POLLEN OF THE NORTH AMERICAN QUATERNARY: 
THE TOP TWENTY

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ABSTRACT

Based on sixty Holocene sections, the most important North American pollen types are: Pinus, Picea, Ephedra, Tsuga canadensis-betulophylla, Pseudotsuga-Larix, Juniperus-Taxodium, Cyperaceae, Gramineae, Betula, Carya, Alnus, Ulmus, Chenopodiaceae, Liquidambar, Acer, Quercus, Nyssa, Fagus, Artemisia, and Ambrosia. The distribution of these taxa is employed to describe six floristic provinces—the Boreal, Lakes, Southeast, Pacific, Plains, and Mountain provinces. These provinces are present during earlier Pleistocene interglacial times, but they are not apparent in glacial-age pollen assemblages, which are dominated by conifers and herbs.

INTRODUCTION

The Quaternary period, approximately the past two and one half million years, is characterized by cold intervals of continental glaciation, alternating with warm interglacials (Shotton, 1973, p. 2). Pollen floras of the present interglacial, the Holocene epoch of the past 10,000 years, generally resemble floras of earlier Pleistocene interglacials (Wright, 1972). Unlike local interglacial assemblages, glacial-age pollen assemblages resemble the Holocene pollen floras that occur in colder, more northern climates.

An estimated 500 to 1000 fossil pollen and spore taxa from the North American Quaternary (north of Mexico) have so far been described. Because these taxa are indistinguishable from pollen of modern species, they are identified with them, rather than being assigned to form genera. Selection of the top twenty is based both on types that are relatively abundant or dominant and on those that are less abundant, but still characteristic components of Holocene assemblages of one or more floristic provinces. None of the top twenty is absolutely restricted to one province, because all are adapted to wind dispersal. The occurrence of stray grains in surface samples found hundreds of kilometers from their closest source has been documented for several taxa, e.g., Ephedra (King and Kapp, 1963) and Sarcobatus of the Chenopodiaceae (Maher, 1964).

According to Leopold (1969), most, if not all, Quaternary pollen types were present from the Miocene onward. The modern floristic provinces of North America appear to have originated in the Pliocene. Since there is no evidence of extinction of the North American flora in the late Cenozoic, the lower boundary of the Quaternary cannot be defined by the stratigraphic criteria of presence or absence of certain pollen taxa.

Previous reviews of Quaternary pollen stratigraphy have attempted to reconstruct vegetation and climatic history (Whitehead, 1965, 1973; Cushing, 1965; Martin and Mehringer, 1965; Davis, 1965; Heusser, 1965; and Wright, 1971). This paper purposes to summarize the geographic occurrence of assemblages that contain the twenty most important stratigraphically recurrent pollen types. We distinguish glacial from interglacial floras and outline six floristic provinces for the interglacial floras (Text-fig. 1, 2). During periods of glacial climatic conditions, the floristic
 provinces are not displaced, but disappear and are replaced by a fairly uniform conifer-herb assemblage. Because of the lack of pollen records from the early Quaternary, the description and distribution of the top twenty pollen types are based primarily on the assemblages of the Holocene interglacial (the last 10,000 years) and the latter part of the Wisconsinan glacial (20,000 to 10,000 years ago).

**POLENN TYPES**

For a pollen type to be included in the top twenty, it must either dominate or characterize interglacial assemblages of one or more of the floristic provinces. Glacial assemblages are composed of taxa that are present during the interglacials. A dominant pollen type contributes more than 20% of most pollen spectra of a glacial or interglacial section. A characteristic type, on the other hand, has similar constancy, but lesser abundance and is generally more provincial. Other abundant types that are not included here occur in isolated parts of sections and are often associated with evidence of local aquatic plant succession, e.g., *Sphagnum* spore in peat. Although only the top twenty types are illustrated (Pl. 1), other important taxa are mentioned. Most of the pollen types are keyed out and further illustrated in Kapp (1969) and McAndrews et al. (1973).

