STRATIGRAPHIC PALYNOLOGY, VEGETATION DYNAMICS AND PALEOECOLOGY OF THE FLORISSANT LAKE BEDS (OLIGOCENE), COLORADO

By

Allan P. Hascall

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Geological Sciences

1988

ABSTRACT

STRATIGRAPHIC PALYNOLOGY, VEGETATION DYNAMICS AND PALEOECOLOGY OF THE FLORISSANT LAKE BEDS (OLIGOCENE), COLORADO

By

Allan P. Hascall

Palynological samples were analyzed from exposures of the Florissant Lake Beds (Oligocene), Colorado. 78 palynomorph types are described, five new to the flora. Most samples are dominated by pollen derived from plants growing close to the lake shore, an observation in agreement with available megafossil data.

Potamogeton pollen appears to provide an indicator of relative water depth. Its presence in the Lower Tuff suggests that this unit was deposited after initial lake formation. Although the lakebed sequence represents basin infilling by ash from proximal volcanic centers, there is no evidence for significant disturbance of terrestrial communities. Spring turnover is proposed to account for the alternating diatomite/sapropel couplets in the laminated lake shales. Palynologic evidence suggests that the lake may have dried at least once late in its history. Accumulation of ash finally ceased and a period of erosion occurred prior to the deposition of the Upper Tuff.

ACKNOWLEDGMENTS

Professors Aureal T. Cross and Ralph E. Taggart have provided the essential guidance to insure that this paper is scientifically accurate and complete. Each demonstrated a sincere personal concern for my academic success and personal welfare. They exceeded the normal expectations of thesis advisors and will always be my friends.

I am indebted to my father, Perry, my mother, Virginia, and my wife, Nancy, for their unwavering encouragement, patience, and financial assistance throughout this project. I appreciate their willingness to let my work often infringe on their lives.

The National Park Service permitted me to excavate and take collections from protected exposures at the Florissant Fossil Beds National Monument. The assistance of the staff and provision of shelter on the property during field study was much appreciated.

I would like to thank Professor Robert L. Anstey for participating on the thesis guidance committee and preparing me for scientific research in the library.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

INTRODUCTION

A complex series of laminated lacustrine shales and associated deposits near Florissant, Colorado, have provided insight into the mid-Tertiary geologic and biotic history of a local intermountain area of the central Rocky Mountains. The Florissant deposits are located approximately 65 km west of Colorado Springs (Figure 1). The lakebeds are widely known for the abundance and delicate preservation of diverse plant and insect fossils, permineralized wood, and fossil vertebrates. Volcanic breccias and andesitic and rhyolitic tuffs are situated above and below the lacustrine shales. A portion of the area of distribution of the deposits was acquired by the federal government in 1969 and designated the Florissant Fossil Beds National Monument and placed under the auspices of the National Park Service. The monument was established "to preserve and interpret for the benefit and enjoyment of present and future generations the excellently preserved insect and leaf fossils and related geologic sites and objects at the Florissant lakebeds" (Root, 1983).

These deposits, of Oligocene age, are currently situated at an average elevation of ~2530 m above sea level near 39° N., 105° W. The region is included in an extended eastward arm of the Thirtynine Mile volcanic field. The Front Range rises from the High Plains 65 km to the east, dominated by Pikes Peak (el ~4300 m, 24 km east). The Florissant basin is arcuate in shape, ~16 km long NW-SE and ~3-4 km wide. Topographic relief is relatively moderate as compared to surrounding mountainous terrain; the rolling hills within the formation vary in elevation by ~150 m.

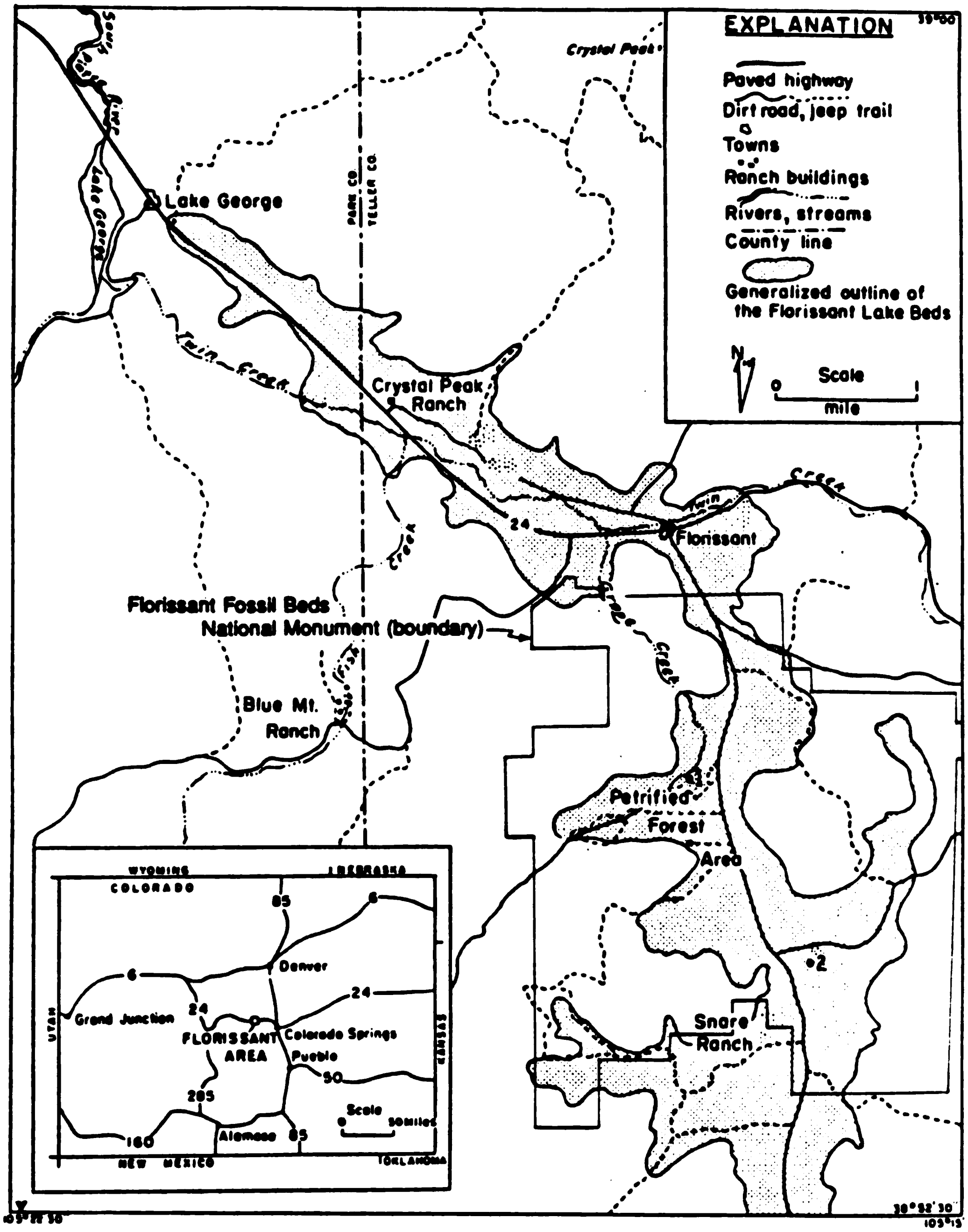


FIGURE 1. Map of Florissant area, Colorado
adapted from McLeroy and Anderson, 1966, p. 606.
1 = section 8/5/84 I   2 = section 8/23/84 I

HISTORY OF RESEARCH

Excellent preservation and intricate detail of the fossil plants, insects and other invertebrates and the geology of these lakebed deposits have attracted paleontologists, sedimentologists, and fossil collectors for more than a century. Extensive collections, both amateur and professional, have been made over the years.

Lesquereux (1872) provided the first known published account of the formation and its fossil flora which initiated scientific interest in the fossils of the deposits and contributed substantially to the identification of the plant material. Between 1872 and 1890, numerous studies were conducted by the United States Geological and Geographical (Hayden) Survey of the Territories; the most comprehensive contributions are Peale (1874), Cope (1875), Scudder (1882), Lesquereux (1883) and Wadsworth (1883).

The fossil insects of the Florissant deposits have been a particular focus of study. Between 1876 and 1900, Scudder described the insect and plant taxa in more than 25 publications. Cockerell produced more than 100 papers on the fossil insects between 1906 and 1941. Brown (1986) has been continuing work on insects.

F. H. Knowlton of the United States Geological Survey published 10 studies devoted to the Florissant plant fossils between 1898 and 1926 and, in 1916, described 121 types held by the United States National Museum (Knowlton, 1916). By the mid-1930's, collections had become extensive but were scattered in museums and other repositories throughout the United States. Need for a systematic revision of this flora was apparent because more than 250 plant species were recorded, many only tentatively. H. D. MacGinitie began an investigation at this time with an interest in integrating, revising, and interpreting the available materials, as well as making additional collections. His publication (1953) is the most comprehensive study of the fossil plants and regional paleoecology to date.

A number of studies have documented the geology of the Florissant deposits. A petrographic study of several thin sections of the lake shales was conducted by Wadsworth (1883). He concluded that the lacustrine deposits resulted from wave redistribution of ash falls and mudflows. Cross (1894) named and defined the formation and published the first United States Geological Survey geologic map of the region. The lakebed laminations represent a period of pulsating volcanism in the region during the Oligocene, according to McLeroy and Anderson (1966), who investigated the lithology and texture of the volcanic sediments as well as their varved interlaminae of biogenic origin. The study focused on the lake chemistry, seasonal variations in deposition, regional climate and total elapsed time of deposition of the lakebed sequence. Epis and Chapin (1974) published a study of the stratigraphy of the Thirtynine Mile volcanic field which includes the Florissant Lake Beds. Their radiometric analysis dates the Florissant deposits at ~34 Ma. A 15-minute United States Geological Survey geologic map which included the entire area of distribution of the Florissant Lake Beds was prepared by Wobus and Epis (1978). In a stratigraphic survey for the National Park Service, Root (1983) refined the delineation and description of units which comprise the lakebeds and differentiated them on a geologic map of the National Monument.

Peale (1874) briefly described the regional physiography and sedimentology and collaborated with Lesquereux to estimate the age of the lakebed deposits as upper Tertiary, possibly Pliocene. Study of the fossil fishes was initiated by Cope (1875, 1879) who suggested an age of late Eocene or early Miocene (prior to recognition of the Oligocene). Cockerell

(1906) and Knowlton (1916) subsequently agreed with Lesquereux's initial estimate of late Miocene based on comparisons with other fossil floras of North America and Europe. A single mammal, (Peratherium sp., a marsupial) recovered from the lake shales, was described by Gazin (1935), who also listed 9 previously described species of fish and 3 species of birds. He suggested an early Tertiary age since marsupials were not known in the Tertiary of North America after John Day time (late Oligocene-early Miocene). More recently, MacGinitie (1953) has supported an early-to-middle Oligocene age which is consistent with Epis and Chapin's (1974) radiometric age of ~34 Ma.

Two studies of the palynology of the Florissant sediments have provided preliminary surveys of the pollen flora. W. S. Ting examined six samples from the varve couplet interlaminae (three of the diatomite and three of the sapropel) for the McLeroy and Anderson (1966) study. These data were used to confirm the seasonality of the varves as postulated by McLeroy and Anderson. The only known illustration with identification of the pollen and spores from the Florissant Formation was prepared by E. B. Leopold (1969 a). Another pollen study, of importance to analysis of the Florissant flora, is the recent discovery of pollen in a fossil flower of the extinct Fagopsis longifolia (Manchester and Crane, 1983), a taxon prominent in the megaflora.

ADVANTAGES AND LIMITATIONS OF PALYNOLOGICAL ANALYSIS

Current paleoecological interpretations of the Florissant sediments are based primarily on analysis of plant megafossils, mostly leaf compressions. Palynological analysis of the sediments has the potential to provide additional information to supplement that available from previous megafossil studies. The pollen representation of a sample must be interpreted in light of several major criteria which are differentially expressed in the various fossil plant taxa: volume and timing of pollen production; pollen dispersal mechanisms and transportation to depositional site; resistance of the wall to natural and laboratory deterioration; precision of assignment to modern plant taxa; and inferred ecological/geographical relationships. These criteria are directly and indirectly addressed throughout this paper.

A study of the stratigraphic distribution of pollen and spores in the Florissant deposits provides a valuable new dimension for the analysis of the composition of the flora and the structure and dynamics of the source plant communities. Any study of fossil plant materials must necessarily deal with <u>parts</u> of plants which represent <u>samples</u> of the regional botanical inventory. Relative to megafossils, particularly leaves, pollen and spores typically cannot be identified with equivalent precision. Under normal conditions, it is possible to document morphotypes within extant or form genera but in the case of some palynomorphs, delineation of morphotypes within a complex of genera or even a group of families is the best that can be expected. In the case of angiospermous pollen, there is also a distinct bias favoring representation of anemophilous forms at the expense of entomophilous forms.

Despite the limitations noted above, palynological data do have several advantages:

(1) Pollen grains and spores are dispersed in much greater numbers than larger plant parts such as leaves.

(2) Palynomorphs tend to be dispersed over greater distances than larger parts, thus improving the geographic sampling of the source flora.

(3) Sufficient numbers of palynomorphs are typically recovered over a much wider stratigraphic range and from more diverse sedimentary environments than plant megafossils.

Fossil pollen grains and spores are subject to representational biases as are any other fossil entities. These biases include the relative production of material in the source flora, the relative importance of taxa in specific communities, the distribution of plant communities, the variations in transport vectors, depositional biases (variable taphonomy), and post-depositional factors. A complete discussion of the interaction of these factors is beyond the scope of this study although specific considerations will be introduced where they seem to be particularly significant.

OBJECTIVES OF RESEARCH

This palynologic study of the Florissant sediments utilized a stratigraphic approach. It involved close sampling through the stratigraphic sections studied. Three objectives or areas of research were planned:

(1) Inventory of floral composition represented by pollen and spores.

(2) Analysis of regional paleoecology (vegetation structure, paleoclimate, paleogeography).

(3) Interpretation of phytogeography and vegetation dynamics (disturbance effects on plant succession).

Floral Composition:

Given the preservational and transportational advantages of pollen and spores over leaves, it was expected that additional taxa would be recognized in the current study. MacGinitie's (1953) systematic list had been extended prior to this study by Ting (in McLeroy and Anderson, 1966) and Leopold (1969 a) by pollen representing additional plants.

Regional Paleoecology:

The composite floral list of megafossils and palynomorphs represents a number of distinct source vegetation communities that intergraded geographically. A uniformitarian approach can be used to subdivide this list into ecologically-distinct source plant assemblages, suggesting a regional mosaic of plant communities that might contribute to both paleoclimatic and paleogeographic reconstruction.

Phytogeography/Vegetation Dynamics:

Comparison of geographically separated florules can increase understanding of the distribution of plant communities within the region. An advantage of stratigraphic palynology over megafossil studies is that productive pollen/spore samples are more common than productive megafossil layers in most stratigraphic sequences, making it easier to determine changes in the source vegetation over time. Floral assemblage changes throughout the stratigraphic column provide the opportunity to look for patterns of succession and shifts in dominance in the communities through the time interval represented by the Florissant deposits.

GEOLOGY

Detailed descriptions of the stratigraphic units of the Florissant deposits have been included in several studies (MacGinitie, 1953; McLeroy and Anderson, 1966; Root, 1983). Description of the internal characteristics of each unit has been quite consistent. However, there are differences of opinion on the stratigraphic position of adjacent beds. Recent studies (Epis and Chapin, 1974; Root, 1983) have provided additional information for the interpretation of stratigraphic relationships.

Earlier Deposits

Currently, the Florissant Lake Beds are known to overlie three earlier rock units at different places. In most areas, the Florissant deposits lie unconformably on the irregular erosion surface of the Precambrian Pikes Peak Batholith (Root, 1983). This extensive crystalline basement is composed of pink-to-red, medium- to coarse-grained, biotite-hornblende granite.

Two depositional sequences of intermediate age have been identified as sporadically occupying the position between the Pikes Peak granite and the Florissant Lake Beds (Root, 1983). The Eocene Echo Park Alluvium has been identified in two small patches on the southeastern section of the Monument. The Wall Mountain Tuff (early Oligocene) forms scattered outcrops throughout the valley margins and marks the onset of the mid-Tertiary volcanism which dominated the region and subsequently provided the sediments of the lake beds. Epis and Chapin (1974) dated the tuff at 34 and 36 Ma using the potassium-argon method. These rhyolitic erosional remnants were once part of a continuous 9,100 km^2 ash deposit of the Thirtynine Mile volcanic field.

Florissant Lake Beds

MacGinitie (1953) and Root (1983) recognize four stratigraphic units in the Florissant Lake Beds. They include: a basal arkosic breccia, a Lower Tuff, the lacustrine shales, and an Upper Tuff. The term "lakebeds" is used throughout this paper to represent the Lower Tuff and the Lake Shales together.

Basal Arkosic Breccia

This unit was first described by MacGinitie (1953) and has been recognized by Root (1983) in two isolated localities in the east-central portion of the Monument. At the exposures of the lower contact, the basal arkosic breccia lies unconformably on the Pikes Peak Granite, or, on the Wall Mountain Tuff, where erosional remnants of that formation are still present. The basal arkosic breccia is made up of homogeneously distributed angular to subangular fragments of partially weathered Pikes Peak granite that range in size from sand to gravel (up to 2.5 cm in greatest dimension). The fragments have been incorporated into a fine-grained, greenish tuff matrix forming a well-indurated rock. MacGinitie (1953) noted that hand specimens are difficult to distinguish from the finer-grained facies of the Lower Oligocene Castle Rock Formation located near Colorado Springs. None of the sections in this palynological study included this basal unit.

Lower Tuff

The Lower Tuff, a series of andesitic beds, is in abrupt contact with the arkosic breccia below (MacGinitie, 1953). More than 11 m of this unit is exposed in one of the sections selected for the present study (8/5/84-1), but its lower contact was not observed because the slope terminates in the wide, nearly horizontal, valley floor. Considerable lateral variation in exposed thickness of this unit exists from outcrop to outcrop with a maximum of ˜15 m (MacGinitie,1953).

The Lower Tuff is divided into two units. The lower half is a complex of alternating fine and coarse beds with gravel lenses composed of andesite cobbles, basaltic lava fragments and partially-weathered granitic material. Cross-bedding is frequently apparent. Hand specimens are predominantly grey in color and irregularly iron-stained throughout. Fossil plant fragments are abundant, but none is of satisfactory size and quality for identification. A fining-upward trend was observed within some units (up to 0.5 m thick) and throughout the lower sequence. Blocky surface weathering and north-south trending vertical fractures are visible in outcrop. The upper half is more uniform and massively bedded. Lithologic breaks for sampling were thus selected arbitrarily at ˜0.3 m intervals. The consistently brown matrix is fine-grained, well-indurated and fractures conchoidally. McLeroy and Anderson (1966) described the composition as predominantly glass, plagioclase, and clinopyroxene minerals. Fossil tree stumps of putative Sequoia spp. and several species of hardwoods are preserved in the upper part of the Lower Tuff, many in their original upright positions. They vary from ˜0.5-4.5 m in diameter.

Size sorting and cross-bedding of the Lower Tuff sediments indicates fluvial transport and deposition. However, MacGinitie (1953) attributes these deposits to mudflows which followed river channels and spread out over the basin. Several sources suggest that deposition of this unit may have ended coincident with the obstruction of the basin drainage system by a lava flow or lahar, choking of the valley with ash fill, or by faulting at its southern end, producing an extensive ponded area known as Lake Florissant

(McLeroy and Anderson, 1966; Root, 1983; Epis and Chapin, 1974). This postulation may be supported by the abrupt lithologic transition of the Lower Tuff unit to the lacustrine shale sequence, above which indicates sudden alteration of depositional conditions.

There is palynological evidence for standing water in the basin during deposition of the upper part of the Lower Tuff, indicated by strong representation of *Potamogeton* pollen in several of the samples studied. The sediment-laden stream(s) may have been ponded at one or more points as it meandered across the broad valley. Alternatively, it is possible that the onset of Lower Tuff deposition was coeval with the obstruction feature to basin drainage since both required an episode(s) of relatively energetic volcanism. The lake would then have formed during Lower Tuff time.

Lacustrine Shales

This highly variable sequence of laminated shales contains the plant and insect compressions that are notable in the Florissant Lake Beds. In the two sections of this study, total thickness of the lake shales is ~4.5 m and ~5.8 m. Root (1983) identified the total thickness to vary between ~1.5 m and ~10.4 m. McLeroy and Anderson's (1966) petrographic study of the Florissant deposits describes four fundamental types of laminae. The volcanigenic sediments are divided into pumice laminae and graded tuff laminae; the biogenic deposits are diatomite and sapropel couplets. In all cases, transitions between laminations are abrupt with no transitional lithotypes.

The pumiceous laminae are the most conspicuous of the lake deposits. They appear yellow in outcrop and vary in thickness from several millimeters to several centimeters, averaging ~1.5 cm. Petrographic analysis (McLeroy and Anderson, 1966) indicates that composition is primarily vesicular, rhyodacitic, glass-froth pebbles averaging 3 mm in diameter, with occasional well-rounded andesitic and trachytic pebbles. Inverse graded bedding is evident when pebbles can be differentiated. The lower bedding plane surfaces are relatively smooth as opposed to upper surfaces which are irregular due to the concentration of the coarser pebbles on top. No leaf or insect compressions have been observed in the pumice laminae.

In contrast with the pumice laminae, the graded tuff laminae are gray in outcrop and contain an abundance of leaf and insect compressions. They grade from a concentration of subrounded to subangular quartz and ferromagnesian minerals at the base to an extremely fine-grained vitric ash at the top (McLeroy and Anderson, 1966). The rhyodacitic ash comprises 90% of the volume of these layers. Vertical distribution is erratic and roughly alternating with the pumice. Like the pumice, the graded tuff is equally variable in thickness, averaging ~1 cm.

McLeroy and Anderson (1966) postulate distinct depositional mechanisms to account for the two types of volcanic lamination and their unique physical characteristics. These depositional mechanisms have winter-spring flooding in common as the underlying cause. The inverse graded bedding and differences in regularity of the upper and lower bedding surfaces of the pumiceous sediments are attributed to delayed deposition of the larger pebbles. Because of their vesicular nature, the larger pebbles were temporarily buoyant upon introduction to the drainage basin. Subsequently, they were deposited over the finer sediments after becoming waterlogged. In contrast, the graded tuff laminae always fine upward because the larger grains lacked vesicles and differentially settled before the ash.

The diatomite and sapropel laminations occur as couplets averaging ~1.0 mm in thickness (McLeroy and Anderson, 1966). Each lamination varies in thickness from ~0.04-2.2 mm. The diatomite is white and composed of 95% opal; a fine silt of orthoclase, plagioclase and quartz contributes 5%. The presence of diatom frustrules is evident at a magnification of 1000 x. In sharp contrast, the sapropel is primarily composed of unidentifiable black organic matter. Up to 50% of the remaining components is a mixture of sponge spicules, pollen, diatoms, and silt particles of quartz, plagioclase and biotite. Limonite and hematite from altered pyrite are common in outcrop samples.

McLeroy and Anderson (1966) suggest the biogenic couplets represent seasonal deposition on the lake bottom. They reason that the diatomite resulted from accumulation after a diatom bloom during spring floods. Diatom growth was favorable at this time because of the nutrient replenishment provided by winter and spring rainfall and subsequent runoff into the ponded basin. Illumination, abundance of dissolved silica, water chemistry and water temperature were also especially suitable for diatom growth during the spring. Once the diatoms depleted the nutrient content in the late spring and the waters had warmed, summer and autumn plankton flourished under the new conditions. The deposition of these organisms resulted in a dark organic layer immediately over the diatomaceous accumulation; therefore, these diatomite/sapropel pairs are varve couplets.

Pollen analysis has been used to substantiate the spring flooding depositional model (W. S. Ting, in McLeroy and Anderson, 1966). Pollen is absent in the diatomite but abundant in the sapropel. McLeroy and Anderson (1966) suggest that this indicates very rapid deposition of the diatoms in the early spring, followed by relatively slow deposition of the sapropelic mud in the summer and fall months.

If significant flooding did occur in the spring, reworked sediments would have been introduced into the lake, and turbidation would have disturbed the fine sediment layering on the bottom. Neither of these is present in the laminated shales examined in this study. In addition, absence of pollen in the diatomite layers may be preservational, and many diatomite deposits are barren of pollen through extensive exposures of section (Prof. R. E. Taggart, pers. comm.).

