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THE BERGEN SWAMP:

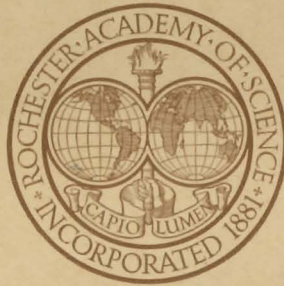
AN ECOLOGICAL STUDY

BY

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THE BERGEN SWAMP: AN ECOLOGICAL STUDY

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* The original draft of this paper was written by Mr. Stewart as a thesis in the department of Botany. In his absence from Rochester I have been asked to prepare his article for publication and to add my name as joint author. It will be understood that the credit for the actual field work and for writing the original paper belongs to Mr. Stewart. Having followed his work closely I have undertaken this revision, and have also contributed the photographs for the four Plates. I have avoided too extensive a condensation for two reasons: first, because of the special interest of local botanists, and second, I wish to retain as much as possible of the personal style and the flavor of discovery seen in the original paper. Any significant additions or amendments on my part will bear my initials. . . . W. D. M.

EXPLANATION OF PLATES

(Somewhat reduced from photographs taken by
Mr. A. A. Lohwater, July 28, 1936.)

PLATE I. View across open marl in rather an advanced stage. *Triglochin maritima*, *Deschampsia caespitosa*, *Cladium mariscoides*, *Scirpus caespitosus*, *Rhynchospora capillacea*. *Salix candida* on mound to left of camera. Pine-Hemlock forest in background.

PLATE II. Open marl close to woodland. *Solidago ohioensis* at left. *Juniperus horizontalis* in tuft at right. Small white pines and larches at border of woodland. Hemlock Knoll in background, large white pines conspicuous.

PLATE III. Border close-up to woodland. Open marl in foreground. Young Secondary Marl, with *Solidago Houghtonii*, *Zygadenus chloranthus*, *Potentilla fruticosa*, *Phragmites communis*. Small white pines and larches bordering the Pine-Hemlock.

PLATE IV. View along outer border of swamp. Less than a rod from mesophytic grassland to a mixture of swamp grasses and sedges, *Aspidium Thelypteris*, and *Typha latifolia*. The trees and shrubs in the background are a part of the Beech-Maple zone.



PLATE I



PLATE II



PLATE III



PLATE IV

INTRODUCTION

In the northern part of western New York there are several large swamps in various stages of transition from an open water condition to the climax forest. They form a series extending westward from the Genesee river toward Lake Erie and the Niagara river. Prominent among these is the Bergen Swamp, which is drained by the Black Creek into the Genesee river. So far as it has been possible to determine, no detailed ecological work has been done on the vegetation of this region, although the Bergen Swamp has long been known to both botanists and zoölogists as an ideal place for collecting purposes, and has been mentioned specifically in the papers by Bray (1930) and Zenkert (1934).

The present paper deals with the general flora of the Bergen Swamp; the ecological formations recognized, with their special floras and underlying soils; the geology of the region; the past history, present status and possible future of the swamp, and a comparison of Bergen with other swamp regions.

Such aspects as the water content of the soil, humidity, light and temperature studies, precipitation and wind records were not worked out in detail, although the government records of average temperatures and precipitation for this region have been used in comparing it with other general localities.

The field work on this problem was carried out during the more open seasons of 1932 and 1933. Fully labeled specimens collected by the writer have been deposited in the University Herbarium. In all cases the nomenclature used is that of Gray's New Manual of Botany, seventh edition.

The method finally adopted for the determination of soil acidity was that of the Youden Hydrogen Ion Determination apparatus as described and discussed by Clark (1922). Clark admits that there are possibilities for error in this method, but for general use it is preferable to the more common colorimetric methods because of its ease of operation and rapidity of determination, combined with a high degree of efficiency.

The writer wishes to express his sincere gratitude to Dr. W. D. Merrell, of the department of Botany, who suggested the problem and aided in the work; to Mr. Milton S. Baxter, curator of the Herbarium; to Dr. J. Edward Hoffmeister, of the department of Geology; and to Dr. Willard R. Line, of the department of Chemistry; also to many others for their helpful suggestions and criticisms.

DESCRIPTION OF BERGEN SWAMP

DEFINITION OF TERMS

Klugh (1913) recommends the following definition of terms used in ecological work, and they will be followed as closely as possible:

Community: an ecological division of unspecified rank ; sometimes called a *society* in a general sense.

Zone: a term used for specific communities which show a well marked concentric or parallel arrangement.

Formation (Grisebach): "a group of plants such as a meadow or forest that has a definite physiognomic character." The Brussels Congress (1910) defined the formation as "the actual expression of certain definite conditions of life. It is composed of associations that differ in their floristic composition, but are in agreement firstly with reference to conditions of habitat, and secondly as regards forms." Klugh, however, would abandon this term.

Association (Brussels Congress 1910): "an association is a plant community of definite floristic composition, presenting a uniform physiognomy, and growing in uniform habitat conditions. The association is the fundamental unit in synecology." Nichols (1923) defines the association as "a community of plants which occupy a common habitat," constituting a "qualitatively and quantitatively homogeneous plant society."

Succession: Clements (1905) defines succession as "the phenomena by which a series of invasions occur in the same spot."

Bog: Rigg (1922a) defines a bog as "that stage in the physiographic succession of an area during which its surface is entirely devoid of ordinary hard soil and is composed completely of living sphagnum moss, under which is to be found fibrous brown peat, composed mainly or entirely of partially decayed sphagnum." Kurz (1928) says that the bog is an area in which the soil is either acid or neutral. Transeau (1903) names *Drosera*, *Sarracenia*, *Larix* and *Vaccinium* as characteristic plants of bog areas.

Swamp: A swamp is usually defined as "soft low ground, saturated, but not usually covered, with water." Kurz says that the characteristic bog plants are absent in the swamp and the substratum is either alkaline or neutral.

The Bergen area is therefore correctly called a swamp because of its general physiognomy, although some portions of it are typically bog like.

GEOGRAPHICAL FEATURES OF THE SWAMP

The Bergen Swamp covers an area of several hundred acres in the townships of Bergen and Byron in the northeast corner of Genesee county, New York. The swamp is about twenty-four miles west of Rochester and about three miles west of the village of Bergen (Figure 1). It is readily accessible by highway at several points. In shape the swamp is generally oval (Figure 2), but on the northeast side its regularity is interrupted by Torpy Hill which runs in toward the center of the swamp. Baxter and House (1924) say of the region that it is an irregular marl bed surrounded by a dense cedar swamp. In dry weather the surface of the marl becomes desiccated and hard, while in wet weather the marl is soft and miry, but at no times dangerous. The original swamp had dimensions considerably greater than those of the present actual swamp, but in general the boundary lines of the older swamp may be recognized by the presence of some swamp vegetation in the otherwise climax forest.

GEOLOGY AND PHYSICAL CHARACTERISTICS OF THE SWAMP

H. L. Fairchild in his contribution to the "Plants of Monroe County" (Beckwith and Macauley 1894), gives the following information regarding this region. The Black Creek, which drains Bergen Swamp, empties into the Genesee River a few miles south of the city of Rochester. The general area along the south shore of Lake Ontario, in which region the swamp is located, is a plain sloping north to the Lake (Figure 1). The altitude at Bergen Swamp is 590-600 feet above tide level.

The rock strata underlying this region rest in a nearly horizontal position, without marks of any serious disturbance. The strike of the formations is nearly east-west and consequently the formations appear as bands running in that direction. These rock formations are however rarely seen at the surface, even in stream beds and other natural depressions, due to the large amount of till deposited upon them by the last glacier. Bergen Swamp proper lies over the shales of the Salina formation of the Silurian age.

Fairchild further states that during the millions of years following the deposition of the Devonian rocks this entire area was exposed to continuous atmospheric erosion and decay. At the close of the Pliocene the climate became considerably colder and resulted in accumulations of snow and ice over Canada and northeastern United States. The natural result of this change was that the former sub-

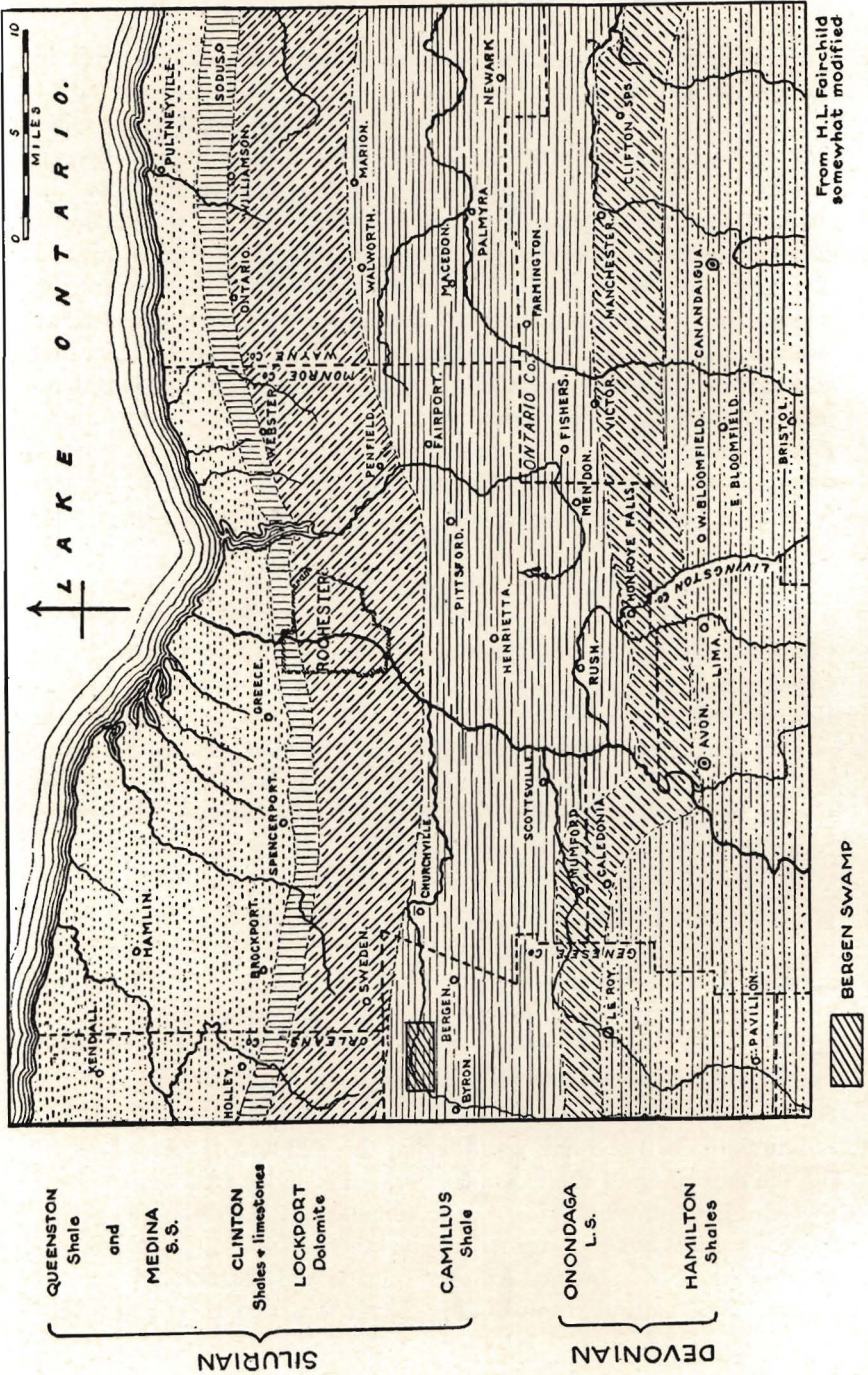


Figure 1. APPROXIMATE LIMITS OF STRATA

aërial denudation of the region became subglacial and consequently much of the superficial rock was crushed and removed to the south with the general movement of the glacier. As the glacier retreated to the north a considerable layer of glacial drift was left over this entire region, and it is this glacial drift which now covers the underlying strata.

As the glacier advanced southward over this general region not only did it remove the superficial rock southward but it also brought from the country north and northeast much of the rock of the Archaean area. Furthermore the lake which washed the foot of the retreating glacier deposited large amounts of silt and clayey soils. As a result of these several factors the glacial till and superficial soils which now overlie the regular subjacent geological formations are extremely heterogeneous. In the region of Bergen Swamp and other localities situated above the Salina shales the drift is comparatively thick and without question contains rocks that have been formed by action of atmospheric agencies, glacial action, stream drainage, lake action, and subsequent exposure following the retreat of the last glacier.

The influence of this geologic glacial activity on the soils and the plant life to be found on these soils will be considered later in the paper.

SOIL TYPES AT BERGEN SWAMP

In the main, two distinct soil types are recognizable. The first of these is the marl type previously mentioned as being located in the central portion of the swamp. Taylor (1928) mentions marl as being one of the two principal types of soil and as being a mineral soil. The marl is not a pure white, even at the surface of those portions least covered with vegetation. At the surface it is tinged with gray, while underneath it is a clean creamy white, the grayish tinge being the result of the decay of the vegetation formerly supported on the marl.

The second type of soil in the swamp is the humus soil, entirely surrounding the marl center. Taylor (1928) states that the humus soil differs from the mineral in that it can be burned off or otherwise destroyed, and also that it varies with the plant life growing upon it. At the Bergen Swamp the humus soil has many types and these are in practically all cases the direct result of the plant types growing in that exact locality. In general there are three main humus soils in the swamp. First, there is the humus that is formed

by decaying sphagnum and associated plants. This is one of the first types to extend out over the marl. The second type is the humus formed by the decaying conifers and the undergrowth associated with them. This humus is punky, acid, and succeeds the sphagnum humus. The third type is the humus formed by the decay of the deciduous vegetation. This is generally darker and sweeter, and is third in the line of succession. It must be remembered that there are variations and all degrees of intergrades of these humus types.

