

STEVENS POND: A POSTGLACIAL POLLEN DIAGRAM FROM A SMALL TYPHA SWAMP IN NORTHWESTERN MINNESOTA, INTERPRETED FROM POLLEN INDICATORS AND SURFACE SAMPLES¹

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INTRODUCTION

The present study comprises a pollen-analytical investigation of a peat core from Stevens Pond, a small depression situated in the coniferous-deciduous forest belt in northwestern Minnesota, about 40 mi east of the present prairie/forest margin (Figs. 1, 2).

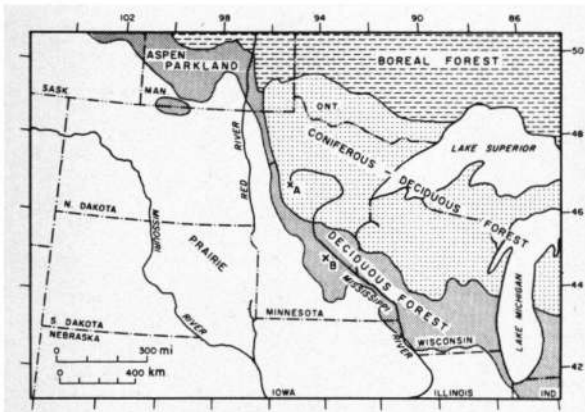


FIG. 1. Location of Stevens Pond and Itasca State Park (A) and Clearwater-Lake Sylvia area (B) in relation to major vegetational formations of Minnesota and adjacent regions.

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FIG. 2. Photograph of Stevens Pond from the west.

A detailed picture of the development of the regional vegetation is already available from the work of Me-Andrews (1966), who analyzed sediments from lakes along an east-west transect across the principal plant formations present today in northwestern Minnesota. For the Itasca State Park area he identified, above the late-glacial sediments, a *Pinus banksiana/resinosa*-

Pteridium assemblage zone, which has no modern equivalent in Minnesota, according to surface-sample analyses. Following this in turn is a *Quercus-Gramineae-Artemisia* zone, a *Quercus-Ostrya* zone, and a *Pinus strobus* zone, which represent respectively the *Quercus* savanna, the deciduous forest, and the coniferous-deciduous forest. The sequence indicates an expansion of the prairie towards the east in mid-postglacial time and a subsequent return of the forest. At the top the *Ambrosia* assemblage zone reflects agriculture developed by white man late in the 19th century.

McAndrews analyzed the sediments of moderately large lakes, so the pollen rain reflected primarily the regional vegetation. He thus interpreted his assemblage zones in terms of vegetation at the organizational level of the plant formation. Now, in each formation the vegetation is not homogeneously distributed. There is a mosaic of plant communities largely dependent on topography and soil differences. The present study had the objective to examine the detailed history of a small segment of this mosaic. Therefore Stevens Pond was selected to reveal such a history, because of two reasons:

1. In a peat bog the vegetation at the sampling site itself can be studied in detail because of the overrepresentation of the local pollen types. These types include several characteristic herbs, as is shown by pollen analyses of surface samples from plant communities prominent in the various stages of recent lake filling (Janssen 1966). Peat thus provides an opportunity to examine the succession in the local bog vegetation.

2. In a small depression the pollen types from the immediately adjacent upland should be better represented than in a larger basin, because of the short distance of dispersal (compare also Tauber, 1965). In an earlier paper Janssen (1966) introduced for such a rise in pollen percentage the concept of extralocal pollen and, for the vegetation that produces it, the extralocal vegetation. The small size of the basin may result in extralocal effects for one or more pollen types. If such pollen types represent species characteristic for the type of upland forest, it may then be possible to determine the nature of the forest surrounding the basin. Finally, after the local and the extralocal effects have been determined, the remainder of the pollen content represents the regional vegetation.

Throughout the discussion the terms local, extralocal, and regional pollen deposition are used as defined earlier (Janssen 1966).

To reveal to what extent extralocal effects occur in present-day basins of the size of Stevens Pond, samples were analyzed from small basins surrounded by various types of deciduous and coniferous-deciduous forests.

To evaluate the ecological significance of species whose pollen grains could be expected in the samples

of Stevens Pond, the modern forests and *Carex* mats in the Itasca State Park region were studied (Janssen 1967). Details of this vegetation study are irrelevant. It will suffice to note that species from vegetation plots (relevés) were arranged according to presence, so that species that tend to grow together are tabulated together in so-called sociological groups (Scamoni & Passarge 1959; Doing 1962). Vegetation plots that are characterized by the same sociological groups are placed together and mark a vegetation type. This is essentially an ordination of plots along some environmental gradient, and one would be inclined to call a sociological group also an ecological group. The difference is that an ecological group is characterized by all environmental factors except competition, and the sociological group includes the factor of competition. The sociological group thus indicates which species tend to grow together in a certain climate, on a certain type of soil, and with a certain regional reservoir of seed sources. A floristic ordination of vegetation plots naturally includes the factor of competition, and groups of species that are derived from such an ordination must be termed sociological, although most of the characterization of the groups is based on factors other than competition.

The nature of a sociological group is illustrated in Figure 3, which shows a simplified ordination of lowland vegetation plots in the Itasca State Park region.

If a stratigraphic pollen diagram is drawn with the pollen types arranged according to these sociological groups, then changes in the environment can be more easily traced. In one of the main pollen diagrams for Stevens Pond (Fig. 5), the lowland pollen types found in Stevens Pond have been so arranged, and the succession shows more clearly. A discussion of the vegetation types involved is contained in the section on lowland vegetation.

In comparing pollen assemblages with recent plant communities it is not implied that on the same type of soil the past vegetation should have had completely the same composition as do the communities today. This might be true if climate and accessibility for the species to an area were the same as today, but such was not the case. Under quite different conditions species now found widely separated may once have been associated. This might be true especially for the vegetation units of lower rank (associations). Units of higher rank (alliances), however, represent types of vegetation that are floristically and ecologically well-defined and often show a typical physiognomy. Probably in the recent past they had the same general species combinations. Moreover, in the late Holocene the competition was not too different from that of today, because the same species were present in the region. On the same type of soil and under similar climatic conditions this would therefore result in species combinations similar to those of today. Thus, for the late Holocene, reference to

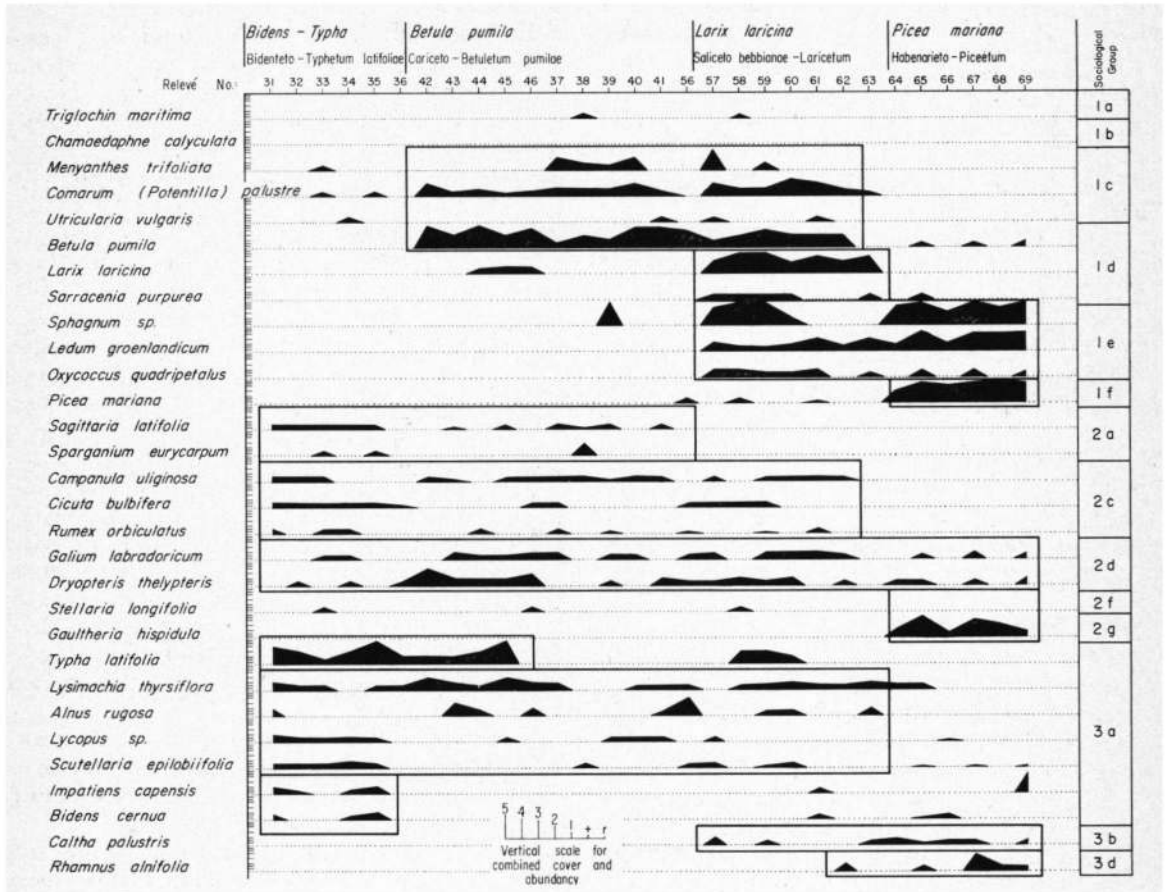


FIG. 3. Arrangement of recent plant communities in vegetation unit B. For explanation, see text under Local Vegetation.

recent plant communities of a fairly high rank is useful.

The more we go back in time, however, the more we find a quite different competition, even with constant climate and soil, because a different set of species was on the stage. The result may be a species composition unknown today anywhere (cf. Iverson 1960). For the early Holocene and before, one might ask whether a purely floristic comparison with recent plant communities is informative. These difficulties can be avoided by use of autecological data rather than floristic. However, the autecology of many species is still poorly known. But much of our knowledge about the ecology of species has been increased considerably by the study of the floristics of whole vegetation types, accompanied by studies of the environment. An arrangement of recent plant communities may tell us as much about ecological requirements of the species as does an autecological study.

By the method of establishing sociological groups, briefly described above, it was difficult to classify groups of vegetation plots in a hierarchic system of vegetation units. Although vegetation units are useful for reference to pollen assemblages in a pollen

diagram, it should be realized that many have sharp boundaries with neighboring ones.

In the following discussion frequent reference will be made to plant communities that were delimited as a result of the vegetation study in the Itasca State Park region. Although the arrangement of the vegetation plots in this region is not strictly according to the methods developed by the Zürich-Montpellier school of phytosociology (Braun-Blanquet 1951), the field methods and the identification of vegetation units are in the tradition of continental European plant ecology, and the plant communities have been named in the tradition of the Z-M school. An additional advantage is that it stresses the floristic concept of these communities. Classes, orders, alliances, and associations recognized according to this method are identified respectively by their suffixes -etae, -etalia, -ion, -etum.

The present paper does not give a full account of the floristic composition of the plant communities investigated (Janssen 1967). Only those data dealing with the various stages of lake filling are reproduced. A description of the present plant formations in the Itasca State Park region and their relation-

ships with physiography, geology, climate, and soil appear in McAndrews (1966).

Laboratory work was done at the Limnological Research Center, University of Minnesota, with the financial support of the Hill Family Foundation. I am much indebted to Dr. H. E. Wright for his helpful discussions and interest in the work, to Dr. E. J. Cushing for his help in identifying pollen types, and to Dr. J. H. McAndrews for introduction to the flora and vegetation of northwestern Minnesota.

The vegetation work was done during the tenure of National Science Foundation summer fellowships at the Lake Itasca Biological Station.

Recalculation of the data according to different pollen sums was carried out by computer according to the DHALL 3 program, designed by K. S. Defeyes and E. J. Cushing.

Pollen counts are on file with the American Documentation Institute, Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington 25, D. C.

METHODS

SAMPLING AND PROCESSING

Stevens Pond was sampled with a Davis corer in December, 1962, when the peat was frozen to a depth of only 2 cm. The core was divided longitudinally, and samples for pollen analysis were taken from the inside. Sample treatment included boiling with 10% KOH for 1 min, sieving through a fine screen, and acetolysis at 95C for 10 min. For microscopic investigation the material was mounted in silicone oil (2000 esk), without stain.

NOMENCLATURE

Nomenclature is that of Fernald (1950) except *Comarum palustris* L., *Melandrium* Roehl, *Ephedra fragilis* Desf., *E. distachya* L., and *Eriogonum heracleoides* Nutt.

POLLEN DIAGRAMS

Main Pollen Diagrams. The main pollen diagram has been divided into two parts. Figure 4 shows the upland pollen types that are included in the pollen sum. Figure 5 shows lowland pollen types as well as those from ecologically indeterminate habitats, all excluded from the pollen sum; the percentage base for each taxon is the pollen sum of Figure 4.

Percentages in both diagrams are shown on two scales; the scale with 10x exaggeration permits the accurate plotting of minor curves and minor fluctuations. The pollen sum is so large (generally more than 1000) that many minor inflections in the curves have statistical significance. For example, a contingency table shows that the drop in *Picea* at the zone 4/5 boundary is highly significant.

Lowland types include pollen from species of the *Ulmus americana-Fraxinus nigra* forest, often pres-

ent in the marginal bog zones. An exception, however, has been made for *Ulmus* itself, because although this tree occurs in this lowland forest it is more frequent in upland forest communities.

Betula has been retained in the pollen sum, although some of the *Betula* pollen grains may be of lowland origin. There are three *Betula* species in the region: *B. papyrifera* is an upland tree, *B. pumila* var. *glandulifera* is a lowland shrub, and *B. lutea* is confined to bogs but is rare in the area today (Christ 1959). Size-frequency curves for *Betula* pollen are shown in Figure 4 beside the *Betula* curve. Size measurements on the two main *Betula* species in the region today are given in the section on pollen morphology and in Table 1 and Figure 6.

Picea also has dual ecological distribution. *P. glauca* is confined to uplands, whereas *P. mariana* is a typical bog tree. Most of the *Picea* pollen grains at Stevens Pond probably are of lowland origin, and for that reason *Picea* was not included in the pollen sum. *Picea* grains were not measured, because preliminary analysis of reference material of the two species showed too much overlap in size.

Other pollen types usually included in the pollen sum, but here excluded because of a possible local origin, are *Salix*, *Alnus*, *Poaceae*, and *Cyperaceae*.

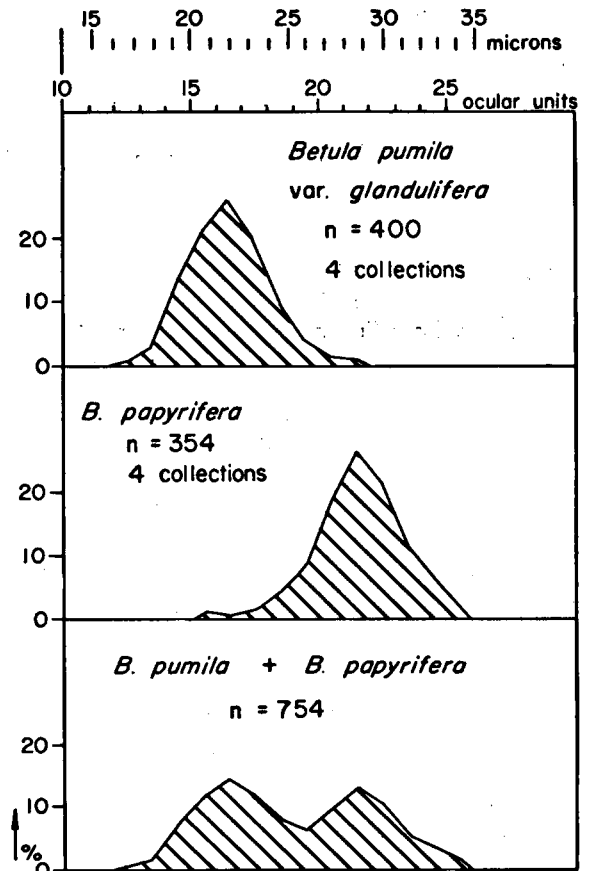


FIG. 6. Size-frequency curves of recent pollen of *Betula papyrifera* and *B. pumila*. See Table 1.

TABLE 1. Data for collections of *Betula papyrifera* Marsh. and *B. pumila* L. var. *glandulifera* Regel used for size-frequency studies. All the collections were treated with 10% KOH (2 min at 100 C), acetylated (1 min at 100 C), and mounted in silicone oil.