**Vesiculate Class**

*Pinus* (Pl. 1, fig. 1, 2) is the most abundant and cosmopolitan Quaternary pollen type and dominates at least part of most sections. When the distal surface is preserved, a verrucate sculpturing identifies the grain as subgenus *Haploxylon* (Pl. 1, fig. 1); a psilate surface indicates the subgenus *Duploxyylon* (Pl. 1, fig. 2). *Haploxylon* pine is absent from the Boreal and Southeast provinces. *Picea* (Pl. 1, fig. 3) dominates the Boreal and characterizes the Coast
provinces; it is either dominant or characteristic southward during glacial. Less important vesiculatates are Tsuga mertensiana in the Coast province and Abies in the Coast and Boreal provinces.

**Polyplicate Class**

_Ephedra_ (Pl. 1, fig. 4,5) is characteristic of the southern part of the Mountain province. Within the genus, two types are readily distinguished, _E. torreyana_ type (Pl. 1, fig. 4), with simple folds and unbranched furrows; and _E. nevadensis_ type (Pl. 1, fig. 5), with complex folds and branched furrows. These two types are geographically separated (King and Sigleo, 1973; Martin, 1963, p. 51). The _E. torreyana_ type is restricted to the southwestern deserts, while the _E. nevadensis_ type occurs mainly in mountainous regions.

**Inaperturate Class**

Fossil pollen of this class are often difficult to identify during sediment analysis because their large size and/or thin exines lead to breakage. _Tsuga canadensis-betuloides_ (Pl. 1, fig. 6), as distinct from the vesiculate _T. mertensiana_, dominates or characterizes sections in the Lakes and Coast provinces. _Pseudotsuga-Larix_ (Pl. 1, fig. 7, 8) is characteristic of the Coast and Boreal provinces, but it occurs occasionally in the Mountain and Lakes provinces. Another gymnosperm pollen type that is less consistently reported, probably because it is overlooked during analysis, is the _Juniperus-Taxodium_ type (Pl. 1, fig. 9, 10). Because these small, relatively sculptureless grains are usually split and crushed, it is difficult to distinguish between types with a tiny pore, such as _Juniperus, Thuja_, and _Chamaecyparis_ (Adams and Morton, 1972), and those with an exuto papilla, such as _Taxodium_ and _Sequoia_. The _Juniperus-Taxodium_ type, as is _Pinus_, is widespread and dominates or characterizes sections in the Southeast, Mountain, Coast, and Lakes provinces.

Cyperaceae (Pl. 1, fig. 11), with its several poroids, is also commonly folded and difficult to identify. It occurs in all provinces and is associated with peat and shallow-water sediment, indicating that its usual source is local aquatic plants. However, it characterizes or dominates deepwater sediments in the Plains province and in the northern part of the Boreal province during the Holocene (Ritchie, 1974), and southward during glacials.

**Monoporate Class**

Gramineae (Pl. 1, fig. 12) is dominant in the Plains and Mountain provinces and characterizes the northern part of the Boreal province. Occasional abundance in sections from other provinces is related to aquatic plants, such as the wild rice _Zizania_ (McAndrews, 1969).
Triporate Class

Betula (Pl. 1, fig. 13) dominates the Boreal province and characterizes the Lakes province. It also characterizes glacial assemblages in the east. Myrica is occasionally present in the Boreal, Lakes Southeast, and Coast provinces. Caryya (Pl. 1, fig. 14) and Ostrya-Carpinus are characteristic of the Lakes and Southeast provinces.

Stephanoporate Class

Alnus (Pl. 1, fig. 15) is dominant in the Boreal and Coast provinces and characterizes the Lakes province. Ulmus (Pl. 1, fig. 16) is characteristic of the Lakes, Southeast, and the northern part of the Plains provinces.

Periporate Class

Chenopodiaceae (Pl. 1, fig. 17), the suborder containing the families Chenopodiaceae and Amaranthaceae, dominates the Plains and Mountain provinces. It is also occasionally abundant in the Southeast province in sections exhibiting aquatic plant succession (Watts, 1969). Although most pollen grains have more than 20 pores, several types with fewer pores are recognized, such as Sarcobatus and Tidestromia of the Mountain province.