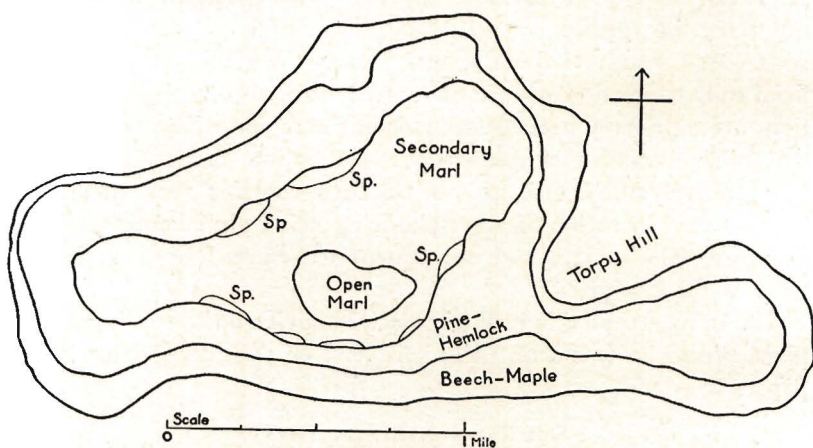


Figure 2. DIAGRAM OF VEGETATIVE ZONES—Sp., Sphagnum

VEGETATIVE ZONES

The following five zones and associations are to be found within the swamp. In each case a list of the dominant or subdominant species characteristic of the community is given.

1. *The Open Marl Association:* This occupies the center of several of the marl beds and has the following typical plants:

Juniperus horizontalis	Solidago Houghtonii
Phragmites communis	Solidago ohioensis
Cladium mariscoides	Deschampsia caespitosa
Scirpus caespitosus	Triglochin maritima
Lobelia Kalmii	Carex Crawei
Senecio Balsamitae	Carex flava

2. *The Secondary Marl Zone:* This zone is so called because, although it is likewise found on the marl, it represents a more ad-

vanced stage in the succession of the swamp vegetation. It is located around the edge of the open marl beds and in a few islands in the middle of some of these beds. Its type plants are:

<i>Larix laricina</i>	<i>Salix candida</i>
<i>Typha latifolia</i>	<i>Gaylussacia baccata</i>
<i>Cypripedium candidum</i>	<i>Ledum groenlandicum</i>
<i>Cypripedium parviflorum</i> var. <i>pubescens</i>	<i>Lonicera oblongifolia</i>

3. *Sphagnum Association*: This association is found on the marl in little humps, but more frequently near the edge of the marl where, at times, it forms a fairly large mat. In most cases it is practically a pure stand of *Sphagnum* and the other plants that may occur with it are *Sarracenia purpurea*, *Gaylussacia baccata*, and *Vaccinium Oxycoccus*.

4. *The Pine-Hemlock Zone*: This zone surrounds all the marl beds and in general extends back from the marl for a considerable distance. It varies considerably within itself between pine and hemlock domination, but not sufficiently, in the writer's opinion, to warrant dividing the zone into separate units. Type plants of the zone are:

<i>Taxus canadensis</i>	<i>Drosera rotundifolia</i>
<i>Pinus Strobus</i>	<i>Chamaedaphne calyculata</i>
<i>Thuja occidentalis</i>	<i>Chiogenes hispidula</i>
<i>Tsuga canadensis</i>	<i>Trientalis americana</i>
<i>Clintonia borealis</i>	<i>Mitchella repens</i>
<i>Coptis trifolia</i>	

5. *The Beech-Maple Zone*: This zone represents the climax association of this general area (Livingston and Shreve 1921). It forms the outer band of vegetation of the swamp and completely surrounds the zones already mentioned. Type plants of this association are:

<i>Aspidium marginale</i>	<i>Populus tremuloides</i>
<i>Aspidium spinulosum</i> var. <i>intermedia</i>	<i>Fagus grandifolia</i>
<i>Pteris aquilina</i>	<i>Ulmus americana</i>
<i>Osmunda cinnamomea</i>	<i>Claytonia virginica</i>
<i>Erythronium americanum</i>	<i>Acer spicatum</i>
<i>Smilacina racemosa</i>	<i>Acer rubrum</i>

The general location of these zones may be seen in Figures 2 and 3.

PLANT LISTS OF THE SWAMP

The following list includes all the species of plants which have been reported from Bergen Swamp in the papers by Beckwith and Macauley (1894) and Baxter and House (1924), together with those collected by the present writer. The list, as a result, is as complete as it is possible to compile at the present time, and only by further collection within the swamp can it be expected materially to enlarge the list.

The plants in this list are arranged by families, the latter being in the systematic order given in Gray's New Manual of Botany, seventh edition. Within each family the genera and species are listed alphabetically. The nomenclature throughout the paper being strictly according to Gray's Manual, the names of the authors of the species have been omitted from all lists except this systematic list.

COMPLETE SYSTEMATIC LIST

Polypodiaceae

- †*Adiantum pedatum* L.
- †*Aspidium Boottii* Tuckerm.
 Aspidium cristatum (L.) Sw.
- **Aspidium Goldianum* Hook.
- †*Aspidium marginale* (L.) Sw.
- **Aspidium noveboracense* (L.) Sw.
- †*Aspidium spinulosum* (O. F. Miller) Sw.
- †*Aspidium spinulosum* var. *intermedia* (Muhl.) D. C. Eaton.
- **Aspidium Thelypteris* (L.) Sw.
- †*Asplenium acrostichoides* Sw.
- **Asplenium filix-femina* (L.) Bernh.
- **Cystopteris bulbifera* (L.) Bernh.
- **Cystopteris fragilis* (L.) Bernh.
- †*Onoclea sensibilis* L.
 Phegopteris Dryopteris (L.) Fee
- †*Polystichum acrostichoides*
 (Michx.) Schott.
- †*Pteris aquilina* L.
- †*Woodwardia virginica* (L.) Sm.

Osmundaceae

- †*Osmunda cinnamomea* L.
- Osmunda Claytoniana* L.

Ophioglossaceae

- Botrychium ternatum* (Thunb.) Sw.
- **Botrychium virginianum* (L.) Sw.

Equisetaceae

- †*Equisetum arvense* L.
- Equisetum fluviatile* L.
- Equisetum hyemale* L.
- †*Equisetum pratense* Ehrh.

Lycopodiaceae

- **Lycopodium clavatum* L.
- **Lycopodium lucidulum* Michx.
- **Lycopodium obscurum* L.

Taxaceae

- **Taxus canadensis* Marsh.

An asterisk () preceding the name indicates a plant previously reported, and collected by the present writer; the sign "†" indicates a plant collected by the writer but not previously reported; names without these marks have simply been reported in previous literature.*

Pinaceae

- **Juniperus horizontalis* Moensch.
- **Larix laricina* (DuRoi) Koch
- **Picea rubra* (DuRoi) Dietr.
- **Pinus Strobus* L.
- **Thuja occidentalis* L.
- **Tsuga canadensis* (L.) Carr.

Typhaceae

- **Typha latifolia* L.

Sparganiaceae

- Sparganium eurycarpum* Eng.
- Sparganium simplex* Huds.

Juncaginaceae

- Scheuchzeria palustris* L.
- **Triglochin maritima* L.
- Triglochin palustris* L.

Gramineae

- Cinna arundinacea* L.
- †*Deschampsia caespitosa* (L.) Beauv.
- †*Deschampsia flexuosa* (L.) Trin.
- Leersia oryzoides* (L.) Sw.
- Panicum Lindheimeri* Nash
- **Phragmites communis* Trin.
- **Sorghastrum nutans* (L.) Nash
- Sphenopholis palustris* (Michx.) Scribn.

Cyperaceae

- Carex aurea* Nutt.
- Carex Bebbii* Olney
- Carex bromoides* Schk.
- Carex cephalantha* (Bailey) Fernald, var. *angustata* Carey
- **Carex Crawei* Dewey.
- **Carex cristata* Schwein.
- **Carex eburnea* Boott
- Carex filiformis* L.
- **Carex flava* L.
- Carex granularis* Muhl.
- Carex gynocrates* Wormsk.
- †*Carex hystericina* Muhl.
- **Carex leptalea* Wahl.
- Carex lupulina* Muhl.
- Carex lurida* Wahl.
- Carex Oederi* Retz.

Cyperaceae—cont'd.

- Carex pedunculata* Muhl.
- Carex polygama* Schkuhr.
- Carex Pseudo-Cyperus* L.
- Carex rosea* Schk.
- **Carex rostrata* Stokes
- Carex scabrata* Schwein.
- Carex siccata* Dewey
- Carex sterilis* Willd.
- Carex trisperma* Dewey
- Carex vaginata* Tausch.
- †*Carex vulpinoidea* Michx.
- **Cladium mariscoides* (Muhl.) Torr.
- Cyperus diandrus* Torr.
- Eleocharis acuminata* (Muhl.) Ness.
- Eleocharis rostellata* Torr.
- Eriophorum virginicum* L.
- Eriophorum viridi-carinatum* (Engelm.) Fern.
- Rynchospora alba* (L.) Vahl.
- **Rynchospora capillacea* Torr.
- R. capillacea* var. *leviseta* Hill
- Scirpus americanus* Pers.
- **Scirpus atrovirens* Muhl.
- **Scirpus caespitosus* L.
- †*Scirpus cyperinus* (L.) Kunth.
- Scirpus pauciflorus* Lightf.
- Scirpus Torreyi* Olney
- †*Scirpus validus* Vahl.
- Scleria verticillata* Muhl.

Araceae

- †*Arisaema triphyllum* (L.) Schott.
- Calla palustris* L.
- **Symplocarpus foetidus* (L.) Nutt.

Juncaceae

- Juncus acuminatus* Mich.
- Juncus balticus* Willd. var. *littoralis* Eng.
- Juncus brachycephalus* (Engelm.) Buch.
- Juncus bufonium* L.
- Juncus canadensis* Gay
- Juncus Dudleyi* Wiegand
- †*Juncus effusus* L.

Liliaceae

- †*Allium tricoccum* Ait.
- **Clintonia borealis* (Ait.) Raf.

Liliaceae—cont'd.

- †*Erythronium americanum* Ker.
- Lilium superbum* L.
- †*Maianthemum canadense* Desf.
- **Medeola virginiana* L.
- †*Polygonatum biflorum* (Walt.) Ell.
- †*Smilacina racemosa* (L.) Desf.
- **Smilacina stellata* (L.) Desf.
- Smilacina trifolia* (L.) Desf.
- **Tofieldia glutinosa* (Michx.) Pers.
- Trillium erectum* L.
- †*Trillium grandiflorum* (Michx.)
Salisb.
- Uvularia grandiflora* Sm.
- Uvularia perfoliata* L.
- †*Zygadenus chloranthus* Richards

Orchidaceae

- Arethusa bulbosa* L.
- Calopogon pulchellus* (Sw.) R. Br.
- Calypso bulbosa* (L.) Oakes
- †*Corallorrhiza maculata* Raf.
- Corallorrhiza trifida* Chatelain
- Cypripedium acaule* Ait.
- **Cypripedium candidum* Muhl.
- Cypripedium hirsutum* Mill.
- **Cypripedium parviflorum* Salisb.,
var. *pubescens* (Willd.) Knight
- Epipactis pubescens* (Will.) Eaton
- Epipactis repens* (L.) Crantz
- Habenaria blephariglottis* (Willd.)
Torr.
- Habenaria bracteata* (Willd.) R.Br.
- **Habenaria dilatata* (Pursh.) Gray
- Habenaria Hookeri* Torr.
- Habenaria hyperborea* (L.) R.Br.
- Habenaria orbiculata* (Pursh.)
Torr.
- Habenaria psycodes* (L.) Sw.
- Liparis Loeselii* (L.) Richard
- Listera cordata* (L.) R.Br.
- Microstylis monophyllos* (L.)
Lindl.
- **Pogonia ophioglossoides* (L.) Ker.

Piperaceae

- Saururus cernuus* L.

Salicaceae

- †*Populus alba* L.
- †*Populus balsamifera* L.
- †*Populus tremuloides* Michx.
- **Salix candida* Flugge
- Salix lucida* Muhl.
- Salix rostrata* Richards

Myricaceae

- **Myrica carolinensis* Mill.

Betulaceae

- Alnus incana* (L.) Moench
- †*Betula lutea* Michx.
- **Carpinus caroliniana* Walt.
- †*Ostrya virginiana* (Mill.) K.Koch

Fagaceae

- **Fagus grandifolia* Ehrh.
- **Quercus alba* L.
- **Quercus bicolor* Willd.
- †*Quercus rubra* L.

Urticaceae

- **Laportea canadensis* (L.) Gaud.
- †*Pilea pumila* (L.) Gray
- †*Ulmus americana* L.
- †*Ulmus racemosa* Thomas
- Urtica Lyalli* Wats.

Santalaceae

- †*Comandra umbellata* (L.) Nutt.

Aristolochiaceae

- †*Asarum canadense* L.

Polygonaceae

- Polygonum dumetorum* L.
- †*Polygonum Persicaria* L.
- Polygonum sagittatum* L.
- Rumex Brittanica* L.
- Rumex verticillatus* L.

Caryophyllaceae

- Stellaria graminea* L.
- Stellaria longifolia* Muhl.
- Stellaria media* (L.) Cyrill

Portulacaceae

- **Claytonia virginica* L.

Ranunculaceae

- †*Actaea alba* (L.) Mill.
- Anemone cylindrica* Gray
- Anemone virginiana* L.
- †*Aquilegia canadensis* L.
- **Caltha palustris* L.
- Clematis virginiana* L.
- **Coptis trifolia* (L.) Salisb.
- Hepatica acutiloba* DC.
- **Hepatica triloba* Chaix.
- Hydrastis canadensis* L.
- Ranunculus abortivus* L.
- †*Ranunculus acris* L.
- Ranunculus aquatilis* L.
- Ranunculus delphinifolius* Torr.
- Ranunculus repens* L.

Berberidaceae

- †*Caulophyllum thalictroides* (L.) Michx.
- **Podophyllum peltatum* L.

Lauraceae

- Benzoin aestivale* (L.) Nees

Papaveraceae

- Sanguinaria canadensis* L.

Fumariaceae

- Dicentra canadensis* (Goldie) Walp.
- Dicentra Cucullaria* (L.) Bernh.

Cruciferae

- Alyssum alyssoides* L.
- †*Arabis hirsuta* (L.) Scop.
- †*Cardamine bulbosa* (Schreb.) BSP
- **Dentaria diphylla* Michx.
- Dentaria laciniata* Muhl.

Sarraceniaceae

- **Sarracenia purpurea* L.

Droseraceae

- **Drosera rotundifolia* L.

Crassulaceae

- Sedum purpureum* Tausch.

Saxifragaceae

- Chrysosplenium americanum* Schw.
- **Mitella diphylla* L.

Saxifragaceae—cont'd.

- Mitella nuda* L.
- **Parnassia caroliniana* Michx.
- Ribes Cynosbati* L.
- Saxifraga pennsylvanica* L.
- †*Tiarella cordifolia* L.

