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# CRITICAL PLANTS OF THE UPPER GREAT LAKES REGION OF ONTARIO AND MICHIGAN

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(Plates 352–379)

## Part I. The Pre-Wisconsin Flora of the Upper Great Lakes Region[1]

Ever since I learned through the distinguished student of the Pleistocene, Professor A. P. Coleman of the Royal Ontario Museum, that "Some suggestions have been made that parts of the north shore of Lake Superior and other high points on the Upper Lakes show little glaciation. On the Slate Islands [only station between the Rocky Mts. and Gaspé for *Dryas Drummondii*] some years ago I was surprised to find no evidence of glaciation"[2]; ever since Professor Coleman wrote these pregnant words I have yearned to see some of the country bordering the Upper Great Lakes. As a field-botanist, realizing the complete disagreement of the botanical evidence, of relic-colonies of remotely isolated or strictly endemic plants about the Great Lakes, and the current interpretation of many geologists, that the flora of the region has been completely wiped out by a wholesale very recent continental glaciation, the "suggestions" referred to by Coleman and his surprise "to find no evidence of glaciation" on the

[1] The substance of Part I was presented to the Royal Canadian Institute at Toronto on January 26 and to the New England Botanical Club at Boston on April 5.

[2] Coleman as quoted in Fernald, *Some Relationships of the Floras of the Northern Hemisphere*, Proc. Internat. Congr. Pl. Sci. ii. 1507 (1929).

Slate Islands in Lake Superior appealed to me. They were what I, as a botanist knowing something of the evidence supplied by the flora, would expect. However, except for the broad-visioned Coleman and one or two others, I could draw from most geologists no admission that any portions of the Upper Great Lakes region could


MAP 1. Availability for Occupation by Plants of North American Areas since the Paleozoic (*Map by* ALFRED W. LOTT).

possibly have passed unscathed through any of the several advances of the Pleistocene ice. The most extensive correlation of the plant-dispersal and geological history of that region is the detailed report of my friend, Gleason, on the *Vegetational History of the Middle West.*[1] There the orthodox interpretation is clearly stated, "the Wisconsin glaciers, which . . . flowed in a southwesterly direction into

[1] Gleason, Ann. Assoc. Am. Geogr. xii. 39–85 (1923).

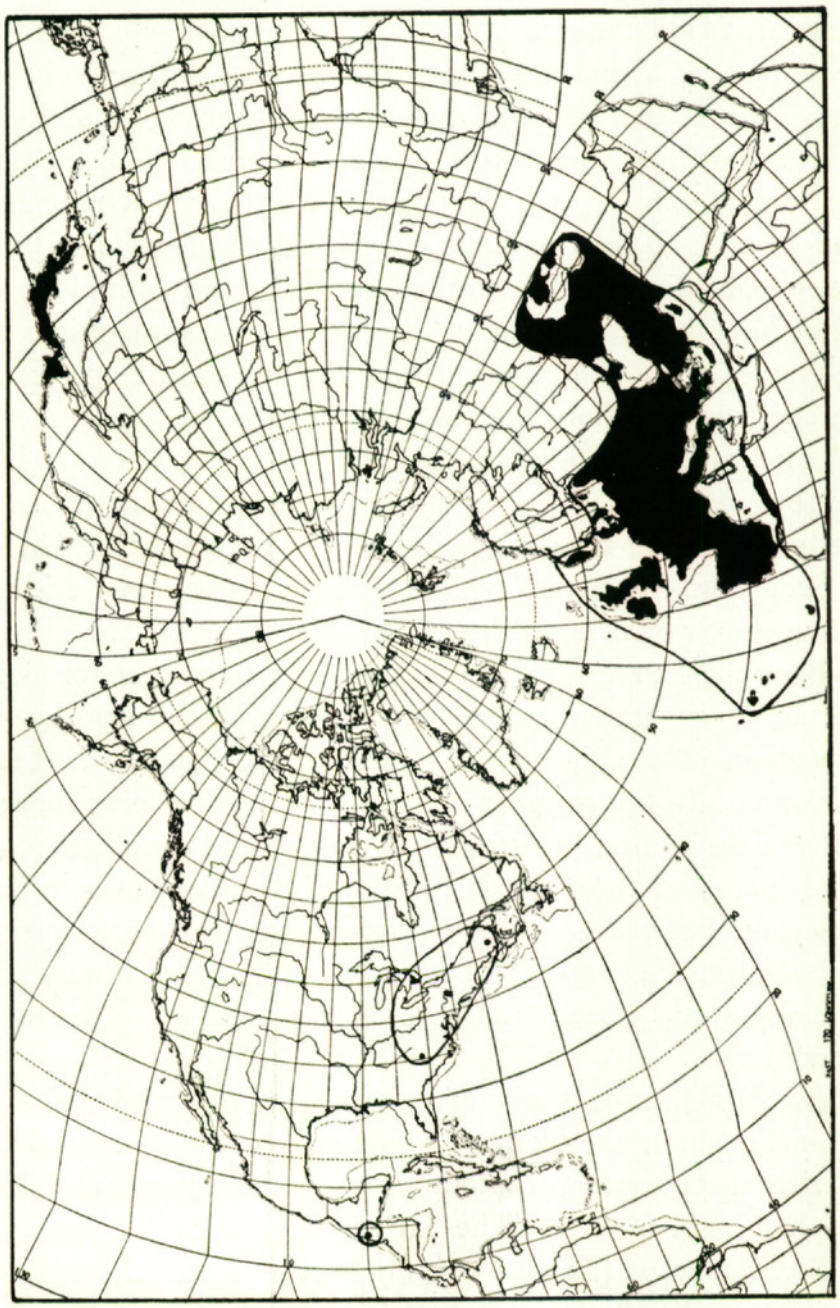
our area, wholly covering the state of Michigan."[1] The elements of the vegetation of the Middle West (including Michigan, where the author had long lived and studied) were enumerated: "THE FIVE ELEMENTS IN THE FLORA OF THE MIDDLE WEST.—. . . .the vegetation of the Middle West . . . is found to be composed of five elements, not of equal importance, centering respectively in the southern Appalachian Mountains, in the southern Coastal Plain and the Mississippi Embayment, in the Ozark Mountains, in the plains of Kansas and Nebraska, and in Canada east of the Great Lakes."[2] Gleason seems not then to have considered (or recognized) the one element which most appeals to my heretical mind as indicating that not all of Michigan was "wholly covered" by Wisconsin ice. I refer to the numerically small but historically significant species of the Pacific slope or the Cordillera which are isolated about the Upper Great Lakes (see MAPS 6–14, 17–20).

The need of much fuller collections of critical plants and a better knowledge of the critical areas in the terrain bordering the Upper Great Lakes was apparent. Consequently, when my enthusiastic (*pulsating* they would say) friends, Pease and Bean (A. S. Pease and R. C. Bean), asked me to recommend a good region for botanical exploration, I suggested the almost inaccessible (except by private boat) portions of the high north shore of Lake Superior and also the Slate Islands. In the summer of 1933 they made successful explorations at various points, centering on Jack Fish and Schreiber, and made a partial survey of the Slate Islands. A full series of the collections of Pease and Bean was most generously deposited in the Gray Herbarium, some species easily identified; others, not so simple, set aside for intensive study, species not heretofore recognized as growing near the Great Lakes.

In June, 1934, it was my great privilege to supply, along with Professor Coleman, the lecture-programme of the Botanical Society of America, meeting at Toronto and then going by automobile to the unique Bruce Peninsula. The latter region, long famous for its several relic-species (*Phyllitis Scolopendrium* (MAP 2), *Polystichum Lonchitis* (MAP 3), *Asplenium cryptolepis* (MAP 5), *Sagittaria cristata*, *Melica Smithii* (MAP 11), *Festuca occidentalis*, *Habenaria unalascensis*, *Goodyera decipiens*, *Draba lanceolata*, *Drosera linearis*, *Rubus parviflorus* (MAPS 14–22), *Epilobium leptocarpum* var. *Macounii*, *E. panicu-*

[1] Gleason, l. c. 62.
[2] Gleason, l. c. 54.