Species	Collector	Locality	Slide No. Limnol. Research Center	No. Mea- sured	Ave. Size (mi- crons)	Median (ocular units)	Mean Size and Standard Deviation (oc. units)
<i>Betula pumila</i> var. <i>glandulifera</i>	C. O. Rosendahl, F. K. Butters	Goodhue Co., Minnesota	2881	100	20.5	15.5	17.5±1.2
	J. W. Moore, B. O. Phinney 12483	Fillmore Co., Minnesota	2886	100	22.0	17.5	18.5±1.4
	J. H. McAndrews	Dakota Co., Minnesota	2898	100	22.6	16.5	17.5±1.2
	O. Lakela 554	Anoka Co., Minnesota	670	100	21.2	14.5	17.5±2.0
<i>Betula papyrifera</i>	E. J. Cushing	Hennepin Co., Minnesota	2080	110	26.7	21.5	21.5±1.6
	M. Fries	Ottawa, Ontario	1676	100	28.6	21.5	22.5±1.2
	O. Lakela 21263	Lake Co., Minnesota	2911	74	29.5	22.5	23.5±1.5
	O. F. Zech 157	Becker Co., Minnesota	2905	70	28.0	21.5	22.5±1.6

Auxiliary diagrams. Figures 6 and 7 are diagrams that show certain pollen types recalculated on the basis of a different pollen sum. These diagrams are especially designed for the two uppermost assemblage zones to allow comparison of Stevens Pond with surface samples and with McAndrews' sites in the Itasca State Park region. The differences reflect sediment type (peat, lake sediments) and differences in cultivation and long-distance transport. The assumptions made in the establishment of these pollen sums are discussed with the descriptions of the assemblage zones involved.

SITE AND PRESENT-DAY VEGETATION

Stevens Pond is the eastern of two ponds north of Itasca State Park along the south side of Minnesota Highway 31 between the village of Lake Itasca and the Mississippi River (Fig. 2). Its longest axis measures about 80 m. It is one of many ice-block depressions in a small outwash valley train of the Mississippi River.

Much of the flat terrain was cleared in the early 20th century and is now used mainly for the cultivation of *Avena*. The woods remaining have a composition typical for sandy soils. *Pinus banksiana* is dominant. *Populus tremuloides* is codominant, and *Pinus resinosa* and *P. strobus* are less common. Except for narrow strips of young planted *Pinus banksiana* along Highway 31, there is no forest

adjacent to the pond. The steep marginal slopes support a ruderal vegetation. In a 64 m² relevé made in 1962 the herb vegetation, covering 90% of the ground, included the following species. The first symbol refers to a 6-point combined scale of cover and abundance, the second to sociability on a 5-point scale (Braun-Blanquet 1951):

<i>Festuca ovina</i>	4.2
<i>Trifolium pratense</i>	3.2
<i>Trifolium hybridum</i>	1.2
<i>Trifolium repens</i>	2.2
<i>Vicia sativa</i>	+2
<i>Erigeron strigosus</i>	+1
<i>Senecio pauperculus</i>	+1
<i>Solidago</i> sp.	1.1
<i>Tragopogon pratense</i>	r
<i>Agropyron repens</i>	2.1
<i>Liatris ligulistylus</i>	+1
<i>Achillea millefolium</i>	r
<i>Berteroa incana</i>	+1
<i>Agastache foeniculum</i>	+2
<i>Phleum pratense</i>	+1
<i>Bromus inermis</i>	+1
<i>Melilotus officinalis</i>	+1
<i>Rosa acicularia</i>	+2

On the side where the angle of slope is the least, *Avena* fields border the pond. The marginal zone between the pond and the upland is characterized by *Salix* shrub (mainly *S. gracilis*). Where the *Salix*

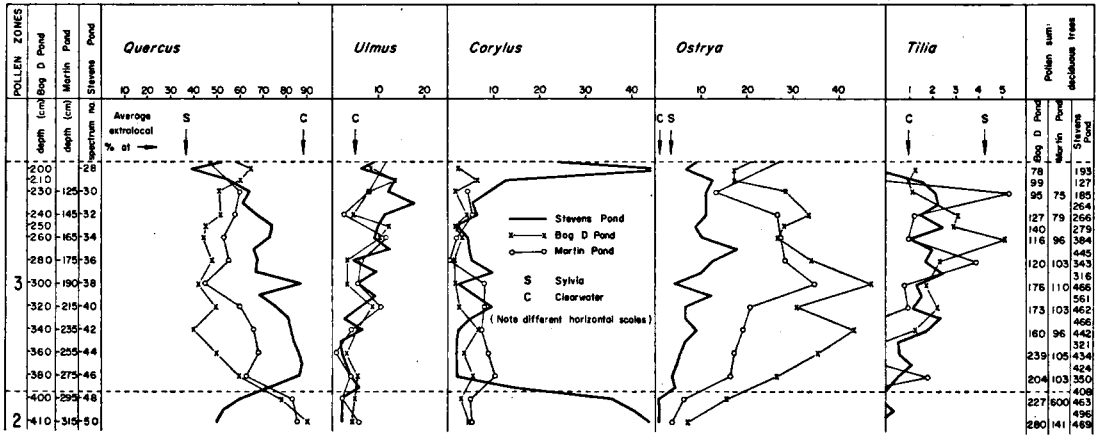


FIG. 7. Comparison of average recent pollen percentages of some deciduous trees for surface samples at Clearwater and Lake Sylvia with zone 3 and the upper part of zone 2 of three sediment cores, based upon the deciduous-tree pollen sum.

shrub is less dense or is lacking, the vegetation is dominated by *Scirpus* and *Carex*, with the following composition:

Shrubs taller than 80 cm	40%
<i>Salix gracilis</i>	+2
Herbs shorter than 80 cm	30%
<i>Scirpus atrocinctus</i>	2.2
<i>Glyceria grandis</i>	+1
<i>Poa palustris</i>	+1
<i>Carex projecta</i>	+1
<i>Carex riparia</i>	2.2
<i>Lysimachia thyrsiflora</i>	r
<i>Rumex crispus</i>	+1
<i>Stachys palustris</i>	r
<i>Solidago graminifolia</i>	+1
<i>Sium suave</i>	+1
<i>Aster puniceus</i>	+1

The pond itself is covered by a floating *Typha latifolia* mat with the following composition:

<i>Typha latifolia</i>	5.5
<i>Lysimachia thyrsiflora</i>	+1
<i>Carex rostrata</i>	+3
<i>Lemna trisulca</i>	+1
<i>Bidens cernua</i>	1.1
<i>Cicuta bulbifera</i>	+1

STRATIGRAPHY

Peat types are shown on the left side of the pollen diagrams (Figs. 4, 5). Symbols follow Troels-Smith (1955). Although no calorific measurements on the humification have been made, the state of humification is roughly indicated in the symbols to show the relative differences.

0-5 cm Undecomposed *Typha* peat. At the time of sampling of the core (Dec., 1962) this thin zone was resting directly upon woody peat, but in spring and early summer the *Typha* mat is floating. In cores taken along the periphery of

the pond, silt and clay occurs below the *Typha* mat. The clay and silt apparently is slopewash that penetrates beneath the mat during times of high water. In the core from the center of the pond the silt layer is absent.

- 5-55 cm Woody peat, gradually more decomposed toward the top. Sphagnum leaves present at 6-12 cm
- 55-73 cm Completely decomposed black amorphous peat
- 73-77 cm Same as above, but less humified
- 77-114 cm Drepanocladus peat with various amounts of moss, rather humified
- 114- cm Calcareous till

PALYNOLOGY

GENERAL STATEMENT

Despite the fact that the core is only 114 cm long, the pollen diagrams (Figs. 4, 5) show basically the same assemblage zones as established by McAndrews (1966). Only the lowest (*Picea*-*Populus*) zone might be absent. Gaps may go unnoticed because of the uniform sediment, especially in the *Quercus*-*Gramineae*-*Artemisia* zone, representing a time when the prairie invaded parts of the state that are now forested. Lake levels were probably lower (Cushing 1963) or fluctuating (Watts & Winter 1966) at this time, and at Stevens Pond peat accumulation may have ceased during dry periods. The abrupt rise and fall of the upland-herb curves at the beginning and end of the zone might mark gaps, which do not, however, eliminate an entire assemblage zone.

DEVELOPMENT OF THE REGIONAL VEGETATION

ZONE 1, SPECTRA 63 THROUGH 91: *Pinus banksiana/resinosa*-*Pteridium* Assemblage Zone

Zone 1 is characterized by very high percentages of *Pinus* (80-90%) and a continuous rather high level of *Pteridium*.

As in the diagrams of McAndrews, most of the pine pollen grains for this zone at Stevens Pond belong to the *P. banksiana/resinosa* type. According to McAndrews *Pinus banksiana* is the species more likely involved because of its more northerly distribution today. McAndrews noted that the absence of *Tilia* and *Acer rubrum* from this zone is an indication of the boreal character of the upland forest. At Stevens Pond, zone 1 has scattered *Tilia* and *Acer rubrum*, as well as *Carya* and *Juglans*, in percentages much the same as in surface samples in the conifer-hardwood formation of the Itasca Park region (Janssen 1966). Although *Tilia* and *Acer rubrum* occur in the area today, *Carya* and *Juglans* do not. It is therefore difficult to decide whether these 4 pollen types in zone 1 reflect the regional vegetation or come from southern Minnesota, e.g. the Anoka sandplain, where they are more consistently found in the correlative pollen zone (Cushing 1963).

Pteridium is recognized as characteristic for pine woods (Butters & Abbe 1953). Cushing (1963) compares the upland vegetation of this zone with the northern dry forest of Curtis (1959). In the Itasca State Park region of today, *Pteridium* is present in almost every type of upland forest but is most abundant on moderately good soils in vegetation types that have been called *Corno canadensis-Pinetalia* (Janssen 1967).

Zone 1 at Stevens Pond has several grains of *Shepherdia canadensis*, a shrub characteristic of the boreal forest today (Ritchie 1960, 1964) but absent from the Itasca Park area. The *Gaultheria procumbens* grains point toward a *Pinus banksiana* forest rather than toward a *P. resinosa* forest, as judged by its present occurrence in the region in poor *P. banksiana* forests on outwash soils (*Arctostaphylo-Pinetalia*; Janssen 1967). Unfortunately, however, in the present forests *Pteridium* is rare or absent where *Gaultheria* occurs. Moss (1953) describes *Pinus banksiana* forests in northwestern Alberta that include *Shepherdia canadensis*, *Vaccinium angustifolium*, and *Gaultheria procumbens*, but not *Pteridium*.

The *Pteridium* percentages found in zone 1 are higher than those in recent surface samples from pine forests and from small bogs surrounded by pine. Probably shading here prevents fruiting, as fruiting specimens of *Pteridium* in these types of vegetation are very rare. In western Europe *Pteridium* is part of the regeneration pattern of the vegetation on poor soils after clearing. Often the occurrence of spores of *Pteridium* is an indication of land occupation on these soils (Smith 1958; Iversen 1964). In the Itasca State Park region *Pteridium* is more abundant in open situations (such as windblown areas) than in closed forests.

The rather high percentages of *Pteridium* thus indicate an open rather than a closed forest, possibly even a jackpine barrens—a savanna in which herbs and forbs are dominant and which is maintained by

frequent fires. This vegetation includes *Pteridium* and *Gaultheria procumbens* (Curtis 1959) and, according to Vogl (1964), several prairie elements as well. Pollen grains of *Shepherdia argentea* found in the zone suggest prairie, but otherwise prairie indicators are absent or rare; for example, *Artemisia* shows a value of 5%, only slightly higher than the percentages found in the forest zones later in the Holocene. But it is definitely much lower than the *Artemisia* percentages in the next zone above, which was deposited during the prairie expansion eastward. Moreover, the genus *Artemisia* includes boreal species (Ritchie 1964).

Thus, in spite of the assumed open character of the pine forests for zone 1 at Stevens Pond, prairie elements were not very important. In addition to *Pteridium*, the understory must have consisted of ericaceous shrubs that usually are very underrepresented, even in small bogs in forested regions (Jonassen 1950; Janssen 1966). Lichens, which in Canada may cover large areas of *Pinus banksiana* savanna (Thieret 1964), may fill a gap in the vegetation yet not contribute to the pollen rain.

Davis (1963) concludes from her comparison with recent pollen spectra in Vermont that *Pinus* played a subordinate role in the forest of zone B, and that the vegetation must have been dominated by *Larix*, *Abies*, *Acer*, and *Populus*, all of which are underrepresented in the pollen record. Absence of pine is accepted by McAndrews for the western part of his transect. At Stevens Pond, however, the pine percentages for zone 1 are at such a high level that pine presumably played a major role in the vegetation.

Perhaps the closest analogues for the vegetation of zone 1 are the jack pine stands on sandy-gley Podzols and Grey Wooded soils studied by Ritchie (1961) in southeastern Manitoba. These stands contain most of the species found in our zone, e.g. *Pteridium aquilinum*, *Gaultheria procumbens*, and *Vaccinium angustifolium*, although *Shepherdia* is absent.

In the Stevens Pond diagram a division may be made between spectra 72 and 73. In zone 1a, *Ulmus*, *Alnus*, *Larix*, *Comarum* type, *Betula*, and *Menyanthes* reach higher percentages than in zone 1b.

The size-frequency curves for *Betula* indicate that in zone 1a, *Betula papyrifera* is involved rather than the smaller-sized *B. papyrifera* at Martin Pond in this zone. The same species has been reported for the correlative zone in southern Minnesota by Watts & Winter (1966).

ZONE 2, SPECTRA 48 THROUGH 62: *Quercus-Gramineae-Artemisia* Assemblage Zone

Zone 2 represents the time in which the prairie/forest border moved east in Minnesota (Wright *et al.* 1963). At Stevens Pond it is characterized by a sharp decrease of *Pinus* and a rise of *Quercus*, *Corylus*, *Ambrosia* type, and *Chenopodiaceae/Amar-*

anthaceae, and by a concentration of occurrences of the prairie herbs *Artemisia*, *Amorpha*, *Petalostemum*, *Lilium philadelphicum*, and cf. *Zizia aurea*. For a similar assemblage, McAndrews postulated that the now forested uplands of his transect were covered by prairie in the structure of a *Quercus* savanna. Because the sediment at Stevens Pond is peat, most of the non-arboreal pollen (Poaceae, Cyperaceae, and Tubuliflorae) may have been of local lowland origin, and thus it cannot be used for an evaluation of the character of the upland vegetation. Some of the grass pollen may have an upland origin, however, because various types within this taxon can be found in the sediments. The same applies for the Tubuliflorae: some species of *Aster*, for example, may be very abundant in a prairie vegetation, but others can be found in *Carex* mats.

In the regional diagram, zone 2 may be divided into subzones 2a (spectra 55-63) and 2b (spectra 48-55). In Zone 2b, *Corylus* shows a maximum, and *Rhus glabra* type, *Symphoricarpos occidentalis*, and *Rosa* type are present. These plants are abundant today in a *Quercus macrocarpa* savanna, a formation that is maintained between prairie and forest as a result of the suppression of *Quercus* seedlings by fire (McAndrews 1966). Ewing (1924) describes for northwestern Minnesota a *Populus tremuloides* brush prairie, bordered on the east by *Quercus macrocarpa* brush prairie with *Corylus americana*, *Rhus glabra*, *Amorpha canescens*, *Rosa* sp., *Petalostemum*, and *Symphoricarpos occidentalis*.

Aikman (1928) found a "Rhus-Corylus chapparal" at the "xerophytic edge" of the *Quercus macrocarpa* forest in Iowa. Curtis (1959) describes for Wisconsin the same type of vegetation as "oak opening." Bray (1960) and Buell & Facey (1960) also describe such savanna vegetation.

Sedvey Lake, a typical site in the *Quercus* savanna of northwestern Minnesota, has mesic forest on the northeast-facing slopes around the lake, but the southeast-facing slope and the crest support a shrub savanna with open-grown *Quercus macrocarpa* and dense shrub in which *Corylus americana* is dominant (McAndrews 1966). *Cornus racemosa*, *Rhus glabra*, *Symphoricarpos occidentalis*, and *Artemisia* sp. are also present. The south-facing slopes support a prairie with e.g. *Amorpha canescens*, *Aster* sp., *Artemisia* sp., and *Petalostemum* sp.

Corylus americana was flowering abundantly at Sedvey Lake in April 1964. In the summer of the same year *Lilium philadelphicum*, a plant from the mesic prairie (Curtis 1955) represented in the Stevens Pond diagram by several pollen grains, flowered at the base of the southern slopes. The higher percentages of *Corylus* found at Stevens Pond (25%) have not been matched in any other diagram from Minnesota. In some of McAndrews' diagrams, especially those at the easternmost part of his transect, a slight rise of *Corylus* is noticeable in this zone. *Corylus* is a good pollen producer, but its grains are

not dispersed readily (Jonassen 1950). For that reason the high *Corylus* percentages may be a result of the short distance to the upland (extralocal effect) rather than a more widespread regional occurrence of *Corylus*.

It is not certain whether the *Ambrosia* type and the *Chenopodiaceae/Amaranthaceae* originate from the upland or from dry lake beds. McAndrews emphasizes the occurrence of *Ambrosia* sp., *Chenopodium hybridum*, *C. rubrum*, and *Amaranthus* sp. on soils near lake shores. Wright *et al.* (1963) and Watts & Winter (1966) favor, for Lake Carlson and Kirchner Marsh, the local occurrence of these plants on bare lake beds or in a broadened shore zone. Indeed the *Ambrosia* type shows very high percentages in diagrams from these sites. At Stevens Pond, however, the peaty sediment may not form such a well-suited seed bed for these plants. Accordingly the values for *Ambrosia* type and *Chenopodiaceae/Amaranthaceae* are relatively subdued. At Thompson Pond, McAndrews found a peak in the curve of *Ambrosia* type at a silt layer in the gyttja. He assumed that *Ambrosia* type pollen was washed into this pond from the upland. However, the *Ambrosia* type pollen in the silt was well preserved in contrast to most of the other types, so it must have arrived by air rather than by inwash from the slopes along with the degraded pollen.