Rosaceae

- †*Agrimonia gryposepala* Wallr.
- **Amelanchier canadensis* (L.) Medic.
- Dalibarda repens* L.
- Fragaria vesca* L.
- **Fragaria virginiana* Duchesne
- **Geum strictum* Ait.
- **Potentilla fruticosa* L.
- †*Prunus virginiana* L.
- Pyrus arbutifolia* (L.) Lf.
- Rosa carolina* L.
- Rubus allegheniensis* Porter
- Rubus hispida* L.
- †*Rubus idaeus* L., var. *aculeatissimus* (C.A.Mey.) Regel & Tiling
- **Rubus odoratus* L.
- †*Rubus triflorus* Richards

Leguminosae

- Apios tuberosa* Moensch.
- Desmodium bracteosum* (Michx.) DC.
- Desmodium canescens* (L.) DC.
- Desmodium grandiflorum* (Walt.) DC.

Geraniaceae

- **Geranium maculatum* L.
- †*Geranium Robertianum* L.

Polygalaceae

- **Polygala pauciflora* Willd.

Limnanthaceae

- Floerkea proserpinacoides* Willd.

Anacardiaceae

- **Rhus Toxicodendron* L.
- **Rhus typhina* L.
- Rhus Vernix* L.

Aquifoliaceae

- **Ilex verticillata* (L.) Gray

Aceraceae

- **Acer pennsylvanicum* L.
- †*Acer rubrum* L.
- Acer saccharinum* L.
- †*Acer saccharum* Marsh.
- **Acer spicatum* Lam.

Balsaminaceae

- **Impatiens biflora* Walt.

Rhamnaceae

- **Rhamnus alnifolia* L'Her.

Vitaceae

- Psedera quinquefolia* (L.) Greene

Tiliaceae

- **Tilia americana* L.

Malvaceae

- Hibiscus Moscheutos* L.

Hypericaceae

- Hypericum boreale* (Britton)
Bicknell
- Hypericum punctatum* Lam.
- Hypericum virginicum* L.

Violaceae

- Viola blanda* Willd.
- †*Viola conspersa* Reichenb.
- **Viola nephrophylla* Greene
- **Viola pallens* (Banks) Brainerd
- Viola palmata* L.
- †*Viola papilionacea* Pursh.
- **Viola scabruscula* Schwein.
- †*Viola renifolia* Gray
- **Viola rostrata* Pursh.
- Viola rotundifolia* Michx.
- Viola sororia* Willd.
- †*Viola canadensis* L.

Onagraceae

- **Circaea alpina* L.
- †*Circaea intermedia* Ehrb.
- †*Circaea lutetiana* L.
- **Epilobium angustifolium* L.
- †*Oenothera biennis* L.

Araliaceae

- †*Aralia hispida* Vent.
- †*Aralia nudicaulis* L.

Umbelliferae

- Cicuta maculata* L.
- Conioselinum chinense* (L.) BSP.
- †*Cryptotaenia canadensis* (L.) DC.
- **Daucus Carota* L.
- **Osmorhiza Claytoni* (Michx.)
Clarke
- †*Sanicula marilandica* L.

Cornaceae

- †*Cornus canadensis* L.
- †*Cornus circinata* L'Her
- †*Cornus stolonifera* Michx.

Ericaceae

- **Chamaedaphne calyculata* (L.)
Moench.
- **Chiogenes hispidula* (L.) T. & G.
- †*Gaultheria procumbens* L.
- **Gaylussacia baccata* (Wang.) C.
Koch.
- **Ledum groenlandicum* Oeder
- Moneses uniflora* (L.) Gray
- Monotropa uniflora* L.
- †*Pyrola americana* Sweet
- Pyrola asarifolia* Michx., var.
incarnata (Fisch.) Fernald
- Pyrola chlorantha* Sw.
- Pyrola elliptica* Nutt.
- Pyrola secunda* L.
- †*Rhododendron nudiflorum* (L.)
Torr.
- Vaccinium corymbosum* L.
- Vaccinium macrocarpon* Ait.
- †*Vaccinium Oxycoccus* L.
- †*Vaccinium pennsylvanicum* Lam.
- Vaccinium stamineum* L.

Primulaceae

- Lysimachia Nummularia* L.
- Lysimachia terrestris* (L.) BSP.
- †*Samolus Valerendi* L.
- **Steironema ciliatum* (L.) Raf.
- **Trientalis americana* (Pers.) Pursh.

Oleaceae

- **Fraxinus americana* L.
- Fraxinus nigra* Marsh.

*Gentianaceae**Menyanthes trifoliata* L.*Apocynaceae*†*Apocynum cannabinum* L.*Asclepiadaceae**Asclepias quadrifolia* Jacq.*Polemoniaceae**Phlox divaricata* L.*Boraginaceae***Myosotis laxa* Lehm.*Labiatae***Lycopus americanus* Muhl.†*Prunella vulgaris* L.*Scutellaria laterifolia* L.*Teucrium canadense* L.*Solanaceae***Solanum Dulcamara* L.*Scrophulariaceae**Chelone glabra* L.*Gerardia purpurea* L.*Mimulus ringens* L.*Veronica americana* Schwein.*Veronica scutellaria* L.*Orobanchaceae**Orobanche uniflora* L.*Phrymaceae*†*Phryma Leptostachya* L.*Rubiaceae**Galium boreale* L.*Galium triflorum* Michx.†*Mitchella repens* L.*Caprifoliaceae*†*Linnaea borealis* L., var. *americana*
(Forbes) Rehder**Lonicera oblongifolia* (Goldie)
Hook†*Sambucus racemosa* L.†*Viburnum acerifolium* L.†*Viburnum cassinoides* L.*Valerianaceae***Valeriana uliginosa* (T. & G.)
Rydb.*Lobeliaceae***Lobelia Kalmii* L.†*Lobelia siphilitica* L.*Compositae*†*Achillea Millefolium* L.†*Anaphalis margaritacea* (L.)

B. & H.

Aster juncus Ait.*Aster macrophyllus* L.*Aster novae-angliae* L.*Aster paniculatus* Lam.*Aster puniceus* L.*Aster Tradescanti* L.†*Aster umbellatus* Mill.**Bidens cernua* L.*Bidens frondosa* L.†*Chrysanthemum Leucanthemum* L.*Erechtites hieracifolia* (L.) Raf.†*Erigeron philadelphicus* L.**Eupatorium perfoliatum* L.**Eupatorium purpureum* L.†*Eupatorium urticaefolium* Reichard**Helenium autumnale* L.†*Hieracium aurantiacum* L.†*Hieracium pratense* Tausch.*Onopordium Acanthium* L.†*Polymnia canadensis* L.**Polymnia uvidalia* L.*Rudbeckia laciniata* L.**Prenanthes alba* L.**Senecio aureus* L.**Senecio Balsamitae* Muhl.*Solidago arguta* Ait.†*Solidago graminifolia* (L.) Salisb.**Solidago Houghtonii* T. & G.†*Solidago latifolia* L.*Solidago neglecta* T. & G.**Solidago ohioensis* Riddell**Solidago patula* Muhl.†*Solidago rugosa* Mill.†*Solidago canadensis* L.*Solidago uliginosa* Nutt.*Solidago ulmifolia* Muhl.**Solidago uniligulata* (DC) Porter†*Tussilago Farfara* L.

The foregoing list contains a surprisingly large number of plants marked "not previously reported" (†), many of which are quite common in and around any swamp region in this general latitude. Reasons for this fact are not difficult to find. The flora of the swamp is constantly changing. Not only have some of the characteristic plants been disappearing, but many other forms have migrated inward from the surrounding mesophytic border. It is also likely that this border area, formerly a part of the swamp, has now been more fully studied than heretofore. Moreover, it is obvious that former reports have paid major attention to the unusual and rare plants, without attempting a complete list,—as is well illustrated by the next list.

RARER PLANTS OF BERGEN SWAMP REPORTED BY BAXTER AND HOUSE (1924)

(An asterisk marks the species collected by the present writer.

The nomenclature follows Gray's Manual.)

- | | |
|---------------------------|---------------------------|
| Aspidium cristatum | *Cypripedium parviflorum |
| *Aspidium Goldianum | var. pubescens |
| Phegopteris Dryopteris | Epipactis pubescens |
| Equisetum fluviatile | Habenaria blephariglottis |
| *Lycopodium lucidulum | Habenaria bracteata |
| *Lycopodium obscurum | *Habenaria dilatata |
| *Taxus canadensis | Habenaria orbiculata |
| *Picea mariana (? M.S.B.) | *Pogonia ophioglossoides |
| Scheuchzeria palustris | Stellaria longifolia |
| Panicum Lindheimeri | *Sarracenia purpurea |
| Sphenopholis palustris | *Drosera rotundifolia |
| Carex aurea | Dalibarda repens |
| Carex Bebbii | Mitella nuda |
| Carex bromoides | *Parnassia caroliniana |
| *Carex cristata | Saxifraga pennsylvanica |
| *Carex flava | Rhus Vernix |
| *Carex granularis | *Acer spicatum |
| *Carex leptalea | *Rhamnus alnifolia |
| Carex pedunculata | Hypericum boreale |
| Carex Pseudo-Cyperus | *Viola nephrophylla |
| Carex rosea | Pyrola asarifolia |
| Carex trisperma | var. incarnata |
| *Cladium mariscoides | Pyrola chlorantha |
| Eleocharis acuminata | Pyrola secunda |
| Rhynchospora alba | *Lonicera oblongifolia |
| Calla palustris | *Lobelia Kalmii |
| Juncus brachycephalus | Aster juncus |
| Juncus Dudleyi | Solidago uliginosa |
| *Clintonia borealis | Solidago ulmifolia |
| Smilacina trifolia | *Solidago uniligulata |
| Cypripedium acaule | |

It is possible that some of the plants reported by Baxter and House have disappeared since their list was compiled. This selected list will be of value in comparing the Bergen flora with that of other regions. The species here mentioned are rarely found elsewhere in northwestern New York.

In addition to the above list Baxter and House (1924) give the following species as being reported from Bergen Swamp by Paine in his "Catalogue of the Plants of Oneida County" (N.Y.) with the statement that they are "common" within the swamp but found sparingly elsewhere. As in the other lists an asterisk marks the species collected by the present writer.

<i>Arethusa bulbosa</i>	<i>Liparis Loeselii</i>
<i>Carex polygama</i>	<i>Microstylis monophyllos</i>
* <i>Carex Crawei</i>	<i>Myrica carolinensis</i>
* <i>Carex eburnea</i>	* <i>Phragmites communis</i>
<i>Carex gynocrates</i>	* <i>Potentilla fruticosa</i>
<i>Carex Oederi</i>	* <i>Rhynchospora capillacea</i>
<i>Carex sterilis</i>	* <i>Salix candida</i>
<i>Carex vaginata</i>	* <i>Scirpus caespitosus</i>
<i>Calopogon pulchellus</i>	<i>Scirpus pauciflorus</i>
<i>Calypso bulbosa</i>	<i>Scirpus Torreyi</i>
* <i>Comandra umbellata</i>	* <i>Senecio Balsamitae</i>
* <i>Cypripedium candidum</i>	* <i>Solidago Houghtonii</i>
<i>Eleocharis rostellata</i>	* <i>Solidago ohioense</i>
<i>Galium boreale</i>	* <i>Tofieldia glutinosa</i>
<i>Juncus acuminatus</i>	* <i>Triglochin maritima</i>
<i>Juncus balticus</i>	<i>Triglochin palustre</i>
* <i>Juniperus horizontalis</i>	* <i>Valeriana uliginosa</i>

Here again the changes which have taken place within the swamp since Paine compiled his "Catalogue," in the latter part of the nineteenth century, have undoubtedly removed or at least made rare some of the species which at that time were found. The present writer, however, wishes to emphasize the fact that he has not attempted to make an exhaustive collection, that work being only one part of the purpose of the present study.

SPECIFIC ZONES AND ASSOCIATIONS OF THE SWAMP

In discussing the specific zones and associations of the swamp the method of presentation will be as follows:

- a. Location of the association within the swamp, and a list of its dominant and subdominant plants.

- b. Characteristics of the association as to physiognomy, plant types, soil types, and soil acidity.
- c. History of the association, so far as it can be determined, and its interpretation *as a unit*.
- d. Relative position of the association in the succession of the swamp as it stands today.

Only those plants which have been observed by the writer will be used in the following lists. Those species which are marked with the letter *b* are either boreal, or at least much more common in latitudes farther north than Bergen Swamp.

It must be remembered that the formations mentioned do not stand as distinct and easily separable units, there being many transitional stages between them. In this way the classification of the associations is more or less artificial, although necessary to a clear presentation.

THE OPEN MARL ASSOCIATION

(Figure 3; Plates I, II)

The open marl association in the swamp is not continuous, but consists of several beds varying in size from small areas of only a few hundred square feet to large tracts several acres in extent. In general these beds are located in the center of the swamp, but some of them extend for considerable distances toward its margins.

