to nearly or quite 2000 feet above tide in the higher parts, and is 100 to 200 feet lower in the valleys. (2) From the fact that the drainage was across this highland and followed preglacial rock valleys. while the ice was piled up around its outer margin, it is evident that this area must have been early abandoned by the local ice cap which covered it. (3) . . . It seems probable that the direct movement of the ice from the northeast was practically checked by the Marquette

¹ Conklin, G. H., A correction, with additions, Bryologist 31: 33, 1928.

² Evans, A. W., loc. cit., 1923.

³ Conklin, G. H., Report of the Curator of the Hepatic Department of the Sullivant Moss Society, Bryologist 32: 21-23, 1929.

⁴ Leverett, Frank, Moraines and shore lines of the Lake Superior region, U. S. Geol. Survey Professional Paper 154-A, pp. 1-72, 1929.

⁵ Davis, C. A., Some interesting glacial phenomena in the Marquette region, Rept. Mich. Acad. Sci. 9: 132-135, 1907.

highland and by the Copper Range." It is intimated, in the same paper, that a similar condition may exist in parts of the Copper Range. Much of the interest in Davis's paper lies in the fact that the criteria used are geological rather than biogeographical. By still other authors, the summits of the Porcupine Mountains are considered to have emerged rather early from the thinning ice sheet, as attested by the distribution of till and erratic boulders. They have not been considered as permanent nunataks, although perhaps the evidence might favor such an interpretation.

The flora of Isle Royale contains several species of curious and anomalous geographical distribution, although the western element does not seem to be as well developed as on the Keweenaw Peninsula. Critical study will perhaps reveal more species. Most of the significant bryophytes are really arctic-alpine ones, reaching a southernmost point here.² The distribution of only Frullania Bolanderi Aust. and Orthotrichum Macounii Aust. appears to be truly significant. The latter is distinctly western and is known from no other part of the eastern United States. Of course, there are several unusual phanerogams, also, of which the most spectacular is Fatsia horrida (Sm.) B. & H., known otherwise only from the northern Rockies and the Pacific northwest.

The presence of western forms on Isle Royale has been known for a long time, and has attracted considerable attention. In 1906 Ruthven³ said: "The occurrence of these western and northwestern elements in the biota of Isle Royale is emphasized because . . . the majority of the species are those of the northeastern North American type. Whatever may be the explanation of the occurrence of these western and northwestern forms this far to the east, an important factor is, no doubt, the peneplain nature of the country, which probably formed an extensive highway for boreal forms along the ice margin during the retreat of the last ice sheet." Ruthven's assumption that the biota of Isle Royale migrated there in post-glacial times is undoubtedly correct, although the source of the plants, at least, need not have been the Rocky Mountains or the west coast, especially if Fernald's proposal is correct. Under any circumstances, the presence

¹ Van Hise, C. R. and C. K. Leith, The geology of the Lake Superior region, U. S. Geol. Survey Monogr. 52: 1-641, 1911.

² Thorpe, Frances J. and A. H. Povah, The bryophytes of Isle Royale, Lake Superior, Bryologist 38: 32-46, 1935.

³ Ruthven, A. G., An ecological survey in the Porcupine Mountains and Isle Royale, Michigan, Ann. Rept. Geol. Survey Mich., 1905: 17-55, 1906.

of Cordilleran species of plants upon Isle Royale is rather remarkable, as the island is known to have been completely submerged under one or more of the relatively recent glacial lakes. Dr. George Stanley (who is probably more familiar than anyone else with the ancient shorelines of Lake Superior) tells me that the conspicuous beaches of Lake Algonquin can be found on the very highest parts of the island, so that a very small part of it, indeed, could have remained above Lake Algonquin, and that part not high. Furthermore, the beaches made still earlier by Lake Duluth are, on the mainland across from Isle Royale, some 200 feet higher than the adjacent Algonquin beaches, so that if Isle Royale was uncovered by an ice sheet, it must have been submerged many feet below the surface of that ancient lake.

In spite of the antiquity of the Algonquin beaches, as shown by the enormous amount of differential uplift which they have suffered, and the still greater age of the lake Duluth beaches, they are almost recent as compared to the Maumee or Arkona lakes, or even to Lake Whittlesey, whose beaches are so conspicuous in southeastern Michigan. It appears that the present flora of Isle Royale must have arrived there, not in interglacial or early postglacial times, but much more recently, in post-Algonquin and pre-Nipissing times. Dr. Stanley says (unpublished manuscript) that there was some as yet unexplained hiatus between Lakes Algonquin and Nipissing, so that the correlation between the two lakes is not well known. It is only in this long and incompletely understood period when Isle Royale first really emerged from the high-level post-glacial lakes that the present flora could have begun to invade the island. It is by no means difficult to believe, however, that the first isolated islands to appear above the ice or the glacial lakes might have received their first plant migrants from relatively close nunataks such as those of the Keweenaw Peninsula (if. for the sake of argument, we accept Fernald's conclusion) rather than from south of the ice border.