An alternative explanation for the origin of the spring diatom maximum is overturn of the lake waters during seasonal temperature cycles. Temperate lakes are commonly thermally stratified in the summer and winter. A thermocline during the summer acts as a barrier to the mixing of warm surface and cool bottom waters due to vertical density differences. Atmospheric warming in the spring causes thermal destratification in lakes, allowing surface and bottom waters to mix freely under the influence of tributary stream or wind-produced currents accompanying winter-spring storms. Such mixing would permit the temporary nutrient enrichment of surface waters that would promote extensive phytoplankton growth. During the warm summer months when thermal stratification would be restored, water below the thermocline would become essentially anoxic and sapropelic debris would thus be protected from degradation. Seasonal turnover would be possible under MacGinitie's estimated average annual range of temperature (~20°F absolute minimum; warmest month ~80°F) for a warm-temperate Florissant paleoclimate. Breakdown of thermal stratification with subsequent turnover would occur twice a year--spring and fall. Phytoplankton blooms are virtually universal in lakes during turnover, particularly in the spring, and this is a likely source for the diatomite (Prof. R. E. Taggart, pers. comm.).

The majority of the lacustrine shale sequences are dominated by alternation of the pumice laminae and the graded tuff laminae, with the biogenic varve couplets as a minor constituent. Two unique bedding types were observed in the measured sections of this study which may not be defined under the four fundamental types of lamination: calcareous layers and homogeneous mudstones.

Previous studies have indicated an absence of calcium carbonate in the lacustrine sediments (e.g., McLeroy and Anderson, 1966). Several calcareous layers were found in disjunct sections of this study. They vary from ~1.5-5 cm in thickness. In all cases, these deposits occurred within 2 m of the Upper Tuff. Thin section analysis of one sample shows vertical fibrous crystals of calcite, the mineralogy supported by x-ray analysis (Prof. D. F. Sibley, pers. comm.). Occasional mud-silt laminae temporarily interrupt the crystal growth. There exists marked lateral variability in thickness and compositional layering in these units, even within a hand specimen. The presence of carbonate deposits may be used to support MacGinitie's (1953) suggestion of periods of aridity in the region which resulted in gypsum layers. It is possible that they are caliche layers which formed 1-2 m below the erosion surface at the Upper Tuff contact (Prof. A. T. Cross, pers. comm.).

Thin laminae ~3 mm thick of interlocking laths of gypsum were found intercalated between volcanic laminae and as fracture-fill in one section. This gypsum is most likely secondary. Gypsum layers as thick as 2.5 cm have been described in previous studies (MacGinitie, 1953; Root, 1983), but none was recognized in the sections of this study.

Layers of indurated volcanic ash occupy positions between the pumice and tuff laminae concentrated in the upper parts of the measured sections. These layers are highly variable in thickness; most ranging from several millimeters to several centimeters, with a single occurrence of more than a meter. They are extremely homogeneous in texture and lack fissility. Larger sediment particles and plant fragments are absent. All are light gray in color, well-sorted and fracture conchoidally. Faint transitions in color of the thick ash unit define the planes of deposition and very fine grading is occasionally present. Cross-bedding, turbidity and other primary sedimentary structures are not evident. Given these characteristics, these massive mudstone layers are considered to be direct airfall ash deposits produced by volcanic eruption.

Upper Tuff

At most lakebed exposures, a highly-indurated breccia lies unconformably on the lake deposits. It is composed of angular-to-subangular fragments of granite, basalt, andesite, and lake shales. The clasts range in size from sand to boulders and no sorting is evident. A light gray to white rhyolitic matrix cements the highly heterogeneous assemblage into a very hard mass up to ~7.6 m thick. This caprock is largely responsible for preservation of the lake shales which are otherwise highly susceptible to erosion upon exposure. Presence of this unit usually indicates the presence of underlying lake shales. Due to its internal characteristics and extensive lateral distribution over most of the basin, the suggestion of a lahar or series of lahars following the lake phase is feasible (Root, 1983).

Later Deposits

One or more of several deposits may overlie the Florissant Lake Beds. MacGinitie (1953) discussed two such deposits under the category "Later Eruptive Rocks". One of these is the continued deposition of the Thirtynine Mile volcanic series that, where present, increases in thickness toward the southern end of the basin and southwestward toward the Guffey volcanic center. MacGinitie (1953) refers to these mudflow deposits as basic (alkaline) agglomerates. The second series, trachytic lava flows, also originating from the southwest after a period of erosion, followed river channels to the basin where they now overlie the Upper Tuff or basic agglomerates in an irregular pattern. A small patch of one of these lava flows was observed above the Upper Tuff at the southernmost collection locality (8/23/84-1) of this study.

Following an extended period of erosion, Quaternary and Recent alluvium and colluvium formed a surficial cover above the Florissant Lake Beds outcrops and throughout the valley floodplain (Root, 1983). These deposits consist of up to ~3.7 m of redistributed clay, mud, sand and gravel. A layer of unconsolidated granitic grus, a partially-weathered gravelly product of eroded Pikes Peak granite, frequently overlies the Upper Tuff unit.

Structure

Field relations of the basin deposits and contiguous rocks suggest that the slopes of the current Florissant valley region can be used to approximate the original outline of Lake Florissant. The highest extent of the paleo-water level and original accumulation of lakebeds is unknown because an undetermined amount of erosion occurred prior to deposition of the Upper

Tuff. MacGinitie (1953) and McLeroy and Anderson (1966) suggest that the current distribution of the Florissant Lake Beds exposures is in part a consequence of post-depositional faulting of the region and that the outline of the outcrops probably does not accurately represent the ancient lake margin. Tilting of the sections of this study appears to be minor; no consistent strike directions were observed and dips ranged from 2° to 8° (av ~4°). There is not substantial evidence for significant change in Florissant basin morphology since the early Oligocene.

A number of depositional and post-depositional factors preclude lithologic correlation of disjunct outcrops. The nature of lake sedimentation was variable. While the sections studied had a common upper stratigraphic reference point, the beds in the 2.4 m immediately below each differed substantially with respect to thickness of the component lithologies. Considerable lateral change in thickness of layers and even pinching out of some layers was generally evident within the 0.5 m wide collection trenches and even within hand specimens. Wind, water or mass movement transported the volcaniclastic material to the basin from different sources and directions. Deposition of the fluvial sediments in the form of deltas was probably greatest near the lake margins at the intersection of tributary streams. This variability and its stratigraphic implications have been discussed in previous studies (MacGinitie, 1953; Root, 1983). It is possible that the lake may not have been a continuous entity, but rather a series of ponded areas which varied in position and time in response to sedimentation and evaporation (MacGinitie, 1953).

Outcropping of the deposits indicates two depositional settings. Most of the deposits appear to represent regions of the lake relatively close to the paleo-shoreline, which may be extrapolated into the basin slopes. Lakebed deposits which completely encircle granitic cored hills suggest the presence of islands during the lake phase (Scudder, 1881). Following deposition and prior to lithification, several factors (subsidence, soft-sediment deformation, compaction) caused distortion of the original bedding and caused local folding and faulting of the strata with displacements as much as 3-4.5 m (Root, 1983).

The first post-depositional regional faulting probably occurred prior to the close of the Oligocene. The basic agglomerates of the Thirtynine Mile volcanic series which immediately overlie the Florissant Lake Beds, at the southern end of the basin, possess the same structural trends as the lakebed units (MacGinitie, 1953). They are considered to be early Oligocene in age. These structures are absent in the trachytic lava flows of the late Oligocene.

Subsequent folding and faulting of the sediments due to regional tectonism during the later Tertiary has produced two complex synclinal structures in which the lake basin sediments are preserved (MacGinitie, 1953). Regional tilting probably reversed the direction of flow of the drainage from southeast to northwest, the direction of flow of Grape Creek today (Scudder, 1882).

METHODS OF STUDY

Field Collection

Collection of samples for palynological analysis was made during August, 1984. Two localities were selected; both are located on the Lake George, Colorado, U. S. G. S. 7.5' series topographic quadrangle map and are plotted on the regional map in Figure 1:

8/5/84-I

CTR., W1/2, NW1/4, SW1/4, SEC. 13, T. 13 S., R. 71 W., Teller County, Colorado.
north-northeast side of "Scudder Hill";
section thickness - 16.8 m
87 samples for palynological analysis

8/23/84-I

NW1/4, SW1/4, SW1/4, SEC. 19, T. 13 S., R. 70 W., Teller County, Colorado.
~150-200 m south of Lower Twin Rock Road along northwest-southeast trending outcrop;
section thickness - 3.8 m
71 samples for palynological analysis

Locality 8/5/84-I was selected because it was the site of the Scudder insect collections and because it is a relatively thick sequence. The upper third of this unit had been previously excavated in 1877 by S. H. Scudder for the collection of insect and plant megafossils. Description of the stratigraphy of the deposits in his (1882) paper was used for comparison with observations in this study. The exposure is situated on the north side of an isolated hill in the interior of the Florissant basin and is commonly referred to by monument staff as the "Scudder site". Since laminated lakebed strata completely surround this hill, which consists of a granite core that crops out on the top of the hill, it may represent a former island.

Locality 8/23/84-I was located ~2.6 km south-southeast of locality 8/5/84-I. Field relations suggest that it represents deposition near the eastern paleo-shoreline of the lake. This section was selected primarily for lithological and palynological comparison with the Scudder site to examine the geographic variability in sediment deposition and palynological assemblages.

These two sections have a common reference point in the form of an unconformable contact between the Upper Tuff and the lacustrine shales. Total thicknesses of the two sections are: 8/5/84-I, 16.8 m; 8/23/84-I, 3.8 m. In section 8/5/84-I, the thicknesses of the lakebed sequence and the exposed Lower Tuff are ~5.8 m and ~11 m, respectively. Near surface distortion of the lakebeds in contact with the Lower Tuff was encountered, apparently caused by gravitational displacement of spoils left behind during Scudder's collections further upslope. The entire 3.8 m of section 8/23/84-I are lakebeds; the Lower Tuff beds are absent because the base of the lakebeds is concealed below by the alluvium/colluvium on the valley floor. Accounting for the unobservable Lower-Tuff contact, extended lakebed thickness in this section is estimated at ~4.5 m by measured thickness of the upper and lower bounded lakebed sequence at a nearby outcrop ~100 m north. The thickness discrepancy of 1.3 m between the two collection localities is reasonable in light of the effects of significant lateral variation in sedimentation and erosion.

The slopes of the eroded exposures average ~18°, with a maximum of 25° near the top flattening to 10° near the base. Weathering of outcrops is rapid and the shales are generally masked by a layer of loose material, making it necessary to excavate the selected exposures in order to minimize the effects of weathering on the palynological samples. Thickness of the loose material and soil averages 3-6 cm on these hillsides. Water has penetrated the fissures and bedding planes to more than a meter below the surface. A trench was excavated with mattock and shovel to a depth of ˜0.4-0.7 m. Since the beds are approximately horizontal in aspect, a terraced approach to excavation was employed because it was least destructive to the lakebed deposits and was convenient for sample collection. The lower end of each trench was commenced at the base of the exposed bedrock above the alluvium/colluvium of the valley; the upper part was terminated at the lakebed-Upper Tuff contact in each section. After sampling, each trench was backfilled and restored to contour.

Following excavation, each trench was measured for thickness from base to top with a 10 X hand level and engineer's rule used as a rod. Vertical control for sampling was maintained by reference stakes placed at regular intervals.

Samples were collected continuously from base to top of each section. Sample thickness was governed in part by lithologic breaks in the sequence. Single lithological units greater than 0.3 m in thickness were usually divided into 0.3 m sampling intervals. Material for each sample was collected throughout the thickness of the sample unit and across the width of the trench. A small plastic bag was filled for each sampling unit. In addition, hand specimens of unusual lithologic units were collected intermittently for possible petrographic analysis in the laboratory. The thickness of sample units ranged from 3 mm to 50 cm , averaging ˜5 cm in the lakebeds and ˜29 cm in the tuff beds. A total of 158 samples were acquired. Each sample was assigned a number (number 1 at base of section) preceded by the section number.

Since this is primarily a palynological study, megafossils were collected only incidentally during sampling or reconnaissance work. Due to the nature of excavation, the fossiliferous shales of the trenches were generally reduced to small fragments and few megafossil specimens were recovered.

Laboratory Preparation

Given the limited scope of this project, 158 samples were more than could be adequately prepared and studied in detail. 69 selected samples were prepared for palynological analysis based on several criteria: (a) even distribution throughout the entire thicknesses of the stratigraphic columns and minimizing the gaps between samples; (b) covering all lithologies; (c) continuous representation of layers which may provide information about disturbance and succession.

Prior to processing, selected samples were recorded in the laboratory catalog and assigned a unique number preceded by 'Pb'. This maceration number is distinct from the sample number assigned in the field.

The objective of chemical maceration was to retrieve the maximum number of palynomorphs preserved in the rock through dissolution of the mineral and organic matter which entombs them. It is desirable to remove as much mineral and extraneous plant material as possible, but a level of tolerance of such matter must be accepted so that loss of smaller palynomorphs and destruction of relatively fragile ones are kept to a minimum during chemical maceration of the rock. Therefore, the treatment employed was the minimum necessary to free the palynomorphs.

The following physical and mechanical treatments were used for macerating the samples. Due to the variability in lithology, organic composition and grain size, the course of treatment differed considerably from sample to sample. Steps were eliminated whenever possible and time of each treatment was highly variable. Samples were often split during processing to apply different subsequent treatments for maximum results. Procedures were modified from Doher (1980), Funkhouser and Evitt (1959), and techniques recommended by Professor A. T. Cross.

Well-consolidated sediment samples were washed in distilled water prior to processing to remove extraneous material. These and other samples were crushed in a mortar with a pestle until the largest fragments were approximately 5 mm in diameter.

7 to 25 gm aliquots of these crushed samples were generally sufficient to produce the desired quantities of pollen residues. Some processed samples were barren. Laminated shales were the most productive and contained the best-preserved grains. Coarse sandstones and massive mudstones, on the other hand, required relatively large samples to obtain satisfactory residues. Carbonates and finer grained pumices and sandstones were intermediate in productivity and preservation. Unproductive samples were usually coarse-grained or highly weathered.

Dilute hydrochloric acid (10% HCl) was applied to all crushed samples for up to 1 hr to dissolve any carbonate sediments and cements that might be present. Some carbonate sediments required 8 hr contact time, using 5% HCl for the first 5 hr. Samples were thoroughly washed and centrifuged between each chemical treatment. Following HCl, hydrofluoric acid (52% HF) was added to dissolve the silicate minerals. Crushed ice was used to control the temperature and speed of the initial reaction. Solution digestion usually was completed in 3-5 hr. but 12-24 hr treatment was necessary in some cases. If solution of carbonates was initially incomplete, a white, granular precipitate (CaF_2) often formed during treatment with HF. If this occurred, the sample was immersed in 20% HCl for up to 2 hours in a steam bath to dissolve the precipitate.

Some samples contained varying amounts of coalified organic material. It was generally desirable to remove or disperse this. If the rock was not significantly weathered, the residue was immersed in a strong oxidizing agent (Schulze's solution: ratio 5 parts nitric acid (HNO_3) to 1 part potassium chlorate ($KClO_3$)) for 1-2 minutes to disaggregate it. Since Schulze's solution is highly corrosive to palynomorphs, especially the thin-walled types, its use was limited. In most Florissant samples, it was found that this treatment could be avoided. Following treatment with Schulze's solution or if organic material was weathered (oxidized), 5% potassium hydroxide (KOH) was applied for a few minutes to dissolve the humic residues.

After release from the organic and inorganic matrix, the palynomorphs were physically separated from undissolved extraneous matter. Ultrasonic agitation was occasionally employed to first loosen flocculates. Specific gravity separation in zinc chloride solution ($ZnCl_2$, sp. gr. 1.95) was quite successful in the separation of the mineral fraction. Alternatively, differential settling in a wetting agent (Calgon, Multiturge) was sometimes used. If clays were abundant, sieving through 7,10, or 15 micron fiber screens was effective in their removal. In all cases where the residue was sieved, it was necessary to check the 'waste' fraction to verify that small pollen grains or spores had not passed through the sieves.

Residues were stained with Safranin O. Some of the residue from each sample processed was suspended in a drop of HEC (Hydroethylcellulose) and evenly distributed over a 22 mm coverslip and allowed to dry. A consistent distribution density of grains on these strewn slides was attempted to facilitate qualitative and quantitative analysis. A drop of Clearmount resin was applied to the cover slip, when dry. A 75 by 25 mm microscope slide was then placed over the inverted coverslip and allowed to harden for two weeks.

Examination

The slides were studied using a Leitz Ortholux research microscope (M.S.U. GG 2667) with a metric calibrated stage. The positions of particular grains were recorded as horizontal and vertical coordinates. For translation of these coordinates to other microscopes, the coordinates of the upper right hand corner of the coverslip of each slide were recorded.

The first step involved scanning the slides randomly, observing and sketching the different morphological types as they were encountered. Subsequently, photographs of the most representative specimens of each type were taken using a Leitz Orthomat automatic microscope camera in conjunction with the above microscope. Kodak Panatomic-X film (ASA 32) produced a fine-grained image with good contrast. Most photographs were taken with the 95 X (oil) microscope objective for maximum resolution of the structural and sculptural details of the pollen walls. Photographs at two or three planes of focus of a single grain were obtained for a three-dimensional perspective in many cases, since any particular plane of focus provides limited information about the whole specimen. A 54 X objective was used in photographing larger specimens. Photographs were printed on Kodak Polycontrast II Rapid R C paper. All photographs were enlarged so that all specimens on the final plates appear at a magnification of 666 X. Specimen dimensions, in micrometers, can be calculated by multiplying plate dimensions in millimeters by 1.5.

Specimens were grouped into differentiated morphotypes and each group was given a unique artificial code name until tentative taxonomic designations were assigned.

The procedures involved in systematic determinations are discussed in the Systematics section.

Counting

All counting was made with a 54 X oil immersion objective and microscope stage graduated in millimeters. The 22 by 22 mm coverslip of each slide was divided into 92 horizontal traverses so that the sum of vertically stacked fields of view provided complete coverage of the coverslip.

For the purposes of this type of study, the necessary quantitative information could be retrieved from a selected number of traverses fewer than the total number possible for any coverslip, assuming the sample was "productive". Each traverse was assigned a reference number so that it could be selected arbitrarily without duplication or overlap with other traverses. Six initial non-random traverses were selected for each slide to insure that the information acquired represented the complete area of the coverslip. Therefore, due to migration of grains of different sizes and densities during slide preparation, areal biases within the coverslip area were accounted for. Subsequent traverses were selected randomly with the aid of a random numbers table until the total predetermined palynomorph count was acquired for each slide.

Sample size was determined by techniques following those used by Thompson (1969) and Gies (1972). The count should be sufficient to give a good approximation of the relative abundance of the complete diversity of types present in the sample. Rarefaction curves were prepared for several samples and all exhibited pronounced flattening beyond counts of 300 grains. 400 grains was selected as a fixed sum to be counted for each sample of this study. In order to overcome additional distributional biases involved in slide preparation, at least two slides were counted per sample and no more than 200 grains were counted per slide. No more than 100 grains were counted on any single traverse. Several samples lacked the fossil pollen recovery necessary to acquire the total count of 400 grains, but were included in the quantitative data if 200-300 specimens could be tallied.

In order to avoid size bias, only those pollen grains and spores with geometric centers within the field of view during the traverses were counted. Grains of uncertain affinity were tallied in the lowest taxonomic rank that they could be assigned to confidently, or included in morphological classes. For counting purposes, the diversity was intentionally inflated, especially early in the examination process. As intra-generic (or intra-typic) variability became better known, previously defined groups were sometimes later combined. The initial 8 samples counted were re-counted to allow for practice and development of confidence in the procedures.

SYSTEMATICS

Nomenclature

The nomenclature of Tertiary palynology is complicated by different authors' use of two contrasting systems. Specimens may be assigned names of extant plants in some cases, indicating relationship to modern taxa, or they may be assigned to artificial groups indicating extinct taxa or uncertain biological affinities. Some studies use both approaches to nomenclature, leading to some confusion. Difficulty arises in the degree of morphological similarity between fossil and modern palynomorphs. The resemblance of Late Tertiary fossils to extant forms is often very close or identical. However, many Early Tertiary and Late Cretaceous pollen morphotypes are distinct from today's. The majority of palynomorphs in rocks of the Oligocene epoch are morphologically similar to modern taxa.

The nomenclatural system to be utilized should be selected in light of the goals of research and comparative utility to other studies. Conventionally, MacGinitie (1953) based his taxonomic designations of leaves and other plant organs on comparisons with modern herbarium material. Since it is a major objective of this study to add light to the paleoecological setting of the Florissant region at the time of deposition, nomenclature will be phylogenetically-based when the morphological evidence is substantial.

Some palynologists employ a purely artificial system of nomenclature in Tertiary studies. It is entirely morphologically-based, and the names are independent of any botanical relationships. Tschudy's (1957) proposed symbolic coding system is tidy, logical, and practical for stratigraphic correlation studies and facies comparison. Schopf (1964) supports this informal system for such limited applications and adds that if identifications are consistent, it may be the preferred starting point to taxonomic treatment.

Taxonomic classification requires exhaustive study of the literature and critical comparisons of specimens, both fossil and living, to establish potential phylogenetic relationships. In addition to distinctive features of morphology and relating different organs to the same plant, assignment of specimens to particular taxa must be consistent with known geographical and stratigraphic ranges of those taxa (Schopf, 1964). Phylogenetic nomenclature is not confused or prejudiced by the purely artificial system and translation from one system to the other is possible.

The rules for the formal treatment of naming the groups are guided by the International Code of Botanical Nomenclature (ICBN). This system is in part arbitrary and artificial because the evidence for phylogenetic relationships is variable and incomplete (Schopf, 1969). "Since the context of phyletic relationship is difficult to establish, the identification of a new taxon is more readily justified than identification with a previously known species" (Schopf, 1969). However, "there are a good many more names now in the literature than the differentiation of material would actually demand" (Schopf, 1964). Confidence in assignment of fossil specimens to modern taxa decreases with antiquity of the associated source sediments because of the variable rates of morphological and physiological change of different plant parts associated with evolution. Nevertheless, in order to integrate the biotic element in a paleoenvironmental interpretation of the source region, it is necessary to assign fossil specimens to extant plant genera and species when comparison of the available morphologic evidence strongly suggests a relationship.

Many palynomorphs from mid-Tertiary or older sediments may be assigned to extant families or higher taxonomic ranks, but supporting evidence is generally lacking to assign them to extant genera. Form genera and organ genera were created to avoid potential misalliances with extant genera. Both have been accepted under the ICBN, but the organ genus concept was removed in 1975 (Pocknall and Mildenhall, 1984). Paleoecological application of these names has been practiced with flawed logic (Tschudy, 1969). For example, a specimen may be placed under the half-natural form genus *Quercoidites*, which implies affinity to the extant genus *Quercus* based solely on morphological resemblance. As long as this designation is restricted in its use to biostratigraphic zonation, as in Pocknall and Mildenhall (1984), it may be useful. However, parallel ecological inference based on relationship to the genus *Quercus* would be erroneous if the author created the fossil genus out of uncertainty. Confusion could be eliminated by assigning a purely morphologically-based generic name and suggesting potential botanical affinities in the systematic description.

The phylogenetically-based nomenclature used in this study requires identification of specimens to the lowest possible taxonomic rank that can be determined with certainty. Accuracy of taxonomic assignment decreases with age of specimens. Many angiosperm palynomorphs from Quaternary sediments can be associated with modern plant species on the basis of morphological criteria. Megafossil studies show that many modern genera and families existed in the Early Tertiary, but there is little evidence that extant species were established in the Paleogene. The Tertiary Period represents a time of significant evolutionary change for the angiosperms. Grasses and forbs (e.g., Compositae) are generally identified at the family level. Since many modern genera, primarily forest trees, are well represented as megafossils during the Oligocene Epoch, it is reasonable and paleoecologically essential to assign the associated palynomorphs to modern genera where possible.

Megafossil specimens collected from the Florissant Lake Beds provide supporting evidence for the taxonomic composition of the palynoflora. Leaf compressions are especially useful because the complex morphological characters preserved provide for identification of many fossils to the genus or species level. MacGinitie's (1953) monographic treatment of the Florissant plant megafossils provided a systematic list of 113 plant species in 87 genera based mostly on leaf identifications. Most of these (99 species, 76 genera) are angiosperms. Only one of the genera, Fagopsis, is known to be extinct.

References

In this study, many references were used in the identification of fossil specimens. It was useful to become familiar with pollen of the modern plant equivalents to those included in MacGinitie's (1953) systematic list of megafossils. The modern pollen reference collection in the paleobotanical laboratory at Michigan State University was an indispensable aid. Two pioneers in pollen analysis, Wodehouse (1959) and Erdtman (1952; 1957; 1965; 1969; 1971), contributed modern pollen handbooks that were important for differentiation and identification of the Florissant types. Other useful texts which focus on North American pollen/spore types are McAndrews, et. al. (1973), Hyde and Adams (1958), Lewis, et. al. (1983) and Sawyer (1981). For comparison with modern pollen/spore floras of other parts of the world, several descriptive texts with abundant photographs were used: Taiwan (Huang, 1972); Argentina (Markgraf and D'Antoni, 1978); and Chile (Huesser, 1971).