Liquidambar (Pl. 1, fig. 18) is distinguished by its relatively simple pore structure and reticulate exine; it is characteristic of the Southeast province.

Tricolporate Class

Acer (Pl. 1, fig. 19) is characteristic of the Lakes province. Quercus (Pl. 1, fig. 20) is dominant in the Southeast province and is characteristic of the Mountain, Lakes, and eastern part of the Plains provinces.

Tricolporate Class

Nyssa (Pl. 1, fig. 21) is characteristic of the Southeast province and often dominates parts of sections exhibiting swamp succession. The morphologically similar Fagus (Pl. 1, fig. 22) is dominant in the eastern part of the Lakes province and characterizes the Southeast province.

Artemisia (Pl. 1, fig. 23) and Ambrosia (Pl. 1, fig. 24), the latter, including other "short-spined" composites such as Iva and Xantbium, are dominant in the Plains and Mountain provinces.

POLLEN FLORISTIC PROVINCES

Six pollen floristic provinces can be distinguished in Holocene and other interglacial deposits. Not surprisingly, these correspond in a general way with the principal vegetation types of North America (Oosting, 1956, p. 271). Our Boreal province includes both tundra and boreal forest. The Lakes province corresponds with the hemlock-hardwood forest around the Great Lakes and St. Lawrence Valley and extends southward and eastward into the deciduous forest. The Southeast province includes both the southern half of the deciduous forest and the southeastern evergreen forest. The region of Pacific forest along the Pacific coast is congruent with the Coast province. The Plains province generally lacks forest and includes the grassland of the Great Plains. The Mountain province contains the partly forested Rocky
Mountains and the shrub-dominated lowland deserts. 
The following discussion of pollen provinces is based on 60 Holocene sections. The sections are located toward the center of any province (Text-fig. 1), and they show relatively little stratigraphic succession when compared with sections located near provincial boundaries. Holocene sections in the transitional areas between provinces have either a mixture of pollen types of two provinces or a stratigraphic succession indicating a shift in boundaries.

Boreal Province

This largest province includes most of Alaska and Canada. Late Quaternary glaciation produced many poorly drained depressions that contain Holocene lake sediments. The cool, moist climate that prevails over this region permits the accumulation of bog pear, another source of fossil pollen. The most widespread dominant is Betula, with values of 40%. Alnus has similar values in the north, but it decreases southward in Saskatchewan, Manitoba, Ontario, Quebec, and Newfoundland. Picea has values above 20% only in the central part of the province, from central Alaska southeast to Newfoundland. Dominance of the Pinus subg. Diploxylon type is restricted to the south, from Alberta to southern Quebec. It is absent in Alaska, the Yukon, and the adjacent Northwest Territories and has values of up to 10% elsewhere. In the north, Cyperaceae values approach 20%, and the values of Gramineae, Salix and Artemisia are 1% to 5%. Pseudotsuga-Larix typically has a value of less than 1%. Abies has similar values everywhere but in Newfoundland, where it has a value of more than 20%.

In unglaciated Alaska and the Yukon, glacial-age sections (Text-fig. 2) have 20% to 40% Cyperaceae and Gramineae, with lesser amounts of Betula and Artemisia. Alnus and conifer pollen are essentially absent.

Interglacial-age spectra or sections from Alaska, northern Ontario, and Baffin Island are typical of the Boreal province. However, they differ from local Holocene assemblages in that the eastern Alaska assemblage is characterized by Pinus and the Baffin Island assemblage is dominated by Betula; thus, they resemble Holocene assemblages farther south. The interglacial abundance of these two taxa indicates that their ranges contracted during the subsequent Wisconsinan glaciation, and these taxa have remained less widespread throughout the Holocene.

Lakes Province

This province centers on the eastern Great Lakes, and it extends west to Minnesota and east to the Atlantic Ocean. Holocene sediments occur in lakes provided by late-Wisconsinan glaciation, but the ice-marginal position of this province also permitted accumulation of sediments during interstadials.