The history of the post-glacial Great Lakes is still incompletely understood, and is without doubt infinitely more complex than the already involved current explanations. The story of plant migrations in the Great Lakes region is inextricably bound up with the geological history of these lakes, and is certainly just as complex.

Many papers have been written on the ecology of bryophytes, and the influence upon them of their environment. Much work has also been done on the associations of bryophytes, but almost completely without regard to the geological history of the species, or even to its distribution as a whole. There are a few species whose present distribution really seems to be influenced by at least the most recent glaciation. When the puzzling distribution of Bryoxiphium norvegicum (Brid.) Mitt. is analyzed, it appears that the species occurs only in areas which have escaped glaciation. The hepatic Frullania Bolanderi Aust. also has a remarkable distribution (Fig. 5). It is common on the west coast, but is also known from the unglaciated parts of the Gaspé Peninsula and from the highlands along the south shore of Lake Superior. In view of the small number of such species, the identification of a disrupted western element in the bryophyte flora of the Keweenaw Peninsula is probably important more as a simple demonstration that the distribution of bryophytes does parallel that of vascular plants, than as bearing on a possible lack of glaciation.

It has certainly not been commonly recognized that many species of mosses and hepatics have a significantly localized rather than a general distribution. Of course, there are so many exceedingly common or even weedy species, that "critical" distribution is usually obscured. From the distribution of such weedy bryophytes as Marchantia polymorpha L.² has come the popular belief in the wide and unlimited distribution and rapid dispersal of bryophytes. As a result, the field of bryogeography in North America has been almost completely neglected. Although several hundred papers have been published on the moss and hepatic floras of restricted areas, no one seems to have analysed the distribution of "critical" species (or any others) over the country as a whole. There are a few comparisons of the hepatic flora of North America with that of other continents, 3,4 but the exact identification of regional elements within this continent is not considered, in American literature, with the exception of some notable work done by Evans in New England and Bartram on the mosses of Central America and Mexico.

One commonly sees species labelled in lists or discussions, vaguely

¹ Steere, W. C., Bryoxiphium norvegicum, the sword moss, as a preglacial and interglacial relic, Ecology, 1937 (in press).

² Graff, P. W., Invasion by Marchantia polymorpha following forest fires, Bull. Torrey Bot. Club 63: 67-74, 1936.

³ Underwood, L. M., The distribution of Hepaticae of North America, Proc. Amer. Assoc, Adv. Sci. 39: 298-304, 1891.

⁴ Müller, K., Die Lebermoose Deutschlands, Oesterreichs u. d. Schweiz 2: 803-860, 1916.

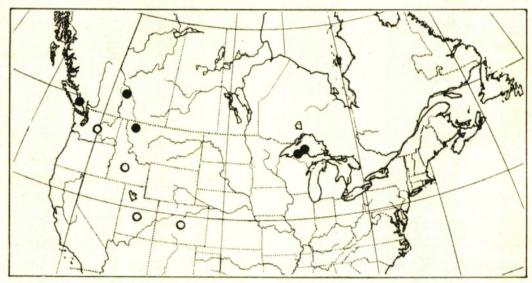


Fig. 3. Range of Pseudoleskea oligoclada.

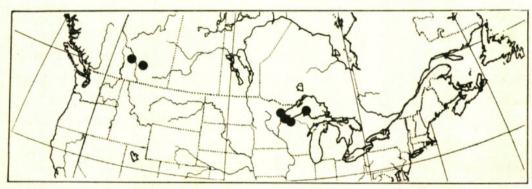


Fig. 4. American Range of Jungermannia Schiffneri.