A plate of selected Florissant palynomorphs prepared by E. B. Leopold (1969 a) was very useful for initial comparison of some specimens. There have been no previous systematic descriptions of the Florissant pollen/spore flora published. Several other studies of North American floras similar in age to the Florissant flora provided systematic descriptions and plates. The late Oligocene Brandon Lignite of Vermont (Traverse, 1955) contains many genera in common with Florissant and was especially useful for its illustration of a diversity of Pinus-types and a discussion on the differentiation of taxodiaceous genera. An early Oligocene flora of the Fraser River Fm., central British Columbia was the focus of a palynological study by Piel (1971). In it, he described and illustrated many genera, most notably Podocarpus, that are found in the Florissant flora. Hopkins (1967) published a study of palynofloras from several formations of the Coos Bay Area of southwest Oregon that range from upper Eocene to middle Oligocene in age. The accompanying plates illustrate many genera present at Florissant. Systematic lists and plates of pollen/spores from other post-Paleocene floras of the Rocky Mountain region and other North American Eocene-Miocene floras were compared: middle Miocene Succor Creek flora, Oregon-Idaho boundary (Taggart, 1971); Miocene-Pliocene Skonun Fm., British Columbia (Martin and Rouse, 1966); middle Eocene Ione Gravels, Chalk Bluffs, California (Leopold, 1969 b); middle Miocene Suntrana Fm., Alaska Range (Leopold, 1969 c); middle Miocene Troublesome Fm, Granby, Colorado (Leopold, 1969 d).

Organization of Descriptive Notes

Systematic descriptions are in phylogenetic order from the sub-class level upward, and families within each class or subclass are arranged alphabetically, following Taggart (1971). The lowest taxonomic rank for identifications in this study is the genus, and designated, for example, Quercus sp.(p.). Genera are organized alphabetically within each family. If generic affinity is uncertain, the grain is classified as Type 1, Type 2, etc., within the family. Differentiation into morphologically-distinct sub-generic categories is also discussed as Type 1, Type 2, and so on. This intra-generic variation may, but not necessarily, represent fossil species. Speculation on botanical affinities to modern equivalents is discussed in a paragraph along with the description. I was not able to identify some differentiated morphotypes to a modern or fossil genus. If specimens could not be identified to any pre-existing taxonomic rank, they are listed at the end of the systematic section, the type preceeded by a "UM" (unidentified morphotype).

Each morphologically differentiated type is described and illustrated with a photograph in one of the plates that follow. Additional information includes: abundance in the mega- and pollen/spore- floras; ecological and geographic indications (based on modern analogs of identified morphotypes), and temporal and spatial distribution of the type during the Tertiary.

FLORAL COMPOSITION

113 plant species were identified (exclusive of 27 incertae sedis), representing 87 genera in 48 families, in MacGinitie's (1953) megafossil study. The species included 4 lower plants, 10 gymnosperms and 99 angiosperms. Two previous pollen studies of the lake shales have added 13 genera to the megafossil list (Ting, in McLeroy and Anderson, 1966; Leopold, 1969 a). Among the 78 pollen/spore types differentiated in this study, 4 additional genera (one is a pair of generic alternatives that were not distinguished) and 1 undifferentiated family type are proposed. All identified and tentatively identified plant genera and families from the four studies are listed in Table 1. The taxa/types in Table 1 are organized in the same fashion as the Systematic Descriptions section.

None of the 5 proposed taxa was abundant in the palynological samples, but specimens observed had the critical morphological characters to justify tentative assignment to unreported genera or families: Mougeotia (Zygnemataceae), Podocarpus (Podocarpaceae), Pseudotsuga/Larix (Pinaceae), Liquidambar (Hamamelidaceae), and undifferentiated Nymphaeaceae. Pollen of three megafossil taxa classified by MacGinitie (1953) as incertae sedis were identified in this study: Potamogeton, Ilex, and Compositae.

The plant specimens of MacGinitie's (1953) study were drawn from one large sample which was the sum of his collections from several localities plus previous collections held in museums and other institutions throughout the United States. 56 species accounted for more than 96% of the megafossil specimens. The 18 genera which contributed 1.0% or more to the total number of megafossil specimens examined by MacGinitie (1953) are listed in Table 2 in contrast to the 12 pollen/spore types which contributed 1.0% or

Table 1. Known composition of the Florissant flora.

Numbers in the "Megafossil Taxa" column represent the number of taxa described by MacGinitie (1953). Parentheses in this column indicate incertae sedis determinations. The "Previous Palynology Records" column represents a composite from Leopold (1969 a), Ting in McLeroy and Anderson (1966), and Manchester and Crane (1983). The "Current Study" column represents observations in this study. Parentheses in the latter two columns represent a degree of uncertainty in the systematic determination. Occurrences at the family level are tabulated only when specimens are noted (typically pollen or spore taxa) which were not assigned to a specific genus.

Bracketed % figures in "Megafossil Taxa" and "Current Study" columns represent contribution of the noted types to composite mega- and pollen/spore floras, respectively. Noted types of "Current Study" column which do not display a % figure were included in "Other" category of pollen counts or were observed in additional traverses.

Abbreviations for groupings of undifferentiated genera or families:

TCT = Taxodiaceae, Cupressaceae, Taxaceae
T/S = Typha/Sparganium
P/S/E = Proteaceae/Sapindaceae/Elaeagnaceae
U/Z = Ulmus/Zelkova

Taxon	Megafossil Taxa	Previous Palynology Records	Current Study
FUNGI	-	-	2
ALGAE	-	-	X
Characeae			
Nitella	1	-	-
Zygnemataceae			
Mougeotia	-	-	1
BRYOPHYTA			
Grimmiaceae			
Plagiopodopsis	1	-	-
Hypnaceae			
Hypnum	(1)	-	-
Sphagnaceae			
Sphagnum	-	-	(X)
LYCOPHYTA	-	X	-
trilete spores	-	-	[0.4%]
Selaginellaceae			
Lycopodium	-	-	(X)
Selaginella	-	X	(X)
SPHENOPHYTA			
Equisetaceae			
Equisetum	1	-	-
PTEROPHYTA			
monolete spores	-	-	[2.1%]
Polypodiaceae	-	-	3
Dryopteris	1[0.4%]	-	(X)
Pellea	(1)	-	-
GYMNOSPERMS			
Ephedraceae			
Ephedra	1	X	2[0.3%]
Cupressaceae		(TCT)	(TCT)[26.0%]
Chamaecyparis	1[7.5%]	-	-
Pinaceae			
Abies	1	X	3[1.4%]
Picea	2	X	2[0.7%]
Pinus	3[1.8%]	X	5[10.6%]
Pseudotsuga/*Larix*	-	-	1
Tsuga	-	(X)	-
Podocarpaceae			
Podocarpus	-	-	1
Taxaceae	-	(TCT)	(TCT)[26.0%]
Torreya	1	-	-
Taxodiaceae	-	(TCT)	(TCT)[26.0%]
Sequoia	1[2.8%]	-	-
Taxodium-type	-	X	-

Table 1 (cont'd.).

MONOCOTS			
Cyperaceae	-	X	-
Cyperacites	1	-	-
Gramineae	-	X	3[0.2%]
Stipa	1	-	-
Liliaceae			
Smilax	1	-	-
Potamogetonaceae			
Najadopsis	(1)	-	-
Palaeopotamogeton	(1)	-	(X)
Potamogeton	(1)[0.4%]	-	1[18.8%]
Sparganiaceae			
Sparganium	-	T/S	2 T/S[0.9%]
Typhaceae			
Typha	1[5.8%]	T/S	2 T/S[0.9%]
DICOTS			
Aceraceae			
Acer	4[0.5%]	X	4[0.1%]
Dipteronia	1[0.3%]	-	(X)
Anacardiaceae			
Astronium	1[0.5%]	-	-
Cotinus	1[1.0%]	-	-
Rhus	3[4.5%]	-	-
Schmaltzia	1[0.1%]	-	-
Aquifoliaceae			
Ilex	(1)	-	1
Araceae			
Orontium	(1)	-	-
Araliaceae			
Oreopanax	1	-	-
Panax	(1)	-	-
Aristolochiaceae			
Aristolochia	1	-	-
Berberidaceae			
Mahonia	3[0.5%]	-	-
Betulaceae			
Alnus	-	X	-
Betula	-	X	-
Carpinus	1[0.9%]	-	-
Burseraceae			
Bursera	1[1.0%]	-	-
Caprifoliaceae			
Sambucus	1	-	-
Celastraceae			
Celastrus	1[0.2%]	-	-
Chenopodiaceae/Amaranthaceae	-	-	3[1.4%]
Sarcobatus-type	-	X	-
Compositae	-	-	1
Aster	(1)	-	-
Convolvulaceae			
Convolvulites	1	-	-

Table 1 (cont'd.).

Elaeagnaceae	-	-	(1 P/S/E)
Eleagnus	-	X	-
Ericales	-	X	-
Eucommiaceae			
Eucommia	-	X	-
Euphorbiaceae			
Croton	(1)	-	-
Euphorbia	1	-	-
Fagaceae			
Castanea	1[0.2%]	X	1
Fagopsis	1[31.4%]	X	1[<0.1%]
Quercus	9(1)[2.0%]	X	4[4.3%]
Hamamelidaceae			
Liquidambar	-	-	1[0.1%]
Juglandaceae			
Carya	1[1.3%]	X	3[4.1%]
Engelhardia	-	(X)	1[0.2%]
Juglans	-	X	1[3.9%]
Platycarya	-	X	-
Lauraceae			
Lindera	1	-	-
Persea	1[0.2%]	-	-
Sassafras	1	-	-
Leguminosae	-[0.7%]	-	-
Caesalpinites	2[0.1%]	-	-
Cercis	1[0.2%]	-	-
Conzattia	1	-	-
Leguminosites	1	-	-
Phaca	1	-	-
Phaseolites	1	-	-
Prosopsis	1	-	-
Robinia	1[0.8%]	-	-
Vicia	1	-	-
Meliaceae			
Cedrela	1[0.7%]	-	-
Trichilia	1[0.4%]	-	-
Moraceae			
Ficus	(3)	-	-
Morus	1	-	-
Myricaceae			
Myrica	-	X	-
Myrtaceae			
Eugenia	1[0.5%]	-	-
Nymphaeaceae	-	-	1
Oleaceae			
Osmanthus	1[0.6%]	-	-
Onagraceae			
Xylonagra-type	-	X	-
Godetia-type	-	X	-
Platanaceae			
Platanus	1	-	-

Table 1 (cont'd.).

Proteaceae	-	-	(1 P/S/E)
Lomatia	1[0.9%]	-	-
Rhamnaceae			
Colubrina	1[0.1%]	-	-
Rhamnites	1[0.4%]	-	-
Zizyphus	1[0.2%]	-	-
Rosaceae			
Amelanchier	1[0.2%]	-	-
Cercocarpus	1[2.7%]	-	-
Crataegus	3(1)[0.6%]	-	-
Malus	2	-	-
Prunus	1[0.1%]	-	-
Rosa	1	-	-
Vauquelinia	2[0.2%]	-	-
Rutaceae			
Ptelea	1	-	-
Salicaceae			
Populus	1(1)[5.0%]	-	1
Salix	4[1.1%]	X	2[1.4%]
Sapindaceae	-	-	(1 P/S/E)
Athayana	1[2.3%]	-	-
Cardiospermum	1[0.2%]	X	-
Dodonaea	1	-	-
Koelreuteria	1[1.0%]	-	-
Sapindus	1[1.1%]	-	-
Thouinia	1	-	-
Saxifragaceae			
Hydrangea	1	-	-
Philadelphus	1	-	-
Ribes	1	-	-
Simarubaceae			
Ailanthus	1	-	-
Staphyleaceae			
Staphylea	1[2.7%]	-	-
Sterculiaceae			
Fremontia	-	X	-
Sterculia	(1)	-	-
Styracaceae			
Halesia	1	-	-
Thymelaeaceae			
Daphne	1	-	-
Tiliaceae			
Tilia	1	-	1
Ulmaceae	-	U/Z	3 U/Z[4.5%]
Celtis	1	X	2[2.3%]
Ulmus	1[1.3%]	-	-
Zelkova	1[9.6%]	-	-
Verbenaceae			
Holmskioldia	1	-	-
Petrea	1	-	-

Table 1 (cont'd.).

Vitaceae			
Parthenocissus	1	-	-
Vitis	1	-	-
All others	[3.2%]	-	[15.9%]
multiporate (UM 1)	-	-	[0.4%]
Additional *INCERTAE SEDIS*			
Antholithes	2	-	-
Archaeomnium	1	-	-
Carpites	2	-	-
Didymosphaeria	1	-	-
Jungermanniopsis	1	-	-
Limnobium	1	-	-
Lomatites	1	-	-
Phenanthera	1	-	-
Normapolles group	-	X	-
unidentified pollen/spore morphotypes	-	?	8

more to the total number of specimens counted in this study. Since discrete samples at known stratigraphic positions were prepared for this palynological study, the relative % contribution of each taxon to the sample sums can be compared and is reflected by the % range data accompanying the list of pollen types. Variablity in taxonomic composition and abundance between pollen samples is discussed in the Vegetation Dynamics section.

The generic diversity represented by pollen is considerably less than that of megafossils (Table 2). The disparity is in part a result of the excellent depositional conditions in the lake for fossilization of leaves, that is, relatively quiet waters with a regular influx of fine clays and silts to entomb the leaves between accreting laminae. Other factors include: limited taxonomic resolution of many pollen/spore types (e.g., TCT), production differences for different organs, restricted dispersal potential of some pollen/spore types (e.g., entomophilous types, such as Sapindus), and fragile pollen/spore types (e.g., Populus). Therefore, each organ assemblage represents a unique and limited sample of the entire regional flora.

Further comparison of the two lists in Table 2 shows that there is also a disparity between the dominant taxa for each category of fossils differentiated. Fagopsis leaves contributed almost one-third of the total megafossil specimens, more than three times the frequency of Zelkova, the second on the list. Fagopsis never contributed more than 0.5% to the pollen sum. The pollen of Fagopsis resembles that of Quercus spp. (Manchester and Crane, 1983). Quercus is abundant in both the mega- and pollen/spore-floras (2.0% of leaves; 4.3% of the pollen). The disparity of the pollen/leaf records between Fagopsis and Quercus may be attributed to various factors. Plants of both genera have coriaceous leaves which preserve relatively well. The overwhelming abundance of Fagopsis leaves suggests that the trees

Table 2. Fossil representation of the Florissant flora.
leaves vs. pollen and spores (genera)

* = taxon common to both lists

LEAVES: COMPOSITE % (MacGinitie, 1953)

30.1	Fagopsis (Fagaceae)
9.6	*Zelkova (Ulmaceae)
6.3	*Chamaecyparis (Cupressaceae)
5.8	Typha (Typhaceae)
5.0	Populus (Salicaceae)
4.5	Rhus (Anacardiaceae)
2.7	Staphylea (Staphyleaceae)
2.3	Athayana (Sapindaceae)
2.2	*Sequoia (Taxodiaceae)
2.1	Cercocarpus (Rosaceae)
2.0	*Quercus (Fagaceae)
1.6	*Pinus (Pinaceae)
1.3	*Ulmus (Ulmaceae)
1.1	*Salix (Salicaceae)
1.1	Sapindus (Sapindaceae)
1.0	*Carya (Juglandaceae)
1.0	Cotinus (Anacardiaceae)
1.0	Bursera (Burseraceae)
sum = 80.7	

all other leaves < 1.0 each
sum = 10.8 (29 genera)
other organs: sum = 5.3
undesignated types: sum = 3.2

POLLEN: % RANGE ALL SAMPLES, COMPOSITE % (current study)

0-75,	26.0	*Taxodiaceae/Cupressaceae/Taxaceae (TCT)
0-79,	18.8	Potamogeton (Potamogetonaceae)
1-68,	10.6	*Pinus (Pinaceae)
0-22,	4.5	*Ulmus/Zelkova (Ulmaceae)
0.5-14,	4.3	*Quercus (Fagaceae)
1-16,	4.1	*Carya (Juglandaceae)
0-57,	3.9	Juglans (Juglandaceae)
0-14,	2.3	Celtis (Ulmaceae)
0-15,	2.1	monolete spores
0-4,	1.4	*Salix (Salicaceae)
0-13,	1.4	Abies (Pinaceae)
0-5,	1.4	Chenopodiaceae/Amaranthaceae (Cheno-Am)
sum = 80.8		

all others < 1.0 each
identified: sum = 3.0 (11 types)
unknown. sum = 16.2

occupied (and possibly crowded) the lake margin. They need not have been abundant in the region as a whole. Therefore, while there may have been local concentrations of the trees which shed a great many leaves directly into the lake, on a regional level the pollen produced by these plants may have been low, relative to the total pollen volume that reached the lake. Oaks, on the other hand, may have been widespread throughout the region, supplying leaves to the lake through stream influx; fewer leaves would reach the lake than those of *Fagopsis*. The anemophilous pollen of the regionally numerous oaks, however, carried by both streams and wind, may well have exceeded the contribution of *Fagopsis* pollen into the lake. It is also possible that pollen production per tree of *Fagopsis* was less than that of *Quercus* or that the pollen of the two genera was differentially degradable, *Fagopsis* being more susceptible to deterioration. Therefore, a preservational bias may distort the actual regional distribution patterns of plants of the two genera.

Six genera are common to both lists in Table 2: *Pinus*, *Ulmus* and *Zelkova*, *Quercus*, *Carya*, *Salix*. These are all arboreal members of the Bottomland/Slope paleoassociation. Their species are wind-pollinated except for some species of *Salix*.

Typha, the third most important megafossil numerically (5.8% of leaves), is also present in the pollen flora, but averages >1.0% only in section 8/5/84-I. Since its pollen is relatively infrequent in section 8/23/84-I, the percent contribution of *Typha* to the composite flora is less than 1.0%. *Populus* is also an important megafossil but is rarely observed as a pollen grain. The pollen of both genera, especially *Populus*, are relatively fragile and low concentrations are to be expected in fossil pollen assemblages, even when the plants reside close to the depositional site.

Numerically important megafossil taxa that are not represented (or perhaps not recognized) in the pollen record include Rhus, Staphylea, Athayana, Cercocarpus, Sapindus, Cotinus and Bursera. Rhus and Sapindus are entomophilous. Plants which are pollinated by insects are generally under-represented in the pollen rain, in part because they produce pollen in much smaller numbers than do wind-pollinated types (Faegri and Iverson, 1974), and in part because of the mode of distribution.

The TCT-type pollen is the most abundant. The large fossil stumps, putatively Sequoia, but quite possibly Chamaecyparis (see TCT discussion in Descriptive Notes for explanation), attest to the fact that the trees were very large. The pollen disparity between TCT and Fagopsis is likely a consequence of significant differences in overall pollen production despite the fact that individuals of both types may have been locally abundant.

Potamogeton pollen varies greatly in abundance and ranks second overall in the composite pollen sum. High levels may be explained by large numbers of source plants and the fact that Potamogeton pollen was actually produced in the lake. Its presence as a megafossil is uncertain. This disparity in records likely reflects rapid deterioration of the succulent leaves.

PALEOASSOCIATIONS

Following the approach of Taggart and Cross (1980), the individual taxa contributing to the pollen sums were grouped into paleoassociations according to related ecological/distributional characteristics of extant equivalents. The 6 paleoassociations selected and their constituent taxa are listed in Table 3. 30 pollen/spore types are included at the genus, family, or larger group level. In addition to the taxa included in the pollen diagrams, the identified types described in the Descriptive Notes section which were not quantitatively significant are listed within brackets to indicate their ecological position in the regional vegetation.

Hypothetically, the paleoassociations together comprise the complete vegetation community mosaic across the topographically variable landscape of the Florissant region. The approximate spatial distribution of these communities with respect to increasing distance and elevation away from the depositional basin may be tentatively arranged: Aquatic/Marsh, Lakeside Forest, Bottomland/Slope Forest, Pine and Xeric/Disturbed Scrub, and Montane Conifer Forest. Like modern landscapes, ecotonal zones would have been present and a dynamic mosaic of community types would have been variably developed on the regional topography under the influence of microclimatic and edaphic factors.

Treatment of data as multiple-taxa paleoassociations tends to buffer the effects of single taxon fluctuations. This lumping is done at the expense of some loss in ecological precision, for patterns of variation of individual taxa are obscurred and their ecological ranges are not accounted for fully. However, shifts in relative importance of the paleoassociations should represent coordinated contributions of the constituent taxa. Such shifts in paleoassociation importance are likely to reflect real changes in the plant

Table 3. Paleoassociations of plant taxa represented by pollen and spores from Florissant.

MONTANE CONIFER FOREST
- *Abies*
- *Picea*
- [*Podocarpus*]
- [*Pseudotsuga*/*Larix*]

PINE
- *Pinus*

XERIC/DISTURBED SCRUB
- Chenopodiaceae-Amaranthaceae (Cheno-Am pollen)
- [Compositae]
- *Ephedra*
- Gramineae

BOTTOMLAND/SLOPE FOREST
- *Acer*
- *Carya*
- [*Castanea*]
- *Engelhardia*
- *Juglans*
- *Liquidambar*
- [Proteaceae/ Sapindaceae/ Elaeagnaceae]
- *Quercus*
- [*Tilia*]

LAKESIDE FOREST
- Taxodiaceae, Cupressaceae, Taxaceae (TCT)
- *Celtis*
- *Fagopsis*
- [*Populus*]
- *Salix*
- *Ulmus*/*Zelkova*

AQUATIC/MARSH
- [Algae]
- [*Ilex*]
- [Nymphaeaceae]
- *Potamogeton*
- *Typha*

OTHER
- spore-producing plants
- unidentified morphotypes and unidentifiable pollen and spores
- (bracketed entities above, except for algae, are included under this category in the pollen diagrams)

community structure, especially when plant diversity within the paleoassociations is high.

At best, the paleoassociation groupings are an approximation of coexisting plants and are not mutually exclusive or precise ecologically or distributionally. Some of the genera or families have broad ecological amplitudes among their species today. For example, the Pine Paleoassociation is completely artificial because in extant floras, pine species may occur in pure or mixed stands or may be scattered widely in open parklands, as *P. ponderosa* currently is at Florissant. *Pinus* spp. may be present in montane conifer communities (e.g., *P. flexilis*, *P. contorta*), bottomland/slope communities (e.g., *P. taeda*, *P. strobus*), xeric/disturbed communities (e.g., *P. edulis*, *P. banksiana*), and in moist lowlands (e.g., *P. elliottii*). Pine pollen is ubiquitous, even in forest soils where it is not locally growing, because of its abundant production and great dispersal potential. Similarly, *Populus* spp. are ecologically diverse. Aspen (*Populus tremuloides*) is the most widely distributed tree in North America (Harlow, et. al., 1979). It is an aggressive pioneer which invades sites in pure stands after disturbances. Cottonwood (*P. deltoides*) is most commonly an occupant of moist alluvial banks. However, open grassy forests of *Pinus ponderosa* with scattered pockets of *Populus tremuloides* in moist bottomlands are common in the Rocky Mountains today. *Quercus* spp., a common element of the palynoflora, may also be found in diverse habitats (e.g., *Q. palustris* and *Q. nigra*: moist bottomlands and swamp margins; *Q. emoryi* and *Q. wislizenii*: shrubby sclerophyllous types of the dry southwest United States and northern Mexico; *Q. alba* and *Q. rubra* of mesic deciduous forests in eastern United States).

The closest existing ecological analog to the Lakeside Forest Paleossociation (dominated by *Fagopsis*, *Sequoia* and *Chamaecyparis*) is probably a combination of the redwood (*Sequoia sempervirens*) forest of the California "fog belt" and the Port-Orford cedar (*Chamaecyparis lawsoniana*) forest of the coastal Pacific Northwest. The leader in overall pollen production is the TCT type. Placement of TCT pollen into particular genera is problematic (cf. TCT discussion in Descriptive Notes section). The most common associates of modern redwoods are *Pseudotsuga*, *Picea*, *Abies*, *Tsuga*, *Lithocarpus* (cf. *L. densiflorus* (Fagaceae)), *Alnus*, *Arbutus*, and *Umbellularia* (Harlow, et. al., 1979). The association inhabits moist benches and alluvial flats. Modern North American *Chamaecyparis* spp. have distributions restricted to the east and west coasts (Harlow, et. al., 1979). *C. thyoides*, the east coast species, is characteristic of freshwater swamps and bogs. *C. lawsoniana* of the Pacific Northwest prefers an abundance of soil and atmospheric moisture, but also frequently occurs on more dry, sandy sites ~45-65 km inland. *C. nootkatensis* occupies a broader, more northerly coastal distribution which extends into southern Alaska. It grows most often on sites with rich soil and an abundance of moisture. Associates include many of the same genera as *Sequoia*: *Pinus*, *Larix*, *Picea*, *Abies*, *Tsuga*, *Thuja*. The available evidence suggests that the Florissant TCT pollen types indicate presence of a rich, moist bottomland environment adjacent to the shallow water body(-ies), possibly affected by periodic flooding.