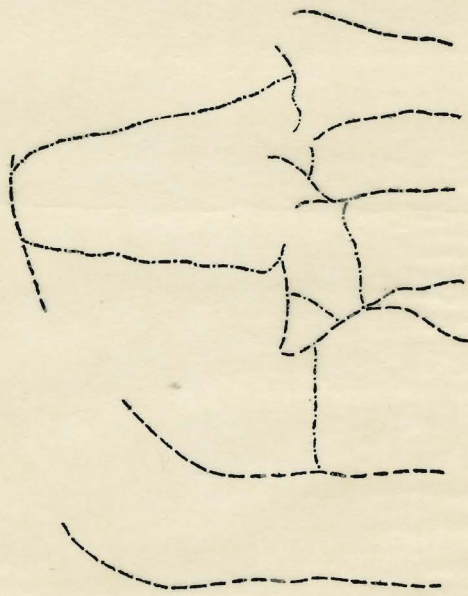
Dominant Species of the Open Marl Association are :

- | | |
|---------------------------|---------------------------|
| b. Triglochin maritima | Cladium mariscoides |
| b. Deschampsia caespitosa | Zygadenus chloranthus |
| Phragmites communis | b. Juniperus horizontalis |
| b. Carex Crawei | b. Scirpus caespitosus |
| b. Carex flava | |

Major Sub-dominant Species are :

- | | |
|----------------------------|--------------------------|
| Deschampsia flexuosa | Lobelia Kalmii |
| b. Rhynchospora capillacea | Senecio Balsamitae |
| Cypripedium parviflorum | b. Parnassia caroliniana |
| var. pubescens | Solidago ohioense |
| Cypripedium candidum | |

The open marl association at first appears to be rather barren of plant life. There are patches of varying size, usually small, upon which there is no vegetation whatsoever, but in general the grasses and sedges have succeeded in covering the marl. The vegetation is all low growing and consequently it is possible to see the entire



----- Good; - - - - - Passable

Trails in Bergen Swamp

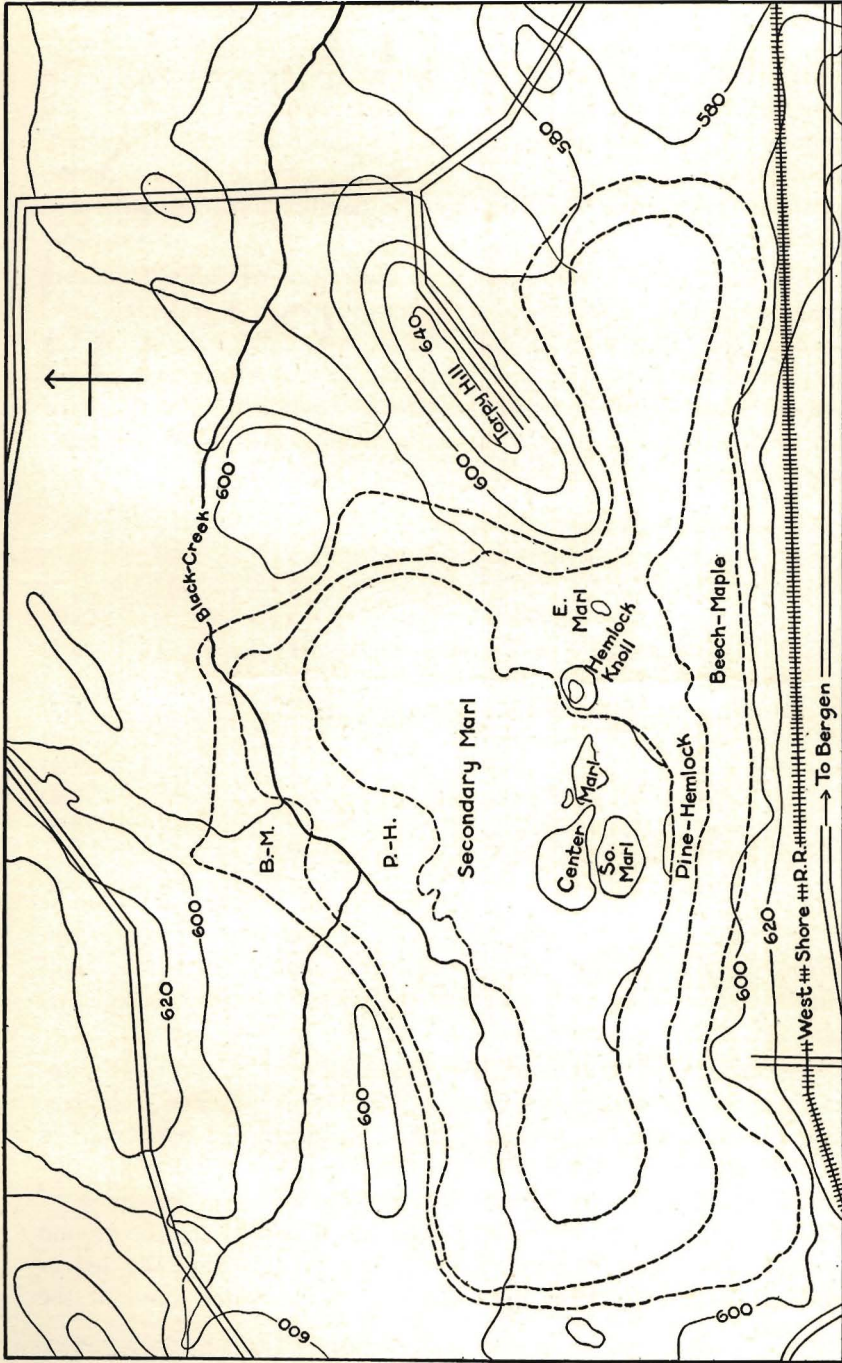
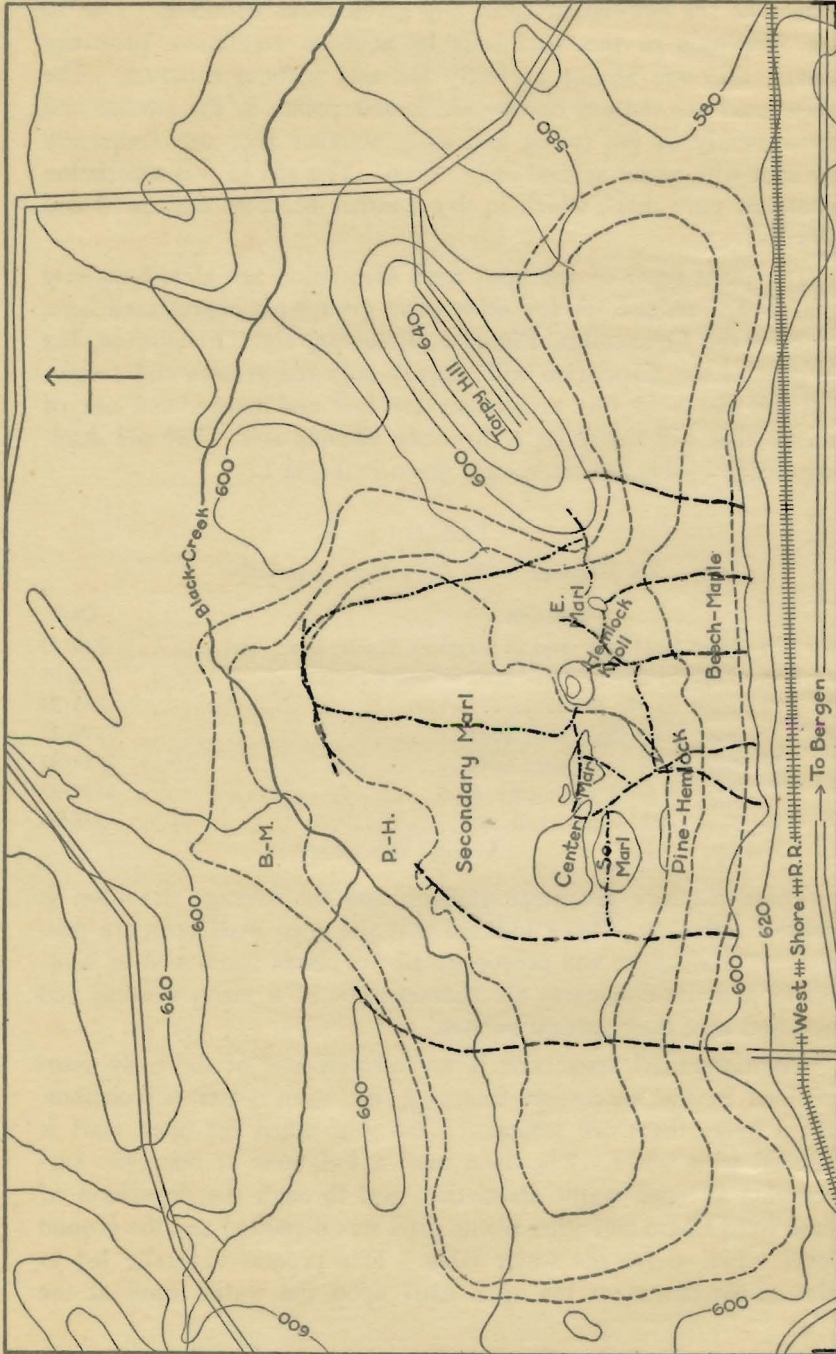


Figure 3. DETAILS OF VEGETATIVE ZONES IN BERGEN SWAMP



--- Good; - - - - - Passable
FIG. 3. DETAILS OF VEGETATIVE ZONES IN BERGEN SWAMP
Trails in Bergen Swamp

extent of the association from any given point within it. Due to the formation of the marl beds by aqueous vegetation, primarily Chara, they are almost perfectly flat and without contours. The open marl associations occupy the lowest points in the swamp and consequently in the spring and early summer they are frequently covered with water several inches deep. The soil in this association is almost pure marl, which in dry weather becomes desiccated and powdery.

The plant types of the open marl association are almost entirely grasses and sedges. A few other plant groups are represented here, such as the Compositae, Pinaceae, Rosaceae, and Orchidaceae, but in general the association will support only the grasses and sedges. All the plants in this association are low and hardy, and are of a type that will thrive on a distinctly alkaline soil. The pH readings made in this association are given in Table I.

TABLE I
pH Readings in the Open Marl Association

pH	Location	Date
1. 7.80	First Marl Bed west of Hemlock Knoll; bare marl	7/2/33
2. 7.53	Same as No. 1. Pure marl 6" below surface	7/3/33
3. 7.20	Same as No. 2	7/3/33
4. 7.20	East Marl Bed; pure marl	7/19/33
5. 7.13	East Marl Bed; pure marl	7/19/33
6. 7.20	Central Marl Bed; pure marl	7/19/33
7. 7.20	Inner end, West Trail	8/5/33
Average = 7.32		Average Dev. = ± 0.19

These readings are quite uniform and the average deviation is consequently low. They indicate that the open marl beds are pronouncedly alkaline; and practically all the plants mentioned as dominants and sub-dominants are characteristic of a marly alkaline soil and find here their natural habitat.

The open marl association is undoubtedly one of the early associations in the succession following the open water associations. Even today there are seasons of the year when the open marl is flooded with water. The open marl associations at one time surrounded an open water association, and through the deposition of lime from Chara and other plants marl was deposited and the ground level raised above the water table. This process naturally led to the encroachment of the open marl upon the water, until at the

present time the marl occupies the center of the swamp, and now represents the earliest successional stage present in the swamp. The open marl is destined to be the first to disappear from the swamp by the encroachment of the zones which now stand adjacent to it. This association at Bergen Swamp is unquestionably a transitional association from the aquatic to the terrestrial, and as it stands today it is in its last stages of existence.

THE SECONDARY MARL ZONE

The secondary marl zone surrounds each of the open marl associations, and stands between the open marl and the pine-hemlock zone (Plates II, III). It varies in width from only a few feet in those places where the pine-hemlock closely approaches the open marl, to several hundred feet; and in some portions of the swamp it has advanced to such an extent that it has completely obliterated the open marl. The secondary marl is also to be found as islands in the center of some of the open marl associations.

Dominant Species of this zone are:

- | | |
|---------------------------------|--------------------------------|
| b. <i>Larix laricina</i> | <i>Cypripedium candidum</i> |
| <i>Gaylussacia baccata</i> | b. <i>Salix candida</i> |
| b. <i>Ledum groenlandicum</i> | <i>Cladium mariscoides</i> |
| b. <i>Lonicera oblongifolia</i> | b. <i>Potentilla fruticosa</i> |
| <i>Typha latifolia</i> | |

Sub dominant Species are:

- | | |
|----------------------------------|------------------------------------|
| b. <i>Juniperus horizontalis</i> | b. <i>Chamaedaphne calyculata</i> |
| <i>Carex hystericina</i> | b. <i>Vaccinium pennsylvanicum</i> |
| <i>Scirpus cyperinus</i> | <i>Solidago ohioense</i> |
| b. <i>Scirpus caespitosus</i> | b. <i>Habenaria dilatata</i> |
| b. <i>Parnassia caroliniana</i> | |

The secondary marl zone shows a distinctly taller growth and is more terrestrial in appearance than the open marl. It is largely composed of shrubs and bushes which grow to a height of ten and twelve feet in many places. The only trees present in the zone are dwarfed *Larix laricina* and an occasional *Thuja occidentalis* which has advanced in from the pine-hemlock zone. The vegetation is quite thick, making the zone almost inaccessible except on well cleared trails (over Figure 3). The under vegetation is composed largely of grasses, a few orchids and other herbaceous plants, but is almost entirely devoid of ferns. The soil is firmer and dryer than in the open marl, but it still is marl, although highly admixed with

humus and in some portions entirely covered with a thin layer of humus. There are practically no mosses present in the zone due to the alkalinity of the soil. As in the open marl this zone is practically level since it rests on a soil formed by the deposition of aquatic vegetation. Wherever there is any distinct rise in the ground level there is a change in the nature of the vegetation. The secondary marl, in spite of its almost level surface, is not subject to such complete coverings of water in the spring as is the open marl, due in part to the increased absorptive power of the soil resulting from the presence of the humus, and also to the slightly higher level of the ground resulting from the superficial humus formation.

The pH readings of the soil in the secondary marl are given in the following table.

TABLE II
pH Readings in the Secondary Marl Zone

	pH	Location	Date
1.	6.52	Rain puddle west of Hemlock Knoll.....	7/3/33
2.	6.94	20 yds. west of Hemlock Knoll; thin humus layer on marl.	7/3/33
3.	7.25	Central Marl Bed,—secondary	7/12/33
4.	7.27	East Marl Bed,—soil under <i>Potentilla</i>	7/12/33
5.	7.12	South Marl Bed,—secondary	8/5/33
6.	7.20	South Marl Bed,—by stream	8/5/33
	Average = 7.05	Average Dev. = ± 0.21	

These pH readings for the secondary marl zone are fairly constant, the only two which deviate radically being the first and second. The first reading was made from the soil in a rain puddle and the writer is at a loss to explain its strong acidity. The reading may possibly be the result of error in determination, or of contamination of the sample; but as three determinations were made from the same sample and all three were in approximate agreement, the average for the three is given in the table. In the second reading, which is just slightly acidic, it is possible that the presence of a very definite humus layer composed of some decaying coniferous vegetation on top of the marl where the sample was taken may have affected the acidity. The remaining readings in the table are considerably less alkaline on the average than those made in the open marl. This decrease in alkalinity is due to a change in the type of the plants growing in the zone, i. e., the inclusion of some coniferous species such as *Larix* and *Juniperus*, which are frequent in occurrence and decidedly acid when in decay, and to the accumulation of some

humus in and on the marl. The average of the pH readings for the zone, 7.05, closely approaches the neutral point and shows an intermediate state in soil acidity between the decidedly alkaline open marl and the pine-hemlock zone which is distinctly acidic.