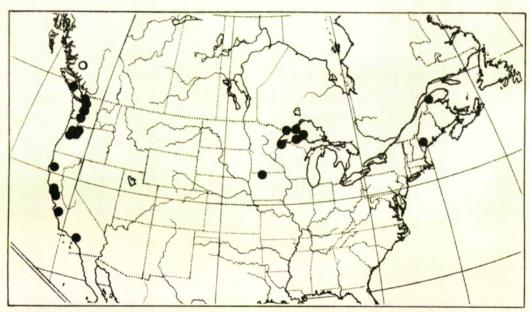


Fig. 5. Range of Frullania Bolanderi.

and often inaccurately, as "northern," "southern," etc. However, when the known geographical distribution of each species is carefully plotted on outline maps, much of the ambiguity and disorder is cleared up. It is not an overwhelming task to prepare such maps for the relatively small groups of the hepatics and mosses, and the illumination which they shed upon the distributional problems has more than repaid the writer's labor in making them. It has become clear that there are many well-defined floristic elements. It is exceedingly stimulating to discover, when reading over a paper on the distribution of flowering plants, in which the floristic elements are tabulated or mapped, that there are almost always exactly parallel species in the bryophytes. The situation is often masked by the presence of large numbers of non-critical, ubiquitous species.

Three floristic elements, each characterized by a disjunct distribution, can be identified tentatively in the Lake Superior region. Arctic species which here reach their southernmost point. Examples of a moss and a liverwort are Timmia austriaca Hedw. (Fig. 1) and Asterella Ludwigii (Schwaegr.) Underw. (Fig. 2). (2) Species which are almost strictly Cordilleran, and usually characteristic of high Examples of a moss and a liverwort are Pseudoleskea oligoclada Kindb. (Fig. 3) and Jungermannia Schiffneri (Loitles.) Evans (Fig. 4). (3) Species which are best known on the Pacific Coast, and usually characteristic of lower levels. An example of an hepatic is Frullania Bolanderi Aust. (Fig. 5). Another element, with which we are not directly concerned here, but which nevertheless is exceedingly significant in its distribution, is composed of Cordilleran species which are also found in "the" driftless area of Wisconsin, Iowa, Minnesota and Illinois. An example from the Hepaticae is Asterella saccata (Wahlenb.) Evans (Fig. 6).

It can be predicted with confidence, on the basis of studies and maps already made that many of the bryophytes will be found to fall into phytogeographic groups with as much precision as do the flowering plants, and furthermore, into the very same groups. The analyses will be possible only after the prolonged and careful collection of specimens in critical areas, and by determining centers of migration.

The topography of Keweenaw County is rather varied, so that a large number of different habitats are available for plants. One of the most conspicuous topographical features is the series of several parallel monoclinal ridges, with longitudinal valleys between them.

The ridges are usually relatively high, with a gradual slope to the north and generally a sheer cliff on the south side. The tops of most of the ridges are treeless and windswept; consequently almost barren of bryophytes. Two species which can be depended upon to occur in

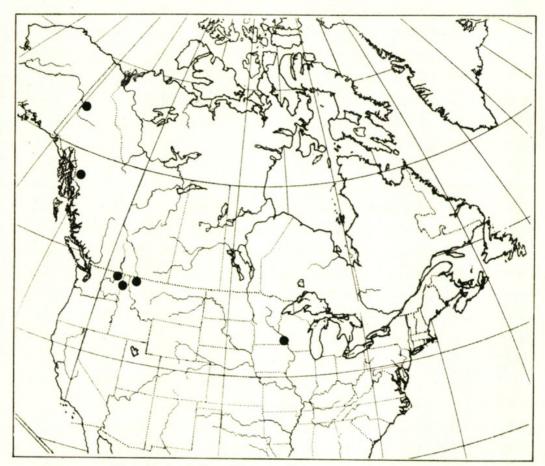


Fig. 6. American Range of Asterella Saccata.

such situations, however, are *Tortula muralis* Hedw. and *Rhacomitrium canescens* (Timm) Brid.

Some high ridge summits in Keweenaw County in addition to West Bluff (735 feet above lake level), which was so thoroughly discussed by Fernald, are East Bluff (726 feet) and Lookout Point (728 feet). The highest point in the county appears to be on an unnamed ridge just north of Gratiot Lake. The altitude of this point is given as 932 feet above lake level. Other high points are the two monadnocks, Mount Houghton and Mount Bohemia, with elevations of 877 and 867 feet, respectively. Most of these highlands have not been collected

¹ Board of County Road Commissioners, Road Map of Keweenaw County, blue print, 22 x 36 inches, 1934.

upon, because of their dryness, so that their bryophyte flora is almost completely unknown, although presumably of little interest.