The topographically variable landscape that Lake Florissant occupied permitted microclimatic and edaphic zonation. Therefore, diverse ecological settings probably coexisted within relatively close proximity to each other. *Pinus*, *Picea*, and *Abies*, which are common associates of extant western North American *Sequoia* and *Chamaecyparis*, are also represented by pollen in the Florissant sediments. This constitutes a mixture of drier upland and slope and moist bottomland plants. *Abies* pollen is generally underrepresented in deposits, even when the trees are abundant regionally, and *Picea* is generally indicative of the local basal area of the existing trees (Leopold, 1964). When the relative effect of TCT pollen is removed from the pollen counts, these two taxa are still poorly represented. Since neither *Abies* nor *Picea* leaves or pollen are abundant in the Florissant sediments, it is difficult to associate them with the taxodiaceous-rich shoreline, but it is possible that they occupied a very minor, scattered position in these forests. Consistently low leaf and pollen levels substantiate MacGinitie's (1953) suggestion that they were cold/dry-adapted members of the montane complex, accompanied by species of *Acer*, *Philadelphus* and *Torreya*.

The leaf margin of *Lithocarpus densiflorus* resembles that of *Fagopsis* (Harlow, et. al.,1979) and their flowers and fruiting structures are comparable (Manchester and Crane,1983). It is postulated here that *Fagopsis* occupied a co-position in the Florissant lakeside forest with *Sequoia* and *Chamaecyparis* in a relationship analogous to the position of modern *Lithocarpus*. This postulation is in agreement with the megafossil abundances. Low levels of *Fagopsis* pollen have been attributed to low production coupled with limited distribution of the trees.

Additional members of the Lakeside Forest Paleoassociation are suggested by MacGinitie (1953). These include: *Populus*, *Salix*, *Zelkova*, *Ulmus*, *Celtis*. Members of the Ulmaceae are relatively abundant in both the pollen and leaf records. MacGinitie (1953) suggests a reciprocal relationship for the abundance of *Populus* and a scarcity of *Salix* fossil foliage, attributed to competition for the same sites. The inverse of this relationship was found in the pollen record, perhaps, in part, a consequence of the relative fragility of *Populus* pollen.

Strong representation of *Potamogeton* in the pollen record documents its widespread occurrence in the ancient lake. Nymphaeaceous plants were also present but probably sparse; only a few grains of pollen and no leaves have been recovered. The existence of cattail marshes is supported by a substantial number of leaf specimens (5.8%, fourth-ranking megafossil) and occasional *Typha* pollen. The algal record consists of *Nitella* (megafossil) and *Mougeotia* zygospores. The Aquatic/Marsh category of Figures 4 and 5 is almost entirely represented by *Potamogeton* pollen.

The Bottomland/Slope Forest Paleoassociation occupied a position on the better-drained flats and hills peripheral to the basin of deposition. On the average, it probably resembled the mixed mesophytic forests of eastern North America and east Asia, dominated by broad-leaved deciduous trees. Mesic species of oak and hickory likely were the co-dominants, on the bases of abundant pollen and leaf records. Trees of secondary importance were species of *Acer* (maple), *Liquidambar* (sweetgum), *Juglans* (walnut), *Castanea* (chestnut) and *Engelhardia*. Sweetgum and walnut may have been locally abundant in pure stands after disturbances. This association was transitional between the lakeside and more upland, drier sites. Hickory may have been ecotonal to the lakeside forest and drier-adapted oaks were probably concentrated on the sparsely vegetated, well-drained slopes.

Exposed areas (e.g. hilltops and steep, south-facing slopes) characterized by poorly developed soils were the likely position within the regional vegetation mosaic for members of the Xeric/Disturbed Scrub Paleoassociation, primarily grasses, members of the families Chenopodiaceae, Amaranthaceae and Compositae, and *Ephedra*. They are poorly represented in the fossil record because of their distance from the sites of accumulation and their limited dispersal potential. MacGinitie (1953) suggested that these herbs and xerophytic shrubs (e.g., Amelanchier, Cercocarpus, Dodonaea, Mahonia, Rhus, Schmaltzia) were intermixed with an open forest of pines and dwarf evergreen oaks, a group characterizing chaparral vegetation.

The "Other" category is completely artificial. In the pollen diagrams, it includes unidentified morphotypes, unidentifiable pollen and spores and all of the bracketed taxa listed within the paleoassociations, because they played a very minor role quantitatively. It also includes the spore-producing plants (monolete, trilete) because the diverse ecological adaptations of these undifferentiated plants precluded classification into any one of the paleoassociations. More than three-fourths of the "Other" category represents pollen and spores which were corroded or deformed beyond identifiability.

Stratigraphic Distribution of Palynomorphs

Pollen diagrams are a useful graphic display for the tabulated sums of the selected samples. They provide a condensed, comparative presentation of changes in vegetation elements and community structure over a particular stratigraphic interval. Two major types of pollen diagrams (or pollen profiles) are used by palynologists: absolute frequency pollen diagrams and relative frequency pollen diagrams.

Absolute pollen counts are useful if the sedimentation rate is known or constant (Moore and Webb, 1978). This method is most appropriate for peats accumulated since the most recent glacial maximum, because the subsequent deposition rates often may be calibrated by incremental radiocarbon dating. Pollen data are expressed as pollen influx, an estimation of the density per unit time (units: # grains of a species/cm^3/yr). The primary application of this method is to identify real changes in the pollen contribution of specific taxa over time, independent of the fluctuations of other taxa.

Relative percentage data are the most widely used in Tertiary sediments, since most allochthonous deposits are less-well time-calibrated. They are used to demonstrate shifts in relative numerical contribution of taxa or groups of taxa among samples. The proportions are calculated according to a fixed pollen sum independent of the relationship of the density of palynomorphs in the sediment. Their limitation is that a change in one component will therefore produce compensatory changes in all other components (Moore and Webb, 1978). This creates the problem of separating real changes in the source vegetation from apparent ones. This problem may be largely overcome by grouping individual taxa into ecologically similar assemblages (paleoassociations), thus damping the effects of single taxon fluctuations.

Due to production, dispersal and preservation biases, pollen analysts have long been aware of the discrepancy between pollen representation in a deposit and source plant abundance and distribution. Correction factors such as Faegri and Iverson's multiplier and Davis' R-value model have been devised to alleviate problems of over- and under-representation (Birks and Birks, 1980). These methods are based on measurement of modern pollen percentages in surface samples in relationship to existing vegetation percentages. The major limitation using these techniques is that correction factors may fluctuate for a single species in different areas; therefore validity decreases when sampling large basins. In addition, these methods are calibrated for modern environmental settings, and it is unlikely that R-values have remained constant over time, especially as far back as the middle Tertiary.. Therefore, correction factors have not been used in this study.

Relative pollen diagrams are used in this study. The palynological samples are arranged vertically to stratigraphic scale and the plant compositional categories are horizontally listed across the top. The sum of the relative compositional contributions at any horizontal level equals 100% for a particular sample. The data are displayed in two primary ways, according to contributions of:

(a) individual taxa

(b) associations of taxa

Figures 2 and 3 are relative frequency pollen profiles of individual taxa, including all taxa which contributed greater than 1.0% relative frequency to the pollen sum of at least one sample of the sections. Taxa/morphotypes of

FIGURE 2. Section 8/5/84 I (taxa)

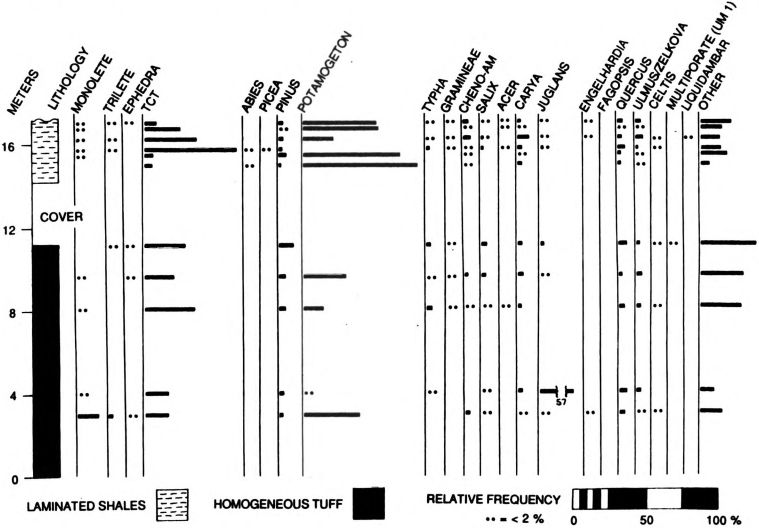
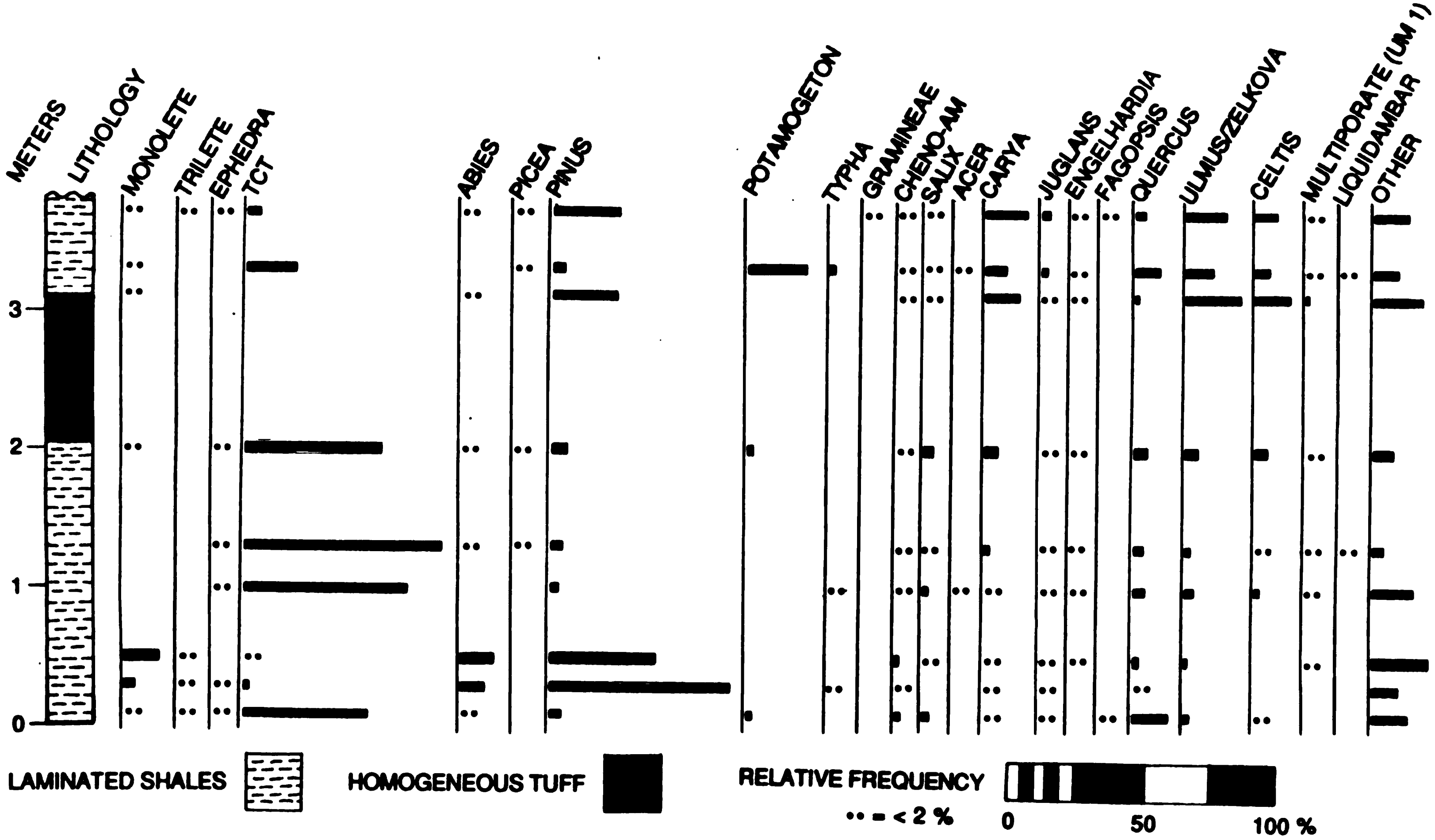


FIGURE 3. Section 8/23/84 I (taxa)



lesser abundance are included in the "OTHER" category. While two taxa (Fagopsis and Liquidambar) contributed very little numerically to the pollen sums, they are retained in the diagrams for their ecological significance when present or absent. These diagrams are useful for comparing the composite pollen spectra of the two sections, and were the starting point for interpretation of vegetation dynamics.

Two individual taxa, TCT and Potamogeton, are disproportionately represented in relation to all the others. Since these are major components of the spectra, any shift in their contribution may consequently cause a major change in the expressed percentages of the other contributors to the pollen sum. Cross and Taggart (1982) remark that such consequential changes may occur without actual changes in the source plant abundance or distribution. Common taxa which may produce this shifting effect in relative frequency diagrams are Pinus, Alnus, Betula and Corylus (Cross and Taggart, 1982; Birks and Birks, 1980). These taxa are either voluminous pollen producers with long-distance dispersal capabilities (e.g., Pinus), or typically grow in dense concentrations close to the depositional basin (e.g., Alnus thickets). The second explanation is probably the case for the abundance of TCT and Potamogeton pollen in the samples. Potamogeton is a ubiquitous aquatic and leaf megafossil data suggest that Chamaecyparis and Sequoia (the probable source of TCT pollen) probably crowded the lake margin as bottomland dominants. In order to mitigate these single taxon biases, the pollen sums were adjusted with the exclusion TCT and Potamogeton; counting was continued for the other taxa until the fixed sum of 400 was reattained. The relative abundance of each type did not change appreciably in either of the two sections after this adjustment.

The relative frequency pollen diagrams in Figures 4 and 5 are based on the ecological associations of taxa described in the Paleoassociations section. TCT pollen is separated from other lakeside taxa so that patterns of variation in the Lakeside Forest Paleoassociation may be separated from the minimizing effects of TCT dominance. The Aquatic/Marsh Paleoassociation is overwhelmingly dominated by Potamogeton; the role of Typha does not exceed 4% (av. 0.85%).

FIGURE 4. Section 8/5/84 I (paleoassociations)

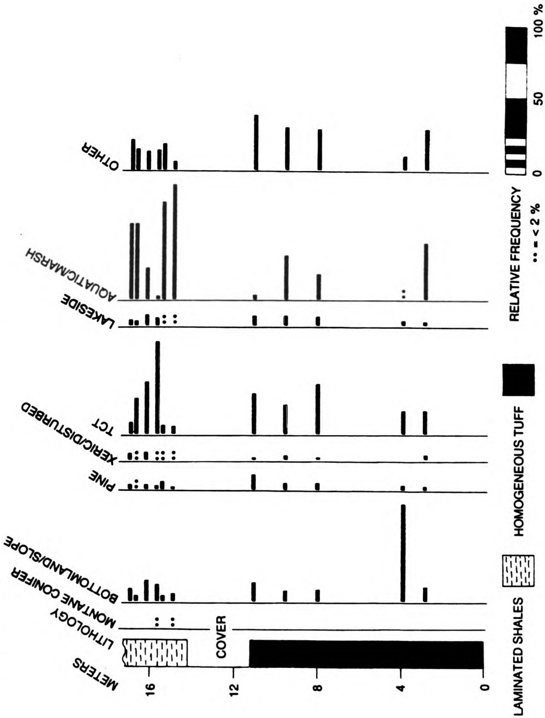
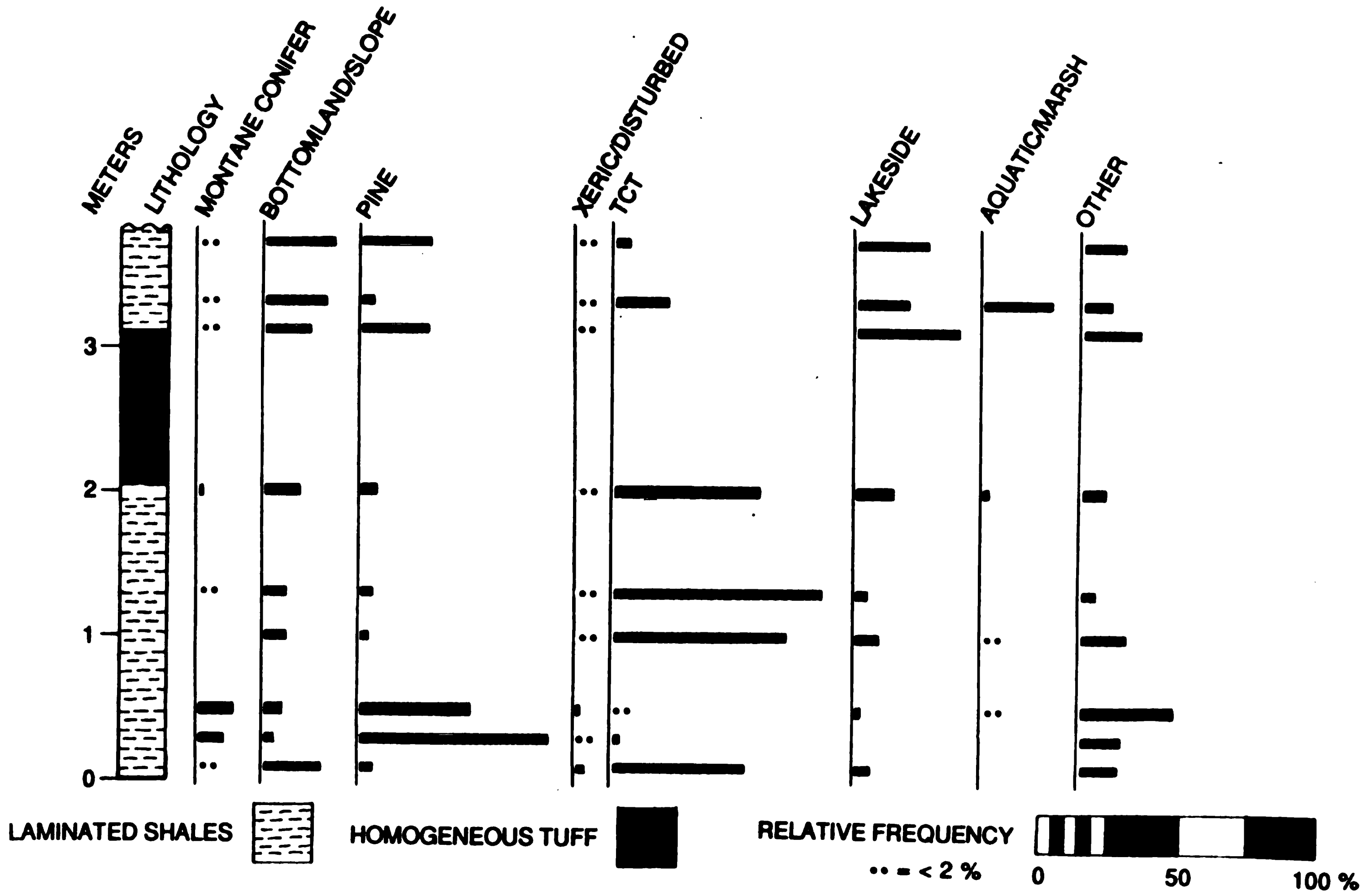


FIGURE 5. Section 8/23/84 I (paleoassociations)



Phytogeography/Vegetation Dynamics

The pollen diagrams which contrast the paleoassociations (Figures 4 and 5) are used for identifying the major shifts in vegetation dominance for the stratigraphic intervals studied. They may also be used to compare the floral composition at geographically separated sites. Figures 2 and 3 are useful for determining the significance of specific taxa/types within each paleoassociation during shifts in dominance.

Because of the complex dynamic nature of plant communities and the limited information preserved in the fossil and sedimentary records, it is difficult to resolve the variables that influence changes in fossil representation. For relative frequency pollen diagrams, shifts in dominance of types may be attributed to changes associated with the source vegetation: (a) numerical abundance, and (b) distribution. The primary environmental factors which control these variables are climate, physiography, and disturbances such as fire, flooding and volcanism. The effects of volcanism and short-term climatic change are recognized in the fossiliferous deposits at Florissant.

Numerical Abundance of Source Vegetation and Geographic Variation in Plant Distribution

The percent range of fossil representation in Table 2 shows considerable variability in relative abundance of the pollen taxa/types for different samples. In all cases, the average percent contribution for each type was much less than the maximum of the range. For several taxa/types, the vertical range of variation within a section was more than 50%. Such dramatic fluctuations should reflect significant changes in the ability of the pollen/spores to reach the depositional site under the prevailing conditions

(Smiley and Rember, 1981). Post-depositional changes may further affect preservation.

The most obvious explanations for fluctuation of a single taxon/type in successive samples are changes in proximity of the source plants to the depositional site, changes in the numerical size of the source plant population (sum of pollen production), and preservation in different types of sedimentary environments. However, the relative representation of a taxon/type in the pollen record may vary with time when these factors are constant for that taxon/type. An additional variable that must be considered is colonization or change in population size of other plants between the taxon/type noted and the depositional site. These other plants contribute pollen to the record, thus decreasing the relative importance of the taxon/type noted, and they may act as a physical barrier to pollen transport from parent plants that were formerly more accessible to the depositional site. When making postulations about the influence of factors such as volcanism and climatic change on source vegetation, these potential biases must be considered.

The Florissant pollen and leaf records indicate that abundant plants of the Lakeside Forest Paleoassociation were capable of acting as buffers to transport of pollen and other organs from plants of the slopes and uplands to the depositional sites.

Volcanism and Pollen/Spore Representation

An important goal of this study was to examine the influence of the regional volcanism on the vegetation in and around the depositional basin. Evidence may be derived from the fossil content and petrology of the basin deposits. The relative frequency pollen profiles do not demonstrate catastrophic destruction of established plant communities here by volcanic activity. Volcanic activity appears to have played a minor role in vegetation dynamics near the depositional basin, indicated by subtle variations in single taxa or coordinated groups of taxa . Other factors may have been more important in controlling the composition and distribution of the regional vegetation.

The extensive deposits of the Thirtynine Mile volcanic field record a highly active interval of volcanism during the early-middle Oligocene. Several types of volcanigenic deposits were observed in the lakebeds. The main stream at the northern end of the basin and tributary streams from the slopes surrounding the basin carried most of the materials into the lake. The homogeneity, coarse character, and cross-bedding of the lower tuffs suggest that loaded streams supplied sediments to the basin in great quantities during early lake history. Relatively quiet volcanic conditions for the latter part of lake history are recorded in the laminated shales above the lower tuffs. The deposits were mainly interbedded pumices and graded tuffs. With respect to overall thickness, direct airfall of volcanic ash played a variable and minor role in lake sedimentation and is the only primary volcanic deposit. Lava flows and ignimbrites are not recorded in the lakebeds.

Volcanism has the potential to destroy or disturb plant communities proximal to the volcanic source. Subaerial deposits of ash and accompanying gasses or heat could temporarily or permanently eliminate some plants. Direct effects include burial, mechanical overloading and suffocation. An indirect but important effect could be alteration of edaphic conditions.

Studies of modern analogs demonstrate highly variable effects of volcanism on vegetation. In studies of the Paricutin eruptions, which began in 1943 in central Mexico, Eggler (1948) and Dorf (1951) showed that plant devastation by accumulated thicknesses of ash is not as severe as might be expected. Mortality of small trees, shrubs and herbs was most extensive, especially in >20 cm of ash (Eggler, 1948). However, many larger trees of the dominant pine-oak forest survived >2 m depth of ash. Grasses (Stipa, included as a Florissant megafossil) and some dicotyledonous herbs colonized bare ash 50 cm thick within two years. Malde (1964) notes that ash falls may even be beneficial to plant growth by enhancing the nutrient content of soils. The immediate effects are usually detrimental, however, because unlike soil, ash is sharply granular, deficient of clays and easily eroded (Malde, 1964). Although episodes of volcanically induced forest destruction have been noted in studies of the Miocene Succor Creek flora (Cross and Taggart, 1982), no such events are evident in the Florissant sections studied.

The best opportunity to investigate the effects of volcanism on Florissant vegetation is a homogeneous volcanic ash layer in the lakebeds of section 8/23/84-I. In Figures 3 and 5, it is represented by the homogeneous tuff zone of the lithologic section. This deposit is ~1 m thick, is uniform gray in color, fractures conchoidally and contains no fragmental plant material or sediment particles larger than the ash. It grades slightly finer upwards throughout its thickness and contains a series of intermittent microlaminations that are evident in thin-section. Cross-bedding and turbidity figures are not apparent in hand specimens or thin-section. Contact with the underlying finely-laminated fossiliferous shale is abrupt with no evidence of scouring or erosion prior to deposition. The underlying shale is uniform in thickness and the upper laminae are continuous; current activity does not appear to have affected it. The intermittent grading may be explained by subaqueous settling of ash particles dropped by fluctuating wind currents transporting the materials from the vent (Guffey volcanic center, ~25 km southwest) to the lake. Three palynological samples representing the total thickness of this bed were barren. This evidence strongly suggests that the accumulation resulted from airfall deposition of volcanic ash into the standing body of water during a geological instant in time, although definitive evidence against fluvial deposition was not found. No counterpart to this deposit has been observed in other exposures of the lacustrine shale unit. It is postulated that it was once a widespread deposit, but has been eroded out of other exposures observed.