*latum*, *Aster ptarmicoides* var. *lutescens*, *Adenocaulon bicolor* (MAP 9), etc.), far-isolated from the main areas of the species, was, necessarily in view of the large and diversely interested (and uninterested) party,



MAP 2. World-Range of PHYLLITIS SCOLOPENDRIUM.

shown us at only a few spots readily accessible to an auto-cavalcade. The botanists of the University of Toronto, notably Professors P. V. Krotkov and Thomas M. C. Taylor and their associates, have for some years been concentrating work on the region; and Dr. Stebbins

of Colgate University recently published[1] his interpretation of the flora and notes on some of the specialties. As to recent glaciation of the Bruce Peninsula and adjacent areas (Grey County, etc.), those of us who had the superlative advantage of riding through the region with Coleman enjoyed his clear exposition, that the lower levels were in many areas most certainly invaded by Wisconsin ice and that the comparatively recent terraces of the Great Lakes were there well displayed; but, and this is the significant point, the highest outcrops of the Niagara escarpment there often display the undenuded and deeply rotted features which seem to indicate that the Wisconsin glaciation left them as nunataks (ice-free areas surrounded by glacial fields).

I am aware that to Stebbins "it seems unlikely that these nunataks were large enough to support a Canadian woodland flora."[2] He may be right; none of us were there to see. Nevertheless, it is most difficult to explain the extreme localization of the Hart's Tongue Fern in Bruce, Grey and Durham Counties unless it had some near-by source from which to spread. The species, *Phyllitis Scolopendrium* (L.) Newm. (*Scolopendrium vulgare* Sm.), has a disrupted range (MAP 2) which was achieved before the Pleistocene: the Mediterranean region from Iberia and northern Africa eastward to northern Persia, thence northward into west-central Asia, southern Scandinavia, Scotland and Ireland; the Macronesian Islands; Japan; and 5 very remote and very restricted areas in North America. Our plants are always on limestone or dolomite: a small colony in a ravine of the Meduxnakeag valley in western New Brunswick; a larger colony with a number of restricted stations "on shaded limestone cliffs and depressions in Onondaga and Madison counties," New York; a tiny colony in a cave near the southeast corner of Tennessee; and, 1450 miles further south, in the mountains of tropical Chiapas, an isolated variety. The one extensive area in North America is on the Bruce Peninsula and adjacent outcrops of dolomite in Ontario. There the Hart's Tongue is a rather frequent and locally abundant fern of fissures and depressions of wooded dolomite. So long as the American plants were considered identical with the European there lingered the possible interpretation that they had been recently brought from Europe and had found a few favorable habitats in which they could spread. Close examination of the American plants shows, however, that they differ in some very essential characters not found in the European plants.

[1] Stebbins, *Some Observations on the Flora of the Bruce Peninsula, Ontario*, RHODORA, xxxvii. 63–74 (1935).

[2] Stebbins, l. c. 69 (footnote).

In the more detailed sections of this paper I am treating them as two geographic varieties (PLATE 355), although the differences are such that some students may prefer to consider them as distinct species. Now, if the strictly North American variety of *Phyllitis Scolopendrium* reached the Bruce Peninsula region in post-Wisconsin time, whence did it come? The New Brunswick and New York stations are all within the area which we are taught to believe was overridden by Wisconsin ice and therefore present the same problem; and the Tennessee station is very tiny, deeply hidden and remote. If the American *Phyllitis Scolopendrium* has been migrating about New Brunswick, Ontario and New York since the Wisconsin (in present time) why have its abundant spores failed to make successful landings on hundreds of thousands of acres of equally available limestones and dolomites in eastern Canada and the northern States? In Bruce, Grey and Durham Counties the fern would rank as frequent and locally abundant and it there grows in the Alleghenian forest with species which abound all over Alleghenian America. Its isolation of colonies is not consistent with post-Wisconsin migration; it seems to me to be a pre-Wisconsin relic, belonging with the other relics to be discussed below.

Dr. Pease was so gratified by the success of himself and Bean in discovering puzzling plants or in extending ranges on the north shore of Lake Superior that he invited me to join him, after the Toronto meeting, for a brief trip to the south shore of Lake Superior, in Michigan. Accordingly, on June 27, I met him and my son, Henry G. Fernald, who accompanied us as alternate driver, photographer and general helper, at North Bay on Lake Nipissing. From there we drove, stopping when inviting territory was found or when some unrecognized plant was seen, by the regular automobile route through "the Soo" (Sault Ste. Marie), thence by the conventional route across the Upper Peninsula as far as the road would take us, nearly to Keweenaw Point. Our brief stops were numerous; but two areas received more attention than others: Cloche Peninsula and Great Cloche Island, on the north shore of Lake Huron, where we spent one very crowded day (with a brief but rather unproductive invasion of much burned Manitoulin Island[1]); and Keeweenaw County, the still gratifyingly wild and natural (except for old mines) tip of the Keweenaw Peninsula, where we had nearly four full days of absorbing botanizing. Much more time could have been advantageously given to the region

[1] See Fassett, RHODORA, XXXV. 389 (1933).

but appointments at home forced us to leave many promising spots unvisited.

This necessary restriction of the time at our disposal forced us to forego the great pleasure it would have been to have accepted the invitations we had received from botanical associates in various parts of Michigan to visit them. If we had used our limited four days in journeys to Lansing, Detroit, Ann Arbor and Douglas Lake, we should never have reached our primary objective, Keweenaw County. It is a real disappointment now to learn that, without swerving from our rigid programme, we might, after all, have combined our Keweenaw trip with a visit to one of the pioneer botanists of that region, Oliver Atkins Farwell, who, quite unknown to us at the time, has returned to the Peninsula (at Lake Linden) and has there renewed[1] his botanical explorations which began in the 80's.

From our non-geological and foreign viewpoint it was difficult for us to see that *everywhere* through this region late Pleistocene activity had been so universal or so uniform as we had been led by many geologists to believe; or that the reputed wholesale and very recent submergence of the land under the lake-water had everywhere left visible evidences. In some areas, for instance much of the region north of Lake Huron, the denudation of the hills (PLATE 353) has been complete. In such tediously uniform country, with the vegetation consisting only of ubiquitous and rapidly invading or aggressive modern species (*Pteridium latiusculum*, *Athyrium angustum*, *Osmunda Claytoniana*, *Pinus Banksiana* and *resinosa*, *Panicum linearifolium*, *Oryzopsis pungens*, *Deschampsia flexuosa*, *Calamagrostis canadensis*, *Glyceria striata*, *Carex aenea*, *Crawfordii*, *gracillima*, *leptonervia*, *flava* and *arctata*, *Iris versicolor*, *Salix humilis*, *Populus tremuloides*, etc.), there was no temptation to linger. When we conscientiously tested such areas, which experience had long ago taught us were "no good," we came back empty-handed or, to save our faces and not be defeated, with a specimen or two "for locality."

In other sections, like portions of the Cloche Peninsula, some areas were thoroughly denuded, others had the ledges of greenstone, quartzite or limestone covered with a frost-broken mantle of unremoved debris *in situ*. In such a place botanizing, as always in spots of weathered rock, was productive: *Festuca occidentalis*, *Carex concinna*, *Habenaria unalascensis*, *Salix serissima*, *Polygonum Douglasii*, *Geum triflorum*, *Astragalus neglectus*, *Lathyrus ochroleucus*, *Epilobium*

[1] See Farwell, RHODORA, xxxvii. 164 (1935).

*paniculatum, Coreopsis lanceolata*, etc. The lowermost levels of Cloche Peninsula and of Great Cloche Island are very flat and, obviously, only recently emerged from the Lake. Their scoured and washed surface is a limestone pavement, often of a beautifully regular cancellate pattern. On this flat limestone pavement of the lakeside or in marshy depressions and savannahs upon it the widely dispersed calcicolous flora of the Great Lakes region luxuriates: *Equisetum variegatum, Agropyron trachycaulum, Eleocharis compressa, Carex Garberi* (described in this paper), *eburnea, Crawei*, etc., *Juncus balticus* var. *littoralis, J alpinus* vars., *Tofieldia glutinosa, Allium Schoenoprasum* var. *sibiricum, Comandra Richardsiana, Arenaria stricta, Potentilla fruticosa* and *Anserina, Polygala Senega, Rhus canadensis, Hypericum Kalmianum, Viola nephrophylla, Shepherdia canadensis, Satureja glabra, Castilleja coccinea, Lobelia Kalmii*, etc.

Similarly, on the Keweenaw Peninsula evidences of extensive and profound work by glaciers were obvious at many low levels; but at the higher levels, such as West Bluff (PLATE 352), 735 feet (224 m.) above Lake Superior, where the deeply weathered trap and conglomerate cliffs stand well above the levels of evident glacial till and denudation, subaerial decay and weathering have obliterated any apparent traces of glaciation, if there ever were any. The day we visited West Bluff (July 4th) the wind blew strongly up the face of the Bluff, which stands surrounded by a vast area of continuous forest. So rotted was the material of which it is composed that we were forced to fight our way against clouds of wind-blown sand and dust of purely local origin. In many areas of unquestioned Wisconsin glaciation which I have visited in New England and eastern Canada the conglomerates have not reached this state of decay, although they are in a region of quite as severe climate as that of northern Michigan. One would suppose that the thousands (probably hundreds of thousands) of years which have elapsed since the subaerial disintegration of West Bluff began should have sufficed to blow away all the dust, but every visitor there, when the wind sweeps up the Bluff, still gets his full "peck of dirt." Such a condition is not consistent with Wisconsin denudation as we understand it farther east.