ZONE 3, SPECTRA 28 THROUGH 47: *Quercus-Ostrya* Assemblage Zone

The base of zone 3 at Bog D in Itasca Park has a radiocarbon age of 3930 ± 100 yr (Y-1328), and the upper part 2730 ± 75 (Y-1156) (McAndrews 1966).

Zone 3 is characterized by a rise in the curves for *Pinus* and *Betula* and a fall in the curves for *Corylus*, *Artemisia*, and *Chenopodiaceae/Amaranthaceae*. At first *Quercus* remains constant, but then its curve starts to drop. Pollen curves of mesic forest elements (*Acer saccharum*, *A. rubrum*, *Ostrya/Carpinus*, *Ulmus*, and *Fraxinus pennsylvanica*) reach maxima in this zone.

McAndrews concluded from his surface-sample transects that for this zone a deciduous forest must have been present on the uplands, where *Pinus* and *Abies* trees were virtually absent. According to him (1966), the tree vegetation was different on the two main till types in the area. On the sandy till of the Wadena Lobe *Quercus* and *Ostrya virginiana* would have dominated on the uplands, *Ulmus* on the more mesic sites, and *Fraxinus nigra* and *Abies balsamea* along bog margins. On the silty till of the Des Moines Lobe, occupying the Big Stone Moraine in the eastern part of Mahanomen County, the uplands contained more *Quercus rubra*, together with *Ulmus americana*, *Tilia americana*, and *Ostrya virginiana*, whereas *Acer saccharum* was confined to the more mesic sites.

In connection with these assumptions made by

McAndrews, largely on the basis of the present ecology of the tree species, it would be interesting to know what particular kind of forest is present on the upland immediately surrounding Stevens Pond. Because of the heterogeneity of the vegetation it is by no means certain that such a forest has the same species composition as the overall forest present in the region. The small size of Stevens Pond, combined with the surface-sample studies along transects in two types of deciduous forest (the Lake Sylvia and Clearwater sites of Janssen, 1966), offers an opportunity to determine the character of the extralocal vegetation. If, for instance, *Tilia* occurred around Stevens Pond then this might be reflected by higher percentages (extralocal percentages) than McAndrews found in his larger basins.

A comparison thus can be made between the pollen percentages at Stevens Pond, those at a number of McAndrews sites, and those found in surface samples at approximately the same distance from upland deciduous forests as the core of Stevens Pond is from the upland. The surface samples were taken in bogs surrounded by two strongly contrasting types of deciduous forest. The forest around the Lake Sylvia Pond is of the Big Woods type, in which *Acer saccharum* is dominant and *Ulmus americana*, *Tilia americana*, and *Ostrya virginiana* are codominant. It contains small amounts of *Quercus rubra*, *Populus tremuloides*, *Betula papyrifera*, and *Carya cordiformis*. The Clearwater Pond is surrounded by a xerophytic forest in which 4 species of *Quercus* are dominant, *Betula papyrifera*, *Acer rubrum*, and *Prunus serotina* are common, and *Populus tremuloides*, *Ulmus americana*, and *Tilia americana* are only minor components (Janssen 1966).

All available data are not comparable without adjustment of the pollen percentages, because:

1. samples come from different sediment types
2. recent surface samples show the disturbing effects of cultivation, and
3. pollen transported from outside the region varies.

Pollen percentages therefore have been recalculated on the basis of a deciduous forest pollen sum including *Populus*, *Fragaria pennsylvanica* type, *Ulmus*, *Quercus*, *Ostrya/Carpinus*, *Tilia*, *Acer saccharum*, *A. negundo*, *A. rubrum*, *A. spicatum*, *Celtis*, *Corylus*, *Humulus*, *Pteridium*, *Carya*, *Juglans nigra*, *J. cinerea*, and *Platanus*. Several pollen types commonly included in the pollen sum are absent. They fall into 3 groups. The first 2 groups are excluded because of assumptions derived from surface-sample analyses and the work of McAndrews.

1. The low percentages of herbs in zone 3 at Stevens Pond point to a forest vegetation. Pollen types that may have originated from non-forest vegetation therefore have been excluded from the pollen sum. This applies in principle to all herbs and forbs except *Pteridium* and *Humulus*. Most of the pollen types that fall in this category show low values, and

an exclusion therefore is not very effective in the adjustment of the other pollen curves. However, *Artemisia*, *Chenopodiaceae/Amaranthaceae*, and *Ambrosia* type may show considerable percentages in some of the samples. Especially *Ambrosia* type shows high and irregular percentages in recent surface samples. Excluding this type facilitates the comparison of recent surface samples with pre-settlement pollen spectra.

2. The upland forest is a deciduous type of forest in which conifers are absent.

Pollen types of upland conifers comprise 3 genera, *Pinus*, *Picea*, and *Larix*:

a. *Pinus*. Pollen grains of *Pinus* are a result of long-distance transport from coniferous forests to the east. Several studies show that the *Pinus* percentages may depend on the distance from such a forest belt. *Pinus* percentages in surface samples are lower in the present deciduous forest belt in the St. Cloud region than in that of the Itasca State Park region (Janssen 1966). Also McAndrews (1966) found decreasing *Pinus* percentages in the outer portion of the present conifer-hardwood forest belt and in the adjacent deciduous forest belt. The general rise of pine through zone 3 therefore might be a result of the approaching coniferous forest from the east, rather than a change in composition in the regional deciduous forest.

b. *Abies*. Most of the pollen grains of *Abies* also may not have originated in the regional vegetation. Although *Abies* occurs in the present deciduous forest belt, it is more abundant in the recent and subrecent conifer-hardwood formation.

c. *Picea*. As will be shown later *Picea* pollen grains also probably came from the conifer region to the east. *Picea* is absent from the present deciduous forest belt.

3. Finally, because some of the samples consist of peat and some of lake sediment, pollen types that might have originated from local bog or lake vegetation must be excluded from the pollen sum because their overrepresentation in only part of the section would prevent a comparison of all data. The most conspicuous representatives of this group are

a. *Poaceae*, *Cyperaceae*. Local values at Stevens Pond and some of the surface samples; possibly also at Bog D.

b. *Larix*. Local values at Stevens Pond.

c. *Betula*. Some of the pollen grains might be *Betula pumila*, especially at Stevens Pond and some of the surface samples. This pollen type was not excluded from the pollen sum of the main diagrams.

Table 2 shows an average pollen percentage for some trees based upon the deciduous-tree pollen sum. Although it is a hazardous procedure to integrate

TABLE 2. Average pollen percentages based upon the deciduous-tree pollen sum for the *Quercus/Ostrya* assemblage zone and for surface samples. *Larix* and *Picea* are excluded from the pollen sum.

Zone 3 in conifer-hardwood formation in Lake Itasca region	Surface samples in deciduous forest formation near St. Cloud in small ponds comparable to Stevens Pond			Quercus/Ostrya assemblage zone in conifer- hardwood forma- tion in Lake Itasca region		Quercus/Ostrya assemblage zone in deciduous forest formation west of Lake Itasca	
	Stevens Pond	Clear- water	Lake Sylvia	Bog D Pond	Martin Pond	Terhell Pond	Reichow Pond
<i>Ulmus</i>	7.3	4.7	43.9	7.0	5.1	9.7	13.7
<i>Quercus</i>	75.2	88.2	37.1	50.5	58.6	55.0	52.0
<i>Ostrya</i>	8.6	1.2	3.7	32.8	22.5	20.2	22.0
<i>Tilia</i>	1.4	1.0	4.3	1.8	1.7	4.7	2.7
<i>Acer saccharum</i>	0.4	0.2	4.1	1.2	0.9	1.1	0.8
<i>Corylus</i>	5.2	0.3	0.4	3.1	6.1	4.6	6.1
Pollen sum	6948	1735	870	4537	1842	2084	2235
<i>Larix</i>	15.2	0.2	0.14	2.1	1.5	0.9	0.6
<i>Picea</i>	2.8	0.1	0.2	1.1	1.8	3.3	3.3
Spectra used	29-47 for <i>Picea</i> ; 32-47 for <i>Larix</i>	4, 5, 6, 11-17	3-13	200- 380 cm	125- 275 cm	40- 510 cm cm	15-97 cm

spectra into an average value from a zone that lasted a long time (it denies changes that certainly took place), still this value will be useful when the variations of the pollen percentages are not too large. This is in a general way one of the very characteristics of a pollen zone.

At any rate, the percentages based upon the deciduous-tree pollen sum of the individual spectra for Stevens Pond, Bog D, and Martin Pond compared with the average percentages from the recent surface samples at Lake Sylvia (S) and Clearwater (C) are shown in Figure 7. For Terhell and Reichow ponds no adjusted curves have been included in Figure 7, mainly because the time-stratigraphic identity that in a general way exists between the spectra of Stevens Pond, Martin Pond, and Bog D pond is certainly lacking between these ponds and the Reichow and Terhell Ponds. For these latter two ponds the only reference to the recalculated percentages is found in Table 2.

From Table 2 and Figure 6 it appears that the pollen percentages of Stevens Pond resemble most those of the xerophytic *Quercus* forest at Clearwater. Both sites show high percentages of *Quercus* and low values of *Ulmus*, *Tilia*, and *Acer saccharum*. The average *Corylus* percentage at Stevens Pond is about the same as in McAndrews sites. The very low values for *Corylus* at Lake Sylvia and Clearwater are a result of its absence in the surrounding forest. The conclusion is that *Corylus* (either *C. americana* or *C. cornuta* or both) was part of the understory of the *Quercus* forest surrounding Stev-

ens Pond in zone 3. That *Corylus* was close by is indicated by its peak at the single sample Nr. 28, where also clusters of *Corylus* pollen were found.

The percentages of *Acer saccharum* and *Tilia* at Stevens Pond are much the same as those at Clearwater. Because at Clearwater *Acer* and *Tilia* are essentially absent, they also must have played but a minor part in the vegetation at Stevens Pond.

I was unable to match in surface samples the percentages found for *Ostrya/Carpinus* in zone 3 for all the sites in the Itasca State Park region. *Ostrya* must have taken a much bigger share in the vegetation than in the present forest at Clearwater.

In Figure 6 the *Ulmus* and *Quercus* values start at the same percentage level as at Clearwater, but *Ulmus* and *Ostrya* rise at the expense of *Quercus* towards the top of the zone, indicating a tendency towards more mesic conditions. *Ulmus*, however, does not reach the values found for the Big Woods at Lake Sylvia. Accordingly it must have been subordinate to *Quercus* in the vegetation at this time.

Thus, in spite of the fact that pollen grains from mesic forest elements reach higher values in zone 3 than elsewhere in the profile, the general impression of the forest around Stevens Pond during deposition of zone 3 is that it was a xerophytic *Quercus* forest. This is in agreement with the assumption of McAndrews that *Quercus* forests dominated the uplands in the Itasca State Park area. The average percentages at Stevens Pond for pollen types are the same as those for Bog D and Martin Pond, except for *Ostrya/Carpinus*, which is much lower,

and Quercus, which is higher. The lower percentages of Ostrya/Carpinus may result from a difference in soil: Stevens Pond is situated on a level outwash plain, which today carries a xerophytic *Pinus banksiana* forest, in contrast to the tills around Bog D and Martin Ponds, which are covered by less xerophytic *Populus tremuloides* or *Pinus resinosa* forests. The higher Quercus values at Stevens Pond may also be a result of these soil differences, although they may be an extralocal effect.

In contrast to the Itasca State Park area, Terhell and Reichow Ponds on tills of the Des Moines lobe show higher values of Tilia and Ulmus in the Quercus/Ostrya assemblage zone, but they are still far lower than in the Big Woods type of forest near St. Cloud, indicating that even here on these rich soils no Big Woods type existed during the time of zone 3.

Sanicula pollen grains are scattered in zone 3. According to the vegetation studies in the Itasca State Park region *Sanicula marilandica*, though present in most of the upland forest types, reaches its optimum in Quercus forests (the so-called *Dier-villete-Quercion*), not in the highly mesic Acer-Tilia-Ulmus communities. This agrees well with conclusions based upon the percentages of the tree-pollen grains.

Although not of primary concern here, *Betula papyrifera* may have been an important component in the Quercus forest, especially in the lower part of the zone. At the boundary between zones 2 and 3 the Betula curve abruptly jumps up to 35%, then drops off slowly. McAndrews found a prominent rise in the curve of Betula at Bog D and Martin Ponds and concluded on the basis of fruits that the species primarily represented was *Betula papyrifera*. It would have been the earliest invader. At Stevens Pond we find at the base of zone 3 a sudden shift in the size frequencies towards the larger-sized Betula

grains, suggesting that indeed *Betula papyrifera* is involved.

If Pinus was absent during zone-3 time, then the rise of pine pollen throughout the zone is a reflection of the approaching coniferous elements from the east. A majority of the determinable pine pollen belongs to the *Pinus strobus* type, as was found also by McAndrews.

ZONE 4, SPECTRA 9 THROUGH 27: *Pinus strobus* Assemblage Zone

In zone 4 Pinus reaches a maximum value exceeding 80%. Quercus, Ambrosia, Artemisia, and Chenopodiaceae/Amaranthaceae have their lowest percentages in the diagram.

The lower boundary of the zone is characterized by the following features:

1. Quercus, Ulmus, and Ostrya/Carpinus complete their steady decrease from the upper part of the previous zone.
2. Pinus exceeds 80%.
3. The Tilia curve becomes interrupted.
4. The Abies percentages show a small but consistent rise.

In Table 3 and Figure 8 all the pollen data were recalculated on a sum that includes the deciduous pollen types of the previous table plus Pinus and Abies, on the assumption that the regional vegetation during this time had the character of a conifer-hardwood forest (McAndrews 1966). Picea and Larix, however, were excluded because of probable local origin.

The surface samples used for comparisons with zone 4 of Stevens Pond were taken at 4 sites of similar size surrounded by different types of upland forest. That at Floating Bog has *Tilia americana* dominant and *Ulmus americana* and *Fraxinus pennsylvanica* codominant. At Bohall *Pinus resinosa* is

TABLE 3. Average pollen percentages for some trees, based upon the coniferous-deciduous pollen sum (excluding Picea and Larix)

Zone	Stevens Pond	Stevens Pond	Bog A Pond	Bog D Pond	Cindy Pond	Martin Pond	Recent				
							Extra-local, Floating Bog	Extra-local, French Creek Bog	Extra-local, Bohall	Extra-local, Beauty	Regional, Itasca area
Abies.....	1.2	3.6	0.65	0.32	0.32	0.39	2.6	5.6	1.6	0.32	1.40
Pinus.....	92.0	85.7	81.1	82.7	83.4	82.2	64.2	78.4	93.2	74.5	80.8
Acer saccharum.....	0.09	0.11	0.35	0.35	0.05	0.23	0.2	0.07	0.04	0.13	—
Ostrya.....	0.63	0.24	3.93	2.4	3.3	4.4	0.95	0.18	0.19	0.29	0.39
Corylus.....	0.91	0.63	0.95	1.47	1.46	1.04	1.9	0.93	1.9	3.8	0.75
Tilia.....	0.08	0.1	0.17	0.03	0.09	0.13	4.8	0.16	0.15	0.09	0.16
Ulmus.....	0.76	1.1	1.58	1.77	1.10	1.26	4.5	1.5	0.35	1.3	1.61
Quercus.....	3.68	6.6	10.2	8.26	8.26	8.23	11.6	9.3	2.4	15.2	8.30
Pollen sum.....	19161	8337	1681	3211	3103	2443	2526	5471	2606	3157	
Picea.....	3.85	1.6	0.45	2.4	1.14	1.42					
Larix.....	0.11	0.26	3.42	3.5	0.55	0.74					
Spectra used.....	10-27	1-9	20-60	40-180	20-90	20-105	4-12	17-22	1-5 3-10	5-10 1-3	

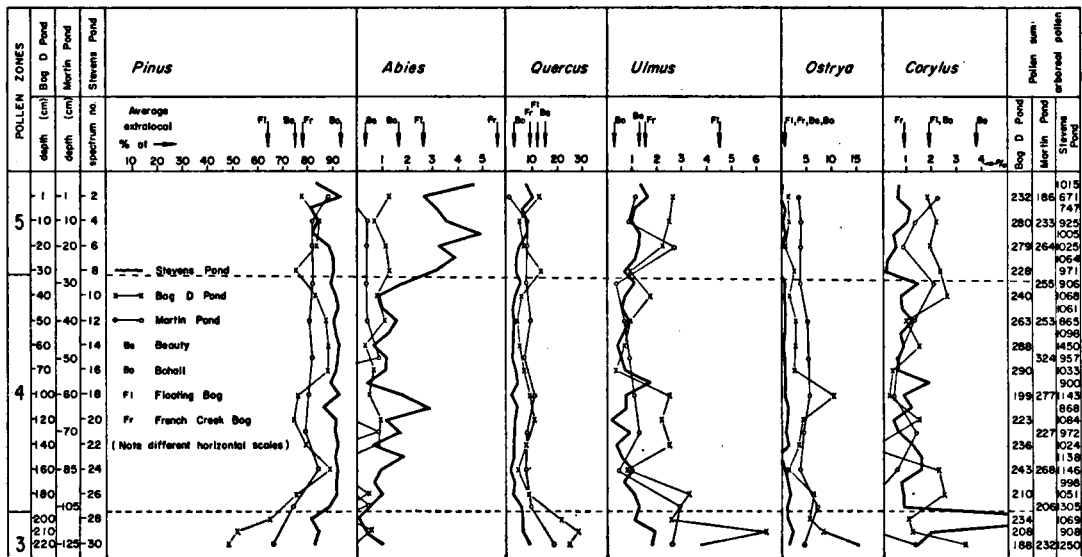


FIG. 8. Comparison of average recent extralocal pollen percentages of some tree for surface samples with zone 4 and 5 and the upper part of zone 3 of three sediment cores, based on the coniferous-deciduous tree pollen sum.

dominant and *Abies balsamea* and *Betula papyrifera* codominant. At French Creek Bog, *Pinus resinosa* and *P. banksiana* are dominant and *Abies*, *Betula*, and *Populus* codominant. The Beauty traverse is characterized by dominant *Populus tremuloides* and *Betula papyrifera* and frequent *Quercus macrocarpa*.