In the fossiliferous shale immediately below the ash deposit, the pollen spectrum is dominated by the Lakeside Paleoassociation (Figure 5: TCT >50%; other Lakeside plants ~14%). All of the other paleoassociations are represented at low levels. Immediately above the deposit, TCT-type and Aquatic/Marsh pollen are absent; other Lakeside members (~37%), Pine (~24%), and Bottomland/Slope (~18%) codominate. Pollen of the Xeric/Disturbed paleoassociation decreases after that sedimentary event.

It is apparent from the pollen spectra below and above the ash deposit that rapid subaerial deposition of more than a meter of ash did not drastically alter the diversity of plants in the basin region. The only plants that were significantly reduced in pollen representation were TCT-types and Potamogeton. Populations of modern Potamogeton spp. are sensitive to reductions in light intensity. It is postulated here that the Potamogeton spp. were catastrophically reduced in numbers by ash burial, change in lake bottom conditions, and decreased photosynthesis in cloudy waters. In the second youngest sample studied from above the ash, Potamogeton recovered from the disturbance and achieved its greatest pollen representation for the section (~22%). The recovery may be attributed to one or more of several factors of lake substrate conditions suitable to growth of rooted, submerged or floating aquatics, e.g., compaction of the ash, alteration of glass and feldspars to clay minerals, increase in organic content (recovery of bacteria, algae, and bottom fauna). Algal spores of *Mougeotia*, rare in the samples studied overall, were abundant in the sample immediately above the ash deposit. Sudden increased nutrient content of water accounts for modern algal blooms, and the nutrient contribution and turbidity associated with the ashfall may have triggered the *Mougeotia* bloom.

The effects of volcanism on the composition of the palynoflora may be compared for the Lower Tuff and Lake Shale units in section 8/5/84-I (Figures 2 and 4). In Figure 4 the plant diversity within the two units appears to be roughly the same. The major difference is the presence of Montane Conifer Forest types (*Abies*, *Picea*) exclusively in the lake shales, but at very low levels. This similarity in diversity suggests that, for the time period represented, the regional vegetation composition was not significantly different during intervals of relatively high and low volcanic influence, or that sampling was not on a fine enough scale. Although not quantitatively significant, the presence of Montane Conifers in the lake shales may represent the colonization of these trees in the uplands after volcanic influences were somewhat mitigated.

Aquatic/Marsh pollen is more abundant in the laminated shales than in the Lower Tuff of section 8/5/84-I (Figure 4). Aquatic/Marsh pollen is overwhelmingly dominated by *Potamogeton*. The turbidity, unstable water level, and rapidly changing lake bottom associated with rapid sedimentation during Lower Tuff time may have limited colonization of *Potamogeton*. The subsequent reduction in volcanic influence may have led to increased stabilization of the lake bottom and clearer water, permitting *Potamogeton* to reestablish itself as a ubiquitous aquatic. Weathered products of the volcanic ash were capable of supplying abundant dissolved nutrients to the water to support rapid growth of extensive beds of Potamogeton. This may account for the abrupt relative increase in Aquatic/Marsh pollen in the lower part of the lacustrine shales of section 8/5/84-I (Figure 4).

Basin Infilling, Climate and Lake Level

Variations in lake level may have caused profound changes in the abundance and type of vegetation in and immediately bordering the lake while not significantly influencing the vegetation of higher, drier sites. It is postulated in this study that during the later lake history, lake levels decreased and became increasingly sensitive to climatic variability.

Following impoundment by a lahar or lava flow, accumulation of sediment and water in the basin may have caused water levels to rise to the top of the containment structure. Additional input of sediment and water could cause water to exceed the capacity of the dam, and progressively erode the top and downstream side. Reduction of dam height or sudden breaching is then possible, causing shallowing of the ponded area. The rate of backcutting would be dependent on the origin of the containment structure; a lahar would be much less resistant to erosion than a lava flow. The reduction in lake level would be permanent, unless a later obstruction of drainage reinitiated the process. Progressive shallowing of the lake would increase sensitivity to fluctuations in the precipitation/evaporation ratio.

Sedimentological evidence in both study sections records a relatively dry climate during the later part of the recorded lake history. Several calcareous layers are present in varying thicknesses near the top of the exposures. In the Geology section, these deposits were suggested to be caliche formed below the erosion surface prior to deposition of the Upper Tuff. Near-surface crystallization of calcium carbonate in the soil is possible under the warm-temperate climatic regime suggested by MacGinitie (1953).

The palynological record of a shale sequence which includes the calcareous deposits in section 8/5/84-I may indicate changes in aquatic plant representation during a dry period. Reduction in fossil representation the aquatic weed Potamogeton may be considered an indicator shallow water and/or decreased lake area. In the upper six samples of Figure 4, Aquatic/Marsh pollen declines from a dominating ~80% to ~2% and then recovers to more than 50% relative abundance. The lowest pollen representation of the Aquatic/Marsh Paleoassociation occurs in one of the thick calcareous layers. The other samples are of clastic origin. Relatively low stream input is indicated by associated thin volcaniclastic laminae as compared to those lower in the lake shales. The same samples in Figure 2 show that fluctuation of Potamogeton pollen is responsible for this shift. There is no Potamogeton pollen in the calcareous layer. Algal growth during a period of high evaporation may have been responsible for the deposition of the calcium carbonate. The Aquatic/Marsh pollen reflects 2.3% Typha, the maximum the genus attains in the lake shales. The Typha spike may represent an increase in marsh conditions created by the receding shoreline.

Diagenetic processes during caliche formation may have resulted in the selective destruction of Potamogeton pollen in the calcareous sample. However, a gradual decrease of Potamogeton pollen in the samples immediately below the calcareous layer followed by a gradual recovery of Potamogeton in the samples above could be used as an argument for real, systematic changes in the parent plant population in response to a temporary dry period.

An abrupt increase in TCT-type pollen accompanies the elimination of Potamogeton. This increase probably does not reflect an increase in the number of associated plants, but a reciprocal decrease in Potamogeton alone could account for this change. However, analagous to an increase in marsh conditions, reduction in water level may have opened flat, moist areas for invasion of TCT-type plants.

Relationship of Collection Localities to Lake Physiography

Field relations of rock units suggest that the two depositional sites studied were situated at different distances from the basin edge. The Tertiary volcanigenic rocks of the region lie unconformably on the extensive and irregular surface of the Precambrian Pikes Peak granite. The granite crops out above the Tertiary rocks sporadically within the basin and dominates the surrounding upland areas. Collection locality 8/5/84-I is positioned in the basin interior, near the western edge, in the form of an isolated hill. The granite is exposed at the top of the hill and the Tertiary lake deposits circumscribe the slopes. The lakebed/Upper Tuff contact extends around much of the hill's circumference near the top. The lower part of the lakebeds completely surrounds the hill and is concealed at the base by the valley fill. The draping of the lake deposits on the granite core at this locality suggests that the hill was an island within the lake during Florissant time. An edge of the lake sediments outcrops a few hundred yards to the northwest.

The deposits of section 8/23/84-I are part of an extensive irregular ring of exposures that outline the slopes near the east edge of the basin. The Upper Tuff is overlain by Quaternary alluvium that covers the gently sloping surface for ~0.8 km to the east where it intersects the exposure of the granite. The exposure of granite is continuous eastward to Pikes Peak and it encircles the upper elevations of the entire Florissant basin. This relationship suggests that the deposits of section 8/23/84-I possibly represent an interior area of the lake, up to ~0.8 km from the shoreline.

The implications of water depth at the two depositional sites may be supported by palynological content of the sediments. Figures 2 and 3 show that Potamogeton pollen was significantly more abundant in the sample suites at locality 8/5/84-I than 8/23/84-I. Water depth requirement varies from shallow to deep among modern Potamogeton species. Comparison of the two localities in light of the above physiographic criteria suggests that the Florissant species of Potamogeton was adapted to shallow water. During lake shale deposition, the island shoreline of section 8/5/84-I was likely relatively nearshore and shallow due to the close proximity of the granite outcrop at the top of the island. Abundant Potamogeton pollen in most samples supports this interpretation of water depth. At locality 8/23/84-I, where the site of deposition was further removed from the shoreline, water depth may have been greater. Deeper water could also be attributed to close proximity (<2 km) of this locality to the postulated site of the dam to the south that formed the lake. The low abundance and common absence of Potamogeton pollen in many samples supports a greater relative water depth. The single spike of Potamogeton pollen near the top of the section may represent an interval of relatively shallow conditions following normal infilling. Alternatively, it is possibly directly related to the sudden >1 m deposition of ash. Temporary absence of Potamogeton pollen in the sample immediately above the ash might be attributed to burial of plants or turbidity of the water as a direct result of the depositional event. Decreased depth may have influenced the subsequent recovery of Potamogeton. The relatively shallow depth requirements suggested for Florissant Potamogeton spp. are conjectural but consistent with available inferences regarding the paleobathymetry of the lake basin. If Potamogeton species adapted to greater water depths were present, it is unlikely that they contributed significantly to the composite pollen data. It should also be emphasized that "shallow vs. deep" water postulations are strictly relative since the absolute bathymetric distribution of rooted, submerged aquatics such as Potamogeton is controlled by factors such as water turbidity, thermal stratification, and seasonal oxygen flux, all relatively unknown for Lake Florissant.

Correlation

Lithologic and stratigraphic correlation of Florissant Lake Beds exposures have been unsuccessful in earlier studies due to post-depositional faulting, strong lateral variation in sediment thickness, and differential erosion. Trends in pollen profiles also have provided no correlation of the two sections studied here.

The base of the Upper Tuff is a consistent time marker. It caps the lakebed exposures in both sections, as well as at most other lakebed exposures throughout the valley, but correlation of the lakebeds immediately below the Upper Tuff is not known. The sequence and thickness of the layers below the Upper Tuff is different in the two study sections. Varying amounts of the upper lakebed layers were probably removed by erosion prior to the deposition of the Upper Tuff.

The two collection localities are approximately equidistant from the center of volcanic activity ~25 km southwest (Guffey volcano). It would be reasonable to expect that an ashfall deposit more than 1 m in thickness (upper surface ~0.6 m below Upper Tuff contact) in section 8/23/84-I would be laterally continuous for more than the ~2.6 km which separates the two localities, although its thickness could be somewhat different. There is no evidence that this unique deposit is present in the section exposed at locality 8/5/84-I. This suggests that one or both of the sections has had a significant amount of material eroded away prior to deposition of the Upper Tuff. Other studies (e.g., MacGinitie, 1953) have suggested that the Upper Tuff was deposited on an erosion surface because fragments of lake shales are embedded in the Upper Tuff matrix and the contact is highly irregular.

The two sections do not necessarily represent different regions of the same water body. If the paleovalley was broad and relatively flat across its width, the lateral meandering of the sediment-laden interdigitating streams would have distributed materials in different areas at different times. If this was the case, it would have been possible for a number of ponded areas, some possibly large, to exist in such a setting (MacGinitie, 1953). At times they would infill with sediment or their containments would be breached and the water would be displaced to a lower location to form a new body of water temporarily. This scenario would account for different depositional sequences of the same types of sediments in disjunct areas.

Calcareous layers were observed in the upper 2 m of the two study sections. They may be a time marker which represents temporary relative aridity in the region. Other mechanisms for deposition of the mineral calcite are possible (e.g., caliche formation, surface weathering, circulation of vadose water, algal activity) and would not necessarily occur in different areas of the lake contemporaneously.

Perspectives on Regional History

Independent studies of the Florissant Lake Beds have provided a large body of information about the biotic and geologic history of the Florissant region 34 million years ago. The history of the region may be summarized from two perspectives. First, the sequence of events that led to the diverse, fossil-rich lake deposits over a moment in geologic time may be assessed. Second, inferences about Florissant paleoecology, paleoclimatology and paleogeography may be compared with inferences from studies of other fossiliferous deposits of the Rocky Mountain region that existed from the Eocene through the Oligocene.

Sequence of Events During Accumulation of the Florissant Deposits

Extrapolation of depositional rates of modern sediments similar to the four types of lamination in the Florissant lacustrine shales was used by McLeroy and Anderson (1966) to estimate the duration of the lake phase. Based on the maximum known thickness of the deposits and the relative proportion of each type of lamination, the estimate at one locality was 2500-5000 yr. It would be increased if erosion of the lakebeds did not precede deposition of the Upper Tuff and if the Lower Tuff represents an early stage of the lake during a period of relatively rapid deposition. Nevertheless, the estimate would probably remain less than 10,000 yr and the deposits may be considered a window into a moment of the early Oligocene.

The volcanic center that supplied the sediments to the Florissant basin was at a critical distance for the quality and quantity of fossil preservation present. MacGinitie (1953) identifies the source as the Guffey "volcano", ~24 km southwest of Florissant. The Lower Tuff represents a relatively active period of volcanism and was deposited more rapidly than the Lake Shales.

During Lake Shale deposition, output of volcanic material was frequent enough to supply fine sediments via stream input, and, to a lesser degree, direct airfall, for the extraordinary preservation of leaves and insects. However, the magnitude of the eruptions was not enough to destroy the previous deposits via lahars, ignimbrites, and lava flows, for perhaps thousands of years.

Continuous, pulsating regional volcanism provided clastic materials that preserved and calibrated the Florissant basin history. Below the volcanic deposits lies the eroded Pikes Peak granite valley and associated alluvium and colluvium. Prior to lake formation, the onset of volcanism is recorded by welded tuffs and lava flows of the Thirtynine mile volcanic field. As the volcanism continued throughout and beyond the lake phase, erosional products of these materials from the uplands were transported to the Florissant basin by the streams of its watershed and deposited as water-laid tuffs.

Formation of the lake was probably caused by a volcanic barrier to drainage, such as a lahar or lava flow that crossed the lower end of the valley. The timing of this event is not certain. Most studies have placed it at the termination of the Lower Tuff. Palynological evidence of standing water suggests the possibility that drainage was obstructed at the onset or during the early stages of Lower Tuff deposition.

The paleoecological, paleoclimatic, and paleogeographic inferences during lake deposition as postulated by MacGinitie (1953) are compatible with the results of subsequent studies. The composite plant megafossil assemblage indicates a warm temperate climate, with less than 50-60 cm of precipitation and an average annual temperature of more than 18° C. Rainfall was concentrated in the late spring/early summer. Absolute minimum annual temperature was greater than -6.6° C. The regional terrain was mountainous; local relief around the Florissant basin was low to moderate. The lake was at an elevation of ~300-900 m, and the surrounding volcanic uplands were at ~1500 m.

In contrast, MacGinitie (1953) noted the presence of megafossils of both fir (Abies) and spruce (Picea) and both taxa are present in the pollen flora. Although not common, both taxa were probably growing at no great diatance from the lake, based on the megafossil occurrences. According to Fowells (1965), no North American species of fir are known where precipitation is less than 51 cm and no spruces occur where precipitation is less than 65 cm. It may well be that MacGinitie's precipitation estimate is low, particularly given his relatively high estimate for paleotemperature.

A similar climate and mosaic of vegetation exists today in the northern Sierra Madre of northeastern Mexico (MacGinitie, 1953). MacGinitie's list of fossil species indicates a mixed conifer forest, woodland, and scrub setting. His list of similar living species in no way implies a tropical or subtropical climate, despite the presence of some hardy subtropical elements that adapted to more temperate climates upon regional cooling after their Eocene northward migration (MacGinitie, 1953).

Entomological evidence, primarily from the Diptera, supports this paleoclimatic interpretation (MacGinitie, 1953). Other fauna that have been recovered from the shales include birds (Cope, 1881; Allen, 1878), fishes (Cope, 1879), and a marsupial (Gazin, 1935).

Probable dessication of the lake was followed by an indeterminate period of erosion prior to deposition of the Upper Tuff. The Upper Tuff represents a relatively violent episode of volcanism where the basin slopes accumulated large amounts of volcanic debris to the point of instability. The subsequent lahar(s) capped the uneroded remnants of the lakebeds in the Florissant valley.

Comparison With Other Early Tertiary Rocky Mountain Floras

A number of other floras that are close to the Florissant flora spatially and/or temporally have been the subject of other studies. Comparison of several of these studies with information from Florissant can broaden the understanding of the development of Rocky Mountain floras and their physical environments during the mid-Tertiary.

Two floras of southwestern Montana have the most striking floral (leaf fossil) similarity to Florissant known to the author. The Ruby paper shales also accumulated in a lacustrine basin, ~1100 km north-northwest of Florissant. Several species are found in only the two floras that have in common 32 species and 36 genera. Given this similarity, Becker (1961) suggested that despite their wide geographical separation, the two floras represent a common botanical province and must have been floristically connected along the central and eastern Rocky Mountains. Becker (1961) estimated the age of the Ruby flora to be late Oligocene and the age has since been refined to 30.8-29.2 ma (Wing, 1987). Approximately 65 km further to the north, the Beaverhead Basins flora is slightly younger (~32 ma) than the Florissant flora and more taxonomically diverse. 40 species are common to both floras (Becker, 1969). All three floras share a strong representation of members of the Pinaceae, Fagaceae, Ulmaceae, Rosaceae, Fagopsis longifolia under a dry/warm-temperate climatic regime.

The Red Rock Ranch flora of the San Mateo Mountains, New Mexico (~625 km south-southeast of Florissant), represents an ecotonal broad-leaved sclerophyll and mixed conifer forest, almost contemporaneous (~35 ma) with

Florissant and at a slightly higher elevation of ~1280 m (Axelrod and Bailey, 1976). The megafossil record shows considerable relationship to Florissant, including abundant <u>Picea</u> and <u>Pinus</u>; <u>Fagopsis</u> <u>longifolia</u> is also present.

The closest flora to Florissant in distance and time is the Silver Cliff flora, ~88 km to the south, dated ~35 ma (Axelrod and Raven, 1985). Diversity is limited to 5 species that represent a semiarid woodland-scrub of southern Cordilleran affinity. It has a drier aspect than Florissant, which Axelrod and Raven (1985) attribute to a site of western exposure.

All of the floras described have been attributed several common characteristics. They represent a mixture of coniferous and broad-leaved deciduous forests growing under a seasonally dry subhumid climate at an intermediate elevation (Wing, 1987). They cover an age range of ~30-35 ma (early Oligocene). The more diverse floras (i.e. Florissant, Ruby, Beaverhead) probably represent a broader region of source plants that were ecologically divided into distinct paleoassociations (see Paleoassociations section).

Early to middle Oligocene floras of the northwest United States and southwestern Canada were generally of lower elevation and received orographic rainfall on the lee side of the uplifting Rockies, as well as higher average temperatures and a narrower annual range of temperature. Therefore, they tend to have more subtropical elements which grew under a relatively humid climate (e.g., Frazer River Fm., British Columbia; Coos Bay and Goshen floras, Oregon).

Early Oligocene floras as a group record a shift to a cooler and drier climate than that of the late Eocene and the boundary between the two periods marks the transition to modernization of angiosperm genera in the Rocky Mountain region (Wing, 1987). Throughout most of the Eocene, broad-leaved evergreens were the dominant component of the forests; broad-leaved deciduous and conifer stands primarily occupied the uplands (Wing, 1987). Examples of the subhumid subtropical to temperate woodlands of the middle to late Eocene are the Yellowstone National Park floras and the Green River flora (Axelrod and Raven, 1985; Wing, 1987). Subsequent climatic deteoriation may be attributed to orographic effects of uplift and the accumulation of thick volcanic piles, as well as southward movement of the North American Plate (Axelrod and Raven, 1985).

CONCLUSIONS

Palynological analysis of the Florissant Lake Beds has contributed to the reconstruction of the regional vegetation and environmental conditions during the early Oligocene. The focus of this study has been primarily to verify or amplify interpretations of former studies which have concentrated on megafossil assemblages (e.g., MacGinitie, 1953) and mechanisms of sedimentation (i.e., McLeroy and Anderson, 1966). The important contributions of this study may be summarized:

(1) The composite palynological record of this study contains many of the plant genera reported in megafossil studies (primarily MacGinitie, 1953) and other palynological studies (primarily Leopold, 1969 a). 78 pollen/spore types are described. Five unreported taxa have been added to the systematic list of plants: Mougeotia (Zygnemataceae), Podocarpus (Podocarpaceae), Pseudotsuga/Larix (Pinaceae), Liquidambar (Hamamelidaceae), Nymphaeaceae (undifferentiated).

(2) Composite abundances of taxa differ significantly between megafossils and pollen/spores (Table 2). Production, transportation and preservation biases account for the disparity in representation of different plant organs in the fossil record.

(3) Stratigraphic comparison of the relative abundance of pollen/spores demonstrates considerable variability in dominance of different plants over the course of the lake history. This variability is attributed to several factors: volcanic disturbances, basin infilling, short-term climatic changes.

(4) The aquatic plant association, dominated by Potamogeton, demonstrates the greatest variability in pollen representation of all paleoassociations.

Variation in *Potamogeton* spp. at different stratigraphic levels indicates response to the marked dynamism of lake conditions (e.g., sudden episodes of deposition, variable lake levels, water quality) regulated by regional volcanism and climate.

(5) As in the megafossil record, Lakeside Forest vegetation dominates the pollen/spore record. TCT-type pollen is the most abundant overall in this study. Limited taxonomic resolution precluded differentiation below the level of the TCT family-group; therefore, ecology based on the pollen is problematic. Of the megafossil taxa present, the pollen most closely resembles that of *Chamaecyparis* and some of the silicified stumps may represent this genus rather than *Sequoia*. Although abundant as leaf megafossils, characteristic *Sequoia* pollen was not encountered.

(6) Paleoassociations representing plants on the mesic bottomlands and slopes of the basin did not fluctuate very much in abundance or diversity. Subaerial deposition from regional volcanism apparently did not significantly alter the terrestrial vegetation near the lake margin for the time interval studied. There is no evidence for catastrophic destruction of terrestrial plants or for succession on a disturbed landscape.

(7) Throughout its history the size of the lake was affected by the efficiency of the containment dam(s), water input from the paleowatershed, and evaporation rates. Late in its history, following extensive infilling, the lake fluctuated in area/volume. The most probable cause for these conditions was relatively dry periods where water input from the watershed declined below the annual evaporative/leakage water loss from the basin. Given the limited size of the watershed and a regionally warm climate, indicated by the flora, this need not have been a "major" climatic event. If similar dry cycles occurred earlier in the lake history,

their effect would probably have been obscured by the buffering effect of a larger lake water volume.

(8) Pollen trends in Potamogeton support inferences of relatively shallow water adjacent to island shorelines and deeper water in the open lake basin.

(9) An alternative model for annual diatom blooms, driven by spring turnover in a thermally stratified lake, is proposed to account for the diatomite/sapropel couplets noted by McLeroy and Anderson (1966).

(10) Palynological correlation of the two sections sampled was not possible.

(11) Fagopsis longifolia, which constitutes >30% of the leaf megaflora, was relatively rare in the pollen record (av. <<1%/sample). This disparity may be a result of low pollen production coupled with a high concentration of plants near the lake margin

(12) Infilling/drainage of the lake(s) had been completed, followed by an indeterminate period of erosion, prior to the deposition of the Upper Tuff unit.

(13) The overall patterns of vegetation dynamics observed in the study sections are compatible with the relatively short lake history suggested by McLeroy and Anderson (1966).

(14) Presence of Potamogeton pollen in the Lower Tuff raises the possibility that the lake may have formed at the onset of or during Lower Tuff time.

Further study of the Florissant Lake Beds should continue to focus on plant succession and correlation of the disjunct exposures. Given the highly dynamic physical conditions of the region during the lake phase, a more detailed palynological analysis utilizing closer sampling, possibly integrated with stratigraphic studies of the megaflora and megafauna, should provide much more information. Interpretation of the geologic and biotic history preserved in these deposits will be fragmented until the temporal relationships of the exposures are better understood.

DESCRIPTIVE NOTES

The average overall abundance and frequency of occurrence of pollen in samples for the described taxa/morphotypes is given according to the following definitions:

highly abundant
- observed in more than 50% of the samples
- average at least 10% per sample

abundant
- observed in more than 50% of the samples
- average 2-9.9% per sample

common
- observed in more than 50% of the samples
- average less than 2% per sample

infrequent
- observed in 20-50% of the samples
- average less than 2% per sample

rare
- observed in 10-20% of the samples
- average less than 0.5% per sample

very rare
- observed in less than 10% of the samples
- 10 or fewer grains observed in the entire study

CRYPTOGAMS

ALGAE

Discussion:

MacGinitie (1953, p. 20) made single mention of the common presence of impressions of the fresh-water alga Nitella (Characeae) but did not include any algae in his systematic list. Algal filaments were observed several times in the palynological samples studied. Their affinity is unknown. Spores from Nitella were not differentiated.

Type 1

(Plate 4-33) Pb 14137-1 40.9/120.8

Description:

Single strands of circular to elliptical cells; average diameter of the cells decreasing from one end of a filament to the other; max. 10 microns, min. 4 microns. Observed length of filaments variable, 15-45 microns.