Likewise, on the crests of more sheltered woodland bluffs and low ridges at elevations of 500 feet (150 m.) or even less above Lake Superior, such, for instance, as those on the north side of the "Mountain Drive" between West Bluff and Eagle Harbor, the angular and slow-weathering debris (PLATE 354), which forms the undisturbed mantle

(just as if it were in the unglaciated southern Alleghenies), is striking evidence to a botanist, at least, that, while a late Pleistocene glaciation rendered botanically uninteresting such country as that shown in PLATE 353, it did not destroy the ancient vegetation on the higher areas (PLATES 352 and 354) of Keweenaw County. In fact, it seemed to us that the later glaciers, just as in eastern Canada, New York and New England,[1] had worked only on the lower levels; and on the Keweenaw Peninsula, as well as in Quebec, the Maritime Provinces and New England, precipitous bluffs and high ridges must have diverted the ice-flow, just as they can be seen to do today in many regions where continental glaciations still prevail.

It is significant, then, that Keweenaw County has a greater assemblage of remotely isolated relic-species and isolated endemics than any other botanically explored region between the Gaspé cliffs and mountains and The Driftless Area of Wisconsin, Minnesota, Iowa and Illinois. Here occur, usually isolated by many hundreds of miles and often by more than a thousand, colonies of such species as *Woodsia oregana*, *Polystichum Lonchitis* (MAP 3), *Asplenium montanum* (MAP 4), *A. cryptolepis* (MAP 5), the Rocky Mountain *Pteridium* (to be discussed later, known between the mountains of Quebec and the Black Hills only on the Bruce Peninsula and in northern Michigan), *Melica* (or *Bromelica*) *Smithii* (MAP 11), *Festuca occidentalis*, *Corallorrhiza striata*, an endemic variety of *Chamaerhodos Nuttallii* (MAP 10) of the Rocky Mountains and the Great Plains, *Crataegus Douglasii*, *Potentilla Blaschkiana*,[2] *Rosa Lunellii*,[2] *Ceanothus sanguineus* (MAP 6), *Chimaphila umbellata* var. *occidentalis*, *Vaccinium membranaceum* (MAP 7) and *ovalifolium*, *Collinsia parviflora*, *Adenocaulon bicolor* (MAP 9), an undescribed *Arnica* of the cordilleran series *Cordifoliae* and several others.

To some, who are unable to visualize the Pleistocene glaciation in the region from Newfoundland to the Great Lakes as NO MORE SEVERE THAN THAT WHICH NOW COVERS GREENLAND, WHERE AN EXTENSIVE TEMPERATE FLORA NOW OCCURS AT THE ICE-FREE MARGIN OF THE CONTINENTAL ICE-CAP, it apparently seems impossible that life could have persisted in the lower latitude of the Great Lakes region through the Pleistocene. It should not be overlooked, however, that the flora of approximately 400 species of vascular plants, which today grows on the ice-free areas of Greenland, is at the margin of a continental

[1] Extended discussion of this feature of New England and adjacent area will appear elsewhere.

[2] See Farwell, l. c.

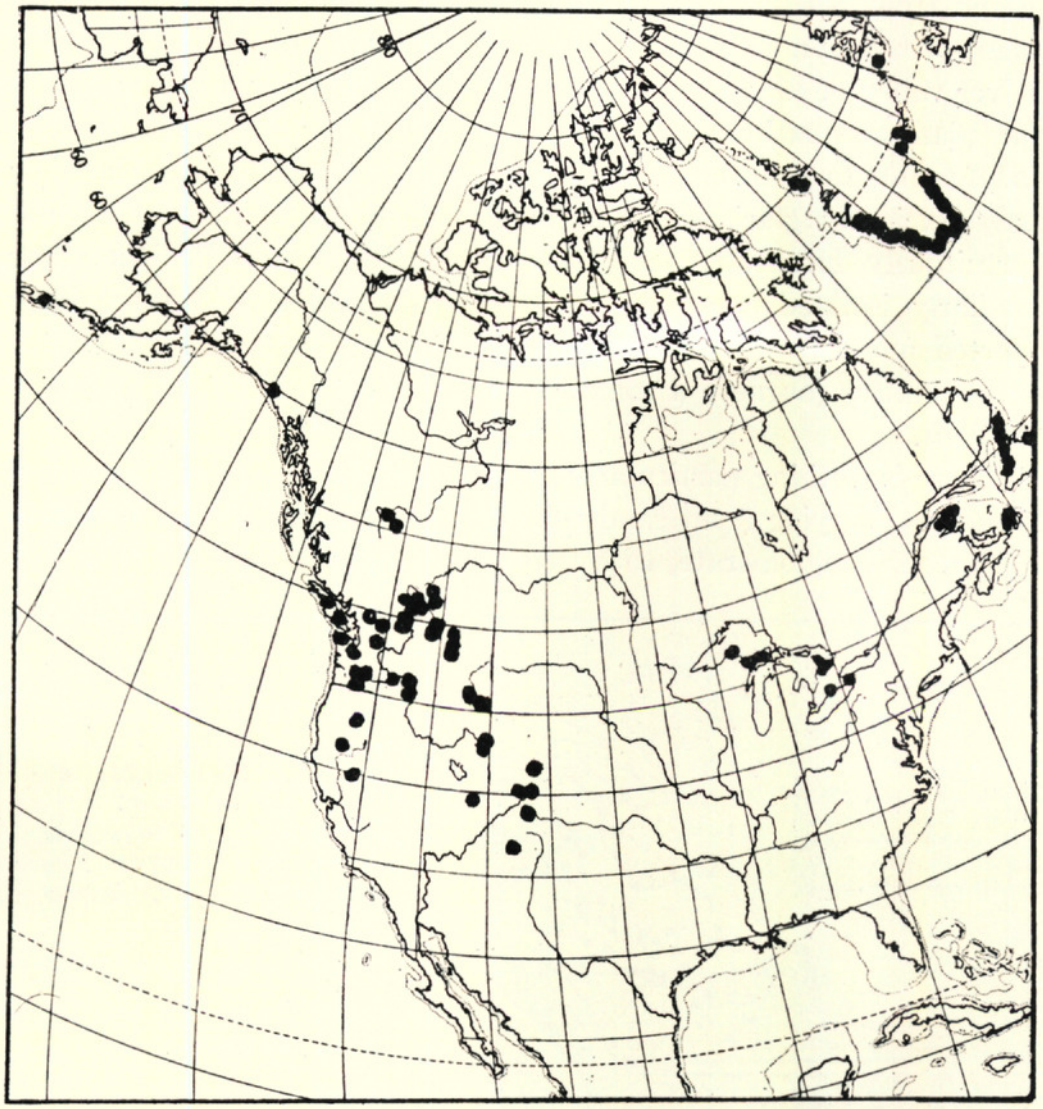
glacier which is often said to be as extensive as any which formerly occupied the median latitudes of North America. It should further be noted that, of the whole vascular flora of Greenland essentially one-third (131) of the species likewise grow as usually common plants in Michigan, Wisconsin, Minnesota or adjacent Ontario. This large (surprisingly large to those who have not previously realized it) group of temperate species, which in Greenland are not seriously disturbed by the proximity of a continental glaciation, includes such very familiar plants as *Woodsia ilvensis, Cystopteris fragilis, Thelypteris Phegopteris* and *Dryopteris, Equisetum arvense* and *sylvaticum, Lycopodium annotinum, clavatum* and *complanatum, Sparganium angustifolium, Potamogeton pusillus, gramineus* and *filiformis, Triglochin palustris, Trisetum spicatum, Deschampsia flexuosa, Eriophorum angustifolium, Carex brunnescens, canescens, deflexa* and *capillaris, Juncus bufonius* and *filiformis, Tofieldia minima, Habenaria hyperborea, Listera cordata, Corallorrhiza trifida, Alnus crispa, Arenaria lateriflora, Stellaria borealis, Ranunculus reptans* and *trichophyllus, Coptis groenlandica, Drosera rotundifolia, Potentilla palustris* and *tridentata, Viola Selkirkii, Epilobium angustifolium* and *palustre, Circaea alpina, Hippuris vulgaris, Cornus canadensis, Pyrola secunda, Ledum groenlandicum, Andromeda glaucophylla, Arctostaphylos Uva-Ursi, Vaccinium Oxycoccus, Menyanthes trifoliata, Utricularia intermedia, Galium triflorum* and *Linnaea borealis* var. *americana.* These are all plants which in much of temperate North America are looked upon as the dominant and progressive or rather ubiquitous species, plants which freely pioneer and readily take possession of newly available land. They have rapidly covered much of the territory which was under Wisconsin ice. They are not, therefore, in the same class as the next element of the living Greenland flora to be considered.