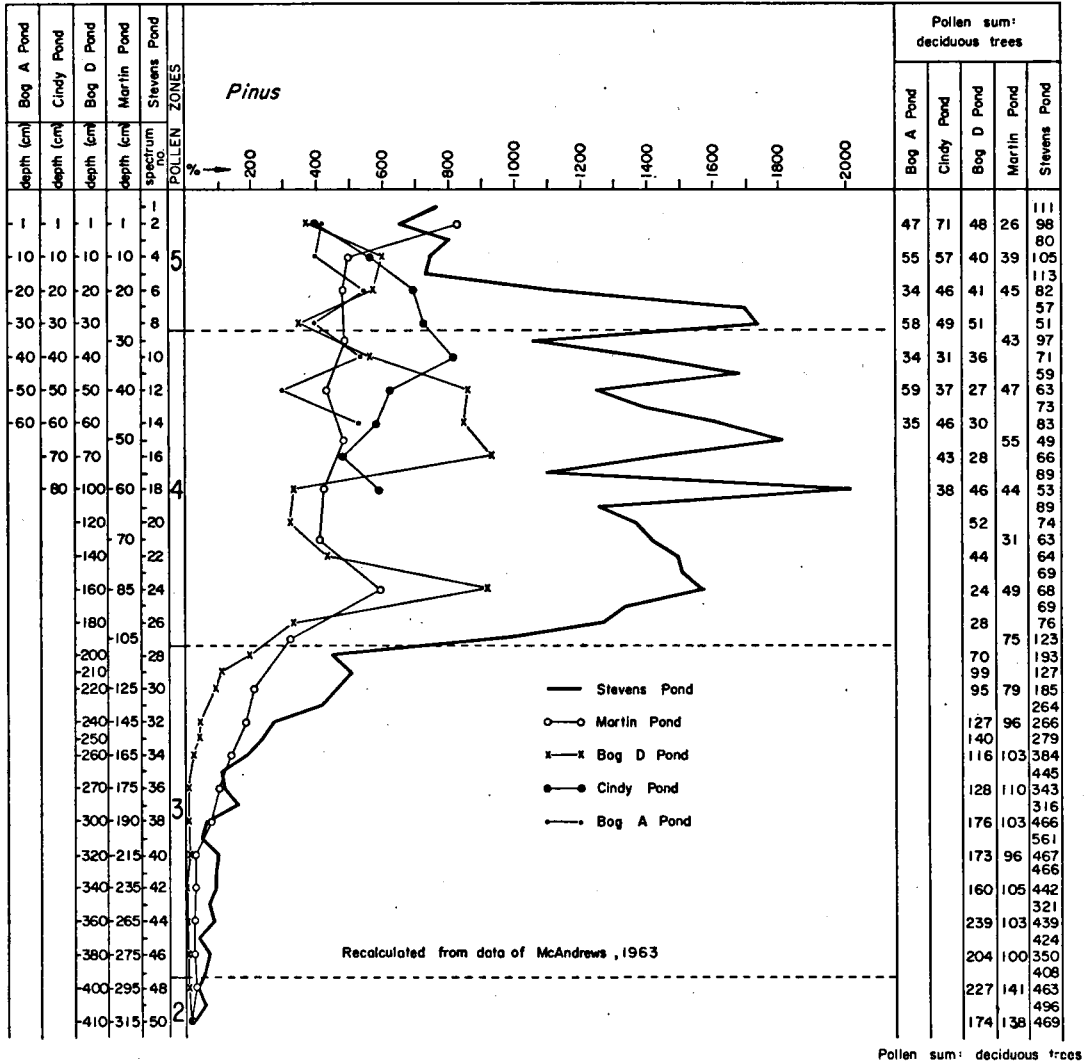
The best correlation is found with Bohall, which has the same high values for pine and same low values for *Quercus*. Deciduous elements such as *Acer saccharum*, *Ostrya virginiana*, *Tilia americana*, *Ulmus americana*, and *Quercus* sp. are completely lacking in the forest at Bohall. Because the pollen percentages of these trees are approximately the same at Bohall and in zone 4 of Stevens Pond, these elements were probably lacking in the pine forest around Stevens Pond at that time.

The mature *Pinus resinosa* forest at Bohall locally has scattered young *Abies balsamea*. For Stevens Pond in zone 4, the values for *Abies* are about the same as the regional recent percentages. They are higher than the regional values found at the sites of McAndrews, but the differences are small, so extralocal *Abies* may not have occurred around Stevens Pond. The rise of *Abies* in zone 4 must have been largely a regional feature.

The values for pine at the 4 sites investigated by McAndrews all are slightly lower than those at Stevens Pond. They are about the same as the average regional recent percentage. Apparently these ponds are of such a size that *Pinus* fails to show an extralocal value, even though they may have been surrounded by pine forests. One might ask whether the difference of ca. 10% that exist between Stevens Pond and the 4 sites of McAndrews is significant. It is, if we realize that a same percentage

rise in the high percentage bracket means a larger increase of actual pollen numbers deposited than in the lower percentage bracket (law of diminishing returns: Faegri & Iversen 1964). The differences between the sites are better demonstrated in Figure 9, which shows the *Pinus* curves based upon a pollen sum of deciduous trees (the pollen sum used in Fig. 7 for zone 3). If we assume that the total pollen deposition of deciduous-tree pollen remained fairly constant throughout zone 3, then the gradual rise of pine in this zone reflects the approach of the conifer-hardwood belt from the east. Alternatively, pines already slowly migrated into the region during zone-3 time and actually replaced deciduous trees, thus resulting in a decline of the total pollen deposition of the deciduous elements and a rise in pine values in zone 3 to levels consistently higher than those at Bog D and Martin Pond. It is not very likely that this difference reflects different distances from a conifer belt in the east, because Stevens Pond and Bog D are very close to each other. Perhaps the regional vegetation on the outwash plain around Stevens Pond already included some pine during zone-3 time. Today we find *Pinus banksiana* on such sandy areas in the Itasca State Park region as well as in the deciduous forest of the Twin Lakes drainageway east of the Big Stone Moraine.

Certainly actual replacement of deciduous elements by pine took place in zone 4. Figure 9 shows in zone 4 *Pinus* percentages between 300 and 900% at Bog D, Bog A, Martin, and Cindy ponds. Stevens Pond however, shows *Pinus* percentages between 1100 and 1800%, reflecting extralocal values. The steep rise of pine at the transition of zone 3 to zone 4 at Stevens Pond may mean that at that level



Pollen sum: deciduous trees

Fig. 9. Curves for *Pinus* at 5 sites in the Itasca State Park region for zones 3, 4, and 5, based upon the deciduous-tree pollen sum. For explanation see text.

Pinus arrived at the shore of Stevens Pond, replacing the xerophytic *Quercus* forest of the previous zone. Such a replacement nearby explains why such a steep rise is absent at the other sites. The *Pinus* curve here merely ends its steady increase of zone 3, and above this it remains at a constant level. The pine forest around Stevens Pond may have been either *Pinus banksiana* or *P. resinosa* rather than *P. strobus*, according to the ratio of pine pollen types (Fig. 4). The increase is present also at Bog D and Martin Ponds, but there it is less important, perhaps because the soils are on till rather than on outwash sand. Between spectra 5 and 6 at Stevens Pond the *Pinus* values decrease to the same level as at the other sites. At this level *Pinus* may have disappeared from around Stevens Pond as a result of clearance by white settlers at the turn of the century, an event also marked by the rise in pollen

of *Ambrosia* type (Fig. 10). Above spectrum 5 the extralocal addition of pine pollen to the total pollen deposition ceases, and as a result a relative rise in percentage of other pollen types is possible. Above spectrum 5 *Pinus* thus shows regional values again.

Betula pollen grains in zone 4 continue to be largely of the *Betula papyrifera* size.

ZONE 5, SPECTRA 1 THROUGH 8: *Ambrosia* Assemblage Zone

Zone 5 is characterized by a rise in the curves for *Ambrosia* type, *Chenopodiaceae/Amaranthaceae*, and *Abies* and the appearance of pollen grains of cultivated cereals (*Avena* type, *Zea mays*). Pollen grains of cf. *Melilotus*, *Trifolium pratense* type, and *Trifolium repens*, all introduced from Europe and present today in disturbed sites, have been found in the samples. Other pollen grains from plants ac-

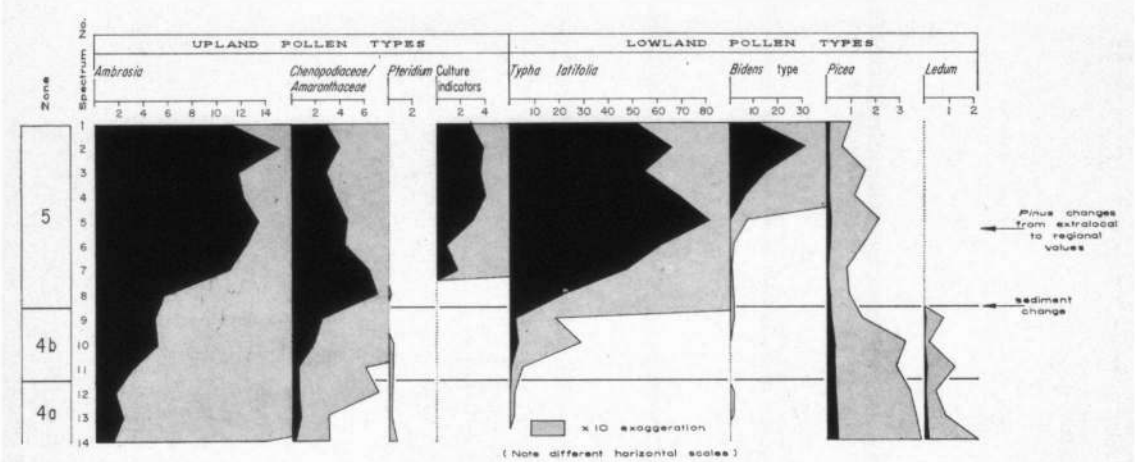


FIG. 10. Selected curves in the upper part of the Stevens Pond diagram.

companion cultivation are *Melandrium* type, *Anthemis* type, and (not exclusively) *Asteraceae* (*Liguliflorae*). The logging and cultivation of the area around Stevens Pond resulted in a complete change of the local vegetation to the *Typha latifolia* mat of today.

Figure 10 shows enlarged some of the events of the transition. Between spectra 8 and 9 the sediment changes from forest peat to *Typha* peat, reflected in the diagram by the drop in *Picea*, the disappearance of *Ledum*, and the strong increase of *Typha latifolia*. Pollen grains from cereals and from plants accompanying cultivation occur above this level only. *Ambrosia* and *Chenopodiaceae/Amaranthaceae* show their highest percentages. Apparently above this level (zone 5) the pine forest around Stevens Pond was logged or burned and transformed to the present fields. Indeed we find in this zone the decrease of pine from extralocal values to regional values (see Figs. 9, 10) at the level where the percentage of *Bidens* type rises. Historic records show that this happened about 1900. Between spectra 8 and 12, before the stratigraphic change, the curves of *Ambrosia* and *Chenopodiaceae/Amaranthaceae* rise (zone 4b), indicating that cultivation was approaching, for the Red River Valley to the west was settled for farming by 1880. Also *Typha latifolia* shows a slight rise. Around Stevens Pond forest was still present, but logging and cultivation elsewhere in the area resulted in a regional rise of these 3 pollen types. Pollen of *Ambrosia* type and *Chenopodiaceae/Amaranthaceae* are easily carried by the wind, and surface-sample studies showed that *Typha* is among the few lowland types that occur in the regional pollen rain in forested regions (Benninghoff 1960; Janssen 1966).

No trees occur at present around Stevens Pond, and the rise of *Abies* pollen therefore must be a regional feature. It may be explained partly by the decrease of pine in the pollen rain, resulting in higher percentages of the other pollen types. On

the other hand, the rise may reflect the expansion of *Abies balsamea* trees with suppression of fires in the past 50 yr (Buell & Cantlon 1951).

DEVELOPMENT OF THE LOCAL VEGETATION

The development of the local vegetation is represented in Figure 5, which shows the pollen curves of the lowland types. In general, the pollen types are arranged according to their stratigraphic appearance, which is closely related to the floristic composition of plant communities representing the stages in lake filling. In Figures 3 and 11 some of

Kalmie- Chamaedaphneta		Fraxinetalia nigrae	Soc. gr.
A	B	C	
←————→			1
←————→			2
←————→			3

FIG. 11. General occurrence of main sociological groups 1, 2, and 3 in three major lowland vegetation types. For explanation, see text under Local Vegetation.

the results of a study (Janssen 1967) of the recent vegetation in the Itasca State Park region are summarized. Only species that disperse recognizable pollen grains have been included. The height of the curves on Figure 3 represent steps in the Braun-Blanquet scale for cover and abundance. At the top of the figure are the vegetation plots (relevés). Relevés and species have been arranged according to presence. As mentioned in the introduction, plant communities have been established on the basis of sociological groups, each group including species that show approximately the same sociological (ecological) amplitude.

To facilitate comparison of the local succession

at Stevens Pond with the recent vegetation types in lowland habitats, a short summary of the results of the vegetation study in lowlands in the Itasca State Park region follows. For reference to the species of the sociological groups, Figure 3 may be used, although it contains only some of the species of the recent vegetation.

The lowland vegetation types can be divided floristically into 3 major units, each characterized by a typical combination of species. Figure 11 shows, simplified, how 3 sociological groups are distributed in these 3 major units.

Unit A (*Kalmio-Chamaedaphneta*) comprises a group of communities especially present in the eastern arm of the Lake Agassiz basin, 200 km northeast of Stevens Pond, covered mostly by *Picea mariana*, *Larix laricina*, and mats of *Carex*. As is shown in Figure 11, species from sociological groups 2 and 3 are absent there. Unit B comprises a group of communities characterized by sociological group 2. These are the types of vegetation that are very widely distributed in the very small depressions of the Itasca State Park region and elsewhere. Species belonging to sociological groups 1 and 3 are also present in some of the communities of this vegetation unit. Unit C (*Fraxinetalia nigrae*) represents communities found in the marginal zones between upland and bogs in the Itasca State Park region. Species from sociological group 3 occur in these communities, as well as species that are found exclusively here (sociological group 4, not mentioned in Figs. 3, 11).

To summarize:

- soc. group 1 may be found in vegetation types belonging to units A and B
- soc. group 2 may be found in vegetation type belonging to unit B
- soc. group 3 may be found in vegetation types belonging to units B and C

Because these 3 vegetation units reflect in a rough way the content of nutrients in the substrate, sociological group 1 thus contains mainly oligotrophic species, and group 3 contains the species adapted to more eutrophic conditions. Accordingly group 2 may be called a mesotrophic group. The trophic designations are of course relative and are used in a loose sense here.

It should be emphasized that the characterization of groups of communities by the main sociological groups does not mean that all species from such a sociological group are found in all communities of the vegetation unit. In each major sociological group a further floristic division is possible. In vegetation units A and B such a division reflects a moisture gradient. Figure 3 shows some of the subdivisions in the main sociological groups that can be made in vegetation unit B. The various stages along the moisture gradient have been indicated by the letters of the alphabet. Sociological groups 1a, 2a, and 3a

thus represent the wettest communities in the lowland vegetation. Sociological groups labeled b, c, etc., represent drier ones. Figure 3 thus shows a division of the 3 main sociological groups along a moisture gradient roughly on 3 levels of nutrient content of the substrate.

The communities heading Figure 3 have been established arbitrarily by combining sociological groups. The pattern of lake filling typical for the not-too-large basins of the region is easily seen. At the margin of a floating *Carex* mat, especially near a creek, a eutrophic vegetation of *Typha latifolia*, *Bidens cernua*, and *Impatiens capensis* occurs. Later stages are represented by *Betula pumila* shrub, *Larix laricina* forest, and *Picea mariana* forest. In this succession the *Typha* mat represents the wettest, most eutrophic stage. The later stages represent communities found in a drier, more mesotrophic environment.