Discussion:

Filaments very rare.

ZYGNEMATACEAE

Mougeotia Agardh.

(Plate 4-29) Pb 14262-4 47.2/128.7

Description:

Zygospores quadrate with two sides more or less straight or concave and two sides with V-shaped indentation in middle which appears to be an incipient fold. Thickness of wall quite variable, psilate. Usually oval depression in center which resembles a pore (dimensions 7 by 4 microns). Size of spores 18-22 microns, square; often clumped together.

Discussion:

The Florissant spores resemble modern *Cylindrocystis* spp. (cf. Bold and Wynne, 1978, fig. 3.173 c,d) and *Netrium* spp. (cf. Bold and Wynne, 1978, fig. 3.174 b,c).

Cosmopolitan in distribution; presence of *Mougeotia* spores may be indicative of oligotrophic lakes in cool to cold climates (Round, 1965) or stagnant, shallow, mesotrophic fresh-water habitats with optimum growth temperature 10-15 °C (van Geel and van der Hammen, 1978).

This green alga is generally very rare but abundant in one sample of section 8/5/84-1.

FUNGI

Discussion:

MacGinitie (1953) did not report any fungi in his study of the Florissant megafossils. Fungal spores were rarely encountered in this study. When present, they were usually clumped together into groups of 4 or 5.

Two morphotypes are recognized; however, few specimens and limited morphological characteristics precluded concise descriptions and the two groupings are generalized. Further study is necessary to develop understanding of the true diversity and systematic relationships of the Florissant fossil fungi. Their affinity is uncertain.

Type 1

(Plate 1-2) Pb 14137-1 46.0/111.7

Description:

Spores circular in outline, usually folded with crease at center; diameter 10-15 microns; when separated, points of former attachment are not easily identified.

Discussion:

Spores very rare.

Type 2

(Plate 1-3) Pb 14137-1 35.9/115.6

Description:

Grains of this type are generally larger than those of Type 1 and are elliptical in outline. Dimensions 20 by 24 microns for the specimen illustrated. Surface is uniformly psilate with random notches at the margins or perforations of the wall. Former points of attachment to adjacent spores are torn in two places on opposite sides along the long axis of the grain.

Discussion:

Spores very rare.

MONOLETE SPORES

Discussion:

Monolete spores are present in more than three-quarters of the samples, usually contributing from 2-4% of the pollen sum (max. 15%). They are more abundant, but less diverse morphologically, than trilete spores.

The monolete spores are probably members of the family Polypodiaceae. The only fern that MacGinitie (1953) included in his systematic list is Dryopteris (Polypodiaceae). Common as a group.

Type 1

(Plate 1-12) Pb 14137-1 30.1/121.9

Description:

Size range 17 by 29 microns to 20 by 36 microns, always folded (usually one major fold). Psilate.

Discussion:

This type accounts for more than 90% of the observed monolete spores.

Type 2

(Plate 1-4) Pb 14038-2 29.8/128.6

Description:

Size range 30 by 35 microns to 42 by 50 microns. Psilate.

Discussion:

Grains of this type comprise approximately 8% of the monolete spores.

Type 3

(Plate 1-9) Pb 14138-1 34.5/116.0

Description:

Reniform, thick-walled and psilate. Dimensions 28 by 37 microns.

Discussion:

Only one specimen encountered. Possibly modern contaminant.

Type 4

(Plate 1-11) Pb 14020-2 31.9/122.0

Description:

Reniform, conspicuously verrucate-coarsely reticulate, size 28 by 38 microns.

Discussion:

One specimen observed.

Possible botanical affinity:

Possibly a modern contaminant. Dryopteris ? (Polypodiaceae) (remark: MacGinitie included Dryopteris guyottii (Lesquereux) MacGinitie in his systematic list.

TRILETE SPORES

Discussion:

Trilete spores are present in about 1/3 of the study samples, never exceeding 3% of the pollen sum. While numerically less abundant than the monolete spores, the trilete types are morphologically more diverse. Leopold (1969 a) illustrated three trilete spores in a plate of selected Florissant palynomorphs. She identified two as Selaginella spp. Infrequent as a group.

Type 1

(Plate 2-15) Pb 14137-1 35.4/119.0

Description:

Trilete suture open, suture radii extending approximately 1/2 way to equator. Amb circular; maximum equatorial diameter 18-23 (av. 22) microns; exine coarsely rugulate.

Discussion:

Accounts for approximately 15% of trilete spores observed.

Possible botanical affinities:

. Sphagnum Erhart ? (cf. Leopold, 1969 c, fig. 3)

. Lycopodium L. ?

Type 2

(Plate 2-12) Pb 14137-1 39.4/123.7

Description:

Trilete suture closed, rays undulatory (highly contorted) and extending almost to equator; lip surrounds triradiate suture. Amb sub-triangular; maximum equatorial diameter 20-24 microns; exine psilate.

Discussion:

Most common trilete spore (approximately 40% of total trilete spore count).

Possible botanical affinitiy:

Sphagnum Erhart ? (cf. Leopold, 1969 c, fig. 2)

Lycopodium L. ?

Type 3

(Plate 2-6) Pb 14134-1 29.7/129.1

Description:

Trilete suture closed, rays extending nearly to equator. Amb sub-triangular with broadly rounded equatorial "apices"; maximum equatorial diameter 25-32 microns. Surface psilate.

Discussion:

Approximately 10% of total trilete spore count.

Type 4

(Plate 2-8) Pb 14137-1 36.4/117.7

Description:

Trilete suture open, rays extending approximately 3/4 distance to equator. Amb sub-triangular with broadly rounded apices; maximum equatorial diameter 23 microns. Exine psilate and very thin.

Discussion:

Spores very rare.

Type 5

(Plate 2-7) Pb 14157-1 29.9/127.9

Description:

Trilete suture closed, rays extending approximately 3/4 distance to equator. Amb circular; maximum equatorial diameter 54 microns; exine sparsely pitted.

Discussion:

Spores very rare.

Type 6

(Plate 2-10) Pb 14137-1 40.1/121.1

Description:

Trilete suture open, rays extending approximately 3/4 distance to equator. Amb sub-triangular with broadly rounded equatorial "apices". Trilete rays narrow abruptly to pointed ends; maximum equatorial diameter 23 microns.

Discussion:

Only one specimen observed. Possibly a modern contaminant.

Type 7

(Plate 2-11) Pb 14137-1 30.0/121.4

Description:

Trilete suture closed, rays extending approximately 2/3 distance to equator. Amb sub-triangular with broadly rounded equatorial "apices"; maximum equatorial diameter 40-55 microns. Surface psilate except on proximal surface where it is granulate.

Discussion:

Accounts for approx 15% of trilete spores.

Type 8

(Plate 2-14) Pb 14038-3 40.2/111.8

Description:

Grains with cingulum; width of cingulum approximately 5 microns. Relatively small trilete suture, closed, rays extending approximately 1/2 way to equator. Amb sub-triangular with broadly rounded equatorial "apices"; maximum equatorial diameter 37 microns (not including cingulum). Surface granulate.

Discussion:

Spores very rare.

Possible botanical affinity:

Selaginella Spring (cf. Leopold, 1969 a, figs. 2,3; Martin and Rouse, 1966, pl. I, figs. 7,8)

Type 9

(Plate 2-16) Pb 14038-2 31.5/119.2

Description:

Grains with cingulum, width of cingulum approximately 2-3 microns. Trilete suture closed, rays undulatory with thickened margins and extending to equator. Amb sub-triangular with broadly rounded equatorial "apices"; maximum equatorial diameter 25 microns (not including cingulum). Surface finely-granulate.

Discussion:

Spores very rare.

Possible botanical affinity:

Selaginella Spring (cf. Leopold, 1969 , figs. 2,3; Martin and Rouse, 1966, pl. I, figs. 7,8)

GNETOPHYTA

Ephedra L.

Discussion:

MacGinitie (1953) tentatively identified one species of *Ephedra* (*Ephedra miocenica* Wodehouse) from the impression of a branch, although he noted that the preservation of the specimen precluded certain identification.

Leopold (1969 a) illustrated one specimen of *Ephedra* typical of those encountered in this study, in her plate of selected Florissant palynomorphs. Similar to modern *E. nevadensis*.

Modern *Ephedra* spp. are xerophytic shrubs restricted to temperate and tropical areas of southwest United States, Mexico, South America and the Old World.

Pollen infrequent in section 8/5/84-1 and common in section 8/23/84-1. Maximum 1.3% in one sample.

Type 1

a (Plate 1-5) Pb 14142-3 32.2/113.9
b (Plate 1-6) Pb 14151-1 34.9/116.1

Description:

Grains polyplicate with meridional folds; prolate. Shape of poles varies from knob-like to evenly and broadly rounded. Ridges (more than 5 discernable) straight and often obscure; furrows branched and extending almost to poles. Branching sometimes circuitous giving a reticulate appearance. Size dimensions 15 by 42 microns to 24 by 58 microns. Two grains are illustrated to show the variation in size and shape.

Discussion:

This type includes almost all of the observed *Ephedra* specimens.

Type 2

(Plate 1-8) Pb 14136-2 39.0/123.1

Description:

Grains relatively small (14 by 41 microns). Furrows not branched and terminate before reaching poles.

Discussion:

Pollen very rare.

CONIFEROPHYTA

PINACEAE

Abies L.

Description:

Grains vesiculate-bisaccate. They closely resemble specimens of Pinus spp. in the distinction between the bladders and the body of the grain, as well as the angle of bladder attachment. Fir pollen, however, is generally significantly larger, with coarser exine on the body, a thicker cap, and loosely appearing attachment of bladders to the body. Exine is reticulate or granulate-reticulate. A prominent "shoulder-like" indentation is evident where the bladder is attached to the cap. Cap 3-6 microns thick, often thinning near proximal pole; marginal ridge rough.

Discussion:

The seed of one species of Abies (A. longirostris Knowlton) was observed by MacGinitie (1953, p.20). He compared the exserted bracts of the cone scales to those of extant A. venusta of California.

Axelrod (1976) discussed the resemblance of A. longirostris seeds from the Creede flora of Colorado to A. chaneyi Mason from the Mascall and Stinking Water floras of Oregon and suggested a relationship to modern A. delavayi of southern China.

Leopold (1964) noted that even when fir trees are abundant regionally, their pollen tends to be under-represented in surface samples due to rapid settling from the air. This suggests that if fir pollen is abundant, fir trees must have grown quite close to the site of accumulation.

Fir trees occupy upland (montane) sites, generally associated with spruce in boreal and alpine forests in North America.

Three types are described and illustrated to demonstrate the range of variability of pollen within the genus. A gradient of types between these three examples characterizes the specimens observed.

Pollen rare in section 8/5/84-I and abundant in section 8/23/84-I. Maximum 12.8% in one sample.

Type 1

(Plate 1-10) Pb 14151-3 36.9/116.0

Description:

Body dimensions 98 by 86 microns in equatorial view, appearing squared-off. Bladders rounded-rectangular, the long axis of each oriented approximately parallel with polar axis.

Type 2

(Plate 1-7) Pb 14151-1 45.2/119.6

Description:

Body more elliptical and elongate in shape than that of Type 1; dimensions 115 by 67 microns in equatorial view. Bladders attached to body at approximately 45 degree angle to the polar axis.

Type 3

(Plate 1-1) Pb 14151-1 35.5/111.8

Description:

Body elliptical, dimensions 113 by 58 microns in equatorial view. Bladders attached to body at approximately 45 degree angle to the polar axis. Bladder outline diffuse at attachment to body, the two separated by a straight boundary. A membrane connects the two bladders at the distal pole.

Picea L.

Description:

Spruce pollen is distinguished from other bisaccate pollen by the characteristic smooth transition between bladder and cap; the bladders and the body together constitute a grain of continuous (uninterrupted) outline which is overall oval-shaped in equatorial view. Body appears granulate with smooth to reticulate bladders. Two morphotypes are illustrated, differing mainly in size.

Discussion:

Two species of Picea (P. lahontense MacGinitie, P. magna MacGinitie) were differentiated by MacGinitie (1953). However, they together comprised less than 1% of the composite megaflora.

Leopold (1969 a) illustrated two specimens of Picea from the Florissant sediments.

Spruce trees typically occupy montane and boreal environments and some coastal lowlands. Associated trees are fir and sometimes birch and aspen in modern high latitudes.

Pollen rare in section 8/5/84-I and infrequent in section 8/23/84-I. Maximum 1.2% in one sample.

Type 1

(Plate 2-1) Pb 14151-2 35.9/124.4

Description:

Grain length 130 microns.

Type 2

(Plate 2-9) Pb 14019-1 38.2/120.1

Description:

Distal polar view of grain (length 90 microns).

Pinus L.

Description:

Florissant pine pollen is here considered as a complex with several uniting characteristics. Grains are vesiculate-bisaccate. Body size ranges from 44 by 22 microns to 70 by 50 microns; body always larger than bladders. Exine of body granulate to finely-reticulate, bladders coarsely reticulate. Body with cap 1 to 2 microns thick. Position of bladder attachment to body is a major differentiating characteristic. Bladders generally appear well fused to body, the margins at edges of attachment usually diffuse. Five specimens are illustrated to show the morphological diversity of the group.

Discussion:

MacGinitie (1953, p. 21) differentiated three species (P. florissanti Lesquereux, P. hambachi Kirchner, P. wheeleri Cockerell) on the basis of leaves and winged seeds, and indicated that more could likely be identified with further analysis. Material from the three species composed 1.6% of the megaflora.

Leopold (1969 a) illustrated one pollen grain of Pinus. Pine pollen is common in all productive samples of this study contributing from 1-68% (av. ~11%) of the pollen sum.

Extant pine species have a very broad ecological amplitude and cosmopolitan distribution. Their anemophilous pollen is produced in large quantities which may travel great distances from the source. Therefore, low to moderate pine pollen levels suggest a relatively insignificant role for pines in paleoecological reconstructions.

Pollen abundant in section 8/5/84-I and highly abundant in section 8/23/84-I. Maximum 67.8% in one sample.

Type 1

(Plate 3-6) Pb 14137-1 39.8/122.8

Description:

Body highly elongate perpendicular to polar axis, dimensions 47 by 23 microns. Bladders small with respect to body and circular in outline; diameter ~22 microns; attached on flattened distal side of body and extending very little beyond body sides.

Discussion:

Pollen very rare.

Type 2

(Plate 3-2) Pb 14144-1 33.0/115.2

Description:

Body dimensions 50 by 35 microns; cap rounded and remaining three sides somewhat polygonal. Bladders large with respect to body, diameter ~30 microns, attached at approx 45 degree angle to polar axis. Bladders almost meet at distal pole.

Discussion:

Pollen very rare.

Type 3

(Plate 3-5) Pb 14151-3 37.3/115.8

Description:

Body dimensions 62 by 34 microns; distinct shoulder at attachment of bladders. Bladder diameter ~37 microns. Bladders meet at distal pole and extend well beyond th width of the body.

Discussion:

Pollen very rare.

Type 4

(Plate 3-3) Pb 14151-1 47.2/119.5

Description:

Body dimensions 57 by 30 microns. Bladders circular in outline, diameter ~35 microns. Bladders attached at approximately 35-40 degrees off polar axis, well separated at distal pole.

Discussion:

About one-half of the Pinus grains observed.

Type 5

(Plate 3-4) Pb 14157-1 36.0/129.0

Description:

Body dimensions 63 by 45 microns. Bladders distinct and elliptical in outline; dimensions 50 by 30 microns. Long dimension of bladders parallel with polar axis; well separated at distal pole.

Discussion:

About one-half of the Pinus grains observed.

Pseudotsuga Carr./Larix Mill.

(Plate 2-13) Pb 14151-4 33.4/118.2

Description:

Ellipsoidal grains, often folded and/or ruptured to form a furrow-like area. Psilate exine. 85->110 microns in long dimension.

Discussion:

Since only two pollen specimens have been observed and the distinguishing exine characteristics are very limited, it is difficult to assign these grains to either Pseudotsuga or Larix. Descriptions and plates of modern species of these two genera usually ally these larger grains to Pseudotsuga spp.

There is no report of either Pseudotsuga or Larix in previous studies of the Florissant fossil leaves or pollen and spores.

Douglas-fir is a common element of coastal and interior forests of northwestern North America. It is also present in scattered forests of southwest China, Japan and Taiwan. These trees are most commonly found on well-drained, loamy sites where an abundance of moisture is present. Some forest associates in the Pacific Northwest include Thuja, Tsuga, Picea and Abies.

Larch and tamarack are widely distributed in north temperate and boreal forests of North America, Europe and Asia. In the southern part of their range, these intolerant trees occupy cool swamps and bogs. Further to the north, they are commonly found on moist benches and better drained uplands. Common associates include Abies, Populus, Betula and some Pinus.

Two specimens were observed in a single sample (8/5/84-I, 61) of this study.

PODOCARPACEAE

Podocarpus L'Herit. ex Pers.

(Plate 3-1) Pb 14016-2 38.2/117.4

Description:

Grains vesiculate-bisaccate. As compared to bisaccate members of the Pinaceae, the body of Podocarpus-types is relatively small with respect to the size of the bladders. Body dimensions 48 by 39 microns; bladder dimensions 60 by 46 microns. Bladders appear loosely attached to body. Cap highly convoluted; bladders coarsely reticulate.

Discussion:

Fossils of Podocarpus have not been noted in any previous studies of the Florissant flora.

These evergreen trees and shrubs today are widely distributed in tropical to warm-temperate moist woodlands and mountains worldwide, but are concentrated in the southern hemisphere (Piel, 1971; Bassett, et. al., 1978). Studies suggest presence of Podocarpus fossils as indicative of upland habitats because representation is generally limited to rare shoot fragments and pollen (Hopkins, 1967; Smiley and Rember, 1981).

Dilcher (1969) identified Podocarpus cuticle from a leafy shoot in Eocene deposits of western Tennessee. He noted that the pollen record of Podocarpus has formerly not been considered to extend into Tertiary sediments of North America. However, megafossil reports of Podocarpus in the Mississippi embayment area and wood from Eocene sediments in Washington indicate that Podocarpus was present in North America during the early Tertiary. He concludes: "The Eocene Podocarpus described in this paper and the numerous reports of Podocarpus pollen from Mesozoic sediments in widely scattered areas of the northern hemisphere are remnants of a much more northern extension of Podocarpus rather than a recent northernmost expansion of a southern element" (Dilcher, 1969, pp. 300-301).

Subsequent reports of Podocarpus pollen have documented its presence in North America well into the Tertiary. In a palynological study of early Oligocene Alexandria-Narcosli sediments from central British Columbia, Piel (1971) identified three distinct types of Podocarpus pollen. Hopkins (1967) identified Podocarpus pollen from Eocene-Oligocene sediments of the Coos Bay area, Oregon. Podocarpus pollen has been recovered from sediments as young as the early Miocene Clarkia Lake flora of northern Idaho (Smiley and

Rember, 1981) and the middle Miocene Succor Creek flora of Idaho-Oregon (Taggart, 1971). It is possible that Podocarpus spp. of western North American Tertiary floras were derived from temperate Asian forms which inhabited sheltered mesic lowlands rather than exposed upland sites as many southern hemisphere types occupy today (Taggart, 1971).

Only three specimens were observed in the samples studied, limited to different samples of section 8/5/84-I.

TAXODIACEAE, CUPRESSACEAE, TAXACEAE

Description:

Pollen of the families Taxodiaceae, Cupressaceae, and Taxaceae (TCT; collectively referred in discussion as "taxodiaceous") are difficult to differentiate with the light microscope. Based on observations of his reference collection, Traverse (1955, p. 40) comments that the generic differentiation of taxodiaceous pollen is not as difficult as some writers indicate, and he assigns Brandon Lignite specimens to a new species of the genus Glyptostrobus (Taxodiaceae). His primary criterion for distinguishing genera is the presence, size and shape of a germinal papilla.

This author's observation of Chamaecyparis lawsoniana, Taxodium distichum, and Sequoia sempervirens in the Michigan State University paleobotanical pollen reference collection suggests that the papilla is a relatively frequent characteristic (approximately 80%) of Sequoia sempervirens and is absent in Chamaecyparis lawsoniana and Taxodium distichum. Also variable within each of these genera is the presence of pores, V-shaped rupture, and elongation of the grains.

On Florissant specimens, the papilla is absent and the other characteristics are highly variable. If the large fossil stumps are properly identified as members of the genus Sequoia, it is possible that the pollen of Florissant grains represents non-papillate Sequoia-type. However, the Florissant pollen specimens are remarkably similar to Chamaecyparis lawsoniana of the Michigan State University reference collection. This is corroborated by the recovery of nearly three times more leaf fossils of Chamaecyparis than Sequoia (MacGinitie, 1953). Therefore, until further taxonomic study of the specimens is completed, assignment of Florissant material to any particular taxodiaceous or cupressaceous genus must be considered untenable; they will be referred to collectively as "TCT".

Leopold (1969 a) illustrated a typical Florissant specimen as "Taxodiaceae, Taxodium-type".

Discussion:

The leaf megafossil record includes Sequoia affinis (Taxodiaceae, 2.2%), Chamaecyparis linguaefolia (Cupressaceae, 6.3%) and Torreya geometrorum (Taxaceae, < 0.1%); Taxodium spp. are absent (MacGinitie, 1953). Therefore, if pollen production volume per plant of each of the represented species is similar and they were growing under the same ecological conditions, Chamaecyparis pollen might be expected to be more abundant than that of Sequoia.

Most studies of the Florissant deposits include mention of the abundant silicified Sequoia stumps (Scudder, 1882, p. 284; Cockerell, 1906, p. 175; Knowlton, 1916, p. 243; MacGinitie, 1953, p. 21; McLeroy and Anderson, 1966, p. 607). While there appears to be a consensus on the generic identity of these stumps, the evidence for this association seems to be based on a uniformitarian analogy (i.e., size of coast redwood) rather than shared anatomical characteristics. The California coast redwood, S. sempervirens, has similar foliage and cones to Florissant material (MacGinitie, 1953, p. 21).

These trees commonly reach 8-12 ft. in diameter and 340 ft. in height (Wodehouse, 1959, p. 269). *Chamaecyparis lawsoniana* of southwest Oregon and northwest California is known to reach 16 ft. in diameter with a height of 240 ft. (Harlow, et. al., 1979, p. 202). *Chamaecyparis formosensis* Matsum. of Taiwan can reach a diameter of 23 ft. (Harlow, et. al., 1979, p. 199). The large diameter of the fossil stumps alone is insufficient evidence for identification. The abundance of *Chamaecyparis* foliage and the comparable size of the mature trees to the fossil stumps must qualify it for further consideration. In the absence of comparative anatomical studies (i.e., thin sections) of a large number of Florissant wood specimens with modern taxodiaceous genera, their designation to the genus *Sequoia* must be tentative.

Sequoia sempervirens is confined to temperate fog-belt areas of west coast North America and inhabits moist, but well-drained slopes and valleys. Extinct *Sequoia* spp. were widespread in forests of the Northern Hemisphere during the Tertiary Period. *Chamaecyparis* spp. typically occupy freshwater swamps and bogs or humid forests of coastal eastern and western North America (Harlow, et. al., 1979).

Type 1

a	(Plate 2-3)	Pb 14142-1	43.9/115.5
b	(Plate 2-4)	Pb 14155-1	28.2/121.9
c	(Plate 2-2)	Pb 14155-1	31.8/118.9
d	(Plate 2-5)	Pb 14020-2	33.9/114.8

Description:

Grains circular in outline, usually (90% of the time) with a ruptured exine. The exine has a finely granulate surface, occasionally with conspicuous, widely and irregularly spaced verrucae. Diameter ranges from 24 to 32 microns, averaging 30 microns.

Four specimens are illustrated to show the range of morphological variability within the type. Type 1 (a) is overwhelmingly the most abundant morphotype encountered.

Discussion:

This is the most abundant pollen type in the Florissant sediments. It is found in almost all samples, reaching a maximum of ~75% of the pollen sum and averaging ~26%.

MONOCOTYLEDONAE

GRAMINEAE

Description:

Given the limited pollen morphological variability between the large number of grass family genera, as well as the relatively broad ecological occurrence of the group, this study will not attempt to identify below the family level.

Three types are differentiated and illustrated. All are monoporate with a pronounced, thickened annulus surrounding the pore.

Discussion:

MacGinitie (1953) identified one species of grass represented by fossil fruits, Stipa florissanti (Knowlton) MacGinitie.

Grass pollen is common in section 8/5/84-I and rare in section 8/23/84-I. Maximum 1.5% in one sample.

Type 1

(Plate 3-10) Pb 14142-2 43.0/116.3

Description:

These grains are psilate and circular in outline, accounting for the majority of observed grass pollen. Diameter ranges from 19 microns to 25 microns (ave. 23 microns). Annulus is very well-developed; thickened. Exine is psilate to faintly scabrate. All grains display one or two folds.

Type 2

(Plate 3-7) Pb 14148-2 29.0/114.3

Description:

Only a few of these grains were observed. It differs from Type 1 grains in having a microreticulate exine.

POTAMOGETONACEAE

Potamogeton L.