This is a more conservative group of species which shares Greenland with the Great Lakes area and other, usually scattered, regions of the Northern Hemisphere. In the Great Lakes region, as in most regions, they are localized or rare species, usually seeming like pre-Wisconsin relics there. They are mostly not pioneers today, but veterans. This list of conservatives contains the following: *Botrychium Lunaria* (K),[1] *Thelypteris Filix-mas* (K) and *fragrans* (K), *Polystichum Lonchitis,* MAP 3 (K), *Lycopodium Selago* (K), *Selaginella selaginoides* (K), *Phleum alpinum* (K), *Poa alpina* (K), *Carex Vahlii* (K) and *scirpoidea*

[1] The species of Greenland which occur as localized plants in Keweenaw County are indicated: (K).

(K), *Orchis rotundifolia*, *Polygonum viviparum* (K), *Stellaria longipes*, *Sagina nodosa* (K), *Ranunculus lapponicus*, *Braya humilis* (K), *Draba incana* (K), *Arabis Holboellii* (K), *Saxifraga aizoides*, *Aizoon* (K), and *tricuspidata* (K), *Pinguicula vulgaris* (K) and *Artemisia borealis* (K).

Such a very distinct and widely dispersed (ancient) but everywhere local fern as *Polystichum Lonchitis* (MAP 3), easily spread by wind-

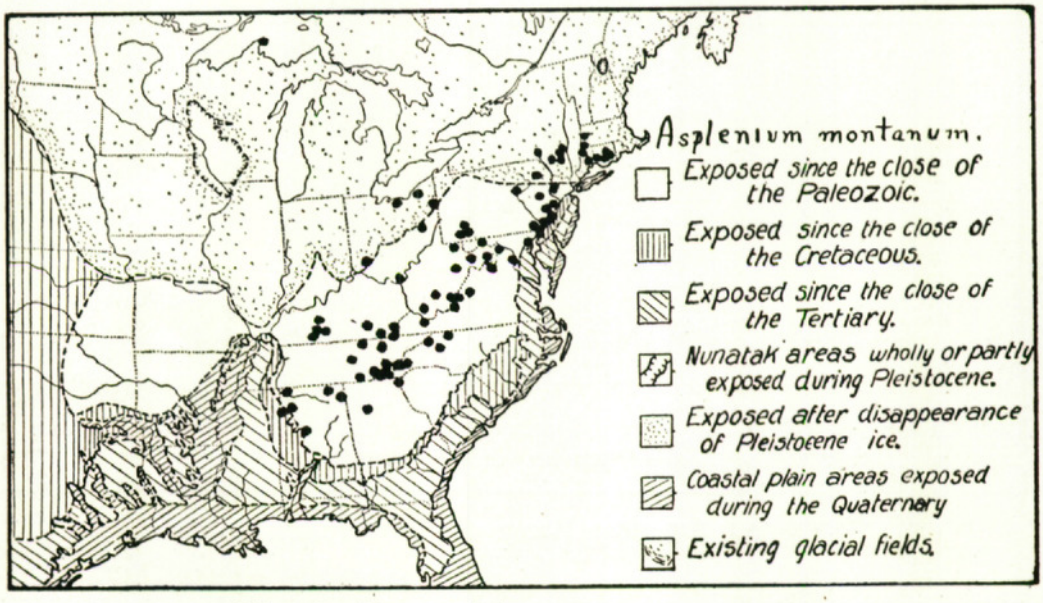


MAP 3. North American Range of POLYSTICHUM LONCHITIS.

borne spores but absent (presumably exterminated by glaciations, increased aridity and other depleting agencies) from large areas within its broad belt of distribution, occurs in Keweenaw County in the richest of deciduous woods, under the shade of ancient Alleghenian trees (like *Juglans cinerea* and *Tilia americana*) with *Adenocaulon bicolor* (MAP 9), of the *Sequoia* forests of the Pacific slope and of cold

ravines in the Black Hills, and *Melica Smithii* (MAP 11), also of the Pacific slope and of the Black Hills, sharing the woodland humus close-by. To me it seems quite illogical to argue that such species and the many other conservative and now unaggressive species with them have been arriving in post-Wisconsin times from different remote centers outside the area of general Pleistocene glaciation, like the Black Hills, 550 miles southwest of Lake Superior and available for plant-occupation since the Cretaceous (see MAP 1), or like the Snake River valley of Idaho, more than 1000 miles to the west and available for plant-occupation since the Jurassic. And it seems especially indefensible to maintain that such plants, coming from unglaciated or only anciently glaciated areas north, south, east and west, should fortuitously have all found the tip of Keweenaw Peninsula (or similarly isolated spots) in post-Wisconsin and should there have started successful colonies, without leaving in their long hypothetical cross-country journeys a somewhat continuous train of intermediate stations.

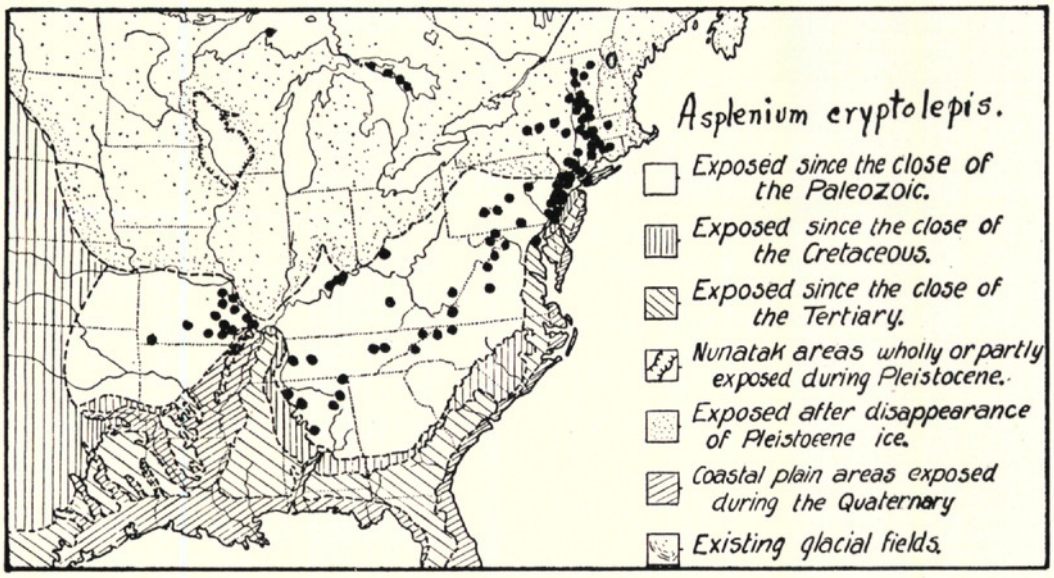
There is nothing particularly unique about the soils of Keweenaw County. Varying from sandstone and greenstones to silicious or to calcareous conglomerate, with frequent iron- or copper-deposits, they




MAP 4. Range of ASPLENIUM MONTANUM.

offer a fair average of diversified soils. Surely, the wind-dispersed spores of *Asplenium montanum* (MAP 4), a species of neutral to acid rock, must, during the last 30,000 years, have fallen somewhere, except locally in Ohio, between the ancient Appalachian core of the

continent and the tip of this remote Peninsula; but not one of the host of ever-enthusiastic hunters for ferns has succeeded in finding an intermediate colony north of Lake Erie. Surely, *Asplenium cryptolepis* (MAP 5), an inhabitant of limestone crevices, must scatter spores on the winds every summer. Why does it shun or fail to start on the limestones between southern Ohio and central New York on one edge of its range and the Bruce Peninsula region and Keeweenaw on the