The local diagram from Stevens Pond shows at almost every level plants belonging to sociological groups 1, 2, and 3 and thus is a typical example of the pattern of succession found today in vegetation unit B. This is not surprising because of the small size of the basin.

ZONE 1

In the lower half of zone 1 several pollen types indicate shallow open water: Nuphar, Nymphaea, Lemna, Myriophyllum, and the alga, Pediastrum. The sediment, however, is not gyttja but Drepanocladus peat. It was impossible to identify the moss to species, but among the possible species several occur in a submerged habitat. In the upper part of the zone these pollen types are gone and Equisetum reaches high percentages. In the lower part of the zone pollen grains of Menyanthes are present, and the values for Alnus and Sagittaria are higher than in the upper part of the zone. All 3 species may have grown along the water edge. Alnus and Sagittaria suggest a eutrophic habitat. Menyanthes, however, indicates more mesotrophic conditions. Myriophyllum is also mesotrophic. It thus remains difficult to get a fitting picture of the local vegetation in zone 1. Perhaps it may be compared to the Myriophylo-Nupharetum from Europe, an association that is the starting point of the succession in mesotrophic water. The Equisetum at the top thus may represent an equivalent of the "reed" stage.

ZONE 2

The composition of the local vegetation of zone 2 is clearer than in previous zones. Pollen grains from plants belonging to sociological groups 2a, 3a, 2d, and 2f show maximum percentages. This combination of species, the high values for *Typha latifolia*, and the presence of *Bidens* type point towards a vegetation comparable to the *Bidentetum Typhetum latifoliae*.

However, *Salix* increases up to 40%; surface sam-

ples indicate that relatively high percentages of *Salix* can be found only where *Salix* shrubs are actually present in the local vegetation, even in treeless regions (Welten 1950). Though not mentioned in Figure 3, *Salix* spp. (e.g. *Salix candida*) are abundant in the Cariceto-Betuletum pumilae. The abundance of pollen of Cyperaceae and *Betula pumila* also point to a vegetation comparable to the present Cariceto-Betuletum pumilae. This contains plants from sociological group 1 (*Comarum palustre* and *Menyanthes trifoliata*); the pollen diagram shows a low percentage of *Comarum palustre* type but no *Menyanthes*. According to Figure 3, *Menyanthes trifoliata* is absent where *Typha latifolia* is very abundant. Surface samples from a *Typha latifolia* mat (Lake Sylvia: Janssen 1966) show relatively high percentages of the same pollen types as found at Stevens Pond in zone 2: *Typha latifolia*, *Sagittaria*, *Lysimachia thyrsiflora*, *Sparganium* type, *Bidens* type, cf. *Stellaria longifolia*, and *Dryopteris* type. *Salix* reaches a value of 10% in one of these samples in a narrow band of low *Salix* shrub. Pollen grains of *Impatiens* found at Lake Sylvia are lacking at Stevens Pond, however, and the values for Cyperaceae are much lower. We thus may conclude from the pollen record that the local vegetation for zone 2 at Stevens Pond was basically a *Typha* mat with much *Salix* shrub, but with some of the elements of a *Carex* mat.

In many pollen diagrams from Minnesota in the assemblage zone correlative with Stevens Pond zone 2, the percentages for aquatic plants are slightly higher than below or above, indicating lower water levels and thereby the expansion of marsh plants and shallow-water plants (e.g. Bog D and Martin Ponds of McAndrews 1966; Kirchner Marsh and Lake Carlson of Wright *et al.* 1963 and Watts & Winter 1966). At Stevens Pond these features are much exaggerated because of the local occurrence of these marsh plants. The same applies for *Salix*, which also shows a slight rise in some of the other Minnesota diagrams mentioned above.

Spores of *Dryopteris* type show an abrupt rise at the base of the zone, but then a decrease toward the top. Such a rise is present at Cedar Bog Lake (Cushing 1963). At both localities spores with a preserved perisporium were present and thus could be identified as *Dryopteris thelypteris*. Cushing considers this zone as the time of maximum dryness, in which *Typha latifolia* and *Carex* mats expanded in former bays as a result of falling lake levels.

As at Cedar Bog Lake, the pollen grains tend to be corroded in zone 2a (see below), especially toward the base. Possibly at Stevens Pond in part of the assumed time of dryness no peat accumulated, and a sharp break at the boundary between 1 and 2 resulted.

ZONE 3

The abrupt change from zone 2 to zone 3 in the upland diagram is present in the lowland diagram

as well. The curves of pollen types belonging to sociological groups 2a, 3a (part), 2d, and 2f, characteristic for the *Typha latifolia* vegetation of the previous zone, decrease strongly or discontinue. However, several pollen types that occur in zone 2b do not decrease (sociological group 2c, as well as *Alnus*, *Scutellaria* type, and *Lycopus* type from group 3a). *Alnus* shows a slight rise at the base of the zone.

Additions to the pollen assemblage are plants belonging to sociological group 1a, 1b, 1c, 1d, and 3b. From Figure 3 it appears that this assemblage fits best that of a *Larix laricina* forest. The continuous presence of pollen types from sociological groups 2c and 3a is perfectly in agreement with this, because the plants involved are also present in the recent vegetation of the *Larix laricina* forests as well as in *Carex* mats. Pollen of *Sarracenia purpurea* also occurs—this plant is found today mostly in *Larix* forests where its pollen shows up in surface samples (French Creek Bog).

Larix pollen reaches a value of 10%, or 15.2% if based upon the deciduous-tree pollen sum (Table 2), much higher than the more regional values found at Martin and Bog D Ponds. *Larix* must have occurred in the local bog vegetation.

A good agreement exists between the pollen assemblage in zone 3 and that found in surface samples in a recent *Larix laricina* bog (French Creek Bog). However, some important constituents of French Creek Bog were probably not very abundant at Stevens Pond (e.g. *Ledum*, *Sphagnum*, *Ericaceae*). Also, the percentages of Cyperaceae pollen are higher at Stevens Pond, perhaps reflecting the *Carex*-mat character of the local vegetation. Altogether, the *Larix* forest in zone 3 shows a vegetation different from that of recent *Larix laricina* forests. This demonstrates clearly that, as stated in the introduction, recent vegetation types are not fully comparable *a priori* to fossil types, even in the late Holocene.

The percentages of the Poaceae pollen are much diminished compared with zone 2. This is in agreement with the change from savanna vegetation, where grasses play a large role, to forest vegetation. The percentages are higher, however, than those found in surface samples in upland forests. In contrast to zone 2, the pollen grains belong to one type only. Probably most of the Poaceae pollen thus is of local origin.

Picea pollen shows a higher percentage than in zone 2. The average for *Picea* based upon the deciduous-tree pollen sum (Table 2) is slightly higher than that found at Bog D and Martin Pond. There is not much difference, however, from the values at Terhell and Reichow Ponds, where *Picea* is absent. *Picea* therefore must have come from the local vegetation at Stevens Pond at the time of Zone 3, and its rise in zone 2 is a regional feature, perhaps a result of the approaching coniferous forests from the east (compare also *Pinus*).

The survey of the recent lowland vegetation (Fig. 3) indicates that *Betula pumila* is an important component in the shrub layer of *Larix laricina* forests. Although at Stevens Pond most of the *Betula* pollen grains belong to the larger *B. papyrifera* type, some of the size-frequency curves for both zones 3 and 4 show a small peak at the smaller size, reflecting the occurrence of local *Betula pumila*. Recent surface samples in comparable vegetation seem to indicate an equally small share of local *Betula pumila* in the pollen rain when *Betula papyrifera* is present on the upland.

A change in the pollen assemblage of zone 3 occurs between spectra 31 and 32. *Larix*, *Salix*, and *Comarum* type decrease, and other pollen grains all belonging to sociological groups 1a, 1b, and 1c disappear. The curve for *Dryopteris* type is still continuous. *Picea* rises. Figure 3 shows that these changes are a reflection of a replacement of the *Larix laricina* forest by a *Picea mariana* forest. The percentage of *Picea* pollen points in the same direction. Table 3 shows that the average *Picea* percentage based upon the coniferous-deciduous pollen sum is 3.85%, well above the regional presettlement percentages for that tree, in spite of the fact that it is depressed by the high extralocal pine values. This indicates that from spectrum 31 upward *Picea* locally occurred at Stevens Pond; on account of its ecology, it was mainly *Picea mariana*.

ZONE 4

At the base of zone 4 *Sphagnum* rises to distinct local values, and *Ledum* and the other ericaceous types appear. The curve for the *Dryopteris* type ends. From this level upward the local bog forest shows the pollen assemblage that is typical for the recent *Picea mariana* forest. There is also a good agreement with the local pollen assemblage found in surface samples in the *Picea mariana* forest at French Creek Bog. There are also pollen grains of *Arceuthobium*, a parasite on *Picea mariana*. The size frequencies for *Betula* continue to indicate that only a small part of the *Betula* pollen rain is from *Betula pumila*. The *Larix* percentages are very low, even lower than the average regional values for the tree found at Martin and Cindy Ponds. The average values at Bog D and Bog A ponds are higher because of the probable extralocal occurrence of *Larix* at these sites. These low values at Stevens Pond indicate that *Larix* was absent in the local vegetation. However, the continuous scattered occurrences of pollen grains of *Utricularia* and, especially in the upper part of the zone, the rise of *Salix* and *Comarum palustre* type indicate that still *Larix* was present, so the local vegetation must have been a mixed *Larix laricina*-*Picea mariana* forest.

ZONE 5

The regional diagram shows in the upper part of zone 4 (zone 4b) the approaching cultivation, but

a change in the vegetation surrounding the pond does not appear until zone 5. Pollen grains from plants belonging to sociological group 3b and 1, including *Larix*, are absent in zone 5. *Picea* drops to regional values, and *Typha latifolia* and *Bidens* type rise to maximum values. The sediment changes from woody peat to *Typha* peat. This pollen sequence suggests the transformation from the oligotrophic bog forest to the recent eutrophic *Typha latifolia* vegetation. The pollen assemblage resembles that found in zone 2 but is much poorer in types, lacking pollen grains from sociological groups 2a, 2d, and 2f.

THE LOCAL LOWLAND VEGETATION AND ITS RELATION TO THE UPLAND VEGETATION

The succession of the local vegetation at Stevens Pond from zone 2 up to zone 5 resembles that of the recent process of lake filling. It starts with a pollen assemblage comprising typical *Carex* mat species, then proceeds through a *Larix laricina* forest into a *Picea mariana* forest. Each successional stage is accompanied by the same associates found today in comparable vegetation. The succession proceeded from a eutrophic wet habitat to a mesotrophic drier environment. Ecologically this is a succession common in most parts of temperate regions with sufficient precipitation. The increasing thickness of accumulating organic matter results in the exclusion of nutrient-rich groundwater and thus in an acidification of the environment.

Indications of the same development can be found in other diagrams from various regions in Minnesota (Bog D Pond of McAndrews; Cedar Bog Lake of Cushing 1963; Weber Lake of Fries 1962), which show after the prairie period a rise in *Larix* and after that at Bog D a rise of *Picea*. The pollen assemblages at these sites, however, do not contain bog herbs, because there the bog forest was not local.

The present bog vegetation of the *Larix* and *Picea* lowland forest shows a strong floristic affinity with both lowland and upland vegetation of the boreal forest. This applies not only for shrubs such as *Ledum groenlandicum* but also for the trees *Larix laricina* and *Picea mariana*. According to Transeau (1903), after the retreat of the ice the bog species were widely distributed all over the region just as they are today in the north. Since then these plants have disappeared except in bogs, where other species invading the area during the Holocene could not follow on account of the extreme environment there. According to him the bog forest thus is a relic from late-glacial time. The diagrams of Stevens Pond, Bog D, and Cedar Bog Lake show that plants characteristic for the bog communities, at least in these parts of the state, are not relics from a once widespread boreal forest. During the time of zone 2 these species were absent. They have been re-intro-

TABLE 4. Relation of local to extralocal vegetation in Stevens Pond sequence, after the prairie period.

Pollen zone	Interpretation of the extralocal vegetation	Interpretation of the local vegetation
5	Cultivated fields after logging of the pine forest.	<i>Typha latifolia</i> mat
4	Pinus forest	<i>Picea mariana</i> forest with <i>Larix</i> . Ericaceae in the understory. Sphagnum important in the moss layer
3	Xeric <i>Quercus</i> forest, increasingly mesic towards the top of the zone	<i>Picea mariana</i> forest with <i>Larix</i> . No Ericaceae <i>Larix laricina</i> forest without Ericaceae and Sphagnum. <i>Salix</i> important in understory
2b	<i>Quercus savanna</i> with <i>Corylus</i> understory. Prairie vegetation present locally	<i>Salix</i> shrub with much <i>Typha latifolia</i>

duced in the lowland vegetation after the prairie period.

The diagram of Stevens Pond reveals a close relationship between the development of the local and the extralocal vegetation. In the upland diagram the top boundaries of zones 2a, 2b, 3, and 4 are all reflected in the local diagram. The regional pollen assemblages for each zone are accompanied by their own local pollen assemblages. In Table 4 these relationships are summarized.

These interrelations are in the first place a result of the way the data are presented. The percentages of the local components have been calculated on the basis of the upland pollen sum. They thus are dependent on the absolute regional pollen precipitation per unit surface. It is not unlikely that a change in the absolute pollen rain occurs especially at the transitions in the regional pollen diagram, thus affecting the local pollen percentages.

The variations in the local diagram, however, are too big to be attributed solely to this phenomenon. There must be some other reason for the simultaneous development of the extralocal and local vegetation. Two factors may be taken into consideration. Changes in climate are probable since the prairie period (McAndrews 1966), and it is not unlikely that they influenced both the upland and lowland vegetation. The present diagram, however, does not particularly show the influence of climate in its pollen curves, because it registers mainly local features.

In a small site like Stevens Pond the extralocal vegetation may influence the local vegetation by means of its runoff. The chemical properties of conifer litter are quite different from those of deciduous trees. As a result the soil underneath a conifer forest or even under a single tree shows a low pH and

a low content of exchangeable bases (Zinke 1962). It is quite conceivable that because of these differences the chemistry of the runoff from a pine forest is quite different from that of a deciduous forest, influencing the nature of the local vegetation in the pond. In the present vegetation of the Itasca State Park region such a relationship often exists. In the contact zone between bogs and a deciduous type of forest, usually a broad belt of eutrophic *Fraxinus nigra-Ulmus americana* forest is present. Between bogs and pine forest, however, such a belt is narrow or lacking. This mechanism would explain why at Stevens Pond there was a delay in the introduction of Sphagnum, *Ledum*, and the other Ericaceae, compared to the usual succession in the lake filling. These elements are present in the recent *Larix laricina* and *Picea mariana* forest, but they were introduced at Stevens Pond no earlier than the postulated change in the extralocal vegetation from *Quercus* forest to Pinus forest (base of zone 4). The runoff from the pine forest would stop the inflow of nutrients into the pond, allowing the introduction of species highly adapted to an acid environment.

The same mechanism would perhaps account for the drop of *Fraxinus nigra* type at the base of zone 4, for *Fraxinus nigra* occurs especially in the marginal zone between bogs and deciduous types of forest.

The recent distribution of Pinus, *Picea mariana*, *Ledum groenlandicum*, and *Larix laricina* point towards the same relationships. Of the 3 pines present

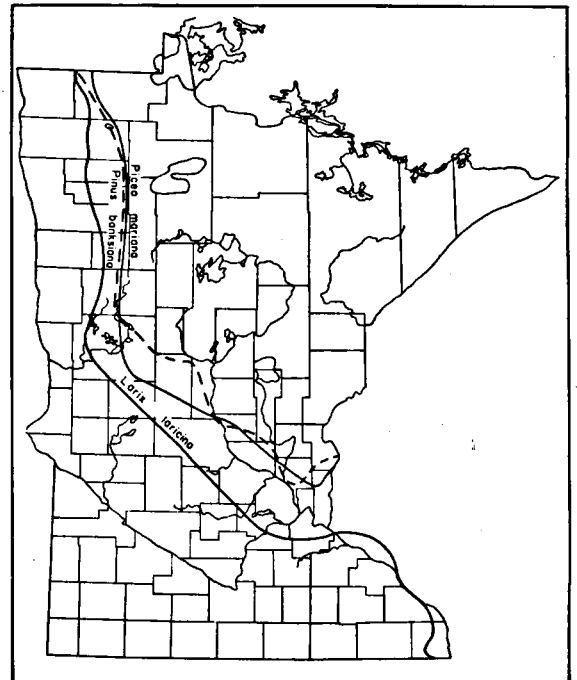


FIG. 12. Distribution of *Pinus banksiana* (from Schoenike 1962), *Larix laricina* (from Rowe 1957), and *Picea mariana* (from Heinselman 1957) in Minnesota.

in Minnesota *Pinus banksiana* ranges most to the west and southwest and therefore has been used in the following comparison of ranges. Figure 12 shows that the western limits of *Picea mariana* and *P. banksiana* are approximately the same. The area of *Larix laricina* extends much more to the west, covering the deciduous forest belt in Minnesota. Distribution maps for *Picea mariana* (Heinselman 1957), *Pinus banksiana* (Rudolph 1958), and *Larix laricina* (Roe 1957) suggest that the same applies for Wisconsin and Michigan.