The Holocene is characterized by Tsuga canadensis-heterophylla and Fagus, but only in sections adjacent to Lake Ontario do these taxa dominate. Tsuga occurs only in the latest Holocene, and Fagus is rare west of Lake Michigan. Both Haploxylon and Diploxylon types of Pinus are dominant northward in Minnesota and Wisconsin. Quercus is characteristic throughout and accounts for half of the assemblages southward in Ohio and Connecticut. Betula is a constant component which increases northward and eastward, with values of 40% in Quebec and Nova Scotia. Ulmus, Acer, Alnus, and Carya are characteristic, with values ranging up to 15%; Carya is more important southward in Ohio.

Glacial sections are dominated by Picea, but the other pollen types show regional variation. In Nova Scotia and Ontario, Pinus is more than 20% and Betula is 10%. In contrast, the glacial section in Minnesota has only 1% Pinus and 5% Betula, but Gramineae, Cyperaceae, and Artemisia are each 10% to 20%.

The interglacial assemblage of southern Ontario is dominated by Quercus, with 5% to 10% each of Pinus, Fagus, Tsuga, Ulmus, Acer, and Carya. In contrast with the local Holocene assemblage, the abundance of Quercus, Carya, and Liquidambar pollen suggests elements of the Southeast province.

Southeast Province

In this province, detailed pollen analyses have been done only in those states bordering the Atlantic Ocean. Holocene, glacial, and interglacial assemblages occur in sediments of sinkhole lakes in Virginia, Georgia, and Florida. Lakes and swamps on the low-gradient coastal plain of Virginia and North Carolina contain Holocene and glacial sediments.

Pinus subg. Diploxylon type and Quercus together contribute about 70% of the Holocene assemblage. Characteristic types, such as Liquidambar, Carya, Juniperus-Taxodium, and Nyssa, are usually 5% or less, with the exception of short-lived peaks for the latter two taxa, which are related to swamp forest
succession. Interglacial sections of Georgia and Florida are similar to local Holocene sections, except that Liquidambar and Carya are each about 10%. The relative abundance of Gramineae, Artemisia, and Ambrosia in the lower part of the Holocene and interglacial sections indicates a connection with the Plains province.

Sediments that date from the interval 22,000 to 10,000 years ago, the maximum ice advance of the late Wisconsinan glaciation, are dominated by 60% to 80% Pinus subg. Diploxylon type. Characteristic Holocene types are essentially absent, except for Quercus, which is 5% or less. Picea is 5% to 20% and, together with 1% Abies, supplies a boreal aspect. However, Betula, Alnus, Cyperaceae, and Gramineae, although present in amounts up to 5% each, are significantly less abundant than they are in the Boreal province.

Coast Province

This province extends along the Pacific coast from southern Alaska to northern California. A generally cool, moist climate encourages peat accumulation, and most Holocene assemblages are known from peat sections.

With the exception of Alnus, with general values of 10% to 40%, all other important types are gymnosperms. Tsuga canadensis-heterophylla has values of 10% to 40%, except in sections in the extreme north and south of the province. Tsuga mertensiana, although not a member of the top twenty, has values of up to 10%, but it is restricted to the northern part of the province. Abies has a more southerly distribution, with values of up to 4%. Picea and Pinus have values up to 25%, with the higher values of Pinus in British Columbia. Pseudotsuga-Larix is absent in the north and reaches a maximum of 5% in southern British Columbia and Washington. Juniperus-Taxodium has values of up to 40% in British Columbia and Washington, but probably it has not been consistently identified elsewhere.

The province is distinguished from the adjacent Boreal province by a virtual absence of Betula. It is related to the distant Lakes province by the presence of Tsuga canadensis-heterophylla, but in general, it lacks the angiosperms of the Lakes province, such as Betula, Quercus, Fagus, Acer, and Ulmus.

Glacial assemblages have relatively high percentages of Pinus subg. Diploxylon type, Gramineae, Picea, Alnus and Tsuga mertensiana, together with variable amounts of Cyperaceae and Gramineae. The Holocene and earlier interglacials are distinguished by abundant Tsuga canadensis-heterophylla and lesser quantities of Gramineae and Cyperaceae.

Plains Province

This province includes the southern part of the Canadian prairie provinces and extends southward through the Great Plains to the Gulf of Mexico. Pollen-bearing deposits are rare in the western part of the province, and the pollen record is best known from the lake and marsh deposits of the less arid north and east.