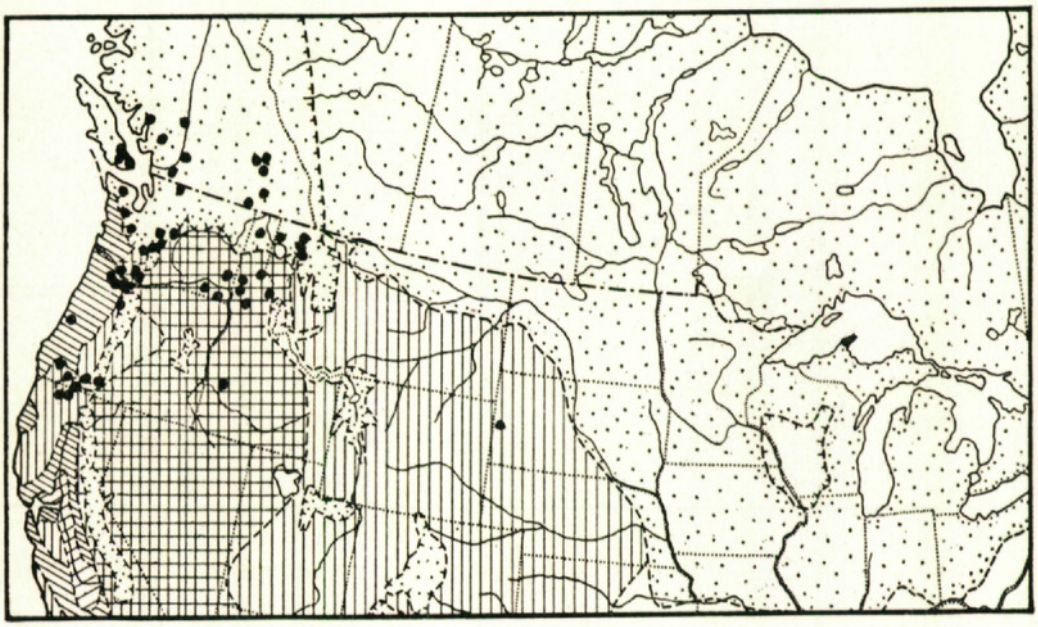



MAP 5. Range of ASPLENIUM CRYPTOLEPIS.

other? There are plenty of limestones in the broad interval but *Asplenium cryptolepis* has not been taking possession of them!

Surely, *Ceanothus sanguineus* (MAP 6), one of the most characteristic large shrubs of the Pacific slope (northern California to Vancouver Island and the Cascades of southern British Columbia, eastward across Idaho into northwestern Montana, with a single record from the Black Hills), if it migrated by means of its heavy, rounded seeds (which roll down- not up-hill) to Keweenaw County in post-Wisconsin time, could have found some dry slope or crest or arid bluff somewhere between western Montana or southwestern South Dakota and the dry bluffs and stony woods (PLATES 352 and 354) of Keewenaw where it grows. It is a tall and handsome shrub, generally known in the Northwest as "Wild Lilac." Why has it not been generally found between western Montana and Keweenaw, if, as some would have us imagine, it has been rolling its large seeds up and over the Rocky Mountains and across the Plains in search of Keweenaw Point in post-Wisconsin time?

Or take *Vaccinium membranaceum* (MAP 7), the "Huckleberry" of the Upper Peninsula of Michigan and especially of Keweenaw. It is there that it is gathered and made into the conserve which reaches the fashionable tables of Great Lakes cities. Having edible berries, it is doubtless locally spread by various animals in northern Michigan. But west of there it is known in typical form (the one in Michigan) only beyond the continental divide. If it is a post-Wisconsin arrival in northern Michigan why, during its imagined migration from west of the Rocky Mountain axis, did it fail to find some place to occupy

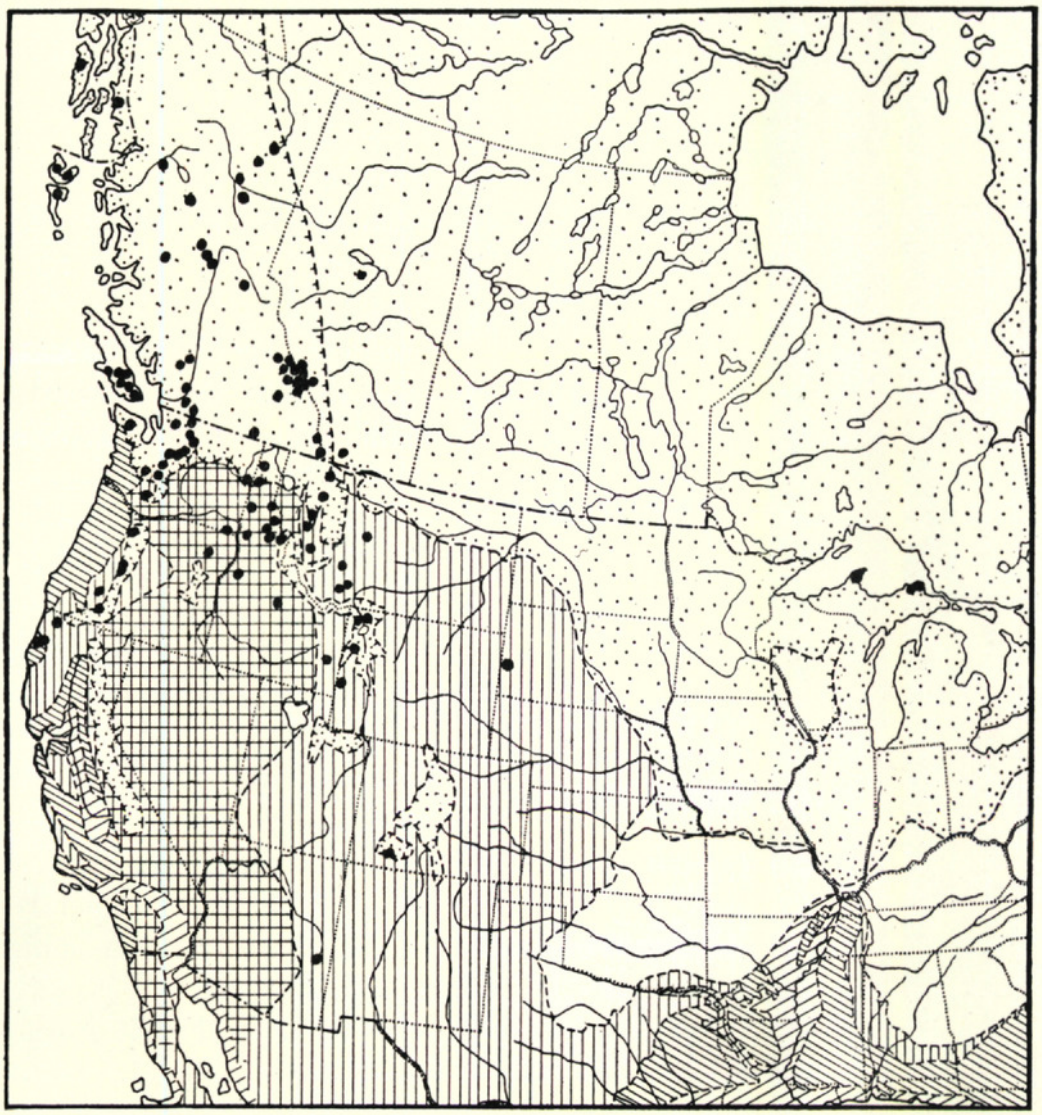


MAP 6. Range of CEANOTHUS SANGUINEUS.

before it reached Lake Superior? It has a xerophytic smaller-leaved variety (sometimes considered a different species, *V. globulare* Rydb.) localized in the Rocky Mountains, south to Arizona; but east of the Rockies and the Black Hills it is quite unknown (and as a shrub bearing edible berries it would be known if present) except on the Upper Peninsula. It there abounds in the dry woods and on slopes of such areas as shown in PLATES 352 and 354.