The development of the secondary marl may be explained as follows: The open marl association, having established itself, naturally deposited some humus resulting from the decay of the vegetation which it supported. This humus served to reduce to some extent the strong alkalinity of the pure marl and to prepare a soil hospitable to those plants characteristic of a habitat not so alkaline. It is known (Taylor 1928) that pioneer plants in a succession are seldom capable of providing for their own perpetuation, that the change of vegetation is normally toward the climax condition, which for the region in which the Bergen Swamp is located is a beech-maple-birch forest (Bray 1930). Further, it is an accepted principle (Clements 1905) that each stage in succession ultimately reacts in such a way as to produce physical and chemical changes more or less unfavorable to its own permanence. In view of these facts it could hardly be expected that the open marl association would be permanent to any degree. Through its own activity the open marl has provided a suitable habitat for the shrubs and other plants characteristic of the secondary marl zone. As a result this zone has succeeded the open marl as rapidly as the open marl has provided the right habitat; the primary requirements for the succession being a reduction in the alkalinity of the soil and the presence of some humus.

THE SPHAGNUM ASSOCIATION

Within the swamp there is a considerable amount of Sphagnum growing in almost a pure stand, there being only a few other plants consistently associated with it. The sphagnum growth within the swamp is minor in comparison with the other type plants to be found; but since it has a soil type distinctly different from that in other zones and associations, and because these sphagnum growths are not consistently to be related to any of the other zones, the writer has chosen to consider them as a separate association. Although the sphagnum areas are arranged in a more or less concentric manner they do not, at least now, show a definite zonal relation to any of the other zones, sometimes even being found growing upon them.

The Sphagnum association is in general located outside the secondary marl zone, but in separate areas as just described. In no places

are these sphagnum areas more than thirty feet in diameter. Since the sphagnum is not continuous the pine-hemlock, which is the next distinct zone, frequently comes in direct contact with the secondary marl. It is interesting to note that small hummocks of *Sphagnum* occur on the secondary marl (Plate IV), and even out on the pure marl where they seem to thrive almost as well as back in the more protected regions outside the secondary marl and nearer to the acidic soil of the pine-hemlock zone. The only species occurring with sufficient frequency in the *Sphagnum* association to warrant mention are *Drosera rotundifolia*, *Sarracenia purpurea*, *Gaylussacia baccata*, and *Vaccinium pennsylvanicum*.

No pH readings of the soil in this association were made, but in view of the findings of other workers (Moore and Taylor 1921, Kurz 1928) we may safely assume that the soil is acidic.

Whether or not the sphagnum has played an important rôle in the filling in of the swamp is a question. It is known that *Sphagnum* is an important factor in the filling in of an acid bog and that the presence of *Sphagnum* has a profound effect upon the acidity of the bog (Moore and Taylor 1921, Kurz 1928). MacMillan (1896) states that the occurrence of *Sphagnum* in a bog is a transitional step from the aquatic toward the climax condition, that it serves both to fill in the swamp and to form a suitable substrate for more terrestrial plants, and finally that the location of the sphagnum within the swamp depends upon the depth of water beneath it; the sphagnum naturally occurring only in shallow places as along the shore line or over old reefs. The Bergen Swamp presents two factors which might explain its filling in: the occurrence of considerable marl and the occurrence of *Sphagnum*. It is known that some bogs left by glaciation are filled in by peat and some by marl, and that the majority of those showing marl action are located in Indiana, Michigan, Wisconsin and Minnesota (Thiel 1930). Since there are such extensive marl beds at Bergen, because marl soil is distinctly alkaline and sphagnum soil is acidic (Kurz 1928), and finally because no reference can be found reporting simultaneous filling in of any swamp by marl and sphagnum activity, the writer prefers to interpret the occurrence of the sphagnum in Bergen Swamp as incidental. Whether the sphagnum has played an important rôle in the filling in of the swamp is another question which will be considered later, but it might be said at this point that there is evidence that such has been the case. In the succession of the

swamp some habitats have been produced which have been well adapted to sphagnum growth and consequently the sphagnum has appeared in those regions. It so happens that most of the proper habitats have been just inside the pine-hemlock zone.

In view of the above, the Sphagnum associations as they occur in the swamp today are interpreted as incidental associations having no definite part in the general succession of the swamp.

THE PINE-HEMLOCK ZONE

(Plates II, III)

In spite of the fact that the white pine, *Pinus Strobus*, is intolerant of the shade of other trees and consequently cannot encroach upon the hemlock growth, and also that it is incapable of existing with the beech and maple growth (Taylor 1928), the writer has chosen to group the pine and hemlock together as one zone because in all other characteristics they are very similar and they are so close to each other in the swamp as to form a regular zone. The pine-hemlock zone is located just outside the secondary marl zone and completely surrounds it. As the form of the secondary marl is affected by the irregularity of the open marl beds so also is the pine-hemlock zone irregular, though not to the same degree as the secondary marl; but in no place does a complete absence of the pine-hemlock zone allow the beech-maple growth to come into direct contact with the secondary marl zone.

Dominant plants in the Pine-Hemlock Zone are:

- | | |
|------------------------------|-----------------------------------|
| b. <i>Taxus canadensis</i> | b. <i>Cornus canadensis</i> |
| b. <i>Pinus Strobus</i> | b. <i>Chamaedaphne calyculata</i> |
| b. <i>Thuja occidentalis</i> | b. <i>Chiogenes hispidula</i> |
| b. <i>Tsuga canadensis</i> | b. <i>Gaultheria procumbens</i> |
| b. <i>Coptis trifolia</i> | <i>Mitchella repens</i> |

Sub-dominant Plants in this Zone are:

- | | |
|---------------------------------|---------------------------------|
| b. <i>Clintonia borealis</i> | b. <i>Linnaea borealis</i> |
| b. <i>Maianthemum canadense</i> | var. <i>americana</i> |
| b. <i>Drosera rotundifolia</i> | b. <i>Lonicera oblongifolia</i> |
| b. <i>Ledum groenlandicum</i> | <i>Viburnum acerifolium</i> |
| <i>Rhododendron nudiflorum</i> | |

In general appearance the pine-hemlock zone is heavily wooded with conifers and possesses a low floor vegetation. There are considerable variations from this condition and in some portions of the zone young trees from the beech-maple zone have begun to appear

and with them has come a light sprinkling of the beech-maple floor vegetation. The floor vegetation of the zone is dominated by ericaceous plants which seem to thrive on the underlying soil (Bird 1923). In the regions bordering on the secondary marl the coniferous trees are younger and smaller than elsewhere and they increase in size back in the older portions of the zone. It is at the inner margin and the outer limits of the zone that the pine occurs in dominant frequency, while in the middle regions the hemlock is dominant. Except in such areas as that found at Hemlock Knoll where there is a considerable rise in the ground level, the soil is quite moist. The zone is almost level but is interrupted at intervals by knolls and slight rises, and at these points the zone vegetation is more advanced than in the other portions. As the soil here is comparatively dry and other factors are favorable, some of the beech-maple vegetation is beginning to appear. The zone is further characterized by heavy shade and a low floor vegetation except at the inner and outer margins where, in the first case, the trees are small and low and where, in the second case, the shrubs characteristic of the beech-maple have begun to appear and make a heavy and impassable ground vegetation.

The soil in the zone is decidedly acidic (Table III) and in appearance varies from a black muck in the more moist portions to a dark, sandy and brownish soil in the dryer parts. All readings reported in Table III were made in portions of the swamp which were undoubtedly pine-hemlock and represent the characteristic pH for that zone. The average deviation of ± 0.66 is relatively large, but may be explained by those readings which are exceptionally low and represent extreme conditions within the zone. The acidity of the zone is caused primarily by the vegetation growing upon it (Bird 1921) and, to a limited extent, by the poor drainage afforded some parts of the zone (Cowles and Schwitalla 1923, Waterman 1926). Ericaceous plants are exceptionally well adapted to the acid condition caused by the rotting of the coniferous vegetation and consequently are frequent in occurrence (Bird 1921). Working on a similar bog at Mt. Desert Island, Maine, Moore and Taylor (1921) found that the humus under the coniferous growth had a pH of 6.0, and Taylor (1928) found that hemlock soil was quite acid, pH 6.2, while a sample from a rotting hemlock log gave a reading of 4.6, which coincides with readings 4 and 5 above. This information indicates that the acid condition in the pine-hemlock zone is of com-

mon occurrence, that the acidity is caused largely by the rotting of the coniferous vegetation, and that the acid soil of the zone makes a good habitat for the ericaceous plants so prevalent in the floor vegetation.

TABLE III
pH Readings in the Pine-Hemlock Zone

pH	Location	Date
1. 8.35	Hemlock Knoll, sandy soil	7/3/33
2. 7.45	20 yds. south of Hemlock Knoll, muck	7/3/33
3. 6.52	Hemlock Knoll, sandy muck on south side	7/3/33
4. 4.49	Hemlock Knoll, soil by rotting log	7/3/33
5. 4.75	Hemlock Knoll, portion of rotting log	7/3/33
6. 6.85	Hemlock Knoll, soil 6" below surface	7/3/33
7. 5.67	Center Trail, $\frac{1}{2}$ way in, spongy soil	7/12/33
8. 6.95	Center Trail, $\frac{1}{2}$ way in, spongy soil	7/12/33
9. 6.69	East of Hemlock Knoll, Arbor Vitae thicket	7/12/33
10. 5.50	Center Trail, $\frac{2}{3}$ way in, Coptis, Cornus	7/12/33
11. 6.18	West of East Marl Bed, zone climax	7/12/33
12. 5.40	East Trail, $\frac{1}{2}$ way in, under moss	7/19/33
13. 7.03	50 yds. north of East Marl Bed	7/19/33
14. 5.53	50 yds. north of East Marl Bed	7/19/33
15. 7.60	50 yds. east of East Marl Bed, 6" depth	7/19/33
16. 5.67	100 yds. north of Hemlock Knoll	7/19/33
17. 6.18	Hemlock Knoll, gray soil	8/1/33
18. 5.74	$\frac{1}{2}$ way in East Trail, rotting stump	8/1/33
19. 6.35	$\frac{1}{2}$ way in East Trail, Pinus, Coptis, Cornus	8/1/33
20. 6.69	South of Hemlock Knoll, pine stump	8/5/33
21. 5.35	Hemlock Knoll, rotting log	8/5/33
Average = 6.12		Average Dev. = ± 0.68

The pine-hemlock zone represents the first forest vegetation to advance into the swamp and the first definitely humus soil to occur. The secondary marl zone supported no trees, with the possible exception of the dwarfed *Larix laricina*, and had primarily a mineral soil. The *Sphagnum* association, which in some portions of the swamp is a forerunner of the pine-hemlock zone, does have a humus soil, but no trees of any kind are present. The pine-hemlock is a transitional zone, not representing the climax vegetation of the region, and being incapable of providing for its own perpetuation.

In the successional filling in of the swamp, the marl vegetation deposited a fairly firm substrate and produced sufficient humus to allow invasion by some pioneer plants which could not be supported on a strongly alkaline soil. In some places *Sphagnum* appeared and

as a result there occurred an acid condition in the soil (Kurz 1928). In addition to these changes in the nature of the soil, the marl zones in their older portions created a somewhat drier condition than had formerly existed, and these factors together made a habitat favorable for the pine-hemlock vegetation. This zone, as it succeeded into the localities formerly occupied by the marl and Sphagnum vegetation, formed a definitely acidic humus soil. The result of this change, brought about by the decay of coniferous vegetation, was that the other plants, not capable of pioneering in a sweet soil, as is the pine, but fond of an acid soil and associated with the pine and hemlock, came in with the association. Most of the plants of this type are herbaceous and form the floor vegetation of the zone.

Starting from the outside of the swamp, the pine-hemlock zone has followed the secondary marl in the general succession and stands today well toward the middle of the swamp, surrounding the marl beds and constantly encroaching upon them. It is logical to assume that in time the pine-hemlock zone will completely obliterate the marl beds. In such a position it would form the center association of the swamp. In the succession we find that the pine sometimes precedes the hemlock. It is seldom found mixed with it, as it is incapable of growing under the hemlock on account of the shade. In other places the pine follows the hemlock, standing thus between the latter and the beech-maple vegetation.

The pine-hemlock zone is thus interpreted as a transitional zone in the general succession and filling in of the swamp. It stands between the pioneer marl vegetation and the climax beech-maple zone, represents the first forest vegetation in the succession, and is found on the first true humus soil occurring in the swamp.

THE BEECH-MAPLE ZONE

This zone, the vegetation of which is the climax for the region of the country in which the Bergen Swamp is located (Bray 1930), forms a complete ring around the outside of the swamp, entirely enclosing the pine-hemlock zone (Figure 3). It follows closely the general shape of the swamp as originally determined by glacial activity. The beech-maple zone is thus the outside zone of the swamp, and in some places fuses directly with the surrounding natural climax forest vegetation, while in other places it is interrupted by clearings and farm land.

Dominant Plants of the Beech-Maple Zone are:

<i>Aspidium marginale</i>	<i>Fagus grandifolia</i>
<i>Aspidium spinulosum</i>	<i>Claytonia virginica</i>
var. <i>intermedia</i>	<i>Hepatica triloba</i>
<i>Cystopteris bulbifera</i>	<i>Acer rubrum</i>
<i>Pteris aquilina</i>	<i>Acer spicatum</i>
<i>Smilacina racemosa</i>	<i>Circaea alpina</i>
<i>Smilacina stellata</i>	<i>Circaea intermedia</i>
<i>Trillium grandiflorum</i>	<i>Circaea lutetiana</i>
b. <i>Populus tremuloides</i>	<i>Eupatorium perfoliatum</i>
b. <i>Betula lutea</i>	b. <i>Solidago graminifolia</i>

Subdominant Plants of this Zone are:

<i>Adiantum pedatum</i>	<i>Sanguinaria canadensis</i>
<i>Aspidium Thelypteris</i>	<i>Mitella diphylla</i>
<i>Onoclea sensibilis</i>	<i>Amelanchier canadensis</i>
<i>Arisaema triphyllum</i>	<i>Rhus typhina</i>
<i>Erythronium americanum</i>	<i>Rhamnus alnifolia</i>
<i>Populus alba</i>	<i>Viola conspersa</i>
<i>Carpinus caroliniana</i>	<i>Cornus circinata</i>
<i>Fraxinus americana</i>	b. <i>Ostrya virginiana</i>
<i>Bidens cornua</i>	b. <i>Caltha palustris</i>
<i>Quercus alba</i>	<i>Eupatorium purpureum</i>
<i>Quercus rubra</i>	<i>Prenanthes alba</i>
<i>Ulmus americana</i>	<i>Solidago serotina</i>

With a few minor exceptions the physiognomy of the beech-maple zone is the same as that of the regular beech-maple climax forest. The soil is more moist than it is in the climax forest and consequently the growth of ferns and mosses is quite luxuriant. The vegetation is varied, there being an abundance of herbaceous, shrub and tree growth; and this vegetation is permanent as it is the climax vegetation of the region. At intervals there are to be found remnants of the pine-hemlock vegetation which formerly occupied the area, such as small growths of *Taxus canadensis* and occasionally some herbaceous forms. A more common remnant of the pine-hemlock vegetation is *Tsuga canadensis*, which stands high and usually above the surrounding beech-maple growth. These trees are lingering and growing old in the beech-maple which has moved in around them. The occurrence of these hemlocks is not of sufficient frequency to affect the type of the zone, and it is a question whether or not they will be able to perpetuate themselves.