The relation between local and extralocal vegetation is most evident at the top of zone 4. The logging of the pine forest around Stevens Pond resulted in an increase of nutrients in the forest soil. Moreover, cores from the margin of Stevens Pond show a cap of sand that can be attributed to the sheet erosion caused by exposure of the soil after logging. The resulting inflow of nutrients in to the pond destroyed the mesotrophic bog forest, turning it to the present eutrophic *Typha latifolia* mat.

The influence of the upland vegetation upon the lowland vegetation is of course most effective in small ponds or along the margin of larger basins. In those areas a non-coniferous vegetation is a restricting factor in the establishment of a true bog vegetation. In the center of larger basins such an influence is less important, but here frequently excessive moisture might be the limiting factor. Thus in regions close to the prairie-forest border, which saw the extermination of the early Holocene pine forests during the prairie period, bog plants are new arrivals in the late Holocene and not relics from the late-glacial. More to the east, however, the impact of the prairie expansion in the mid-Holocene was less, and *Pinus* is present in relatively high values throughout the Holocene (Weber Lake of Fries 1962). Persistence of bog plants might be most likely in those regions.

LOCAL, EXTRALOCAL, AND REGIONAL POLLEN RAIN

As mentioned in the introduction, the small-sized Stevens Pond was selected to determine the influence of a particular type of upland forest close to the sampling site, i.e. the extralocal effect of pollen types.

The Stevens Pond diagram shows 2 or 3 features that may be considered a result of the extralocal effect. In zone 2 *Corylus* shows high values not yet found in diagrams from larger basins in Minnesota. In zone 3 *Quercus* is higher in the adjusted diagrams, and in zone 4 the percentage of *Pinus* shows a distinct rise compared with the values from larger basins. In the latter case the *Pinus* rise also has been found in surface samples from a small bog surrounded by pine forests.

Although for some tree elements an extralocal effect is present, the influence of this phenomenon

on the pollen diagram is not so large that correlation with diagrams from larger basins becomes difficult. The relative unimportance of the extralocal effect at Stevens Pond may result from 2 factors:

1. The dispersion curves fall very rapidly even over short distances as was also noted in the surface-sample study.
2. The extralocal vegetation (the vegetation on the uplands adjacent to Stevens Pond) was not markedly different from the overall vegetation in the region. A larger extralocal effect might be expected when the extralocal vegetation is quite different.

The Stevens Pond diagram does not show clearly a raised percentage of upland herbs because of the short distance to the upland (except perhaps *Sanicula* in zone 3). Apparently most pollen from herbs has short dispersal. This means that for small ponds the upland forest type can not be determined from the pollen of characteristic upland-forest herbs. This result also is essentially the same as found in surface samples from comparable small basins.

A completely different picture, however, is shown by the local vegetation. Local pollen types are many and characteristic, and each type is represented in the sediment and in surface samples by relatively large numbers. Because of this local effect the development of the vegetation in the basin can be followed in detail.

SUMMARY

The pollen assemblages of a core in the conifer-hardwood formation in northwestern Minnesota are compared with the floristics of the recent vegetation in the region. Percentage levels of the main tree components have been compared first with those from recent surface samples taken at the same short distance from various types of upland forests and second with the regional values of the pollen rain in this area (McAndrews 1966). To that end all the data were recalculated on the basis of special pollen sums.

The regional diagram of Stevens Pond shows basically the same assemblage zones as established by McAndrews but without the late-glacial *Picea*-*Populus* assemblage zone. The pollen in the following *Pinus*-*Pteridium* assemblage zone has been interpreted as derived from a pine forest. During the mid-postglacial expansion of the prairie eastwards the regional vegetation must have been a *Quercus* savanna, locally with prairie. *Corylus* reaches relatively high percentages in this zone. Among the prairie elements especially the occurrence of *Lilium philadelphicum* may be noted. In the next zone the pollen diagram shows a rise of the curves of mesic elements. In spite of this the comparison with recent surface samples indicates a xerophytic *Quercus* forest rather than a mesophytic deciduous forest. In the following *Pinus* assemblage zone pine was

present along the margin of Stevens Pond and is therefore overrepresented in the diagram. In the uppermost zone the pollen curves show the effect of logging of the forest about 1900. Pollen of cultivated and introduced plants appear in this zone.

Many local pollen types were found, on account of local overrepresentation. This made it possible to compare the local Stevens Pond sequence with the composition of recent lowland vegetation types. The pollen sequence was similar to a large extent to the recent pattern of lake filling, starting with a eutrophic vegetation of *Typha latifolia* and *Salix* in the prairie period and leading to a *Larix* forest and then to a mesotrophic *Picea mariana* forest, the present edaphic climax on peaty soils. There is a delay, however, in the introduction of acidophilous species, the *Larix* forest being without *Sphagnum* and *Ericaceae*. This is explained by assuming an influence of the vegetation of the surrounding slopes upon the local vegetation. About 1900 the bog forest was destroyed by logging operations and replaced by the present *Typha latifolia* mat.

LITERATURE CITED

- Aikman, J. M. 1928. Competition studies in the ecotone between prairie and woodland. *Proc. Iowa Acad. Sci.* 35: 99-103.
- Anderson, S. Th. 1961. Vegetation and its environment in Denmark in the early Weichselian Glacial (Last Glacial). *Danmarks Geologiske Undersøgelse*, R. 2, Nr. 75, 175 p.
- Benninghoff, W. S. 1960. Pollen spectra from Bryophytic moss polsters, Inverness Mud Lake Bog, Cheboygan County Mich. *Pap. Mich. Acad. Sci. Arts & Letters* 45: 41-60.
- Beug, H. J. 1961. *Leitfaden der Pollenbestimmung für Mitteleuropa und angrenzende Gebiete*. Gustav Fischer, Stuttgart. 63 p.
- Braun-Blanquet, J. 1951. *Pflanzensoziologie: Grundzüge der Vegetationskunde*. Springer, Vienna. 631 p.
- Bray, J. R. 1960. The composition of savanna vegetation in Wisconsin. *Ecology* 41: 721-732.
- Buell, M. F. & J. E. Cantlon. 1951. A study of two forest stands in Minnesota with an interpretation of the prairie-forest margin. *Ecology* 32: 294-306.
- Buell, M. F. & V. Facey. 1960. Forest prairie transition west of Itasca Park Minnesota. *Bull. Torrey Bot. Club* 87: 46-58.
- Butters, F. K. & E. C. Abbe. 1953. A floristic study of Cook County, northeastern Minnesota. *Rhodora* 55: 21-201.
- Chanda, S. 1962. On the pollen morphology of some Scandinavian Caryophyllaceae. *Grana Palynol.* 3: 67-89.
- Christ, J. D. 1959. A study of yellow birch (*Betula lutea*) in the bogs of Itasca Park, Minnesota. *Amer. Midland Natur.* 61: 580-583.
- Curtis, J. T. 1955. A prairie continuum in Wisconsin. *Ecology* 36: 558-566.
- . 1959. The vegetation of Wisconsin. An ordination of plant communities. Univ. Wisconsin Press, Madison. 657 p.
- Cushing, E. J. 1963. Late-Wisconsin pollen stratigraphy in east-central Minnesota. Ph.D. Thesis, Univ. Minnesota. 165 p.
- Davis, M. B. 1963. On the theory of pollen analysis. *Amer. J. Sci.* 261: 897-912.
- Doing, H. 1962. Systematische Ordnung und floristische Zusammensetzung Niederländischer Wald- und Gebüschgesellschaften. *Wentia* 8, 85 p.
- Erdtman, G. 1943. An introduction to pollen analysis. *Chronica Botanica Co.*, Waltham, Mass. 239 p.
- . 1952. Pollen morphology and plant taxonomy. Angiosperms. *Chronica Botanica Co.*, Waltham, Mass. 539 p.
- Erdtman, G., B. Berglund & J. Pragowski. 1961. An introduction to a Scandinavian pollen flora. Almqvist & Wiksell, Stockholm. 92 p.
- Ewing, J. 1924. Plant succession of the brush prairie of northwestern Minnesota. *J. Ecol.* 12: 238-266.
- Fægri, K. & J. Iversen. 1964. *Textbook of pollen analysis*. Munksgaard, Copenhagen. 237 p.
- Fernald, M. L. 1950. *Gray's manual of botany*, 8th ed. American Book Co., New York. 1632 p.
- Fries, M. 1962. Pollen profiles of late Pleistocene and Recent sediments from Weber Lake, Minnesota. *Ecology* 43: 295-308.
- Heinselmann, M. L. 1957. Silvical characteristics of black spruce. *Lake States Forest Exp. Sta. Pap.* 45, 30 p.
- Helmich, D. E. 1963. Pollen morphology in the maples (*Acer* L.) *Pap. Mich. Acad. Sci. Arts & Letters* 48: 151-162.
- Iversen, J. 1960. Problems of the early Post-glacial forest development in Denmark. *Danmarks Geologiske Undersøgelse*, R. 4, 4(3), 32 p.
- . 1964. Retrogressive vegetational succession in the post-glacial. *J. Ecol. (Suppl.)* 52: 59-70.
- Iversen, J. & J. Troels-Smith 1950. Pollenmorphologische Definitionen und Typen. *Danmarks Geologiske Undersøgelse*, R. 4, 3(8), 52 p.
- Janssen, C. R. 1966. Recent pollen spectra from the deciduous- and coniferous-deciduous forests of northwestern Minnesota: a study in pollen dispersal. *Ecology* 47: 804-825.
- . 1967. A floristic study of forests and bog vegetation mainly in the Itasca State Park area, northwestern Minnesota. *Ecology* 48 (in press).
- Jonassen, H. 1950. Recent pollen sedimentation and Jutland heath diagrams. *Dansk Bot. Arch.* 13. 168 p.
- McAndrews, J. H. 1966. Postglacial history of prairie, savanna, and forest in northwestern Minnesota. *Torrey Bot. Club Mem.* 22(2), 72 p.
- Moss, E. H. 1953. Forest communities in northwestern Alberta. *Can. J. Bot.* 31: 212-252.
- Reitsma, T. 1966. Pollen morphology of some European Rosaceae. *Acta Bot. Neerl.* 15: 290-307.
- Ritchie, J. C. 1960. The vegetation of northern Manitoba VI: The lower Hayes region. *Can. J. Bot.* 38: 769-788.
- . 1961. Soil and minor vegetation of pine forests in southeast Manitoba. *Can. Dep. Forest., Forest Res. Div., Tech. Note* 96.
- . 1964. Contributions to the paleoecology of west-central Canada. 1: The Riding Mountain area. *Can. J. Bot.* 42: 181-193.
- Roe, E. I. 1957. Silvical characteristics of tamarack. *Lake States Forest Exp. Sta., Pap.* 52, 22 p.
- Rudolph, P. O. 1958. Silvical characteristics of jack pine. *Lake States Forest Exp. Sta., Pap.* 61, 31 p.
- Scamoni, A. & H. Passarge. 1959. Gedanken zu einer natürlichen Ordnung der Waldgesellschaften. *Arch. Forstwesen* 8: 386-426.
- Schoenike, R. E. 1962. The distribution of jack pine

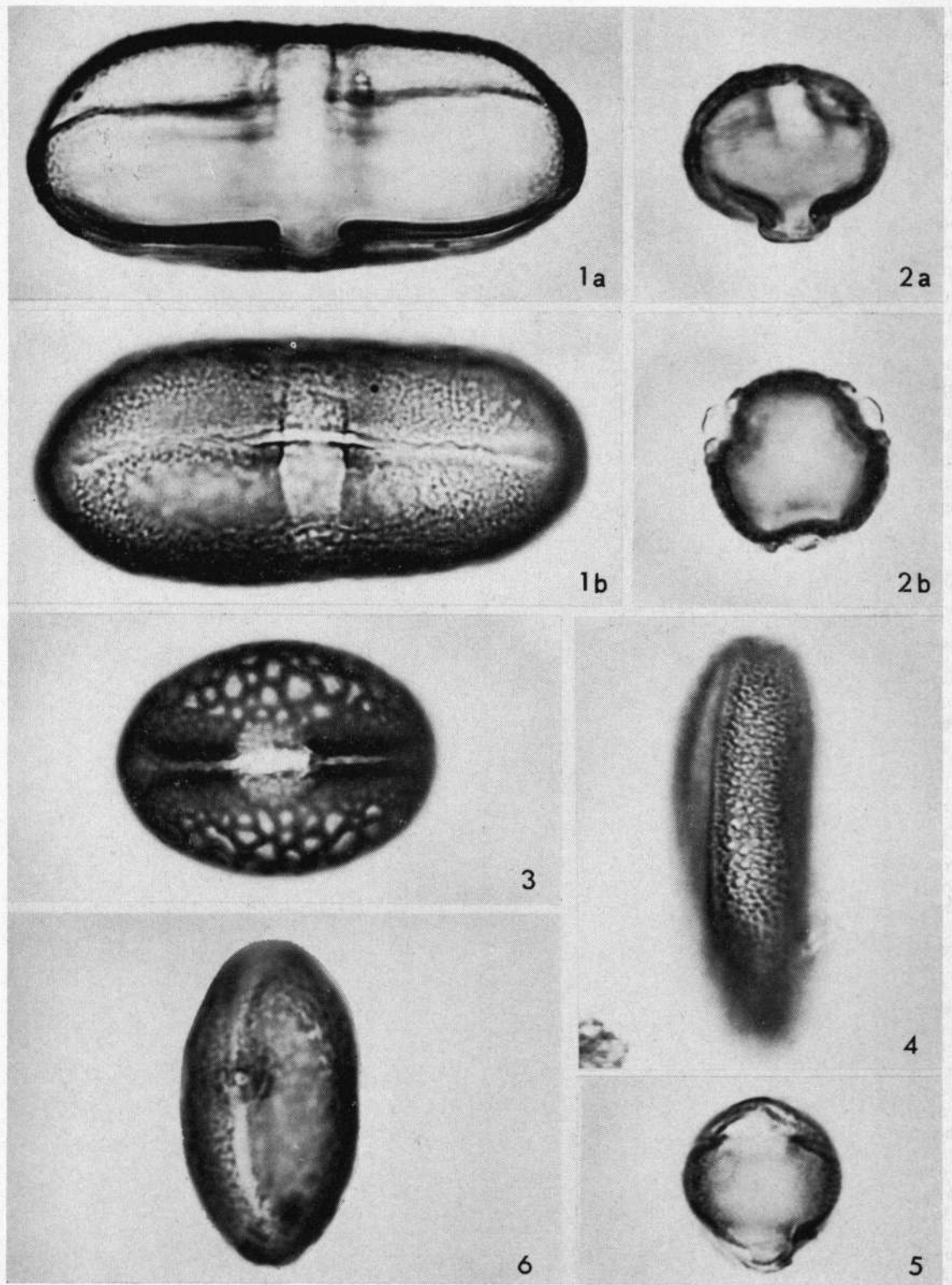


FIG. 13. 1. *Sanicula marilandica*, fossil, spectrum 41, 2. *Comarum palustre* type, fossil, spectrum 47, 3. *Trifolium pratense* type, fossil, spectrum 2, 4. *Petalostemum purpureum*, fossil, spectrum 59, 5. *Amorpha canescens*, fossil, spectrum 53, 6. *Shepherdia canadensis*, fossil, spectrum 87. Ca. 1700x.