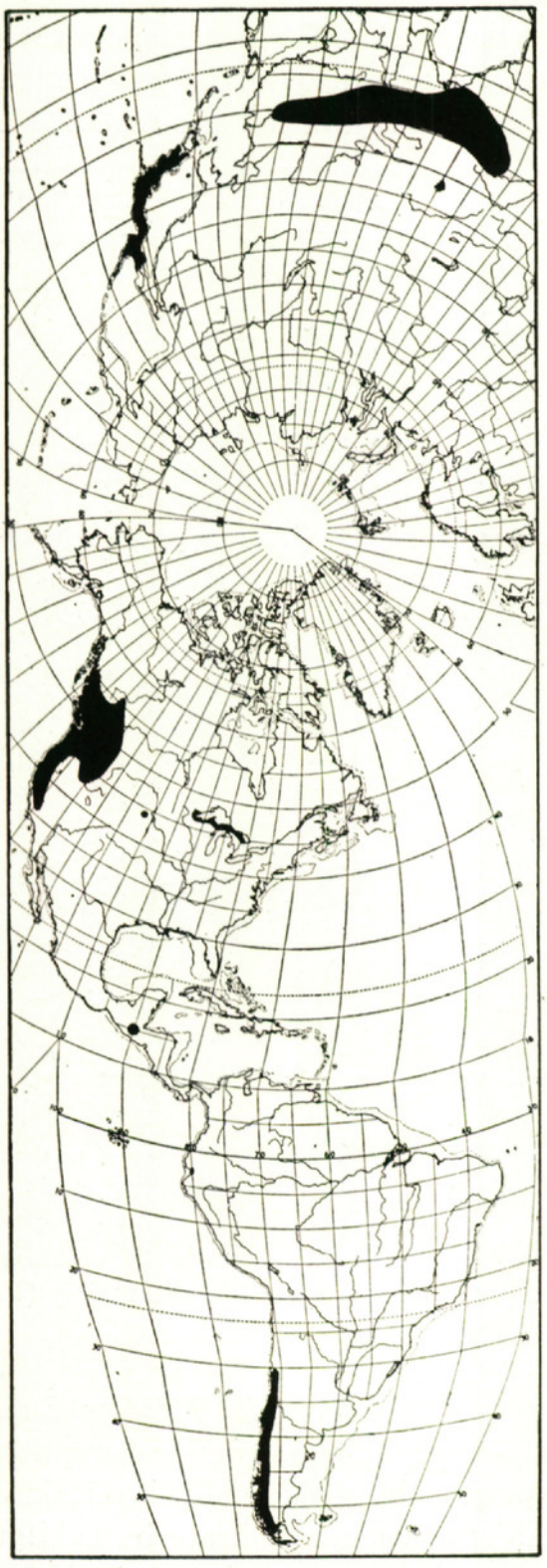
*Adenocaulon* (MAP 8) is a genus very much older than the Wisconsin glaciation. It has five or six species: *A. adhaerescens* Maxim. and *A. himalaicum* Edgew. of the ancient floras of eastern and south-central Asia; *A. chilense* Lessing, of Chile, and possibly a second Chilean species; a recently discovered species in the mountains of Guatemala (*fide* S. F. Blake); and *A. bicolor* Hook. *Adenocaulon bicolor* (MAP 9), the North American representative of this ancient genus, has three

areas: from California to southern British Columbia, eastward to northwestern Montana; valleys of the Black Hills; and from northern Minnesota to the Bruce Peninsula. It belongs in a family which has many modern weeds; but in a tribe (*Inuleae*) which has a remarkable



MAP 7. Range of VACCINIUM MEMBRANACEUM; the small-leaved variety (*V. globulare*) in the Rocky Mountains.

percentage of local endemics (species of *Antennaria, Leontopodium*, etc.). It is most emphatically not a weed. The geographic disruption of the genus indicates that it is comparatively old; and it is certainly significant that many of the Californian labels indicate its habitat there as being frequently under redwoods ("among redwoods," "Mariposa Big Trees," "*Sequoia gigantea* region," "among redwoods"), that Gray, in the *Botany of California*, should have given its habitat



MAP 8. Range of the Genus ADENOCAULON.

as "Redwoods," and that Greene, in *Flora Franciscana*, should explicitly describe its habitat as "Redwood forests of the Coast Range." It also grows in other forests, but its frequent association with ancient *Sequoia* and its occurrence on the Pacific Slope or in the Black Hills, largely in areas which had their present floras developed in pre-Pleistocene time, indicate that it is a plant of early, rather than of post-Wisconsin dispersal. *Adenocaulon bicolor* has achenes with one of the best adaptations for easy dispersal, glandular processes; nevertheless, it has failed to occupy any of the broad area between northwestern Montana and the Lake Superior-Bruce Peninsula country, except the ancient Black Hills, where Over records it as "rare in moist ravines."

If it be said that *Adenocaulon* requires moist woodland and, therefore, was unable to get a start in the broad areas between the continental divide and the Black Hills, and thence to Lake Superior, it may be pointed out that one of its associates in Pacific Slope-Great Lakes disruption of range, the "Salmon Berry" of the West, the

*Photo. H. G. Fernald.*

West Bluff, Keweenaw Peninsula.

*Photo. H. G. Fernald.*

DENUDED HILLS, NEAR WASAPITEI, SUDBURY DISTRICT, ONTARIO

*Photo. H. G. Fernald.*

UNDISTURBED MANTLE OF ROTTED ROCK, MOUNTAIN DRIVE, KEWEENAW PENINSULA.

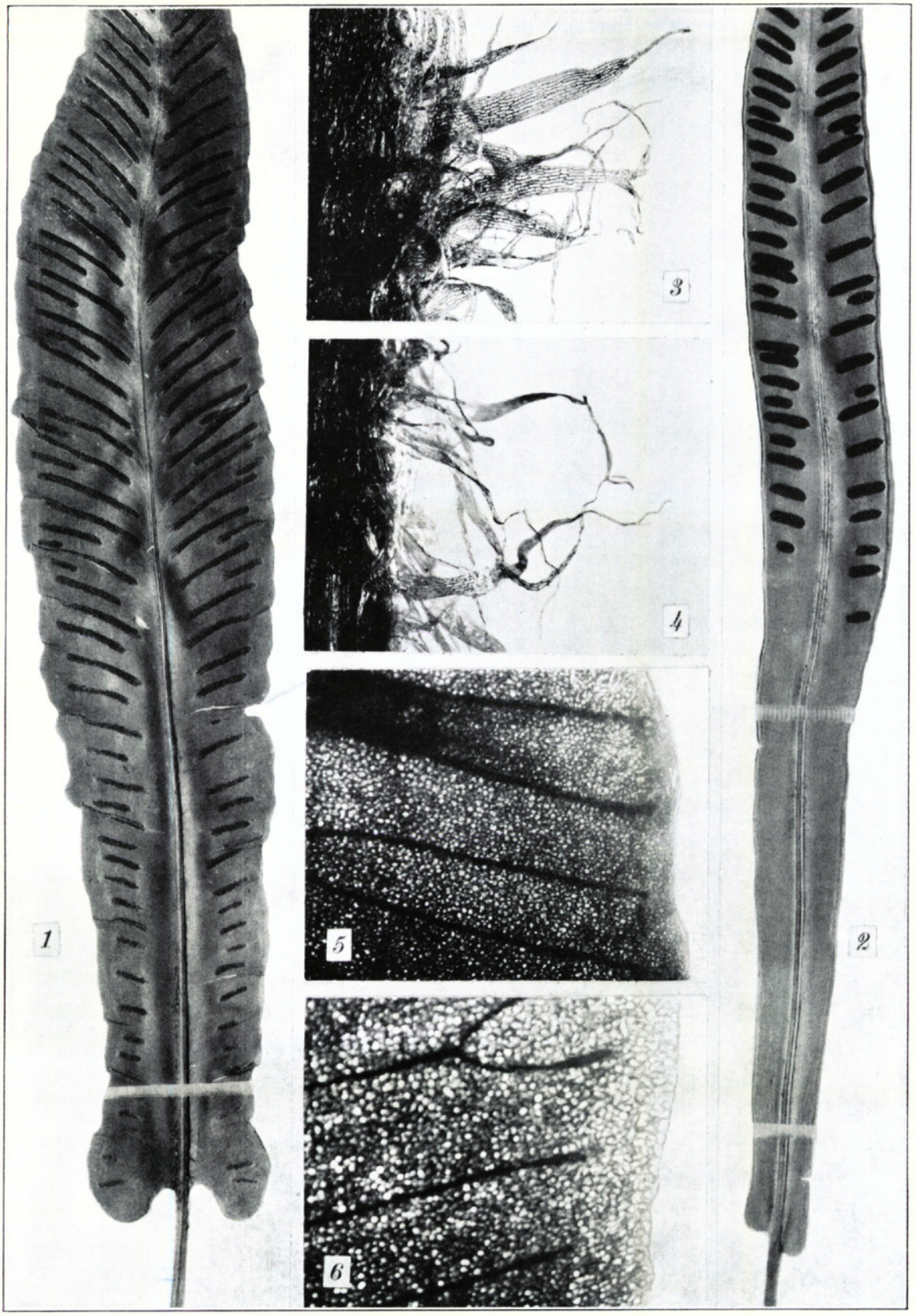
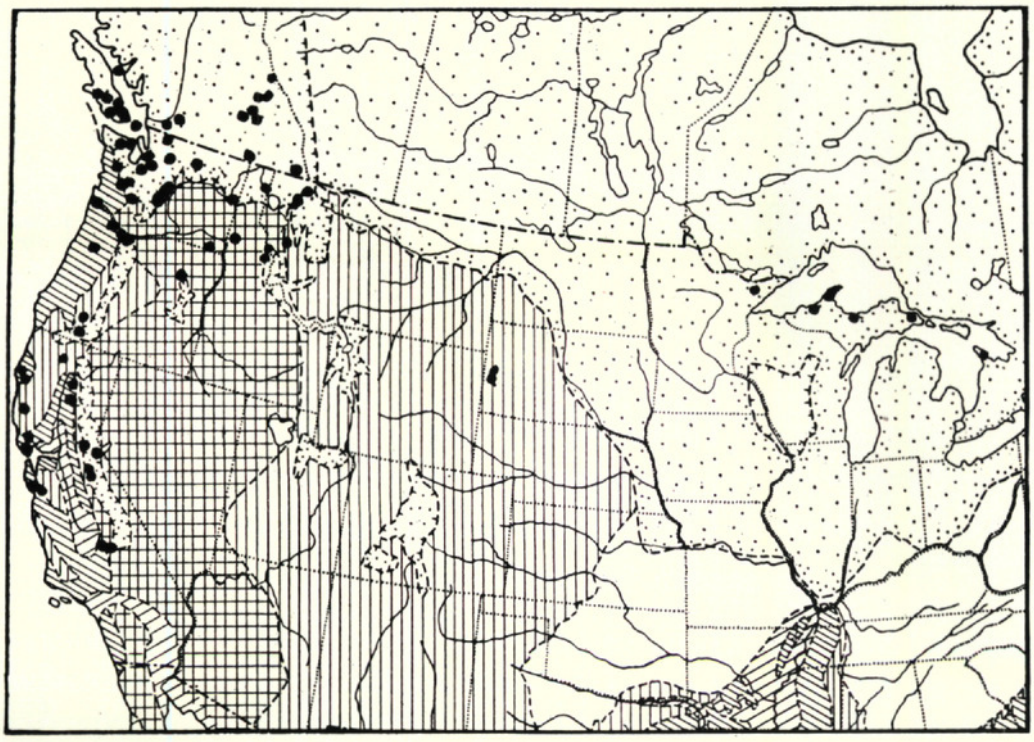