The region now occupied by the beech-maple zone was undoubtedly at one time open swamp. This is proved by the occurrence at

the outermost reaches of the zone of a minor growth of *Thuja occidentalis* and *Typha latifolia* (Plate IV). Such forms as these do not grow in normal forests of beech-maple. Their occurrence at the outside of the swamp may be explained only by the assumption that the original limits of the swamp included the localities now occupied by these plants, and that their persistence there is possibly due to poor drainage and other sufficiently favorable environmental factors.

The soil within the beech-maple zone is still slightly acidic (Table IV), somewhat drier than that of the pine-hemlock zone, and nowhere does it have the sandy quality of the soil of the pine-hemlock. The abundant humus at the surface is composed almost entirely of decaying deciduous vegetation. In Table IV the readings vary from pH 5.00 to pH 7.69 and consequently the average deviation, ± 0.72 , is high. It is possible, however, to derive from the table a general idea as to the soil acidity within the zone, and more than 50% of the readings are on the alkaline side of the neutral point. This would indicate that the vegetation of the beech-maple zone has a decided effect as a neutralizing agent on the acid soil left by the pine-hemlock. The fact that the average of the readings, 6.45,

TABLE IV
pH Readings of the Beech-Maple Zone

	pH	Location	Date
1.	5.84	Southern edge, moist soil	7/12/33
2.	6.69	100 yds. from south edge, black soil	7/12/33
3.	6.85	50 yds. from south edge, black soil	7/19/33
4.	7.60	Entrance, east trail	7/19/33
5.	6.69	100 yds. south of Torpy Hill, dry soil	7/27/33
6.	7.37	South edge of Torpy Hill	7/27/33
7.	7.53	Clearing on Torpy Trail, black humus	7/27/33
8.	6.69	West end of Torpy Hill, gray soil	7/27/33
9.	7.20	Clearing on Torpy Trail, dry soil	7/27/33
10.	7.37	Torpy Hill, black humus	7/27/33
11.	7.37	Clearing on Torpy Hill, gray soil	7/27/33
12.	7.53	East Trail, $\frac{1}{2}$ way in, whitish soil	8/1/33
13.	5.00	East Trail, $\frac{1}{2}$ way in	8/1/33
14.	7.37	Southeast edge, moist soil	8/1/33
15.	6.75	Southeast edge	8/1/33
16.	7.20	South edge, black soil	8/5/33
17.	7.12	Center Trail, $\frac{1}{2}$ way in	8/5/33
18.	6.93	South edge	8/5/33
	Average = 6.45	Average Dev. = ± 0.72	

is acidic would indicate that the acid soil of the pine-hemlock zone, upon which the beech-maple is constantly encroaching, has not as yet been completely neutralized by the invading vegetation. This process of neutralization is very likely being retarded by the presence of remnants of the pine-hemlock vegetation still persisting.

The history of the beech-maple zone, when compared with that of the other zones and associations which have preceded it, is comparatively simple. Before it was possible for the vegetation of the beech-maple zone to appear within the swamp several environmental factors had to become adjusted in such a manner as to form a suitable habitat for the zone. The more important adjustments in the environment were a firm substrate, sufficient drainage, and a terrestrial humus soil not as distinctly acid as that found in the pine-hemlock zone. Practically all these conditions were supplied by the zones preceding the beech-maple in the succession of the swamp. In the older portions of the pine-hemlock zone the only major factor not suitable for the beech-maple invasion was the excessive acidity of the soil. For every vegetational zone there are those plants which will act as pioneers (Taylor 1928). These pioneers are seldom capable of providing for their own perpetuation, are seldom found growing in the true climax forest, but will repeat themselves in a given locality until they have created conditions sufficiently favorable for the establishment of the new type to which they really belong. Among the more important pioneers for the beech-maple vegetation are *Populus tremuloides*, *Pteris aquilina*, *Solidago rugosa*, *Aspidium marginale*, and the like. These pioneer plants have been able to encroach on the soil of the pine-hemlock zone and reduce the acidity sufficiently to allow the beech-maple vegetation to come in on a soil formerly unsuited for it. It is perfectly natural that the climax forest of the surrounding country should commence to advance into the swamp as soon as conditions were even partially favorable for its entrance, and this is exactly what has happened in the case of the beech-maple zone.

This zone, having commenced its succession into the swamp, will undoubtedly continue its advance until it ultimately reaches the center of the swamp and covers the entire area with true climax forest. The zone as it stands today around the edge of the swamp is not a pure beech-maple growth in the climax state. It has not been within the limits of the swamp long enough to thoroughly establish itself as such, and there are still some aspects of the zone which

are quite transitional. On the other hand the zone is sufficiently climactic to indicate beyond doubt that the filling in of the swamp by a climax vegetation has finally set in, and no further type of vegetation will succeed it as the climax of the region has already begun its invasion. The presence of the beech-maple zone thus marks the beginning of the end of the Bergen Swamp.

HISTORY AND DEVELOPMENT OF THE SWAMP

ORIGIN OF THE DEPRESSION

One of the primary requirements for the swamp condition is a depression in the surface of the land in which the drainage is not complete. Regarding the origin of such a depression it is only possible to theorize, since we have no direct evidence as to its exact cause. It is possible that the general east-west depression running from Lake Erie to the Genesee River, in which Bergen Swamp rests, is correlated with the underlying rock formations. This depression, as already mentioned, is directly above the soft Salina shales, and these shales are bounded on the north by the hard Niagara limestones and on the south by the equally hard Onondaga limestones (Figure 1). It is easy to imagine that during the ice erosion of the glacial periods more rock was removed from the comparatively soft shales than from the harder neighboring limestones and that a trough was thus formed over the Salina shales. This will explain the general east-west depression, but not the limited depression in which Bergen Swamp itself rests.

Transeau (1903) states that frequently those swamps found on glacial deposit, as is Bergen Swamp, are due to the breaking off of a portion of the glacier as it retreated. Such a detached ice cake would remain for some time after the departure of the main glacier and prevent the deposition of silts and like material from the post-glacial lake. When such a portion of the glacier finally melted it would leave a depression in the area it formerly occupied, due to the deposition of silts around its resting place but not under it. Bray (1930), on the other hand, is of the opinion that many of the depressions on glacial till now occupied by swamps and bogs have been caused by deposition of till and débris in such a manner as to prevent proper drainage of an otherwise well-drained depression. These two ideas are not so different in final analysis as they may at first appear. The breaking off of a portion of a glacier,

as suggested by Transeau, would prevent deposition of glacial débris in the one locality in which it was forming the depression and allow deposition in the surrounding areas, thus preventing drainage of the depression. Bergen Swamp is located on glacial till and we may be reasonably sure that it was through some activity of the glacier that the depression it occupies was formed. We are unable to tell the exact cause of the depression and the two theories presented above are merely suggestions as to how the original swamp bed may have been formed.

CAUSES OF THE FILLING IN OF THE DEPRESSION

Any poorly drained depression, such as that which must have been left at Bergen following the glacier, would naturally become filled with water and form a pond or small lake. We know, as has previously been stated, that for every given region there is a climax vegetation, that toward such a vegetation all portions of a given region will tend to progress, and finally that for the region in which Bergen Swamp is located the climax vegetation is a beech-maple forest. Any changes necessary to produce the climax vegetation are of course possible only if the environmental factors are of such a nature that it is possible to modify them and produce a habitat suitable for the climax. As Bray (1930) pointedly states, it is obvious that there must be intermediate stages in the succession from the original non-climax habitat to the climax. Clements (1905) indicates that the reproduction of a plant in a locality gives rise to a potential, if not an actual association. Now the permanence of such an association is dependent upon the immobility of the individuals which compose it. Hence it is perfectly natural to assume that those aquatic and semi-aquatic transitional individuals which normally would occur around and in such a pond would by their own reproduction tend to form an association or zone which, not being climactic, would be transitional in the general succession and filling in process. Since the individuals in these associations possess a high degree of mobility, as has been formerly demonstrated, they were capable of migrating into the open water and acting as agents in its filling in. Following these primary associations came the secondary more terrestrial zones. The fact that such an invasion of one zone after another has occurred indicates that the environmental factors have not been such as to prevent the gradual creation

of a habitat suitable to the climax forest. The causes of the filling in of the swamp are, then, that the open water flora does not represent the climax vegetation of the region, that the environmental factors have been susceptible of modification, and finally that there have been transitional forms and associations of sufficient variety to be capable of modifying these factors and preparing a climax habitat.

STAGES IN THE FILLING IN OF THE DEPRESSION

In order to derive a complete picture of the stages of swamp succession we shall compare the known steps at Bergen with those found by workers in other localities. As has already been stated, the order of associations and zones now present in the swamp is: open marl, secondary marl, Sphagnum, Pine-Hemlock, and finally the near-climax Beech-Maple zone. We have, at Bergen, the last half of the story of the succession; of what has gone before, we can only surmise.

Bray (1930) gives the order in which he believes that plant types succeed into a lake as follows:

1. Floating plants (microscopic, visible algae, duckweeds)
2. Wholly submerged vegetation (pondweeds, etc.)
3. Floating-leaf plants (water lilies, etc.)
4. Marsh plants (sedges, bulrushes, cattails, etc.)
5. Marsh-meadow plants (sedges, grasses)
6. Marsh-shrub or swamp-shrub (willows, alders, etc.)
7. Swamp-forest (black ash, red maple)
8. Climax forest (maple, beech, birch, pine, hemlock, etc.)

Of the stages mentioned by Bray we have at Bergen stages four to eight inclusive, although they are not in exactly the same groupings as Bray indicates.

Transeau (1905) states that in the normal succession of the bogs of the Huron River Valley the order is: bog sedge, bog shrub, and then conifer. This is exactly the condition at Bergen, under different descriptive terms.

Cowles (1901) in his report on Chicago and vicinity states that following the advance of the shrubs into the swamp the first trees to appear are *Larix laricina* and *Thuja occidentalis*, and that closely following comes *Pinus Strobus*. Under these coniferous trees he reports the dominant herbs as being *Coptis trifolia*, *Cornus canadensis*, etc. Again we report an identical condition at Bergen Swamp.

Transeau (1903) in discussing the bogs of northern Michigan

gives a gradation of vegetation from the center of a swamp to the outside. His list of plants is too long to present in full, but his groupings of plant types are as follows:

1. Aquatic Society,—Potamogeton, Nymphaea, Castalia.
2. Cattail-Dulichium Society,—Typha, Phragmites, etc.
3. Cassandra Society,—Chamaedaphne, Kalmia, Ledum, etc.
4. Shrub and young tree Society,—Aronia, Ilex, Larix.
5. Conifer Society,—Larix, Pinus, Thuja, etc.
6. Climax forest,—Acer, Betula, etc.

At Bergen all the above stages of succession with the exception of the first are found and they occur in this same order.

Waterman (1926) lists the stages found in the swamps of northern Illinois as follows:

1. Free-floating aquatics.
2. Aquatics whose roots are in the soil at the bottom.
3. Aquatics whose roots are in the soil at the bottom and which extend above the surface.
4. Plants which grow in very shallow water, as the sedges.
5. Water-loving shrubs.
6. Swamp trees.
7. Vegetation of the surrounding uplands (climax).

The condition at Bergen is very similar to this plan, presenting the stages four to seven inclusive.

From a comparison of the above plans of succession with the stages now existing at Bergen, it is obvious that this swamp now presents the last portion of a perfectly normal program of succession, a program which in general is followed in practically the same manner in all swamps. As to what stages have gone before the earliest ones now existent at Bergen we can only theorize. The close similarity of the present stages to those reported by Waterman, Transeau, and Bray leads us to think that very likely Bergen Swamp had earlier stages likewise similar to those reported by these other workers. The occurrence of considerable marl in the swamp indicates the former presence of aquatic vegetation. We are therefore safe in believing that in the past history of the swamp, as well as in its present condition, a normal pattern of succession has been followed.

Bray (1930) states that the swamp forest, which merges into the climax and in many cases is identical with it, is the result of a relatively high water table due to poor drainage. He states further that peat and marl are characteristic of such regions where the drain-

age is poor and that conifers, as *Larix*, *Pinus* and *Tsuga*, are quite characteristic of such a forest. Bray lists two main effects of such a swamp forest upon the substratum:

1. Rapid and unequal elevation of the land, due to the spreading rather than the penetration of the roots.
2. Dead trees accentuating effect No. 1, both No. 1 and No. 2 tending to bring about a rapid change in the soil environment.

The swamp forest now existent at Bergen has, in the main, the characteristics just mentioned. The forest floor is quite uneven, the roots spread over the soil rather than penetrating it, the forest is primarily coniferous and follows the peat and marl in the general succession, these features being closely similar to those reported from other localities.

CAUSES OF THE SEQUENCE OF STAGES

It has already been made clear that the filling in of the swamp has taken place in definite stages, each with its typical floral structure and each to be designated as a zone or formation; that this filling in has of necessity been gradual; and that its success has been due largely to pioneer plants. The next question is why the stages follow each other in the succession of the swamp in the order we have observed.

It is a well-known ecological principle that within any given locality the vegetational structure will change unless that structure is the climax for that locality. As Taylor (1928) points out this change may be in either of two possible directions: toward the climax, which is the more normal condition, or away from it, as in the case of fire. It is difficult to tell by mere observation in what direction the succession is moving, but in the absence of marks of serious fires, storms, or cuttings, and for other reasons mentioned above it is safe to assume that progress is being made toward the climax vegetation.

Clements (1905) states that this process of invasion, or succession, depends upon the ability of some plants to enter a region of a certain character different from that from which they have come. If these two regions are in close approximation, as is the case at Bergen, the invasion is continuous. It is obvious that no change in the vegetational make-up of a locality could ever come about if the above were not true; it would be impossible to reach the climax condition if there were not those plants which were capable of

leaving one environment and entering another, and by their presence in the second environment so modify it as to eventually bring it into close likeness to the first. Such plants are the pioneers. It is obvious that no plant, no matter how active a pioneer it might be, could be capable of modifying the open water condition, which was originally present within the swamp, directly into the climax beech-maple forest. This process must be accomplished by a series of pioneers, which will create environments suitable for their own types of vegetation and will be merely transitional. When one such step has been taken a second will follow, and so on until the climax is reached.