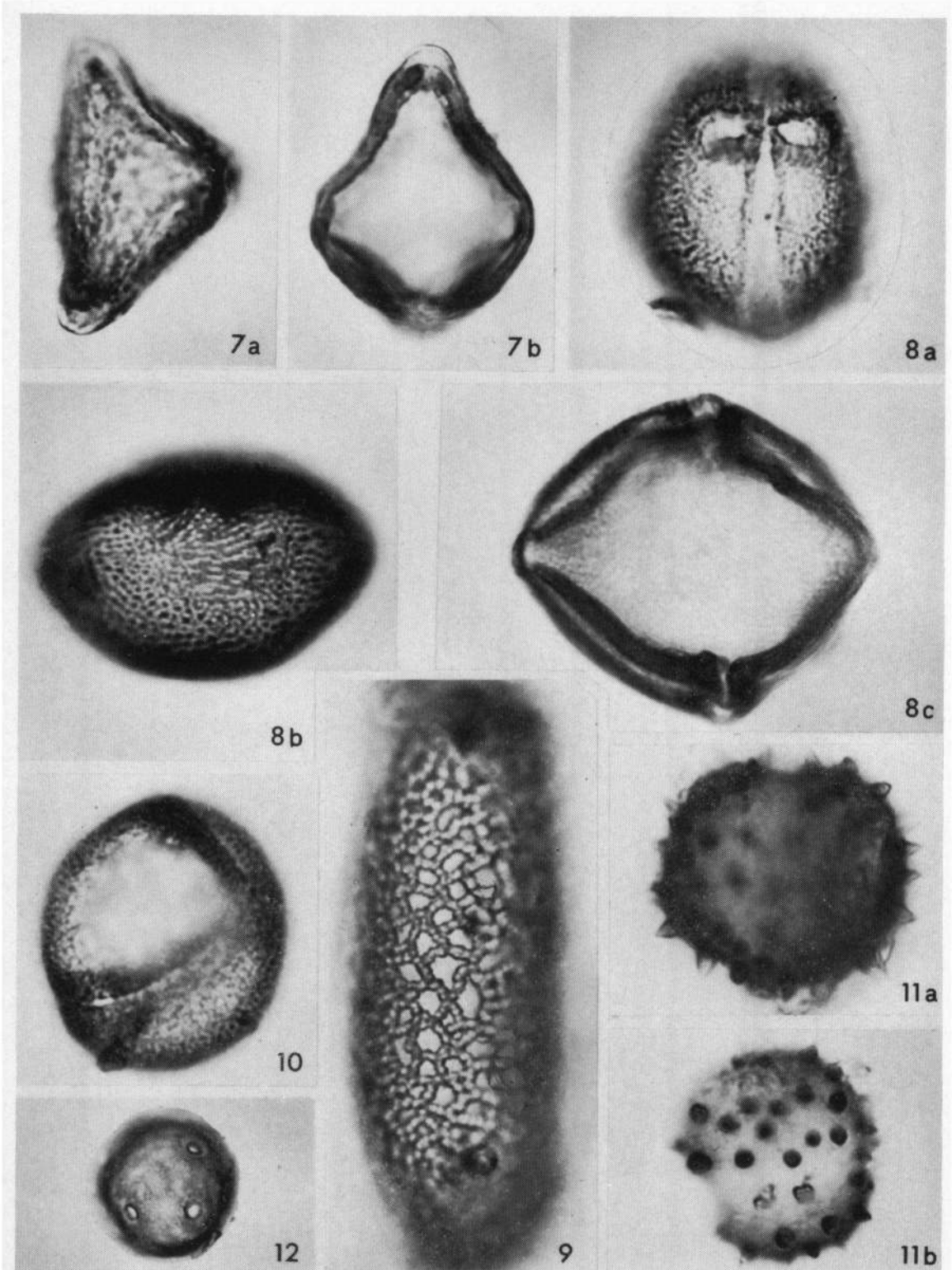


FIG. 14. 7. *Shepherdia argentea*, fossil, spectrum 84; 8. *Rhus glabra* type, fossil, spectrum 86; 9. *Lilium philadelphicum*, fossil, spectrum 48; 10. *Rumex orbiculatus* type, fossil, spectrum 51; 11. *Arceuthobium*, fossil, spectrum 16; 12. *Sarcobatus*, fossil, spectrum 36. Ca. 1700x.

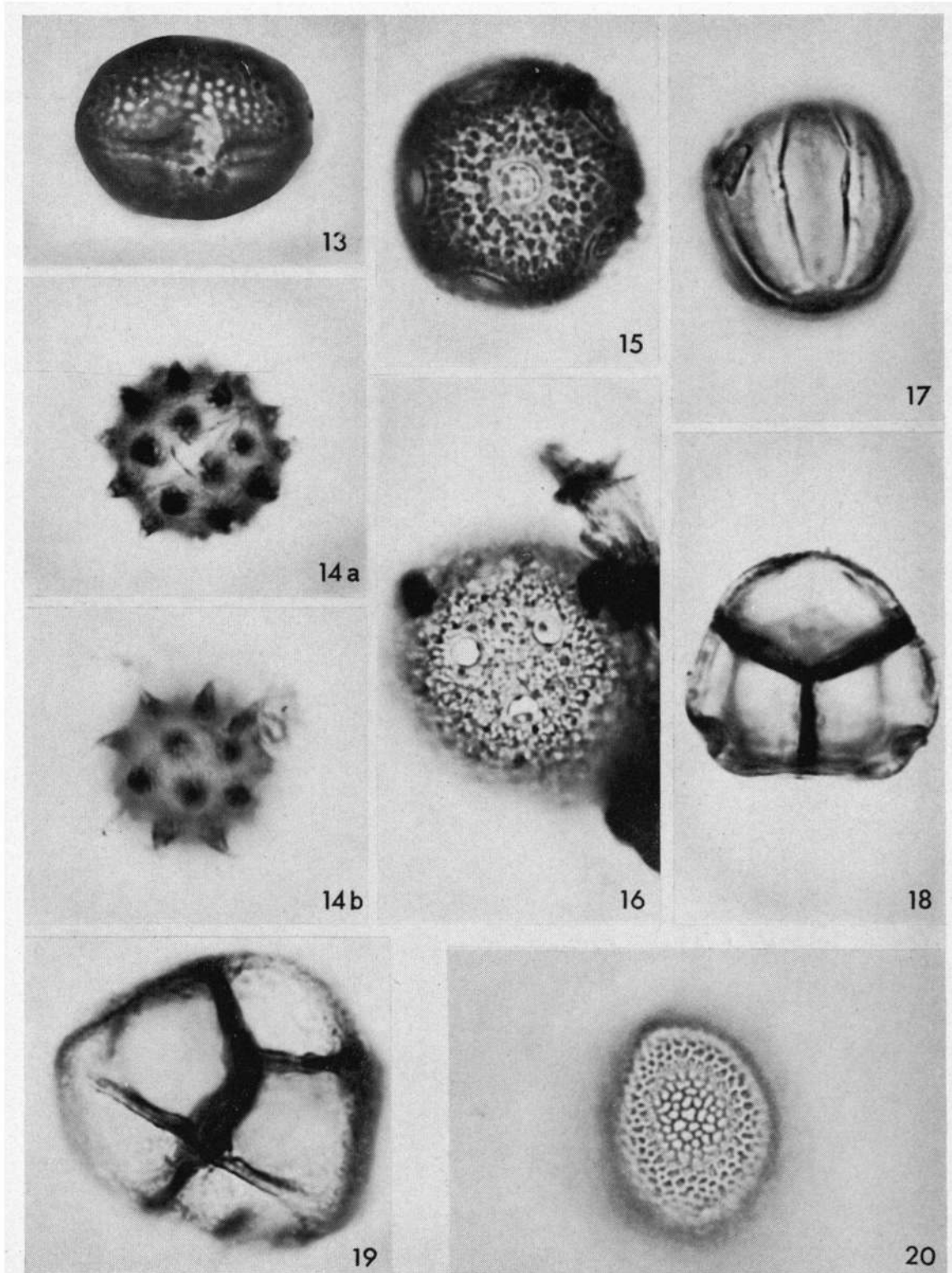


FIG. 15. 13. *Lysimachia thyrsiflora*, fossil, spectrum 27; 14. *Bidens* type, fossil, spectrum 3; 15. cf. *Stellaria longifolia*, fossil, spectrum 50, 16. *Melandrium* type, fossil, spectrum 3; 17. *Sarracenia purpurea*, fossil, spectrum 40; 18. *Ledum*, fossil, spectrum 18; 19. *Gaultheria procumbens*, fossil, spectrum 84; 20. *Triglochin*, recent. Ca. 1700x.

- in Minnesota. Univ. Minn. School Forest. Spec. Publ. 1, 57 p.
- Smith, A. G. 1958. Pollen analytical investigations of the mire at Fallaholgy Td., Co. Derry. Proc. Royal Irish Acad. 50 B(16): 329-343.
- Styz, E. 1960. Pollenmorphologische Untersuchungen an Compositen. Grana Palynol. 2: 41-104.
- Tauber, H. 1965. Differential pollen dispersion and the interpretation of pollen diagrams. Danmark Geologiske Undersögelse, R. 2, Nr. 89, 69 p.
- Thieret, J. W. 1964. Botanical survey along the Yellowknife Highway, Northwest Territories, Canada. So. Methodist Univ., Sida, Contrib. Bot. 1: 187-256.
- Transeau, E. N. 1903. On the geographic distribution and ecological relations of the bog plant societies of northern North America. Bot. Gaz. 36:401-420.
- Troels-Smith, J. 1955. Karakterisering af løse jordarter. Danmarks Geologiske Undersögelse, R. 4, 3(10), 73 p.
- Vogl, R. J. 1964. Vegetational history of Crex meadows, a prairie savanna in northwestern Wisconsin. Amer. Midland Natur. 72: 157-175.
- Watts, W. A. & T. C. Winter. 1966. Plant macrofossils from Kirchner Marsh, southeastern Minnesota—a paleoecological study. Bull. Geol. Soc. Amer. 77: 1339-1360.
- Welten, M. 1950. Beobachtungen über den rezenten Pollenniederschlag in alpiner Vegetation. Berichte Geobot. Inst. Rübel, Zürich (1949): 48-57.
- Wright, H. E., T. C. Winter & H. L. Patten. 1963. Two pollen diagrams from southeastern Minnesota: Problems in the regional late-glacial and post-glacial vegetation history. Bull. Geol. Soc. Amer. 74: 1371-1396.
- Zinke, P. J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43: 130-133.

Notes on pollen morphology

This section describes pollen-morphological features that serve to separate the pollen types mentioned. No attempt has been made to give a complete morphological diagnosis of the types.

Most of the pollen morphological terms are from Faegri & Iversen (1950, 1964) and Iversen & Troels-Smith (1950).

Pollen types described by Cushing (1963) have been omitted, for instance Aceraceae, many Fabaceae types, Pinus, and Populus.

For the sake of unity the conventions on identification used by Cushing are also applied here. Names without any suffix indicate a reasonably certain identification within the flora of the Midwest. The suffix "type" is added when there are alternatives; in the description the taxa that are included within the pollen type are mentioned. "Cf." indicates an uncertainty in the identification, resulting from insufficient reference material. The number of collections studied for the separation of the pollen types is stated in parentheses.

Microphotographs (Figs. 14-16) were taken with a Leitz Orthomat camera and Orthodox microscope with apochromatic objective x63 and eyepiece x10. Sizes apply to acetolyzed grains mounted in silicone oil.

ACERACEAE. For morphology see Cushing (1963) and Helmich (1963). *Acer spicatum* and *A. negundo* occur scattered in all zones.

ANACARDIACEAE

Rhus glabra type (Fig. 14-8). Tricolporate, striato-reticulate, distinct costae endocolpi, apiculate in

equatorial view. Grain large (36-42 μ). Includes *Rhus glabra* (4) and *R. typhina* (2), both upland species.

Rhus radicans type. Also tricolporate and striato-reticulate, but size smaller (ca. 24 μ). Includes *Rhus radicans* (2) and *R. vernix* (3), both lowland species.

APIACEAE

Cicuta type. Tricolporate, shape compressed-constricted, oval. Structure rather coarse. Costae colpi thick, broad. Borders of endocolpus parallel. Colpus in equatorial view visible up to the margin of the grain. Polar axis 25-30 μ long; ratio of length of polar to equatorial axis (P/E) 1.9-2.1. Includes *Cicuta bulbifera* (1) and *C. maculata* (2).

Sanicula (Fig. 13-1). Tricolporate, shape compressed-oval or very slightly constricted-oval. Perprolate, P/E 2.0-2.3. Grain large, polar axis ca. 50 μ . Colpus in equatorial view visible up to the margin of the grain. Borders of endocolpus parallel, or endocolpus slightly oval. Endocolpus broad, up to ca. 6 μ . Costae endocolpi medium. Includes *S. marilandica* (1) and *S. europaea* (3).

Cf. *Zizia aurea* (2). Size 28-35 μ . Shape strongly apiculate in equatorial view. Endocolpus oval. Exine much thicker in equatorial plane.

ARALIACEAE

Cf. *Aralia nudicaulis*. Tricolporate, spherical, reticulum irregular with small lumina and broad muri. Borders of endocolpus parallel. Endocolpus relatively broad (ca. 3 μ). Grains are much like *A. nudicaulis* (1), which is the smallest of the species seen (ca. 24 μ), does not have well-developed costae colpi and costae endocolpi, and has a slightly rugulate pattern. *A. racemosa* (1) has similar shape and endocolpus, but structure is slightly coarser. *A. hispida* (1) is larger and apiculate in equatorial view and has thick costae colpi and costae endocolpi. In *A. spinosa* (1) the columellae are larger than in any of the preceding species.

ASTERACEAE

Anthemis type (Stix 1960). Tricolporate, tectae, echinate. Spines equilateral triangular. Intercolpi along equatorial limb with 12 spines. Exine thick in intercolpium with coarse, often branched columellae. Includes *Achillea borealis* (1), *A. lanulosa* (1), *A. sibirica* (1), *Chrysanthemum leucanthemum* (1), *Matricaria matricarioides* (1), *M. chamomilla* (1), *Tanacetum huronense* (1), *T. vulgare* (1), *Anthemis arvensis* (1), *Achillea ptarmica* (1), *A. millefolium* (1).

Bidens type (Fig. 15-14) (*Helianthus* type p.p.; Stix 1960). Tricolporate, tectate, echinate. Spines long, triangular, in fossil material often bent. Columellae fine. Intercolpium along equatorial limb with 15-17 spines. Colpus long, acuminate. Endocolpus short. Includes *Bidens cernua* (3), *B. connata* (3), *B. comosa* (1), *B. discoidea* (1), *B. coronata* (2), and *Echinacea angustifolia* (1). In *Bidens frondosa* (2) and *B. tripartita* (3) the number of spines is larger (up to 20 along equatorial limb). The *Helianthus* species seen (*H. laetiflorus*, *H. petiolaris*, *H. tuberosus*) have shorter colpae and an oblate shape.

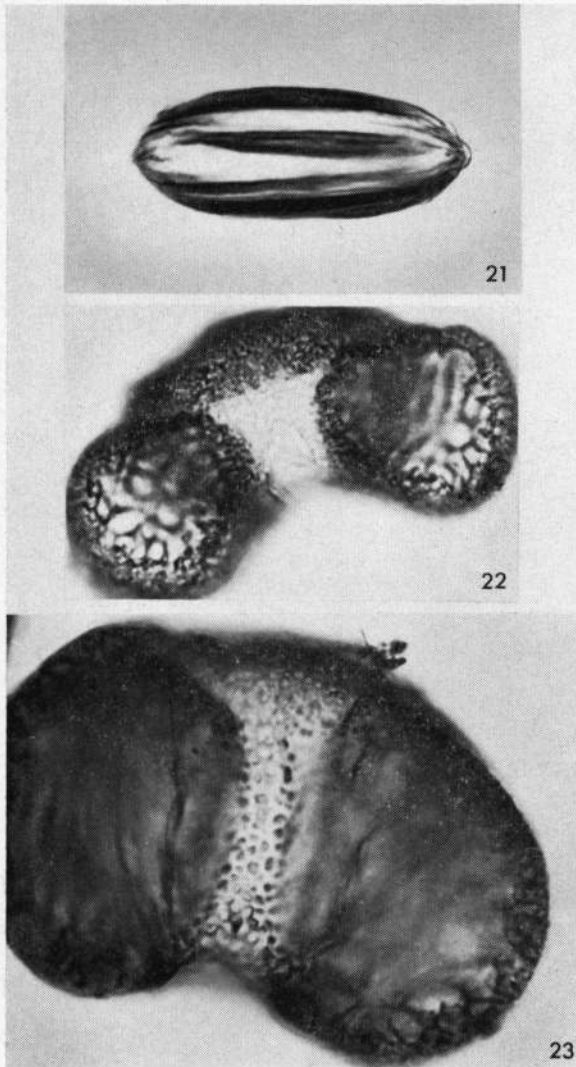


FIG. 16. 21. *Ephedra* cf. *fragilis* type, fossil, spectrum 37; 22. *Pinus banksiana/resinosa* type, fossil, spectrum 87; 23. *Pinus strobus* type, fossil, spectrum 29. Ca. 1200x.

Ambrosia type (Cushing 1963). Includes *Ambrosia* (9 spp.), *Franseria* (8 spp.), and *Iva axillaris* (1). *Iva ciliata* (Cushing 1963). Includes *Iva ciliata* (2), *I. microcephala* (1), *I. frutescens* (1), *I. imbricata* (1), and *I. angustifolia* (1).

Iva xanthifolia type (Cushing 1963). Includes *I. xanthifolia* (2), *I. dealbata* (1), and *I. ambrosiifolia* (1).

Asteraceae tubuliflorae. All *Asteraceae* tub. types not included in the types described above. Includes especially the genera *Aster* (10 spp.), *Solidago* (6 spp.), *Erigeron* (6 spp.), and *Eupatorium* (2 spp.).

BETULACEAE

Betula. Size measurements were made of recent pollen of *B. pumila* and *B. papyrifera* (Table 1). *Betula lutea* was omitted from these studies because of its rarity in the present flora. It has its main area in the eastern United States. Its recent range makes

it improbable that it occurred during the post-glacial in the Itasca State Park region. The same may be true for all the species of *Betula* with eastern or western ranges. Possible exceptions are species (*B. glandulosa*) with northern ranges that might have been present in the region in the early Holocene. The size-frequency curves for *B. pumila* and *B. papyrifera* and for a mixture of the two species show that the peaks are sufficiently far apart to result in a bimodal frequency curve for a mixture (Fig. 3). The most striking change in size of *Betula* pollen grains occurs at the boundary between zones 2 and 3, where the sediment changes from amorphous peat to woody peat. Because of the possible effects of sediment type on pollen size (Wenner 1953), the interpretations based on size are not completely conclusive.