*Photo. E. C. Ogden.*

PHYLLITIS SCOLOPENDRIUM: FIG. 1, frond, × ½, from Ireland; FIG. 3, scales of stipe, × 10, from Ireland; FIG. 5, venation, × 10, from Savoy.

Var. AMERICANA: FIG. 2, frond, × ½, from New York; FIG. 4, scales of stipe, × 10 from Ontario; FIG. 6, venation, × 10, from New York.

"Thimble-berry" of Lake Superior, *Rubus parviflorus* (MAPS 14–22, PLATES 363–365), has cordilleran varieties in cool and damp forested cañons all along the Rocky Mountains into Mexico, as well as in the Black Hills. And it certainly cannot be said that *Ceanothus sanguineus*, *Asplenium montanum* and *A. cryptolepis* are intolerant of some aridity; and surely *Chamaerhodos Nuttallii* (MAP 10, PLATE 366), which occupies the arid and windswept crests, crevices and talus of West

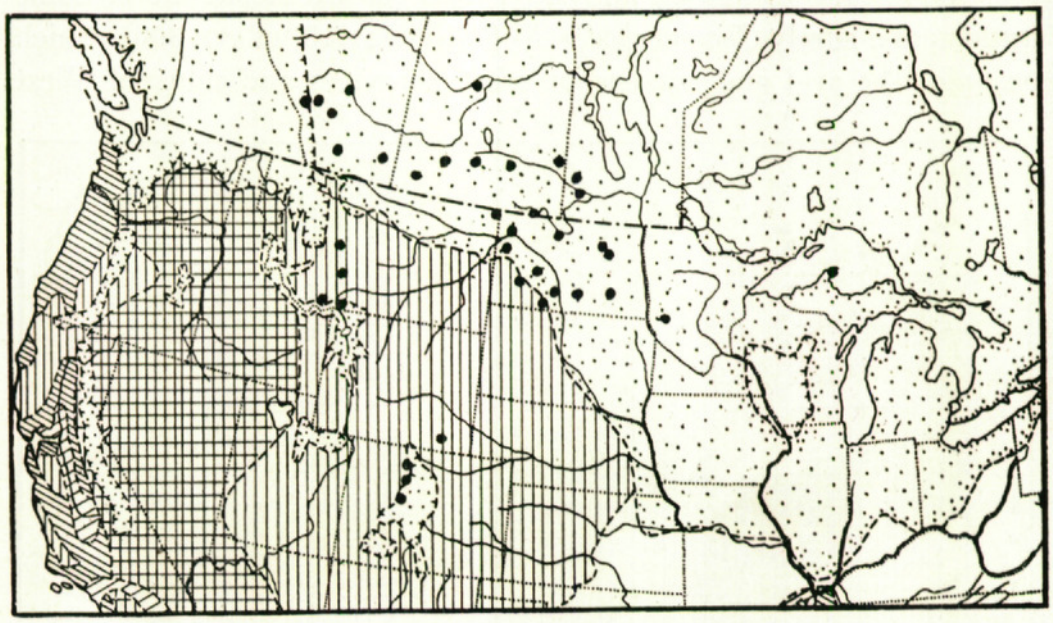


MAP 9. Range of ADENOCAULON BICOLOR.

Bluff, along with the cordilleran *Carex Rossii* Boott, *Woodsia oregana*, *Collinsia parviflora* and several other western types, is a xerophyte, and so is the misnamed *Potentilla pensylvanica* of the Cordillera and the Great Plains, growing with them. The type of *Chamaerhodos Nuttallii* came from "the highest gravelly hills" of the Mandan region; but the Keweenaw plant, also of "the highest gravelly hills," has been long enough isolated from the nearest area of the species (375 miles to the west, in western Minnesota) to have developed a marked varietal difference (PLATE 366).

The fixing of such a difference requires time, much more time than many modern laboratory experimenters imagine; and, certainly, the complete morphological segregation of a species from its geographically remote allies takes, except in the cases of hybrid-blends, a time

much longer than post-Wisconsin. In the ancient and long-weathered mantle shown in PLATE 354 we find *Ceanothus sanguineus, Collinsia parviflora* and several other isolated plants; but in the shaded gravel near-by the most interesting plant is an undescribed and very distinct



MAP 10. Range of CHAMAERHODOS NUTTALLII; var. KEWEENAWENSIS on Keweenaw Peninsula.

*Arnica* (PLATE 380), which is related only to a series of cordilleran species. Its nearest relative, *A. cordifolia* Hook., is unknown east of the Black Hills; the other members of the § *Cordifoliae*, as recognized by Rydberg (N. Am. Fl.) are restricted to the mountains from Alberta to Utah and westward.

One of the most elementary principles of the history of vegetation is that the species which make up the natural associations of plants successfully migrate together, not helter-skelter, into country favorable to them and, once occupying the territory, make "closed associations," *i. e.* they take such possession that later invaders have no entry, except as the natural and primitive habitat is disturbed (by clearing, plowing, land-slides, etc.). It will be noted from the maps that the western types which are isolated about the Upper Great Lakes are, in the Black Hills, in the Rocky Mountains or on the Pacific slope (south of north-central Washington, northern Idaho and northern Montana), in country which they undoubtedly occupied before Pleistocene time. They extend northward slightly into the region of the Cordilleran glaciation. The latter region, however, was un-

questionably quite as available to plant-occupation in the Pleistocene as are the ice-free forelands and cliffs of Greenland and Novaya Zemlya today. Here are the words of Chamberlain and Salisbury: "The whole Cordilleran ice-sheet was the product of a confluence of mountain glaciers deploying on the intervening plateau; but there appears to have been plateau glaciation not solely dependent on contributions of ice from the mountains. . . . The northern lobes descended the valleys tributary to the Yukon. . . . On the west, the plateau ice-cap seems to have sent tongues of ice through the gaps in the coast ranges at many points, and to have discharged thence into the Pacific. . . . Much the greater part of the 4,000,000 square miles of the ice-fields lay on the plains of Canada and in the upper Mississippi valley."[1] There is no more reason to suppose that the plants of the Pacific slope under discussion have invaded southern British Columbia since the waning of the Pleistocene valley- and plateau-glaciers than there would be to insist that Ellesmereland, Greenland, Spitzbergen, Novaya Zemlya, Switzerland, Glacier National Park, the Malaspina Glacier (covered with heavy forest) and the valleys of southern New Zealand are now destitute of vegetation. Everyone knows that they are not so.