The cliffs which are so prominent a feature of the linear ridges rather generally face to the south and receive maximum insolation. Consequently they harbor few bryophytes. The talus slopes below conglomerate cliffs are also relatively barren, partly because of their dryness and partly because of their mobility, although they are often well vegetated. The talus slopes of trap-rock cliffs, on the other hand, are among the most favorable habitats for bryophytes. Even the dry slopes exposed to the full force of the sun support xerophytes, as Andreaea petrophila Ehrh. and several species of Grimmia. On the shaded lower talus slopes, which have been invaded by the forest, are found many species of bryophytes in enormous quantities. great rock fragments are covered with thick mats of mosses and hepatics, and the chasms between the blocks are often bridged by a carpet suspended only at the margins, a condition which is apt to result in embarrassment or damage to the unwary collector. Perhaps the most productive trap-rock cliffs are those extending for many miles on either side of the settlement appropriately named Cliff. The most important species which were found here, all in quantity, were Metzgeria furcata (L.) Dumort., Tritomaria quinquedentata (Huds.) Buch, Orthotrichum strangulatum Schwaegr., Homalia Jamesii Schimp., Pseudoleskea oligoclada Kindb., Isopterygium Muellerianum (Schimp.) Lindb., and Rhytidium rugosum (Ehrh.) Kindb.

The habitats which are richest in species of bryophytes are the sheltered bays or "harbors" along the northern shore of the Keweenaw Peninsula. On the sheltered, shaded conglomerate and trap-rock shores of Agate Harbor, Copper Harbor, and the less easily accessible Horseshoe Harbor are often solid carpets of mosses and hepatics. At the water level and to a foot or so above it are mats of Leiocolea Gillmanni (Aust.) Evans [Lophozia Kaurini (Limpr.) Steph.], Scapania cuspiduligera (Nees) K. Müll., and Oncophorus virens (Sw.) Brid. Farther up on the rock ledges are Blindia acuta (Huds.) Bry. Eur., Hypnum arcuatum Hedw., Dicranoweisia crispula (Hedw.) Lindb., Brachythecium plumosum (Sw.) Bry. Eur., and Grimmia alpicola Hedw. var. rivularis (Brid.) Broth. Above the water level, but within the reach of spray and storm waves are species of a more mesophytic character. On the dry faces of the higher shore cliffs Leiocolea heterocolpa (Thed.) Buch, Saelania glaucescens (Hedw.) Broth., and Encalupta ciliata (Hedw.) Hoffm. are not uncommon.

In the moist forest along the lake shore, mosses and hepatics cover the ground and boulders in a thick mat. The most important species are Lophozia incisa (Schrad.) Dumort., L. longidens (Lindb.) Macoun, L. Hatcheri (Evans) Steph., L. Kunzeana (Hüben.) Evans, L. obtusa (Lindb.) Evans, L. attenuata (Mart.) Dumort., and Tritomaria quinquedentata (Huds.) Buch. The disjunct western species, Timmia austriaca Hedw., was locally common in a few places at the edge of the forest just above the rocky shore ledges. Most of the swamps and bogs were too dry to make satisfactory collecting or even survey work possible, so that the work in these habitats was postponed until a more favorable season.

(To be continued)

THE TYPIFICATION OF ACALYPHA VIRGINICA L.

C. A. Weatherby

ACALYPHA VIRGINICA has no original diagnosis in the Species Plantarum. It rests on citations from the Hortus Cliffortianus, Flora Zeylanica and Hortus Upsaliensis of Linnaeus, from Plukenet and from Gronovius. There is a specimen in the Linnaean herbarium, presumably there in 1753 and labelled by Linnaeus "1 virginiana." In the Hortus Cliffortianus, there is a brief original diagnosis, or rather phrase-name, insufficient to determine what Linnaeus had before him; but there is no specimen in the Clifford herbarium. There is no original diagnosis in the Hortus Upsaliensis. The citations from Plukenet and Gronovius are represented by specimens.

When I revised the group of A. virginica in 1927 I had seen none of the above specimens. I had before me the statement of Mueller Argovensis that the specimen in the Linnaean herbarium represented the plant of the Upsala garden and certain notes most generously lent me by Dr. S. F. Blake who had himself been interested in the group and who had looked up the material in the herbaria at London. These notes stated that although, as I pointed out, Plukenet's figure resembled rather A. virginica β intermedia Muell. (A. digyneia Raf.), the specimen back of it was actually A. virginica α genuina; also that Clayton 201, on which the Gronovian citation rests, was A. virginica

¹ Rhodora, xxix. 193-204 (1927).

² in DC. Prod. xv. pt. 2, 869 (1866).



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