Holocene sections are dominated by 5% to 40% Gramineae and by Artemisia, Ambrosia, and Chenopodiaceae, which together total 25% to 50%. Among tree pollen, Pinus is 1% to 20% north of Iowa, but it is essentially absent southward. Quercus and Ulmus are absent in Saskatchewan, but they have values, respectively, of 5% to 30% and 1% to 5% from Manitoba southward. Cyperaceae commonly has minimum values of 5%.

Glacial-age sections are known only from Missouri northward, and they are dominated by up to 70% Picea. Like the Holocene assemblage, these sections contain significant amounts (5% to 20% each) of Pinus, Artemisia, Gramineae, and Cyperaceae, but unlike the Holocene, Quercus, Ambrosia, and Chenopodiaceae are virtually absent.

The interglacial assemblage of southern Manitoba is similar to the local Holocene assemblage. However, the interglacial section in Illinois is unlike the overlying Holocene assemblage; it is dominated by Quercus and Juniperus-Taxodium and also shows significant amounts of Carya and Liquidambar. Thus, it appears that the flora of the Southeast province extended farther westward during the interglacial than during the Holocene. Similar but more local floristic displacements from the Holocene are documented along the northern and eastern margin of the Plains province, from Alberta (Lichti-Federovich, 1970), Saskatchewan (Mott, 1973), Manitoba (Ritchie, 1964), and Minnesota (McAndrews, 1966; Waddington, 1970).

Mountain Province

The Mountain province includes the Rocky Mountains and the deserts of the Great Basin and Southwest. Permanent lakes and peat bogs occur at higher elevations; and spring mounds, playa sediments, and alluvium serve as sources of fossil pollen at lower, more arid elevations, where permanent lakes and bogs are absent. Because of the altitudinal zona-
tion of the vegetation, the pollen flora reflects sources from both high-altitude forest, as well as shrubs and herbs of lower-elevation grassland and desert.

Holocene assemblages from high-elevation sections in Wyoming, Colorado, eastern California, and New Mexico are dominated by 50% to 75% Pines, in contrast to assemblages at lower elevations, where Pines is 20% or less, Chenopodiaceae is dominant (10% to 50%), and Ambrosia is 20% or more. Artemisia is 5% to 10% in all sections, except those in Idaho, where it is 20% to 40%, and in southern Arizona, where it is absent. Gramineae ranges up to 20%, and Quercus and Juniperus-Taxodium have values of 1% to 5%. Ephedra, the characteristic endemic of the province, is present only from Colorado southward, where its values range up to 5%. Picea is significant only at higher elevations, e.g., 5% to 10% in Colorado.

Glacial sections in Texas and Nevada are dominated by 60% to 80% Pines; other pollen types are less than 5%, except in Nevada, where Juniperus-Taxodium and Gramineae are each 10%. The higher elevation of the New Mexico site is reflected by the lower values of Pines (30%); it shows 50% Artemisia and 5% to 10% Picea. Ephedra is virtually absent from all glacial sections. Interglacial deposits frequently are devoid of pollen (Martin and Methinger, 1965).

CONCLUSIONS

A study of the relative abundance of twenty pollen types in Holocene sections makes it possible to describe six pollen floristic provinces. These same provinces occur in the preceding interglacial, although they are somewhat displaced geographically. Pollen assemblages from the intervening glacial period 20 25 generally resemble Holocene floras of subarctic and alpine regions and display little provincialism.

Work on the objective delimitation of pollen provinces is in progress. For example, Webb and McAndrews (1975) make use of percentage contours and principal component analysis on pollen in surface samples to describe the modern pollen rain in parts of the Plains, Lakes, and Boreal provinces. However, application of these techniques to fossil assemblages is hampered by a lack of information from critical areas, such as British Columbia, Alberta, Mississippi, Alabama, California, and the Plains province. Thus, future objective work may not only revise provincial boundaries, but it may also distinguish other provinces and subprovinces. However, the top twenty pollen types are unlikely to be extensively revised.

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