Alnus. The grains are similar to *A. rugosa*.

Ostrya/Carpinus. See Cushing (1963).

BRASSICACEAE

Tentatively a separation has been made between: *Cardamine* type. Brassicaceae with large lumina. Includes *Brassica* (2 spp.), *Cardamine* (3 spp.), *Dentaria* (1 sp.), and *Erucastrum* (1 sp.).

Cf. *Lepidium densiflorum* (2). Size extremely small (14-17 μ) but columellae relatively large.

Brassicaceae. All Brassicaceae pollen grains not included in the types mentioned above.

CAMPANULACEAE

Campanula. The number of spines and pores agrees well with *Campanula uliginosa* (2).

CAPRIFOLIACEAE

Lonicera hirsuta type. Tricolporate, echinate, with short colpi and endocolpi. Spines small (ca. 1.5 μ long), ca. 15 along the equatorial limb. Columellae larger than in the following type. Includes *L. hirsuta* (1), *L. prolifera* (1), *L. sempervirens* (1), *L. oblongifolia* (1), and *L. dioica* var. *glaucescens* (1).

Lonicera canadensis type. Differs from the previous type by its verrucate-echinate structure, its stout spines (often obtuse at the top), fine columellae, and not very distinct composite aperture. Includes *Lonicera canadensis* (1). *Diervilla lonicera* (1) is triplicate with very thick annuli and few spines and verrucae.

Symphoricarpos occidentalis. Resembles *Lonicera hirsuta* type but is densely echinate (30-40 spines along equatorial limb) and has much smaller columellae. *S. albus* (1) is psilate.

Viburnum lentago and *Viburnum trilobum* (Cushing 1963).

Cf. *Viburnum rafinesquianum* (1). Lumina and columellae larger than in *V. trilobum*.

CARYOPHYLLACEAE

Melandrium type (Fig. 15-16) (Chanda 1962). Grain rather large with distinct (1 μ) spines. Includes *Melandrium album* (2).

Cf. *Stellaria longifolia* (Fig. 15-15). Periporate, subangular, ca. 30 μ . Pores with distinct narrow annulus. Pore membrane with 6-10 granules. Tectum with microechini (smaller than 1 μ). Fossils

are closest to *S. longifolia* (1) and *S. longipes* (2).

Caryophyllaceae. All the other Caryophyllaceae types not described above.

CORNACEAE

Cornus stolonifera type. Tricolporate, grain large, 40-70 μ . Structure coarse. Costae colpi broad, thick, interrupted in equatorial plane. Shape prolate, apiculate in equatorial view. Includes *Cornus alternifolia* (2), *C. obliqua* (1), *C. racemosa* (3), *C. rugosa* (1), *C. stolonifera* (3). *Cornus canadensis* is much smaller (20-25 μ), with narrow costae colpi.

ELEAGNACEAE

Shepherdia canadensis (1) (Fig. 13-6) (Erdtman 1952). Tricolporate, prolate, polar axis 27-35 μ . Colpus membrane psilate, without costae, ca. 3 μ wide. Endoaperture circular, within the colpus, with small costae. Structure scabrate.

Shepherdia argentea (1) (Fig. 14-7). Oblate, apiculate. Endoaperture circular with distinct fastigium. In polar view semi-triangular-semilobate, polar area small.

EPHEDRACEAE. Distinctions according to Beug (1961).

Ephedra distachya type. Longitudinal furrows branched. Synonym: *E. viridis* type (Cushing 1963). Includes *E. viridis* (2), *E. cutleri* (1), *E. funera* (1), *E. antisiphilitica* (1), and *E. nevadensis* (1).

Ephedra fragilis type (Fig. 16-21). Longitudinal furrows unbranched. Synonym: *E. trifurca* type (Cushing 1963). Includes *E. trifurca* (2), *E. californica* (1) and *E. torreyana* (2).

ERICACEAE

Ledum-Chamaedaphne complex. Tetrads subtriangular, ca. 35 μ . Colpi longer than 3 μ , with distinct costae. *Ledum* (5) (Fig. 15-18). Inner walls of tetrad thicker than outer walls. (Cf. Beug 1961; Erdtman 1943).

Chamaedaphne type (5). Inner walls of tetrad usually not thicker than outer walls. Costae colpi tend to be broader, and colpi ends are often more obtuse than in *Ledum*. Includes *Chamaedaphne calyculata* (5) and *Kalmia polifolia* (3).

Ledum/Chamaedaphne. Grains of the complex for which no distinction could be made.

Gaultheria procumbens (2) (Fig. 15-19). Tetrads globular-shaped with long colpi (14 μ). Size ca. 40-45 μ . Structure scabrate to faintly rugulate. *Arctostaphylos uva-ursi* (3) has a finer structure and broader costae colpi. *Gaultheria hispidula* (3) is smaller and has a different structure.

Vaccinium angustifolium (2). Tetrads globular-shaped, 40-45 μ , but colpi short without distinct costae. Structure coarsely scabrate-rugulate.

Other ericaceous tetrads. Includes all the other Ericaceae and Pyrolaceae except *Chimaphila* (2) and *Arctostaphylos* (3). Includes *Pyrola asarifolia* (2), *P. elliptica* (2), *P. rotundifolia* (3), *P. virens* (2), *Vaccinium myrtilloides* (2), *V. vitis-idaea* (2), *V. oxycoccus* (2), *Moneses uniflora* (2), *Gaultheria hispidula* (3) and *Epigaea repens* (1).

FABACEAE

Petalostemum purpureum (Fig. 13-4) (Cushing 1963).

Petalostemum candidum (Cushing 1963).

Amorpha (Fig. 13-5) (Cushing 1963).

Cf. *Amorpha*. Corresponds closely with *Amorpha* but has no operculum in the colpus.

Cf. *Amorpha nana* (1). Reticulum coarser than in *Amorpha canescens*.

Trifolium pratense type (Fig. 13-3). Tricolporate, prolate, large (32-45 μ). Endoaperture circular, without costae. Supra-reticulate, heterobrochate. Colpi with costae. Includes *T. pratense* (3), *T. procumbens* (1), and *T. hybridum* p.p. (2), but the latter two tend to be smaller and have smaller lumina.

Trifolium repens type. Lumina often very small, often indistinct. Includes *T. repens* (2).

Vicia type (Faegri & Iversen 1964). Tricolporate, depressed oval-prolate. Structure almost psilate or faintly reticulate. Costae endocolpi well-developed, endocolpus oval. Includes *Lathyrus venosus* (1), *L. ochroleucus* (1), *L. palustris* (1), and *Vicia americana* (1). Most grains are probably *Lathyrus venosus* on account of shape and costae endocolpi.

Cf. *Melilotus*. Perhaps synonymous with *Ononis* type of Faegri & Iversen (1964). Tricolporate, prolate, compressed at the poles, finely reticulate. Endoaperture circular. Colpus narrow with one row of granules. Polar axis 30-37 μ . Fossil grains agree well with *M. alba* (1) and *M. officinalis* (1).

HYDROCHARITACEAE

Sagittaria. Periporate, echinate with numerous spines. Pores without annulus. Spines also present on pore membrane. *Sagittaria latifolia* (1).

JUGLANDACEAE

Juglans nigra (Cushing 1963). Pore number greater than 10.

Juglans cinerea (Cushing 1963). Pore number 10 or less.

LAMIACEAE

Agastache type. 6-colpate, supra-reticulate, subspheroidal. Synonyms: *Prunella* type (Faegri & Iversen 1964), *Dracocephalum* type (Cushing 1963). Includes *Agastache foeniculum* (1), *A. Urticoides* (1), *A. nepetoides* (1), *Dracocephalum parviflorum* (1), *Nepeta cataria* (1), and *Prunella vulgaris* (1).

Lycopus type. 6-colpate, intectate, reticulate. Synonym: *Mentha* type (Faegri & Iversen 1964). Includes *Blephilia* (1 sp.), *Salvia*, *Hedeoma* (1 sp.), *Lycopus* 5 spp., *Mentha* (3 spp.), *Monarda* (2 spp.), *Satureja* (2 spp.), *Pycnanthemum* (2 spp.).

Scutellaria type. *Stachys* type p.p. (Faegri & Iversen 1964). Tricolpate, subspheroidal, finely supra-reticulate. Lumina size decreases towards the pole. Includes *S. epilobifolia* (1), *S. parvula* (1), *S. lateriflora* (1).

Stachys type. Tricolpate, reticulate, lumina uniform. Includes *Stachys* (3 sp.) and *Galeopsis* (3 spp.). In *Lamium* the reticulum is almost indistinct at 600X.

LILIACEAE

Lilium philadelphicum (1) (Fig. 14-9). Monocolpate, reticulate, prolate-perprolate. Muri width variable,

up to 6 μ , decreasing towards the poles and colpi. Dupliaculate. Polar axis 60-75 μ . *Lilium michiganense* (1) is less prolate and has a different pattern.

LORANTHACEAE

Arceuthobium (Fig. 14-11). 6-colpate, echinate with blunt spines. Three colpi are long, with psilate colpus membrane; 3 colpi are short, with granulate-echinate colpus membrane. Grain intertriangular in polar view, suboblate in equatorial view. Size ca. 35 μ . Includes *Arceuthobium pusillum* (1), *A. americanum* (1), and *A. douglasii* (1).

LYCOPODIACEAE (Cf. Erdtman et al. 1961).

Lycopodium annotinum (2). Reticulate, lumina ca. 6 μ . Triangular in distal view.

Lycopodium inundatum (1). Irregularly rugulate, circular in distal view.

Lycopodium clavatum type. Reticulate, lumina smaller than 6 μ , triangular in distal view. Includes *L. clavatum* (3), *L. complanatum* (2), *L. tristachyum* (1). Perhaps from the local Picea-Larix bog forest.

OLEACEAE. Distinctions according to Cushing (1963).

Fraxinus pennsylvanica type. Colpus margin irregular, usually 4-colpate. Includes *F. pennsylvanica* (6), *F. americana* (2).

Fraxinus nigra type. Colpus margin distinct, usually 3-colpate. Includes *Fraxinus nigra* (2), *F. quadrangulata* (2).

Fraxinus undiff. No reliable distinction between the above two types was possible.

OSMUNDACEAE

Osmunda. Includes *O. regalis* (2), *O. claytoniana* (2). Material very variable (cf. Andersen 1961).

PINACEAE. Distinctions according to Cushing (1963).

Pinus strobus type (Fig. 16-23). Ventral face of the grain coarsely verrucate.

Pinus banksiana/resinosa type (Fig. 16-22). Ventral face of the grain scabrate-psilate. The *Pinus strobus* type also tends to be larger, but this character has not been used here. Not all of the pine pollen grains could be assigned to a type. Fig. 4 shows the ratio of the two pine types based upon a sum of determinable pine pollen grains.

POACEAE (CEREALES)

Zea mays (2). Grain larger, more than 45 μ .

Avena type (1) (cf. Beug 1961).

POLYGONACEAE

Rumex orbiculatus type (Fig. 14-10). Synonym: *Rumex aquaticus-hydrolapathum* (Andersen 1961). Periporate, large (ca. 35 μ). Pore relatively small. Includes *R. orbiculatus* (2), *R. hydrolapathum* (1), and *R. fenestratus* (1).

Rumex undiff. All other *Rumex* types, smaller than 30 μ .

Polygonum persicaria type. Synonym: *P. lapathifolium* type (Cushing 1963). Periporate, reticulate. Includes *P. arifolium*, *P. careyi* (1), *P. hydro-piper* (1), *P. sagittatum*, *P. persicaria* (1), *P. hydro-piperoides* (1), *P. lapathifolium* (1), *P. pennsylvanicum* (1), *P. punctatum* (2).

Eriogonum heracleoides. Tricolporate. Colpi narrow,

endoporus small (ca. 4 μ), often longitudinally elongated, exceeding the colpus width. Ektexine thick. Capita united in small groups or united in a coarse broken rugulate pattern. Resembles *Fagopyrum*. Includes *Eriogonum heracleoides* (2) and *E. microthecum* (1). *E. umbellatum* has a coarser structure.

POLYPODIACEAE

Dryopteris type. Monolete spores with perisporium incomplete or absent. Includes *Cystopteris*, *Athyrium*, *Onoclea*, *Dryopteris*, *Woodsia*, and *Matteucia*. *Dryopteris thelypteris*. Perisporium wrinkled, with small spines.

Dryopteris spinulosa type. Perisporium folded, with numerous small spines. Includes *D. spinulosa* (1) and *D. cristata* (2).

Dryopteris filix-mas (1). Perisporium folded, without spines.

PRIMULACEAE

Lysimachia thyrsiflora (Fig. 15-13). Tricolporate, subspheroidal, small (ca. 22 μ), reticulate with broad muri. Granulae not easily resolvable at 600x. Endocolpus oval, often constricted in colpus area. Colpus provided with a broad margo. *Lysimachia ciliata* (1), *L. lanceolata* (1), *L. quadrifolia* (1), and *L. terrestris* (1) show differences in distinctness of the structure and in width of the endocolpus.

RANUNCULACEAE

Caltha type (Faegri & Iversen 1964). Tricolpate, microechinate. Includes *Caltha palustris* (2), *Aquilegia canadensis* (2), *A. coerulea* (2), *Delphinium virescens* (1), and *D. nelsonii*.

Ranunculaceae. Synonym: *Ranunculus* type (Cushing 1963). Includes all the other Ranunculaceae with scabrate-verrucate structure.

Thalictrum has been left undivided.

ROSACEAE

Comarum palustre type (3) (Fig. 13-2). A subtype of the *Potentilla* type (Faegri & Iversen 1964) characterized by its protruding operculum and lack of anastomosing valvae (Reitsma 1966). Fastigium sharply protuberant, which together with size and structure serve to distinguish the type from other *Potentilla* species.

Rosa type. Tricolporate, operculate, costae colpi distinct. Fastigium large. Grain distinctly striate. Shape almost spheroidal. The difference from *Potentilla* lies in the shape, the well-defined endocolpus and the presence of costae colpi. Includes *R. macounii* (1), *R. arkansana* (2), *R. blanda* (1), *R. acicularis* (1).

Spiraea type (cf. *Filipendula* in Faegri & Iversen 1964). Grain small, spheroidal to slightly prolate. Endocolpus margins parallel. Structure microechinate. Includes *S. alba* (3), *S. tomentosa* (2), *Filipendula ulmaria* (3).

Prunus-Amelanchier complex. Tentatively divided into:

Prunus type. Synonym: *Geum* type (Faegri & Iversen 1964). Not operculate, distinctly striate, distinct costae colpi. Includes *Prunus* (6 spp.), *Geum alleppicum* (2), *G. canadensis* (1), *G. macrophyllum* (1).

Amelanchier type. Not operculate, indistinctly striate or psilate. Includes *Amelanchier* (9 spp.), *Sorbus* (2 spp.), *Pyrus* (1 sp.).

RUBIACEAE

Houstonia. Tricolporate, reticulate with broad muri and distinct capita. Lumina of variable size, up to 2.5 μ . Colpus membrane psilate. Polar axis 35 μ . Polar area small. Typical are the double costae of the endoaperture; one set borders a wide, more or less oval endocolpus with diffuse ends; the second set is much thicker and borders a smaller endoporus. *Houstonia longifolia* (1).

Galium labradoricum type. 5-7-colpate, small, relatively coarse structure. Includes *Galium boreale* (1), *G. labradoricum* (2), *G. longifolia* (1).

Galium undiff. Stephanocolpate grains with structure finer than in the previous type.

SALICACEAE

Populus tremuloides type (Cushing 1963). Includes *P. tremuloides*, *P. grandidentata*, and *P. deltoides*.

SARRACENIACEAE

Sarracenia (Fig. 15-17). Grain small (ca. 20 μ), tectate, psilate, 7-colporate. Colpus in equatorial plane irregular or interrupted. Sometimes a small

endoporus present. Slightly depressed-oval in equatorial view. *Sarracenia purpurea* (1).

SCHEUCHZERIAEAE

Triglochin (Fig. 15-20). Inaperturate, reticulate, homobrochate. Columellae not easily resolvable (cf. Beug 1961, Faegri & Iversen 1964). *Triglochin maritima* agg. (2), *Triglochin palustris* (1).

SPARGANIACEAE

Sparganium type (cf. Beug 1961). Monoporate, reticulate, no annulus around pores. Includes *Typha angustifolia* (3) and *Sparganium* (2 spp.).

ULMACEAE

Celtis (Cushing 1963).

VITACEAE

Parthenocissus. Tricolporate, prolate, ca. 40 μ , often slightly apiculate in equatorial view. Intectate, reticulate, elements much fused. Muri thick, lumina small. Endoporus provided with thick costae, ca. 3 μ , slightly exceeding the colpus. Colpus membrane psilate, with costae and margo. Polar area small. Exine ca. 2.5 μ thick. *Parthenocissus inserta* (1) and *P. quinquefolia* (1).

Vitis (Faegri & Iversen 1964). *Vitis riparia* (1), *V. rotundifolia* (1), and *V. aestivalis* (2).