(Plate 3-14) Pb 14023-2 43.6/117.5

Description:

Aporate pollen grains with distinctive coarsely reticulate-rugulate exine. Grains spherical, ranging from 30-37 microns in diameter (av. ~34 microns), commonly with 3 or 4 folds. They often (approx. 40% of grains) have a rounded to angular dark spot (occasionally 2 or 3) which sometimes appears pore-like, up to 6 microns in diameter; a ghost of the exine generally appears through the spot.

Discussion:

The genus Potamogeton is classified by MacGinitie (1953) in the category incertae sedis, comprising 0.4% of the leaf megaflora. He also includes in this category Najadopsis and Paleopotamogeton.

Pondweed is a floating or submerged aquatic which may occupy positions from shallow ponds to deep areas of lakes, sometimes forming extensive beds. Preferred temperature of the water body is variable among species, and some species are tolerant of calcareous or brackish conditions. Because of these broad ecological requirements, evidence of Potamogeton pollen will not provide much insight into the depth, temperature or chemistry of Lake Florissant. Its many species are distributed throughout the northern United States and Canada.

Lewis, et. al. (1983) note that most Potamogeton spp. are anemophilous and produce small quantities of pollen.

Potamogeton pollen occurs in most of the palynological samples, contributing up to 79% of the pollen sum (av. 18.8%) and is co-dominant in most pollen spectra with TCT-types.

The large quantities of pollen noted in this study are therefore suggestive of extensive development of Potamogeton "beds" and possibly of relatively shallow water and/or high water clarity.

TYPHACEAE (SPARGANIACEAE)

Typha L. (Sparganium L.)

Discussion:

Typha lesquereuxii Cockerell comprises 5.8% of the leaf fossils, ranking fourth in abundance among all plant species (MacGinitie, 1953). Since no megafossil specimens of Sparganium have been reported, the Florissant pollen is likely Typha. For inventory and paleoecological discussions in this study, the grains will be referred to Typha even though, in the absence of other evidence, pollen of the two genera is difficult to distinguish.

Leopold (1969 a) illustrated one specimen of Typha/Sparganium in a plate of Florissant palynomorphs which resembles a cross between the two grains illustrated here.

Cattail can be found along riverbanks and in swamps and marshes in temperate to tropical climates throughout the world, except south of the equator in Africa. Species of bur reed are widespread temperate to subtropical aquatics, occupying swampy margins of ponds, lakes and streams. Some species may be found in deeper waters. Most extant western North American species are tolerant of acidic, shallow, soft-bottomed, temporary ponds.

Type 1

(Plate 3-12) Pb 14143-1 35.4/118.3

Description:

Grains monoporate, spherical and often folded. Pore margin indistinct. Thin exine with reticulate thickenings. Diameter 25-30 microns.

Discussion:

These specimens occurred in about 1/2 of the palynological samples, averaging about 1% overall and about 2% when present (maximum 4%).

Pollen common in section 8/5/84-I and infrequent in section 8/23/84-I. Maximum 4.0% in one sample.

Type 2

(Plate 3-13) Pb 14249-3 36.5/117.5

Description:

Tectate, circular grains, less commonly folded than Type 1. Diameter 30-35 microns. Single pore usually evident but margin merges with sculpturing pattern. Reticulation coarse. Closely resembles *T. angustifolia* (cf. Huang, 1972, pl. 177)

Discussion:

Pollen rare.

DICOTYLEDONAE

ACERACEAE

Acer L./*Dipteronia* Oliv.

Description:

Grains tricolpate with furrows extending almost to the poles which are indented. Exine is conspicuously striato-baculate or striato-granulate, the striations generally oriented longitudinally. All grains are prolate. Three types are differentiated.

Discussion:

MacGinitie (1953) recognized 5 species of Aceraceae in the leaf fossil record: *A. coloradense* MacGinitie, *A. florissanti* Kirchner, *A. heterodentatum* (Chaney) MacGinitie, *A. oregonianum* Knowlton, *Dipteronia insignis* (Lesquereux) Brown. Only one of these species, *A. florissanti* (0.5%), is represented in his list of species occurrences contributing greater than or equal to 0.1% of the total.

The family is equally low in abundance in the pollen record. *Acer* spp. were infrequent in the palynological samples of both sections. Leopold (1969 a) illustrated a specimen which resembles *Type 3*.

Maple pollen is generally highly under-represented in pollen records, probably because most species are entomophilous and produce small amounts of pollen per flower (Leopold, 1964; Meeuse, 1961).

Dipteronia leaf fossils also occur in the Republic flora of Washington and the Bridge Creek flora of Oregon. Its present distribution is confined to central and southern China. Erdtman (1952) describes and illustrates modern pollen of the genus. The description cannot be differentiated from *Acer* but the striations of his pen drawing appear to be less conspicuous than striations on Acer. He also notes that pollen of the Aceraceae is similar to that of the Sapindaceae.

Maple trees are a common element of the mixed mesophytic deciduous forest of North America.

Type 1

(Plate 4-7) Pb 14154-4 28.7/109.4

Description:

These grains measure 27-33 microns in the polar dimension and 19-23 microns equatorially. The striations are relatively coarse.

Type 2

(Plate 4-6) Pb 14249-2 45.6/128.0

Description:

These grains measure 18-23 microns in the polar dimension and 16-19 microns equatorially. The striations are relatively fine.

Type 3

(Plate 4-8) Pb 14143-1 31.0/128.1

Description:

Only one of these grains was observed. In polar view, its equatorial dimension is 45 microns. The colpi are very broad and open. The striato-baculae are very narrow and randomly oriented.

Type 4

(Plate 4-9) Pb 14144-1 45.6/123.2

Description:

Tricolp(or)ate (?), spherical, diameter 35 microns. Characteristically baculate (baculae up to 2 microns long), arranged in short striae.

Discussion:

One specimen observed; possibly a modern contaminant.

AQUIFOLIACEAE

Ilex L.

(Plate 4-12) Pb 14143-1 43.4/116.4

Description:

Grains tricolporate with wide furrows narrowing at the equator and transversely elliptical ora. The exine is conspicuously clavate, the individual clavae more than 2 microns in length. Polar diameter of these prolate grains is 30 microns and equatorial diameter 20 microns.

Discussion:

MacGinitie (1953) has classified Ilex knightiaefolia Lesquereux in the category incertae sedis and it contributed less than 0.1% to the leaf fossils.

This is the first known occurrence of Ilex in the Florissant pollen record. One specimen was observed; therefore, it may be a contaminant.

Modern holly consists of nearly 400 species of evergreen or deciduous trees and shrubs distributed throuthout the world, except Australia. It is entomophilous and typically occupies warm-temperate to subtropical bogs and swamps (Gibson, 1901; Hopkins, 1967).

CHENOPODIACEAE/AMARANTHACEAE

Description:

Grains periporate (pores 15-35), pores strongly aspidate and evenly dispersed over the entire grain. Specimens are spherical and rarely folded. Grains are thickly tectate (up to 2 microns thick) with finely-granulate surface. Three types are differentiated and may represent individual species.

Discussion:

Since pollen of the families Chenopodiaceae and Amaranthaceae are difficult to morphologically differentiate with the light microscope, the families are generally discussed together in pollen studies under the designation "Cheno-Am", a convention that will be followed here. Neither family was represented in the megaflora reported by MacGinitie (1953).

Cheno-Am pollen occurs regularly in the samples studied, but is rarely abundant; most is Type 1. It usually contributes to between 1% and 5% of the pollen sum of a sample (av. 2%).

Lambs Quarters, Sarcobatus spp., and other members of these two herbaceous families are generally characteristic of xeric sites and often indicate the re-establishment stage of secondary succession.

Type 1

(Plate 4-32) Pb 14151-1 46.7/122.8

Type 2

(Plate 4-30) Pb 14138-1 29.6/119.4

Description:

Type 1 is differentiated from Type 2 based exclusively on size criteria. Leopold (1969 a) illustrates two grains resembling these types and designates them Chenopodiaceae, Sarcobatus-type. The pores of both are relatively large (dia. 2-4 microns). Histogram representation of size variation of observed specimens shows a bimodal distribution clustering at 25 microns and 30 microns. Type 1 includes all specimens whose diameter falls between 17 microns and 27 microns (av. 24 microns). Type 2 includes grains within the 28 microns to 33 microns diameter range.

Discussion:

Pollen common in both sections. Most observed Cheno-Am grains were <u>Type 1</u>.

<u>Type 3</u>

(Plate 4-31) Pb 14154-4 33.7/122.5

Description:

The grains are small (dia. 17-22 microns) and have distinctly small (dia. 1-1.5 microns) pores whose annuli may be inconspicuous.

Discussion:

Pollen very rare.

COMPOSITAE

(Plate 4-16) Pb 14262-4 43.2/126.1

Description:

Grains tricolpate, colpi deeply-incised in polar view, amb sub-triangular. Diameter from side to opposing colpus 18 microns. Exine thick, very coarsely echinate (2-3 microns long, spaced 1-2 microns.

Discussion:

Very rare. Possibly a contaminant.

FAGACEAE

<u>Castanea</u> Mill.

(Plate 4-23) Pb 14143-1 43.5/117.0

Description:

Grains tricolporate and prolate, 14-16 by 11-14 microns. Pores transversely elliptical. Exine psilate.

Discussion:

MacGinitie recovered a small number (0.2% of total examined) of Castanea dolichophylla Cockerell leaves from the lake shales.

Modern chestnut trees may be found in mesic woodlands throughout the northern hemisphere.

Pollen very rare in section 8/5/84-I and infrequent in section 8/23/84-I).

Fagopsis longifolia (Lesq.) Hollick

(Plate 4-18) Pb 14249-3 36.2/123.3

Description:

Grains tricolporate and spherical, furrows extending almost to poles and generally appear as closed partings in the exine. Diameter 20-25 microns (av. 22 microns); exine psilate to finely-verrucate or granulate.

Discussion:

This extinct monotypic genus was first classified as Planera (Ulmaceae) by Lesquereux (1883). Hollick (1909) reclassified and renamed it Fagopsis longifolia (Lesq.) Hollick and attributed it to the Fagaceae. MacGinitie (1953) further classified it as a member of the Betulaceae based on "cones".

Leopold (in MacGinitie, 1969) and Manchester and Crane (1983) have since confirmed its membership to the Fagaceae in detailed studies of the leaves, flowers, fruits and pollen utilizing SEM and TEM. Manchester and Crane (1983) isolated and described pollen removed from an anther of a staminate inflorescence. This has provided evidence for the pollen morphology and has therefore been particularly useful in this study.

Fagopsis leaves have also been found in the Republic flora of Washington (early-middle Eocene), the Red Rock Ranch flora of New Mexico (early Oligocene), the Beaverhead Basins (early-middle Oligocene) and Ruby Paper

Shales (middle-late Oligocene) floras of Montana, and in unspecified Miocene sediments (Becker, 1961, p. 18; Becker, 1969, p. 22; Manchester and Crane, 1983, p. 1162; Axelrod and Bailey, 1976, p. 237).

Fagopsis longifolia is the most abundant leaf fossil in the Florissant megaflora, accounting for 30.1% of the specimens (MacGinitie, 1953). Paradoxically, its contribution to the pollen flora is negligible (absent in section 8/5/84-I; very rare in section 8/23/84-I). According to Manchester and Crane (1983), the pollen of Fagopsis longifolia, although distinctive, is quite similar to that of Quercus spp. Quercus pollen is quite abundant in the microflora, averaging 4.3% of the pollen sum of the samples. Suggested explanations for the leaf/pollen representational disparities of these two genera are offered in the Floral Composition section.

Quercus L.

Type 1

(Plate 4-22) Pb 14249-3 28.4/119.6

Type 2

(Plate 4-20) Pb 14138-1 40.6/113.5

Type 3

(Plate 4-26) Pb 14157-1 32.5/123.2

Type 4

(Plate 4-19) Pb 14151-1 41.8/126.0

Description:

Grains tricol(por)ate, prolate with deeply dissecting furrows commonly extending almost to poles and spread apart. Broad range of sizes varying from 16 by 20 microns to 28 by 38 microns. Exine faintly- to coarsely-granulate or irregularly spaced warty verrucae.

There is no clearcut morphological division to separate the observed specimens into separate species, although it is expected that at least several of the 10 oak species listed by MacGinitie (1953) are represented. Therefore, Quercus pollen is considered as a complex and four grains are illustrated to show the gradient of sizes and sculpturing elements which were encountered in the samples studied.

Discussion:

MacGinitie (1953) recognized 10 species of oak in the leaf flora, contributing 2.0% of the total: Q. dumosoides MacGinitie, Q. knowltoniana Cockerell, Q. lyratiformis Cockerell, Q. mohavensis Axelrod, Q. orbata sp. nov., Q. peritula Cockerell, Q. predayana MacGinitie, Q. scottii (Lesq.) MacGinitie, Q. scudderi Knowlton, incertae sedis, Q. balaninorum Cockerell.

Leopold (1969 a) illustrated one specimen of Quercus pollen from the Florissant shales.

The genus has relatively broad ecological amplitude and wide modern distribution. Oak is commonly a dominant tree of the mesic deciduous forests of the temperate northern hemisphere. Some dwarf evergreen species are adapted to xeric habitats of northern Mexico and southwestern United States. MacGinitie (1953) suggests that the Florissant oaks were like the latter ecotype, occupying the high-ground of the region.

Pollen abundant in both sections.

HAMAMELIDACEAE

Liquidambar L.

(Plate 4-27) Pb 14154-1 37.1/120.8

Description:

Grains 8-15+ periporate; pores covered by characteristic persistent membrane with verrucae; pores large (dia. 3-5 microns), irregularly outlined, and unevenly but randomly scattered. Grains finely-reticulate; dia. 27-38 microns (av. 29microns). The distinctive appearance of these grains is not easily confused with any of the other Florissant palynomorphs.

Discussion:

This is the first record of any organ of Liquidambar in the Florissant shales.

Pollen very rare in section 8/5/84-I and infrequent in section 8/23/84-I.

Liquidambar fossils are also present in many other mid-Tertiary floras.

Sweetgum is often a component of oak-hickory forests of warm-temperate regions of the northern hemisphere (Hopkins, 1967). It also occurs in almost monotypic stands following clear-cuts in both Illinois and montane Mexico (Prof. R. E. Taggart, pers. comm.).

JUGLANDACEAE

Carya Nutt.

Discussion:

Carya leaf fossils contributed 1.0% of MacGinitie's (1953) systematic list.

Pollen of the genus has also been reported by Leopold (1969 a, figs. 26, 27).

Hickory is commonly a dominant tree of the mesic deciduous forests of the temperate northern hemisphere on bottomland or upland sites; commonly co-dominant with oak.

Pollen abundant in both sections.

Type 1

(Plate 3-16) Pb 14016-1 40.4/117.3

Description:

Triporate pollen grains with relatively large; circular pores (dia. 3-5 microns). Pores heteropolar; equally spaced near the equator. Amb circular to sub-triangular (pores near "apices"); grain dia. 31-45 microns (av. approximately 40 microns). Exine faintly scabrate to granulate.

When grain diameters are plotted on a histogram, a unimodal curve results with a peak in the 40 to 43 microns range. While the size range of the grains is quite broad, the histogram data does not suggest that the genus should be divided into distinct types based on size criteria.

This type accounts for most of the tabulated Carya grains.

Type 2

(Plate 3-18) Pb 14249-3 27.8/128.5

Description:

Grains triporate with very large pores relative to the size of the grain; pore diameter 4 microns; strongly heteropolar. Grains thin-walled and often folded into a distorted shape; however, unfolded grains are circular in outline. Grain diameter 22-28 microns. Exine finely-granulate to psilate.

Discussion:

The few samples containing these specimens are primarily from section 8/23/84-I.

Type 3

(Plate 3-17) Pb 14262-4 29.8/124.8

Description:

Grains triporate, heteropolar, with large (dia. 3-4 microns), annulate pores. Average grain diameter 28 microns. Amb circular; intectate; exine granulate.

Discussion:

Specimens of this type have been observed in only two samples of section 8/23/84-I.

Engelhardia Lesch. (Momipites Wodehouse)

(Plate 3-20) Pb 14157-1 37.2/124.4

Description:

Grains triporate, amb straight- to slightly convex- triangular with pores at the rounded apices. Diameter from pore to opposite margin 20-28 microns. Exine surface finely-granulate to scabrate.

Some of these grains possess two white streaks resembling the description of Momipites coryloides Wodehouse by Frederiksen (1980). Occasionally, a trans-polar crease is evident as in Platycarya described by Leopold and MacGinitie (1972).

Discussion:

Dilmy (1955) discusses the confusion of the spelling of the genus in the literature (Engelhardia vs. Engelhardtia). He notes the correct original spelling to be Engelhardia.

Engelhardia was not included in MacGinitie's (1953) systematic list of megafossils.

Leopold (1969 a) illustrated a Florissant specimen with uncertain identity to Engelhardtia.

Extant species of the genus exist in tropical to subtropical climates of Mexico, Central America, and southeast Asia (Piel, 1971). The pollen appears in early Tertiary sediments when its geographic range was much more extensive than that of today (northern S. America to arctic) (Graham.1972).

Pollen infrequent in section 8/5/84-I and common in section 8/23/84-I.

Juglans L.

(Plate 4-17) Pb 14138-1 27.9/122.8

Description:

Grains periporate (12-25 pores, av. 16) and spherical; heteropolar with many of the pores concentrated near the equator; pores aspidate (annular thickenings 5-7 microns across); pore dia. approximately 2 microns. Exine surface finely-granulate to psilate. Grain diameter 27-40 microns (av. 35 microns).

Discussion:

Juglans leaves do not occur in the megaflora (MacGinitie (1953). However, walnut pollen appears in most samples of this study and usually contributes about 4% to the pollen sum.

Leopold (1969 a, fig. 31) illustrates one grain of Juglans from the Florissant sediments.

Walnut trees are a common deciduous element of the mixed mesophytic forest and are usually characteristic of rich soils.

Pollen abundant in section 8/5/84-I and common in section 8/23/84-I. In one sample, Juglans accounts for almost 60% of the pollen sum.

NYMPHAEACEAE

(Plate 4-2) Pb 14249-2 45.6/128.0

Description:

Grains tri(tetra-?)porate, spherical, diameter 30-34 microns. Distinctly echinate (spines 1-3 microns long), spines distributed evenly and spaced approximately 3-4 microns apart.

Discussion:

Pollen very rare.

Potential affinities:

Lotus ?, Nelumbo ?, Nymphaea ?, Nuphar ?

All are aquatic plants of cosmopolitan distribution in tropical to temperate climates. All are entomophilous and therefore generally poorly represented in palynological samples.

alternative family: Malvaceae?

PROTEACEAE/SAPINDACEAE/ELAEAGNACEAE

(Plate 4-1) Pb 14154-4 28.6/115.0

Description:

Grains triporate; oblate; amb triangular with irregular (undulating) margins; indented at poles with creases extending from equatorial pores to poles. Pores ragged and V-shaped from polar view and located at "apices" of amb. Diameter from pore to opposite side ranges from 30-45 microns. Exine surface reticulate-rugulate.

Discussion:

Pollen very rare.

Remark: MacGinitie (1953) lists two species of Sapindaceae, Athayana (2.3% of leaves), Sapindus (1.1% of leaves).

Potential affinities:

-Proteaceae?: MacGinitie (1953) identified *Lomatia lineata* (Lesq.) comb. nov., from leaf fossils.

Most modern genera are xerophytic and restricted to the southern hemisphere, indicative of a long annual dry season (Hopkins, 1967).

-Sapindaceae?: Leopold (1969 a), fig. 18, *Cardiospermum* !! L. (from Florissant); Huang (1972), pl. 138 figs.14-15, *Cardiospermum*.

-Elaeagnaceae?: Leopold (1969 d) figs. 34-35, *Shepherdia* Nutt.; Frederiksen (1980), pl. 14, fig.14, *Boehlensipollis hohlii*; McAndrews, et. al. (1973), fig. 13 B, *Shepherdia argenta*.

SALICACEAE

Populus L.

(Plate 3-9) Pb 14143-1 39.0/128.7

Description:

Grains inaperturate; spherical but usually folded around edges. Diameter 20-24 microns. Exine scabrate-verrucate.

Discussion:

MacGinitie (1953) identified three species of poplar based on leaf compressions: *Populus crassa* (Lesq.) Cockerell (5.0% of leaves); *Populites heeri* (Lesq.) MacGinitie *incertae sedis*; and *Populus pyrifolia* Kirchner. The disparity between the pollen and leaf records may be a consequence of the high susceptibility of pollen to destruction prior to fossilization.

Aspen, poplar or cottonwood trees have a cosmopolitan distribution in temperate to tropical climates. They may be found on riparian sites (lakes or streams) or as opportunists on disturbed sites.

Pollen very rare.

Salix L.

Description:

Grains tricolpate, colpi extending nearly the full length of the grain.

Discussion:

MacGinitie (1953) includes four species of Salix in his systematic list, comprising 1.1% of the leaf fossils in sum: Salix libbeyi Lesquereux, S. ramaleyi Cockerell, S. coloradica MacGinitie, S. taxifolioides MacGinitie.

Leaf fossils are common in the middle and upper Tertiary, but rare in the lower Tertiary (MacGinitie, 1953).

Leopold (1969 a) illustrated one specimen of Salix? pollen.

Willow often holds a dominant position along streams and lakes of temperate regions worldwide.

Pollen common in both sections. More than 95% of the grains are Type 1.

Type 1

(Plate 4-11) Pb 14038-2 32.7/114.5

Description:

Shape prolate; dimensions 17 by 22 microns to 22 by 32 microns. Exine distinctive coarsely-reticulate between the furrows but diminishing within them.

Type 2

(Plate 4-10) Pb 14157-1 33.4/118.5

Description:

Same characteristics as Type 1 but more spheroidal and larger (diameter 26-38 microns)

TILIACEAE

Tilia L.

(Plate 4-14) Pb 14262-1 39.2/116.1

Description:

Grains tetraporate (tetracolpate?); pores U-shaped and equatorial. Amb circular to rounded quadrangular. Diameter approximately 20 microns. Exine reticulate.

Discussion:

MacGinitie (1953) identified *Tilia populifolia* Lesquereux leaf impressions which are extremely rare in the Florissant shales.

Alternative affinities:

Intratriporopollenites stavensis Frederiksen (triporate, but discussed as rarely tetraporate), Frederiksen (1980), pl. 14, fig. 17 (bot. aff. Tiliaceae)

Fremontia Torr.? (*Fremontodendron* Cov.?) (Sterculiaceae) ; Leopold (1969 b, #33)

Basswood occurs in temperate deciduous forests and along streams throughout the northern hemisphere.

Pollen very rare.

ULMACEAE

Celtis L.

Discussion:

MacGinitie (1953) recognized one species of hackberry in the leaf flora. *Celtis mecoshii* Lesquereux.

Leopold (1969 a, #30) illustrated a *Type 1* specimen without systematic designation.

Pollen common in section 8/5/84-I and abundant in section 8/23/84-I.

Modern hackberry trees are often found on disturbed sites.

Type 1

(Plate 4-21) Pb 14149-1 32.7/119.2

Description:

Grains triporate; two of the pores heteropolar, the other pore equatorial. Pores incipiently aspidate; pore diameter 2 microns. Amb sub-circular to rounded triangular. Exine finely-granulate to psilate. Grain diameter approx. 22-28 microns (av. 25 microns). One or two folds typically cross the grains.

Discussion:

More common than Type 2.

Type 2

(Plate 3-15) Pb 14151-3 37.8/119.2

Description:

Grains triporate (rarely tetraporate), slightly heteropolar. Pores large (4-5 microns) and strongly aspidate with narrow but highly protruding annulus. Amb circular. Exine psilate to finely-granulate. Grain diameter 28-33 microns. Most grains have small folds which do not affect shape.

Ulmus L./Zelkova Spach.

Discussion:

Elm pollen is well represented in both the fossil pollen and leaf floras. The genera Ulmus and Zelkova are discussed together because their pollen are difficult to differentiate morphologically.

MacGinitie (1953) reported one species of each genus, Ulmus tenuinervis Lesquereux (1.3% of leaf fossils) and Zelkova drymeja (Lesq.) Brown (9.6% leaf fossils). Together, they contributed 10.9% of the Florissant leaf megafossils, ranking second in abundance to Fagopsis longifolia.

Ulmus/Zelkova spp. are common elements of other western North American mid-Tertiary floras.

Leaf fossils of Zelkova spp. are also present in the Green River, Bridge Creek, and Latah floras.

Elm trees are widespread in temperate regions of the northern hemisphere, occupying an often dominant position in lowland deciduous forests; often early successional.

Pollen abundant in both sections.

Type 1

(Plate 4-5) Pb 14252-2 37.3/112.5

Description:

Grains 5-stephanoporate (common range 4-6); heteropolar; pores large (3-5 microns) and sometimes slightly annulate; amb semicircular-subangular (polygonal); exine surface coarsely rugulate, giving a distinctive faint convoluted appearance; diameter 25-40 microns (av. 31-33 microns). Histogram representation of the range in size shows no bimodal distribution that might suggest separation into more than one type.