So far the question of the cause of the arrangement of the successive stages in the filling in process has been approached almost entirely as being a function of the activities of various pioneer plants. It is quite possible that there are some physical factors which are important in causing this succession and which function entirely independently of the vegetation of the region. Shaw (1902) is inclined to place these physical factors first in importance. The main physical factor which Shaw mentions is the deposition of silts from the drainage of the surrounding territory. It is undoubtedly true that in regions where the contour of the land is such as to cause active drainage into the swamp such a factor might be important. In so far as the writer has been able to determine there are, today, no physical factors of any major importance functioning in the succession at Bergen. As far as the past is concerned no definite statement can be made, but it is very doubtful whether such physical factors have played any important rôle in the history of this swamp.

A final question on this point is why the climax remains the climax and does not lead to something else. Taylor (1928) answers the question by pointing out that the beech-maple climax, such as is found at Bergen, reacts in the forest in such a manner as to give it its main characteristics. The beech and maple are very tolerant of shade and consequently the young trees are not suppressed by the shade from the dense canopy created by the older trees: i. e., these trees are self-perpetuating in their own shade. This shade further serves to keep out the seedlings of other trees and plants which might disrupt the climax condition. The only factor which will allow outside plants to get into the beech-maple climax forest is light, and in the climax at Bergen there are several light spots

where timbering has been going on. In such places pioneer plants have rushed in, plants not characteristic of the climax, but plants which will make for an environment suitable to the climax. Hence the climax is permanent because it is able to endure in the environment created by itself and this environment keeps out non-climax plants.

As a fitting conclusion to this discussion some of the laws of succession as set down by Clements (1905) might be mentioned. Clements states that the causation of succession is either the creation of a new habitat or the efficient change of an existing one. At Bergen both causes have operated. The new habitat was created by glacial activity, and was later modified by the activity of pioneer plants. The second law is that each stage in the succession reacts in such a manner as to make its own permanence more or less impossible, with the exception of the climax stage. Thirdly, stabilization is the normal tendency of all vegetation, and finally the pioneer plants are those plants in the closest proximity and possessing the greatest mobility. The initial pioneers in swamp succession are usually the algae and fungi. These laws have all been found operative in the succession at Bergen.

CERTAIN ASPECTS OF THE MARL AND PEAT WITHIN THE SWAMP

Regarding the source of the marl, such as is found in the extensive and deep beds in Bergen Swamp, Bray (1930) says "the formation of the numerous and rather extensive marl beds in lake bottoms and in swamp soils built up under water is now ascribed largely to water vegetation; in part the blue green algae . . . and particularly to *Chara* and to a lesser degree to the *Potamogetons*, etc."

The action of *Chara* in the deposition of marl is described by Davis (1900) as follows: "We have in *Chara* a plant of relatively simple organization, able to grow in abundance under most conditions of light and soil which are unfavorable to more highly developed types, a chief agent in gathering and rendering insoluble calcium and other mineral salts brought into the lake . . . by springs, streams and seepage water. After precipitation is accomplished and the plant is dislodged or dies, it drifts ashore, where, after the decomposition and drying out of the relatively small amount of vegetable matter, the various erosive agents along the shore break up the encrusted chalky matter, and the finer fragments are carried into the deeper water and the coarser are left along the lines of wave action." This

explanation seems plausible, especially when Bray indicates Chara as a very active plant in this process. At Bergen it is possible to find a small amount of Chara in a few of the more moist portions of the marl beds, but practically all deposition has ceased.*

Oosting (1933) does not attribute marl formation to any specific plant, but states that the filling in is due primarily to accumulations of marl and that "all borings in the filled areas showed, at depths of more than a few feet, a mere scattering of plant fragments appearing superficial to almost pure marl." This same condition was found existing at Bergen and will be commented upon later.

Thiel (1930) in a paper bearing directly upon the question of marl beds states that the marl is composed largely of CaCO_3 and that its hardness is dependent upon the degree of drainage in the region. These two factors were found to be in perfect accord with the conditions at Bergen. Thiel gives us some valuable information on the source of the lime for the formation of marl. He attributes it directly to the heterogeneous masses of clay, sand, boulders, and drift deposited upon an area of glaciation. Water percolates through this mass and carries the lime dissolved from the rocks and clay to the center of drainage,—the lake or pond. Thiel points out a nice correlation between the areas affected by glacial activity and those in which marl is deposited. Regarding the method of deposition he mentions three theories:

1. A direct chemical precipitation of CaCO_3 resulting from the release of CO_2 from $\text{Ca}(\text{HCO}_3)_2$, the loss of CO_2 being caused by a reduction in pressure and an increase in temperature as the underground water is released into the lake.
2. Mechanical precipitation as carried out by Chara and possibly some other algae.
3. Mechanical sedimentation.

It is quite possible that all three of these theories are based upon fact, but the writer is inclined to agree with Bray (1930) and Davis (1900) in believing that Chara is chiefly responsible for marl

*The active formation of marl by Chara is beautifully seen in Blue Pond, in the town of Wheatland, Monroe County, a few miles southeast of Bergen. Here the Chara is piled in great masses near the shore, in all stages of disintegration. As late as sixty years ago the pond was partly fenced in to prevent cattle from being bogged down in the "quicksand." The open water is now surrounded by a wide border of totally bare marl, into which the sedge vegetation is encroaching.—(W. D. M.)

deposition in swamps. The extensive and deep marl beds at Bergen need more than chemical precipitation or mechanical deposition to explain the large amounts of marl present.

All theories regarding the formation of marl agree that it was produced under aquatic conditions. It is logical to assume, therefore, that the region now occupied by marl beds at Bergen was formerly covered by open water. Now we also find at Bergen considerable *Sphagnum* growing upon the marl. In this connection Transeau (1905) states that as a result of his work on marl beds in Indiana and Michigan it is evident that the marl usually forms the substratum upon which the peat is later deposited, due to the fact that marl is formed by aquatic plants (*Chara*), and peat by swamp forms. In other words the aquatic stage, which would naturally precede the swamp stage, deposits the marl and through this action creates a habitat adverse to its own permanence (Clements 1905). This results in the formation of a swamp condition and at this time *Sphagnum* becomes active and forms peat over the marl. MacMillan (1896) considers the occurrence of muskeg (peat) a normal transitional step in the filling in of glacial depressions. He says that "typical muskeg may clearly be taken as an intermediate physiognomic distribution of vegetation linking the original open lake with the later glade or forest." The statements of these authors coincide perfectly with the conditions found at Bergen. The marl has been deposited primarily through the action of *Chara*, and represents the aquatic stage in the succession. Following the disappearance of the aquatic stage the swamp appeared and with it *Sphagnum*, which has formed the peat layer on the marl in many places. The arrangement found at Bergen is apparently quite normal.

On December 1, 1933, Dr. Merrell and the writer investigated the marl beds to a depth of two to three feet. It was discovered that the marl was interrupted at a depth of 20-25 inches by a layer of peat varying in thickness from three to eight inches. Below this peat layer pure marl was again found. Investigation at several points in the marl beds indicated that this condition was general throughout the swamp. Microscopic examination of this sub-marl peat indicated that it was an almost pure *Sphagnum* deposit. No exact explanation of this sub-marl peat layer can be offered at this time, but it seems logical that it may be the result of a sudden raising of the level of the water table in the swamp. It is possible that the water table was at one time lower than it is today and

that the succession in the swamp had reached such a point that marl deposition had ceased and Sphagnum had formed on top of it to quite an extent. At this time a blocking of the drainage, or any other activity which might suddenly raise the water table would re-create aquatic conditions over the sphagnum. As a result marl deposition would be resumed and consequently bury the sphagnum between two layers of marl. The writer offers this merely as a possible explanation of the condition existing.

The idea of a change in the level of the water table as just presented is again offered as a possible explanation of a second curious condition found. On some of the open marl beds there are found a great many large dead trees, easily identified as arbor-vitae (Thuja). These trees could not have started upon the open marl. It is thought that the marl was at one time covered by Sphagnum peat, upon which the trees gained a foothold. A subsequent rise of the water table would have drowned out the trees and left them standing as they are today. An alternative idea is that possibly a swamp fire in the peat may have burned it off, killing the trees, and exposing the marl. Some char-markings on the trees indicate that fire has occurred at some time in this part of the swamp. The writer makes no attempt to prove either of these two ideas.

EFFECTS UPON THE VEGETATION CAUSED BY THE SOIL LEFT BY THE GLACIER

In a discussion of the stages of succession within the swamp it is important to consider the soil and its possible effects upon the vegetational composition of zones present. The glacial till, which through subsequent erosion formed the soil of the region, has no effect upon the vegetation of Bergen Swamp because this vegetation is supported entirely upon the humus formed by the decay of former vegetation. Even the vegetation outside the swamp which does grow upon the glacial till is not affected because the till was so heterogeneous and evenly mixed that a uniform soil has resulted. The underlying sedimentary rocks have no effect upon the vegetation because, with the exception of small outcrops, they are entirely covered by glacial débris (Beckwith and Macauley 1894). The only noticeable effect of the soil upon the vegetation is that in the central portion of the swamp some of the peat soils of the Sphagnum and Pine-Hemlock zones seem to be comparatively cool, possibly as a result of a high rate of evaporation from their surfaces, and this

coolness seems to create a condition quite satisfactory for some plants which are boreal. This idea is suggested by Bray (1930), and the writer is convinced that it is in effect at Bergen Swamp.

In the foregoing paragraphs we have considered the history of Bergen Swamp in so far as it has been possible to tell anything of its past. The present status of the swamp has been discussed earlier in the paper. For the future of the swamp we can only say that if left to its natural development it will in time become stabilized as a climax forest, which at Bergen would be of the beech-maple type.

ON THE BOREAL NATURE OF BERGEN SWAMP

EVIDENCES OF BOREALITY

Since no weather observations were made at Bergen Swamp, it is impossible to compare the swamp itself with the various surrounding regions as to climate. It being safe to assume, however, that the general weather conditions of the swamp, with the possible exception of temperature, are approximately the same as those at Rochester, 23 miles distant, the weather reports at Rochester (Vanderpool 1933) may be used as a basis for a general comparison with other portions of the country.

Using the U.S.D.A. Report for 1932, Vanderpool gives us the following information regarding the climatic conditions at Rochester. Table V, based on records for the last 103 years, gives the mean monthly and annual temperatures.

TABLE V

Mean Monthly and Annual Temperatures, Rochester, N. Y.

January	25.1°F	May	56.4	September	61.8
February	24.4	June	62.2	October	49.4
March	32.6	July	71.0	November	38.9
April	44.6	August	68.6	December	28.6
		Annual	47.0		

The average date for the last killing frost in the spring is April 29, and the average date for the first killing frost in the autumn is October 20.

The monthly and annual precipitation records, Table VI, from the same source, are adequate for the purpose of a general description. This rainfall record, the writer believes, is almost directly applicable to Bergen Swamp.

TABLE VI

Mean Monthly and Annual Precipitation, Rochester, N. Y.

January	2.59"	May	3.01	September	2.78
February	2.40	June	3.10	October	2.91
March	2.64	July	3.13	November	2.67
April	2.47	August	2.78	December	2.62
Annual		33.10			

According to Vanderpool Rochester has a frostless season which averages 153 days in duration. The figures in Table VII, from Livingston and Shreve (1921) will orient the Rochester region in respect to other general localities.

TABLE VII

Length of Average Frostless Season

New Hampshire	131 days	Ohio (north)	163 days
Vermont	132	Indiana (north)	163
Maine	135	Massachusetts	163
Wisconsin	136	Illinois	165
Minnesota	138	Pennsylvania	162
Michigan	147	New Jersey	177
New York	154	Delaware	181
Connecticut	158	Rhode Island	197

The frostless season, as an index of climatic conditions, would indicate that the climate of Rochester was in general similar to that of the state as a whole, and also to that of Michigan, northern Ohio, northern Indiana, and Massachusetts.

The above information is given for two reasons, first to make clear the climatic conditions of the general region in which Bergen Swamp is located, and second to indicate to what general regions the Rochester climate is similar and with what regions it differs and in what respects these differences are expressed. The information presented in the first part of the section may give some idea of the climate in the swamp itself.

VEGETATIONAL ASPECTS

The comparison of the vegetation of Bergen Swamp with that of general regions will depend upon the distribution of swamps which are similar to Bergen and would consequently have a like vegetation, and also upon the distribution of those regions in which the climax vegetation is similar to the typical vegetation found

at Bergen. It must be remembered that, while the climax vegetation now encroaching upon Bergen Swamp is the Beech-Maple forest, the typical swamp vegetation is that found in the Pine-Hemlock, Sphagnum and marl zones.

Transeau (1903) states that the maximum occurrence of the typical bog which he describes, and which is very similar to Bergen, is an area extending from the Mackenzie basin to the Atlantic, and lying in general to the north of a line passing through northern Minnesota, Wisconsin and Michigan, across Ontario to Kingston, across northern New York, Vermont, New Hampshire and Maine, and thence easterly to Newfoundland. He speaks of a secondary band of swamp occurrence south of this area which runs as far south as Chicago, Detroit, Buffalo, Scranton, and New York.

This information would indicate that the general territory occupied by the swamps of which Bergen is a type is located well to the north of New York State. An indication that Bergen Swamp is very similar to the "typical swamp" upon which Transeau has based the boundaries mentioned above is seen in the fact that of the fifteen species which he reports as being especially typical of the boreal swamp, we report 70% from Bergen, most of them occurring in abundance.

Livingston and Shreve (1921), speaking of the northern evergreen mesophytic forest, state that it occupies all alpine regions, portions of the Pacific coast to the north, northern Minnesota, Wisconsin and Michigan, and from northern Maine to the south along the Alleghenies as far south as North Carolina. They report as type species of this forest *Pinus Strobus*, *Larix laricina*, *Picea mariana*, *Picea canadensis*, *Thuja occidentalis*, *Tilia americana* and *Acer saccharum*. All of these, with the exception of *Picea mariana*, are reported in abundance from Bergen. They also report *Cornus canadensis* as being one of the most typical herbs of this northern transcontinental range, and again we report it as abundant in Bergen. In Figure 4 the dotted line marks the southernmost distribution of *Cornus canadensis*, showing clearly that the principal occurrence of *Cornus canadensis* lies well to the north of western New York.