Consequently, the occurrence of such plants on the Keweenaw Peninsula, in or adjacent to habitats where there are no obvious glacial drift or large transported boulders and where the long-continued subaerial weathering has produced a loose carpet or crust of angular gravel *in situ*, forces me to the conclusion that this region, like some others about the Upper Great Lakes, did not suffer a complete extermination of its flora in the Pleistocene, at least during the later glacial developments called the Wisconsin glaciation. In 1925, still retaining a naïve faith in what I had been taught but realizing that the considerable relic-flora about the Upper Great Lakes needed explanation, I wrote: "All geologists whom the author has consulted are in agreement, that the shores of the Great Lakes were all eroded or covered in the Wisconsin glaciation and even that some of the region (Isle Royale, for example) has been submerged beneath the surface of the lakes. It would, therefore, be hardly justifiable to account for these plants of the Pacific slope isolated on Isle Royale, Isle St. Ignace, Keweenaw Peninsula or Bruce Peninsula, as relics which there outlived the Wisconsin glaciation."[2] I then suggested

[1] Chamberlain & Salisbury, Earth Hist. iii. 330–333 (1906).

[2] Fernald, *Persistence of Plants in Unglaciated Areas of Boreal America*, Mem. Amer. Acad. xv. (Mem. Gray Herb. ii), 317 (1925).

that they might have survived in the Driftless Area to the southwest and thence later migrated to Lake Superior.

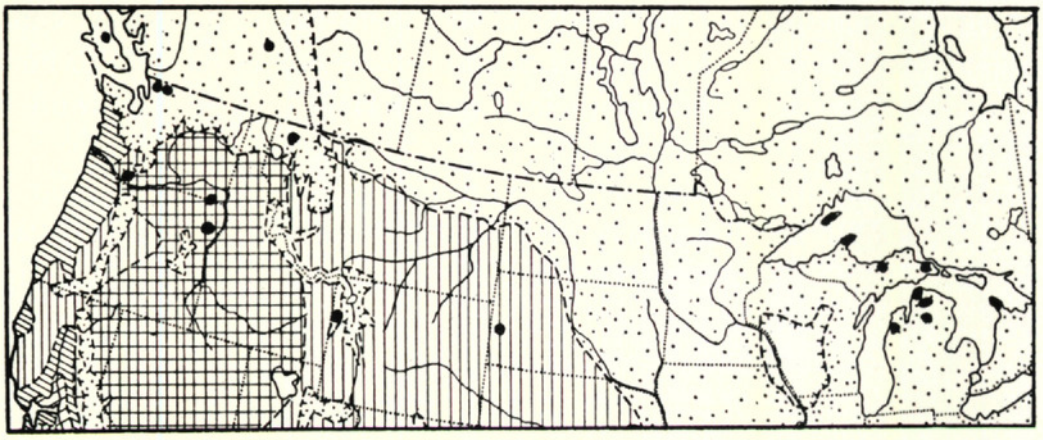
Fassett,[1] however, finds it difficult to conceive several of the isolated species of northern Michigan and northern Wisconsin (*Rubus parviflorus, Arenaria macrophylla, Goodyera decipiens, Osmorhiza divaricata,* etc.) as having been in The Driftless Area without leaving colonies in habitats there which would be favorable for them. Fassett continues: "The apparently preglacial flora of northern Wisconsin and neighboring territory has its affinities with the Rocky Mountains, with the Gaspé Peninsula, and with the Torngat Mountains. There is another relic flora in The Driftless Area . . . which has its affinities mostly with the region south of the area of Wisconsin glaciation. . . . This distinct relic flora, practically confined to The Driftless Area, with several endemics, having its affinities in unglaciated areas to the westward or to the southeastward, may be clearly interpreted on the basis of lack of glaciation in southwestern Wisconsin. But the occurrence in the Lake Superior region of plants of the Rocky Mountains and of the Gulf of St. Lawrence area is a problem that cannot at the present be solved with any degree of certainty."

Our experience in Keweenaw County leads us to the belief that Fassett's contention is well founded and that the isolation of plants in the Lake Superior region, some from the Rocky Mountains or the Black Hills (or from the Gaspé region), some from the arid high Plains, some from the Ozarkain and Appalachian plateaus (but none, I think, with distinctive Torngat relationship, except species of broad boreal dispersal), does not require the Pleistocene invasion by them of The Driftless Area. The Driftless Area (with emphasis on THE) was not the only haven in the Great Lakes region during the Wisconsin glaciations. The high bluffs of Keweenaw evidently were not denuded by Wisconsin ice and, consequently, they served as centers on which many species survived (just as hundreds of species are living today on the available slopes and ice-free forelands of Greenland or of Novaya Zemlya), some later to spread slightly to lower levels and, in case of readily dispersed species, like *Rubus parviflorus* (MAPS 14–22), *Vaccinium ovalifolium* and *membranaceum* (MAP 7), *Osmorhiza divaricata, Goodyera decipiens, Melica Smithii* (MAP 11), *Festuca occidentalis* and *Adenocaulon bicolor* (MAP 9), to extend over much of the Upper Lakes region, while annuals, such as *Polygonum Douglasii, Epilobium paniculatum* and *Collinsia parviflora,* tend to become local weeds.

[1] Fassett, RHODORA, xxxiii. 226. 227 (1931).

Other species, such as *Asplenium montanum* (MAP 4) and *cryptolepis* (MAP 5), *Carex Rossii*, *Ceanothus sanguineus* (MAP 6), *Chamaerhodos Nuttallii* (MAP 10), *Potentilla Blaschkiana* and the endemic *Arnica*, have apparently not spread far or at all from their old havens.

These observations on the Keweenaw Peninsula inevitably suggest that similar conditions will be found in other sections of the Upper Great Lakes area, especially where elevated and vertical escarpments and sharp bluffs stand high above the general level.[1] So long as the botanist meekly accepts, without personally checking, the proposition that *all* the Upper Great Lakes region was completely under Wisconsin ice (and to a depth sometimes said to be 2,000 feet!) and then under the water of the Lakes he will fail to solve this striking



MAP 11. Range of MELICA SMITHII.

phytogeographic problem. If he will visit the high bluffs and escarpments and himself SEE the conditions, he is likely to find that the bluffs of Keweenaw are not alone in lacking the abundant transported drift with which orthodox geology has blanketed them. He is likely to find that their crests and slopes have, instead, a rotted and angular crust or deeply weathered mantle *in situ*. It will then be demonstrated that there were in the Upper Great Lakes region SEVERAL DRIFTLESS AREAS, limited in extent but sufficient to have maintained colonies of the formerly wide-spread and somewhat generalized Tertiary flora, species which, in areas of active Wisconsin glaciation, were eliminated in favor of a younger and more aggressive series of plants.

I realize that the current interpretation of many ecologists favors

[1] One such area has been reported to me. It is hoped that its discoverers and explorers will soon give an account of it. Two others, where Wisconsin activity seems to have been slight, are awaiting examination.

an arid ("xerothermic") climate following the Wisconsin glaciation and a migration then into the areas which had been covered by Wisconsin ice of a flora which has subsequently become segregated or disrupted by a post-Wisconsin climatic change. Personally "I am from Missouri" regarding this proposition. If *Ceanothus sanguineus* (MAP 6), *Woodsia oregana*, *Carex Rossii* and other western xerophytes are interpreted as relics of colonies which extended across the Great Plains to Keweenaw in the reputed early arid spell, why have they so completely disappeared from the great arid stretch of Plains, with their bluffs and crests, which should now suit them? They are accompanied in Keweenaw by western mesophytes, such as *Melica Smithii* (MAP 11), *Corallorrhiza striata*, *Vaccinium membranaceum* (MAP 7), *Rubus parviflorus* (MAPS 14–22), *Adencaulon bicolor* (MAP 9) and others. Would those who believe in the "xerothermic" post-Wisconsin climate maintain that these mesophytes also crossed the Plains and reached Keweenaw during their "xerothermic" stage? I cannot believe it.

Altogether these recent short excursions of New Englanders about the Upper Great Lakes have yielded many species apparently little known or hitherto unreported in the region. In so far as they are yet worked out they are here reported; and in a few instances noteworthy species, although not collected by us, are specially discussed. The photographs of the terrain and of growing *Rubus parviflorus* here reproduced were taken by HENRY G. FERNALD. The maps of ranges have been prepared by my daughter, MISS KATHARINE FERNALD, with a contribution of data from the Ozark Plateau from JULIAN A. STEYERMARK. The smaller-scale base-map used for several species was prepared for me by the geologist, ALFRED W. LOTT. It is presented in full as MAP 1, which gives the necessary explanations. The other base-map of eastern North America carries its own explanation. The world-projection used is Goode's no. 201 Pc, copyrighted by the University of Chicago. The photographs of herbarium specimens and their details have been prepared by my student and special assistant, E. C. OGDEN. The expense involved in the preparation and reproduction of the plates and maps has been met in part from the Wyeth Fund of the Division of Biology, in part through a grant from the Milton Fund for Research, both of Harvard University.