Discussion:

This type accounts for more than 95% of Ulmus/Zelkova pollen grains in the samples studied.

Type 2

(Plate 4-4) Pb 14023-2 30.6/113.3

Description:

Grains triporate and smaller (diameter av. 26 microns) than Type 1. Characteristic Ulmus/Zelkova rugulate appearance.

Discussion:

Very rare.

Type 3

(Plate 4-3) Pb 14019-3 37.0/119.8

Description:

Grains tetraporate; pores situated along the equator; pore diameter 3 microns; slightly aspidate. Amb circular-quadrangular. Exine tectate and very thick; the grains appear very rigid and dense, never folded. Surface coarsely foveolate. Grain diameter 25-30 microns.

The surface of the specimens has a coarse topography which closely resembles that of other Ulmus/Zelkova types, but the muri are definitely more circular than elongate (i.e. not rugulate). The wall is thicker than the other Ulmus/Zelkova types described and heteropolarity is not apparent.

Discussion:

Pollen limited to one sample.

UNIDENTIFIED MORPHOTYPES (UM)

UM 1 (MULTIPORATE in pollen diagrams)

(Plate 4-13) Pb 14138-1 37.5/113.2

Description:

Grains 5-7 stephanoporate; heteropolar; aspidate to varying degrees (ranging from thickened annulus to unraised darkened rim around pore); pore large (dia. 4 microns). Grains spherical; diameter 28-24 microns; amb often elliptical. Occasionally, the equatorial outline is angular when the pores are thickly aspidate. Exine surface finely-granulate.

Discussion:

One specimen observed in section 8/5/84-I and common in section 8/23/84-I.

Possible affinities:

Pterocarya? [cf. Traverse (1955), p. 45; Leopold and MacGinitie (1972), pp. 181-182; Frederiksen (1981), p. 43, pl.8]

Ulmaceae?

Juglans?

Nyssa? Leopold (1969 c), #42

see also Leopold (1969 a), p. 363, pl. 16-6 (undetermined specimen from Florissant)

UM 2

(Plate 3-19) Pb 14135-1 40.0/117.0

Description:

Grains triporate, pores strongly aspidate with operculum(?). Amb triangular; grain diameter approximately 30 microns.

Discussion:

Very rare.

Possible affinities:

<u>Betula</u> ?

<u>UM 3</u>

(Plate 4-15) Pb 14143-1 39.2/112.8

Description:

Grains tricolpate; very coarsely reticulate between furrows, diminishing within. Shape prolate, size 15 by 12 microns.

Discussion:

One specimen observed.

Possible affinities:

poss. <u>Salix</u> ? <u>Fraxinus</u> L. ? (Oleaceae); Caprifoliaceae?

<u>UM 4</u>

(Plate 4-28) Pb 14031-3 36.9/114.6

Description:

Diporate, oblate, with pores equatorial. Thickening of exine near pores but not aspidate. Exine psilate-granulate; dimensions 19 by 22 microns.

Discussion:

One specimen observed.

Possible affinities:

<u>Corylus</u> (Corylaceae) [see Traverse (1955), pp. 46-47]

<u>UM 5</u>

(Plate 3-11) Pb 14142-1 29.6/117.5

Description:

Grains aporate, spherical, and usually characterized by many jagged folds. Exine psilate; diameter 22-32 microns

Discussion:

Rare.

Possible affinities: ?

UM 6

(Plate 4-25) Pb 14148-3 47.0/123.9

Description:

Grain tricolporate, prolate and inflated at equator. Size dimensions 38 microns by 24 microns. Exine tectate; surface baculate (densely packed baculae).

Discussion:

One specimen observed.

Possible affinities:

Fagus ?

UM 7

(Plate 4-24) Pb 14138-1 33.3/119.5

Description:

Grain triporate(?); spherical; densely echinate; spines short (length less than 1 microns). Diameter 15 microns.

Discussion:

One specimen observed.

Possible affinities:

bryophyte spore?

Compositae ? (remark: no Compositae in MacGinitie (1953) systematic list)

UM 8

(Plate 3-8) Pb 14137-1 31.5/120.3

Description:

Spherical entities of unknown biological origin. Diameter 14-18 microns. Linear surface features radiate from central "pore". Pore outline unclear (dia. approximately 3-4 microns).

Discussion:

Infrequent and limited to a few samples.

Possible affinities:

Wing segment of moth or other insect?

References Cited

Allen, J. A. 1878. Description of a fossil passerine bird from the insect bearing shales of Colorado. United States Geological and Geographical (Hayden) Survey of the Territories, Bulletin, 4: 443-445.

Axelrod, D. I. 1976. Evolution of the Santa Lucia fir (Abies bracteata) ecosystem. Annals of the Missouri Botanical Garden, 63:24-41.

Axelrod, D. I. and H. P. Bailey. 1976. Tertiary vegetation, climate and altitude of the Rio Grande Depression, New Mexico. Paleobiology, 2: 235-254.

Axelrod, D. I. and P. H. Raven. 1985. Origins of the Cordilleran flora. Journal of Biogeography, 12: 21-47.

Bassett, J., C. W. Crompton and J. A. Parmelee. 1978. An Atlas of Airborne Pollen Grains and Common Fungus Spores of Canada. Canada Department of Agriculture, Research Branch, Monograph 18, 321 p.

Becker, H. F. 1961. Oligocene plants from the Upper Ruby River Basin, southwestern Montana. Geological Society of America, Memoir 82, 127 p.

____. 1969. Fossil plants of the Tertiary Beaverhead Basins in southwestern Montana. Palaeontographica, Abt. B, 127: 1-142.

Birks, H. J. B. and H. H. Birks. 1980. Quaternary Palaeoecology. University Park Press, Baltimore, 289 p.

Bold, H. C. and M. J. Wynne. 1978. Introduction to the Algae, 2nd ed. Prentice-Hall, New York, 720 p.

Brown, F. M. 1986. The tsetse flies of Florissant, Colorado. Pikes Peak Research Station, Bulletin 1, 12 p.

Cockerell, T. D. A. 1906. Fossil saw-flies from Florissant. American Museum of Natural History, Bulletin, 22:499-501.

Cope, E. D. 1875. On the fishes of the Tertiary shales of the South Park. United States Geological and Geographical (Hayden) Survey of the Territories, Bulletin, 1:3-5.

_____. 1879. The Amyzon Tertiary beds. American Naturalist. 13:332.

_____. 1881. On a wading bird from the Amyzon shales. United States Geological and Geographical (Hayden) Survey of the Territories, Bulletin, 6: 83-85.

Cross, A. T. and R. E. Taggart. 1982. Causes of short-term sequential changes in fossil plant assemblages: Some considerations based on a Miocene flora of the northwest United States. Annals of the Missouri Botanical Garden, 69:676-734.

Cross, W. 1894. Description of the Pikes Peak sheet, Colorado. United States Geological Survey, Geological Atlas, Folio 7, 5 p.

Dilcher, D. L. 1969. Podocarpus from the Eocene of North America. Science, 164:299-301.

Dilmy, A. 1955. Nama jang sjah untuk keluarga Bischoffia Bl. dan Engelhardia Lesch. Rimba Indonesia, 4(1-2): 29-37.

Doher, L. I. 1980. Palynomorph preparation procedures currently used in the paleontology and stratigraphy laboratories, U. S. Geological Survey Circular 830, 29 p.

Dorf, E. 1951. Lithologic and floral facies in the Paricutin ash deposits. Mexico. New York Academy of Sciences Transactions, Series 2, 13:317-320.

Eggler, W. A. 1948. Plant communities in the vicinity of the volcano El Paricutin, Mexico, after two and a half years of eruption. Ecology, 29:415-436.

Epis, R. C. and C. E. Chapin. 1974. Stratigraphic nomenclature of the Thirtynine Mile Volcanic Field, central Colorado. United States Geological Survey, Bulletin 1395-C, 23 p.

Erdtman, G. 1952. Pollen Morphology and Plant Taxonomy I, Angiosperms (An Introduction to Palynology. I). Almqvist & Wiksell, Stockholm, 539 p.

_____. 1957. Pollen and Spore Morphology/Plant Taxonomy II, Gymnospermae, Pteridophyta, Bryophyta. (Illustrations). Almqvist & Wiksell, Stockholm, 151 p.

____. 1965. Pollen and Spore Morphology/Plant Taxonomy III, Gymnospermae, Bryophyta. (Text). Almqvist & Wiksell, Stockholm, 191 p.

____. 1969. Handbook of Palynology. Hafner Publishing Company, New York, 486 p.

Faegri, K. and J. Iverson. 1974. Textbook of Pollen Analysis, 2nd Revised Edition. Hafner Publishing Co., New York, 237 p.

Fowells, H. A. 1965. Silvics of forest trees of the United States. United States Department of Agriculture, Handbook 271, 762 p.

Frederiksen, N. O. 1980. Sporomorphs from the Jackson Group (Upper Eocene) and adjacent strata of Mississippi and western Alabama. United States Geological Survey, Professional Paper 1084, 75 p.

Funkhouser, J. W. and W. R. Evitt. 1959. Preparation techniques for acid-insoluble microfossils. Micropaleontology, 5:369-375.

Gazin, C. L. 1935. A marsupial from the Florissant beds (Tertiary) of Colorado. Journal of Paleontology, 9:57-62.

Geel, B. van and T. van der Hammen. 1978. Zygnemataceae in Quaternary Colombian sediments. Review of Paleobotany and Palynology, 25:377-392.

Gibson, W. H. 1901. Blossom Hosts and Insect Guests. Newson and Company, New York, 197 p.

Gies, T. F. 1972. Palynology of sediments bordering some Upper Cretaceous strand lines in northwestern Colorado. Ph. D. Dissertation (Geology), Michigan State University, East Lansing, Michigan, 355 p.

Graham, A. 1972. Outline of the origin and historical recognition of floristic affinities between Asia and eastern North America, p. 1-18, *In* A. Graham (ed.), Floristics and Paleofloristics of Asia and Eastern North America. Elsevier, New York, 278 p.

Harlow, W. M., E. S. Harrar and F. M. White. 1979. Textbook of Dendrology, 6th ed. McGraw-Hill, New York, 510 p.

Heusser, C. J. 1971. Pollen and Spores of Chile. University of Arizona Press, Tucson, Arizona, 167 p.

Hollick, A. 1909. A new genus of fossil Fagaceae from Colorado. Torreya, 9: 1-3.

Hopkins Jr., W. S. 1967. Palynology and its paleoecological application in the Coos Bay area, Oregon. Ore Bin, 29:161-183.

Huang, T. C. 1972. Pollen Flora of Taiwan. National Taiwan University, Botany Department Press, 297 p.

Hyde, H. A. and K. F. Adams. 1958. An Atlas of Airborne Pollen Grains. MacMillan and Co., London, 112 p.

Knowlton, F. H. 1916. A review of the fossil plants in the United States National Museum from the Florissant lake beds at Florissant, Colorado, with descriptions of new species and list of type specimens. United States National Museum Proceedings, 51:241-297.

Leopold, E. B. 1964. Reconstruction of Quaternary environments using palynology, p. 43-52. *In* J. J. Hester and J. Schoenwetter (eds.), The Reconstruction of Past Environments (Proceedings of the Fort Burgwin conference on paleoecology:1962, no. 3), Fort Burgwin Research Center, New Mexico.

____. 1969 a. Selected pollen and spores of the (upper Oligocene) Florissant Formation (plate of 40 grains), pl. 16-6, p. 363. *In* J. S. Penny, Late Cretaceous and Early Tertiary Palynology, ch. 16. *In* R. H. Tschudy and R. A. Scott (eds.), Aspects of Palynology. Wiley-Interscience, New York, 510 p.

____. 1969 b. Selected pollen and spores from the (middle Eocene) Ione gravels, Chalk Bluffs, Calif. (plate of 43 grains), pl. 16-5, p. 358. *In* J. S. Penny, Late Cretaceous and Early Tertiary Palynology, ch. 16. *In* R. H. Tschudy and R. A. Scott (eds.), Aspects of Palynology. Wiley-Interscience, New York, 510 p.

____. 1969 c. Selected pollen and spore types of the Suntrana Formation of Middle Miocene age from the Alaska Range (plate of 45 grains), pl. 17-1, p. 403. *In* E. B. Leopold, Late Cenozoic Palynology, ch. 17. *In* R. H. Tschudy and R. A. Scott (eds.), Aspects of Palynology. Wiley-Interscience, New York, 510 p.

_____. 1969 d. Selected pollen and spore types of the Middle Miocene age from the Troublesome Formation, Granby, Colorado (plate of 44 grains). pl. 17-2, p. 408. *In* E. B. Leopold, Late Cenozoic Palynology, ch. 17. *In* R. H. Tschudy and R. A. Scott (eds.), Aspects of Palynology. Wiley-Interscience, New York, 510 p.

Leopold, E. B. and H. D. MacGinitie. 1972. Development and affinities of Tertiary floras in the Rocky Mountains. ch. 12, p. 147-200. *In* A. Graham (ed.), Floristics and Paleofloristics of Asia and Eastern North America. Elsevier, New York, 278 p.

Lesquereux, L. 1872. Lignitic formation and fossil flora. United States Geological and Geographical (Hayden) Survey of the Territories, Annual Report, 6:317-427.

_____. 1883. Contributions to the fossil flora of the Western Teritories. III. The Cretaceous and Tertiary flora. United States Geological Survey. Annual Report 8, 283 p.

Lewis, W. H., P. Vinay and V. E. Zenger. 1983. Airborne and Allergenic Pollen of North America. Johns Hopkins University Press, Baltimore, 254 p.

MacGinitie, H. D. 1953. Fossil Plants of the Florissant Beds, Colorado. Carnegie Institution of Washington Publication 599, Contributions to Paleontology, 198 p.

Malde, H. E. 1964. The ecological significance of some unfamiliar geologic processes, p. 7-15. *In* J. J. Hester and J. Schoenwetter (eds.), The Reconstruction of Past Environments (Proceedings of the Fort Burgwin conference on paleoecology:1962, no. 3), Fort Burgwin Research Center, New Mexico.

Manchester, S. R. and P. R. Crane. 1983. Attached leaves, inflorescences, and fruits of Fagopsis, an extinct genus of fagaceous affinity from the Oligocene Florissant flora of Colorado, U.S.A. American Journal of Botany, 70:1147-1164.

Markgraf, V. and H. L. D'Antoni. 1978. Pollen Flora of Argentina. University of Arizona Press, Tucson, 208 p.

Martin, H. A. and G. E. Rouse. 1966. Palynology of the late Tertiary sediments from Queen Charlotte Islands, British Columbia. Canadian Journal of Botany, 44:171-208.

McAndrews, J. H., A. A. Berti and G. Norris. 1973. Key to the Quaternary Pollen and Spores of the Great Lakes Region. Royal Ontario Museum, Publications in Life Sciences Miscellaneous Publication, 61 p.

McLeroy, C. A. and R. Y. Anderson. 1966. Laminations of the Oligocene Florissant lake deposits, Colorado. Geological Society of America, Bulletin, 77:605-618.

Meeuse, B. J. D. 1961. The Story of Pollination. Ronald Press, New York, 243 p.

Moore, P. D. and J. A. Webb. 1978. An Illustrated Guide to Pollen Analysis. John Wiley and Sons, New York, 133 p.

Peale, A. C. 1874. Report of South Park Division. United States Geological and Geographical (Hayden) Survey of the Territories, Annual Report, 7:193-273.

Piel, K. M. 1971. Palynology of Oligocene sediments from central British Columbia. Canadian Journal of Botany, 49:1885-1920.

Pocknall, D. T. and D. C. Mildenhall. 1984. Late Oligocene-early Miocene spores and pollen from Southland, New Zealand. New Zealand Geological Survey, Paleontological Bulletin 51, Science Information Publishing Center, Wellington, New Zealand, 66 p.

Root, R. R. 1983. Stratigraphic surveys for site selection of visitor and administration facilities, Florissant Fossil Beds National Monument, Colorado. Denver Service Center, National Park Service, United States Department of Interior, 39 p.

Round, F. E. 1965. The Biology of the Algae. Edward Arnold Publishers, Ltd., London, 268 p.

Sawyer, R. 1981. Pollen Identification for Beekeepers. University Cardiff College Press, Great Britain, 111 p.

Schopf, J. M. 1964. Practical problems and principles in study of plant microfossils, p. 29-57. *In* Cross, A. T. (ed.), Palynology in Oil Exploration--Symposium, San Francisco, 1962. Society of Economic Paleontologists and Mineralogists Special Publication 11, Tulsa, Oklahoma, 200 p.

____. 1969. Systematics and nomenclature in palynology, p. 49-77. *In* R. H. Tschudy and R. A. Scott (eds.), Aspects of Palynology. Wiley-Interscience, New York, 510 p.

Scudder, S. H. 1882(1881). The Tertiary lake basin at Florissant, Colorado, between South and Hayden Parks. United States Geological and Geographical (Hayden) Survey of the Territories, Bulletin, 6:279-300.

Smiley, C. J. and W. C. Rember. 1981. Paleoecology of the Miocene Clarkia Lake (Northern Idaho) and its environs, ch. 17, p. 551-590. *In* J. Gray, A. J. Boucot and W. B. N. Berry (eds.), Communities Of The Past. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

Taggart, R. E. 1971. Palynology and paleoecology of the Miocene Sucker Creek flora from the Oregon-Idaho boundary. Ph.D. Dissertation (Botany), Michigan State University, East Lansing, Michigan, 173 p.

____ and A. T. Cross. 1980. Vegetation change in the Miocene Succor Creek flora of Oregon and Idaho: a case study in paleosuccession, ch. 7, p. 185-210. *In* D. L. Dilcher and T. N. Taylor (eds.), Biostratigraphy of Fossil Plants. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania.

Thompson, G. G. 1969. Paleoecology of palynomorphs in the Mancos Shale, southwestern Colorado. Ph. D. Dissertation (Geology), Michigan State University, East Lansing, Michigan, 199 p.

Traverse, A. 1955. Pollen analysis of the Brandon lignite of Vermont. United States Department of Interior, Report of Investigations 5151, 107 p.

Tschudy, R. H. 1957. Pollen and spore formulae--a suggestion. Micropaleontology, 3:277-280.

____. 1969. Applied Palynology, Ch. 7, pp.103-126, *In* R. H. Tschudy and R. A. Scott (eds.), Aspects of Palynology. Wiley-Interscience, New York, 510 p.

Wadsworth, M. E. 1883. Tufa from Florissant (Colorado). United States Geological and Geographical (Hayden) Survey of the Territories, Annual Report, 12:276-278.

Wing, S. L. 1987. Eocene and Oligocene floras and vegetation of the Rocky Mountains. Annals of the Missouri Botanical Garden, 74: 748-784.

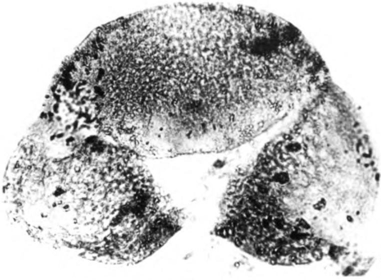
Wobus, R. A. and R. C. Epis. 1978. Geologic map of the Florissant 15-minute quadrangle, Park and Teller Counties, Colorado. United States Geological Survey, Miscellaneous Investigations Series, Map I-1044.

Wodehouse, R. P. 1959. Pollen Grains: Their structure, identification and significance in science and medicine. Hafner Publishing Co., New York. 574 p.

PLATE 1

Illustration	
1	*Abies* Type 3
2	*Fungi* Type 1
3	*Fungi* Type 2
4	Monolete Type 2
5	*Ephedra* Type 1 a
6	*Ephedra* Type 1 b
7	*Abies* Type 2
8	*Ephedra* Type 2
9	Monolete Type 3
10	*Abies* Type 1
11	Monolete Type 4
12	Monolete Type 1

All illustrations 666X.

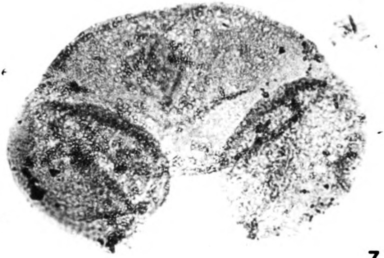


1

2

3

4



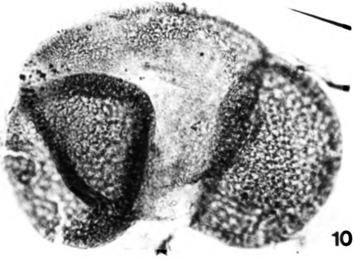
5

6

7

8

9



10

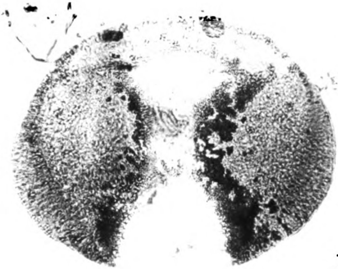
11

12

PLATE 2

Illustration	
1	*Picea* Type 1
2	Taxodiaceae/Cupressaceae/Taxaceae Type 1 c
3	Taxodiaceae/Cupressaceae/Taxaceae Type 1 a
4	Taxodiaceae/Cupressaceae/Taxaceae Type 1 b
5	Taxodiaceae/Cupressaceae/Taxaceae Type 1 d
6	Trilete Type 3
7	Trilete Type 5
8	Trilete Type 4
9	*Picea* Type 2
10	Trilete Type 6
11	Trilete Type 7
12	Trilete Type 2
13	*Pseudotsuga*/*Larix*
14	Trilete Type 8
15	Trilete Type 1
16	Trilete Type 9

All illustrations 666X.


1

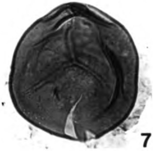

2


3

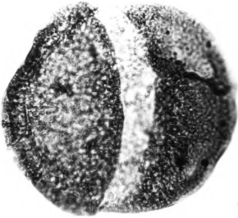

4


5

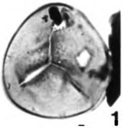

6


7


8

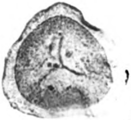

9


10


11


12


13


14

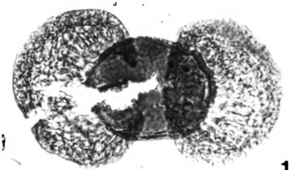

15

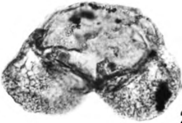

16

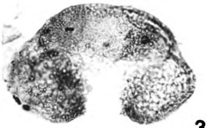
PLATE 3

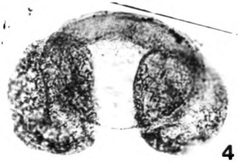
Illustration	
1	*Podocarpus*
2	*Pinus* Type 2
3	*Pinus* Type 4
4	*Pinus* Type 5
5	*Pinus* Type 3
6	*Pinus* Type 1
7	Gramineae Type 2
8	UM 8
9	*Populus*
10	Gramineae Type 1
11	UM 5
12	*Typha*/*Spargnium* Type 1
13	*Typha*/*Sparganium* Type 2
14	*Potamogeton*
15	*Celtis* Type 2
16	*Carya* Type 1
17	*Carya* Type 3
18	*Carya* Type 2
19	UM 2
20	*Engelhardia*

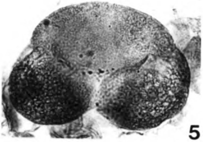
All illustrations 666X.


1


2


3


4


5


6


7


8


9


10


11


12


13


14


15


16


17


18

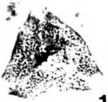

19


20

PLATE 4

Illustration	
1	Proteaceae/Sapindaceae/Elaeagnaceae
2	Nymphaeaceae
3	*Ulmus*/*Zelkova* Type 3
4	*Ulmus*/*Zelkova* Type 2
5	*Ulmus*/*Zelkova* Type 1
6	*Acer*/*Dipteronia* Type 2
7	*Acer*/*Dipteronia* Type 1
8	*Acer*/*Dipteronia* Type 3
9	*Acer*/*Dipteronia* Type 4
10	*Salix* Type 2
11	*Salix* Type 1
12	*Ilex*
13	UM 1
14	*Tilia*
15	UM 3
16	Compositae
17	*Juglans*
18	*Fagopsis longifolia*
19	*Quercus* Type 4
20	*Quercus* Type 2
21	*Celtis* Type 1
22	*Quercus* Type 1
23	*Castanea*
24	UM 7
25	UM 6
26	*Quercus* Type 3
27	*Liquidambar*
28	UM 4
29	*Mougeotia*
30	Chenopodiaceae/Amaranthaceae Type 2
31	Chenopodiaceae/Amaranthaceae Type 3
32	Chenopodiaceae/Amaranthaceae Type 1
33	Algae Type 1

All illustrations 666X.


1


2


3

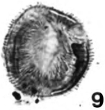

4


5


6


7


8


9


10


11

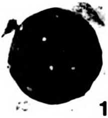

12


13

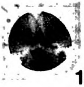

14


15


16


17


18


19


20


21


22


23


24


25


26


27


28


29


30


31


32


33