Campbell (1926), in speaking of the vegetation of northern Maine and the adjacent islands, says that it is distinctly northern and in some cases almost subarctic. He continues his description by stating that "an undergrowth of such boreal plants as *Linnaea borealis*, *Cornus canadensis* and *Coptis trifolia* is characteristic."

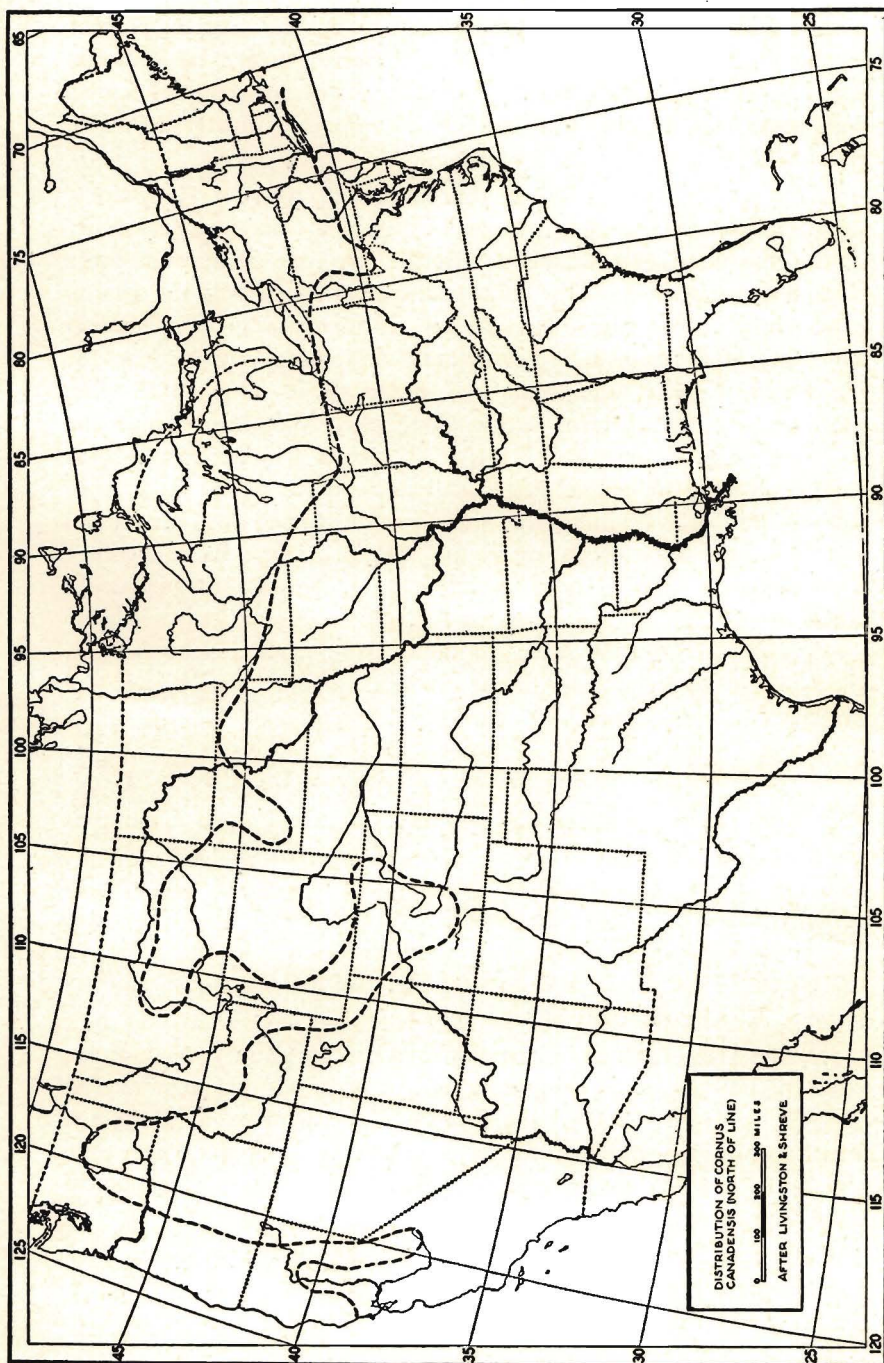


Figure 4. DISTRIBUTION OF CORNUS CANADENSIS

The fact that he mentions these species as "boreal," that they occur in abundance in Bergen, and that the region of which he is speaking, Maine, is decidedly cooler than New York, as reported above, would seem to indicate that Bergen Swamp is distinctly boreal in relation to its surrounding vegetation.

Eaton (1909), in discussing the climate of western New York, says that the northeastern corner of Genesee County is decidedly in the Canadian climatic zone. Bergen Swamp occupies a large portion of this corner of the county and it is undoubtedly the swamp to which he is referring. Bray (1930), in mentioning this Canadian zone, says that it is the southernmost and most valuable part of the boreal conifer vegetation and describes its extent as being Maine, New Hampshire, south along the Alleghenies, and the southern part of Canada. Of the 22 species which Bray lists as being especially typical of the Canadian zone we report 60% from Bergen, and of the sixteen he gives for the Canadian Transitional zone there are 68% occurring in the swamp. These facts, together with those mentioned above, point very strongly to the decidedly boreal nature of the vegetation in Bergen Swamp. Comparison of the location of these boreal vegetations, aside from that of Bergen, shows a nice correlation with the climatic factors mentioned in the first part of this section.

COMPARISON OF THE SWAMP WITH SPECIFIC LOCALITIES

In order to substantiate the general idea that Bergen Swamp is boreal, as mentioned above, the following comparisons with specific localities are listed. In all cases comparisons are based upon species actually collected within the swamp by the writer. Plant lists are not given because they would not materially add to the value of this phase of our study and because they are too large and cumbersome to handle efficiently at this point.

Rowlee (1897), studying the bogs of Oswego County, New York, reported 54 species as being especially typical of that region. At Bergen we report 65% of those reported by Rowlee, a percentage which would indicate that the bogs of the two regions were quite similar in character, as might be expected from their geographical proximity.

From a glacial moraine bog located in the Allegheny State Park in the southern part of this state, House and Alexander (1927) report a list of 70 typical species of which we report 62% at Bergen.

The bog reported is similar to Bergen and probably boreal, even though some distance to the south, because of the elevation of the region it occupies.

Taylor (1828) reports 108 species from the entire Allegheny State Park and from Bergen we report 50% of his list. Taylor states that some of the species reported are typical of the vegetation to the south and it is possible that for this reason our correlation is low.

In reference to a bog on Mazuma Dome, Rigg (1922b) states that the bog is 6000 feet above sea level and decidedly alpine in nature. Of his list we report 80% from Bergen Swamp.

Cooper (1913) reports 27 species as especially typical of the vegetation of Isle Royale in Lake Superior, and of that number we report 68%.

MacMillan (1892) reports 200 species from the swamps and bogs of Minnesota, and of this list we report 58% from Bergen.

Transeau (1905) gives a list of 106 species from the bogs of the Huron River Valley in Michigan. Of his list 58% occur in Bergen Swamp. Again Transeau (1903) in his report on the swamps of northern Michigan presents a list of 52 species, of which we have 63% at Bergen. These two comparisons indicate that Bergen Swamp resembles the bogs of northern Michigan more than it does those of the southern part, the Huron river being located in the extreme southeast corner of the state.

Reference at this point to the plant lists given under the discussion of the specific zones and associations of the swamp will strengthen the argument for the boreal nature of the swamp. In those lists the boreal species are indicated by the letter *b*. It is interesting to note that the percentage of boreal species is high in the associations which are not climactic and are considered boreal, whereas in the beech-maple, which is climactic, the percentage of boreal species is quite low.

The percentages listed above may at first appear to be low, but when it is remembered that in nearly all cases, including Bergen Swamp, the lists were not complete, it will become evident that the percentages, in most cases, represent higher correlations than would be indicated by their numerical values. This fact will become more evident when we compare the vegetation at Bergen with that of Spruce Mountain, West Virginia, as reported by Core (1929) and find that the correlation value has dropped to 40%.

The comparisons presented above indicate rather strongly that the Bergen Swamp is boreal in nature, especially when compared with the vegetation of the region in which it is located. The climatic factors show that the general region surrounding the swamp is perfectly normal; and yet when the vegetation of the swamp is compared with that of the Canadian zone there is a high degree of correlation, indicating that Bergen Swamp is a "little island of boreal vegetation" representing the Canadian zone and located in the transitional zone of western New York State.

THEORIES REGARDING THE BOREAL NATURE OF THE SWAMP

The theoretical causes of the boreal condition in swamps and bogs, such as that at Bergen, will be discussed in the next paragraph, while at this time we mention briefly the one outstanding theory regarding this boreal nature of bogs. This theory is that the soil in these bogs has a lower temperature than that in the surrounding regions. Transeau (1905) has found this to be the case in his investigations of the bogs of the Huron River Valley. He is of the opinion that this cold soil has a very definite effect upon the natural selection of the plants struggling to occupy the bog and that only those plants best fitted for such a cold soil are successful in invasion. For this reason, he claims, the vegetation of these bogs is typically boreal since the boreal plants are best adapted to invade such a soil. Working his argument backwards we might reason that the occurrence of boreal species in Bergen Swamp indicated a comparatively cold soil. On the same question Bray (1930) states that "certainly it is a common experience that bog waters are cold;" and further regarding the bogs of New York State he mentions that in every case there is a predominance of boreal species and that the bog is a "boreal island." It is obvious that if the bog waters are cold the soil will likewise be cold, and hence we have a probable explanation of the occurrence of so many boreal plants. No completely satisfactory reason has yet been given as to why the bog water and the bog soil should be cold in comparison with the surrounding territory, although Bray believes that the rapid evaporation from Sphagnum peat and similar soft soils in the swamp serves materially to reduce the temperature of the soil. It is clear, then, that the main theory of the boreal nature of these bogs is that the soil and soil water are comparatively cold and hence form a better habitat

for boreal plants than for those of the climax vegetation of the surrounding regions.

CAUSES OF THE BOREAL CONDITION OF THE SWAMP

Bray and Transeau thus present very similar and satisfactory explanations of the boreal condition as it exists in such swamps as Bergen. Other theories have been presented by various workers, most of which are modifications of those offered by Bray and Transeau.

Bray makes the following additional statements: that at the advent of the glacier the present floristic make-up of the country was in existence, with the present types of adaptations in effect and with the vegetation segregated into floral zones much as they are today. He then points out that the glacial invasion destroyed the floral cover of New York State and that the species existent in the state were either forced to migrate to the south or were exterminated. He continues that the present floristic make-up of the state has been derived from the vegetation to the south at the time of the glacial retreat; and that the New York species as well as those from farther north, having been forced southward by the advancing glacier, migrated north again following its retreat and reoccupied the regions they had formerly inhabited. This northward migration of the plants was, of course, possible only as the climate became milder with the retreat of the glacier. It is normal to assume that the boreal species came back first and were followed by the transitional and austral vegetations. This migration was subject to the same ecological rules as were mentioned earlier in the paper.

Transeau (1903) presents the same idea and in addition makes the very interesting speculation that during the duration of the glacial invasion the bog species had the same position in relation to the ice lobe as they now have in relation to the timber line. Regarding the postglacial northward migration Transeau says "With the renewal of a milder climate and consequent recession of the glacier the plant societies would gradually spread . . . and generally northward. The bog and tundra types would be the first to push into the barren ground left by the retreating ice. In the small glacial depressions where the absence of wave action would favor littoral vegetation, the bog plants would become firmly estab-

lished." Transeau attributes the continuance of these bog plant societies in the poorly drained depressions to the following factors:

1. The lower temperatures prevailing in the bogs.
2. The sterile nature of the substratum.
3. The completeness with which the substratum is occupied by bog plants (preventing other invasion).*

Transeau concludes from his study of the bogs that these boreal habitats, which are relics of early postglacial times, are due to the favorable low temperatures of the undrained depressions.

The above explanation of how the boreal vegetation came to occur in the swamps and bogs, such as Bergen, when the surrounding vegetation is far from boreal, seems to be quite satisfactory. In brief it may be stated that the glacier, as it moved south, either exterminated all the vegetation in its path or drove it south; the vegetation south of the glacier bearing the same relation to the glacier as it now bears to the timber line. During its invasion the glacier created the depressions now occupied by the swamps. As the glacier retreated the vegetation naturally migrated to the north to occupy the barren ground left by the glacier, the boreal types coming first. Finally the boreal plants in their migration northward found in the depressions left by the glacier suitable habitats and became well established in those places and have remained there ever since. These plants have remained in the depressions in spite of the development of a transitional and partially austral vegetation in the surrounding regions because the habitat has been especially well suited to their ecological needs. The writer is satisfied that some process similar to that just described is responsible for the boreal vegetation at Bergen Swamp.

SUMMARY

1. Bergen Swamp has been described as to its geology, soil types, and general physical features and it has been found to be normal in every respect.

2. The flora of the swamp, in so far as possible, has been studied and a list of those species collected and identified, combined with a list of species formerly reported from the swamp.

3. The type associations within the swamp have been described as to their floral structure, position in the succession, soil acidity,

*Parentheses the writer's.

and history within the swamp. The floral structure of the associations is perfectly normal, and the succession within the swamp today is in the order of open marl, secondary marl, *Sphagnum*, pine-hemlock, and beech-maple zones. The soil acidity readings indicate that the marl zones are pronouncedly alkaline, the pine-hemlock zone is decidedly acidic and the beech-maple zone is nearly neutral. No explanation of the relation between soil acidity and plant types is offered, although certain plants are noted as being characteristic of soils of limited acidity.

4. The history and development of the swamp has been discussed. The depression in which the swamp rests is ascribed to glacial activity and the cause of the filling in is thought to be the tendency of every region to move toward stabilization in the climax type of vegetation. The succession in the filling in is attributed to pioneer plants which act to modify the soil and create habitats favorable for the next step in succession.

5. The occurrence of sub-marl peat has been mentioned and no explanation has been offered, although an idea that secondary inundation has caused its being covered by marl has been suggested.

6. The idea that the soils left by the glacier might have had some effect upon the vegetation in the swamp has been considered and the conclusion reached that no such effects are visible.

7. Evidences of the boreal nature of the swamp have been presented; these evidences being based upon climatic factors, vegetational comparison of the swamp with both general areas and specific localities, and the theories and findings as presented by other workers. The results of these comparisons indicate that the Bergen Swamp is, in fact, a "boreal island" located in the temperate climate.

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