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FOSSIL FLORA AND STRATIGRAPHY OF THE FLORISSANT FORMATION, COLORADO

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INTRODUCTION

The Florissant fossil beds of Colorado hold a special place in the study of North American Cenozoic floras. In 1967, a section of the Florissant exposures were designated as the Florissant Fossil Beds National Monument. Florissant's fissile shale yields far more than its share of well-preserved plants and insects. Its giant sequoia-like trunks are some of the most dramatic petrified trees in the world. Collections from Florissant are present in most museums that claim to have paleobotanical holdings. Although the Rocky Mountain and Great Plains regions are rich in Cretaceous and Paleogene fossil floras, the floral record becomes very sparse in rocks younger than the middle Eocene. This change is due to regional climatic and depositional conditions that were not favorable for the preservation of plant parts. In this context, the late Eocene Florissant flora is particularly important. With the exception of some newly discovered floras near Florissant that are associated with the Thirtynine Mile volcanic field, the nearest coeval floras occur in western Montana, eastern Oregon, and along the Pacific Coast of California, Oregon, and Washington. The Florissant flora is a single bright light in a large and dark room.

It has been almost a half-century since Harry D. MacGinitie published his monograph on the Florissant flora. *Fossil Plants of the Florissant Beds, Colorado* is an early masterpiece by one of the most talented angiosperm paleobotanists of the 20th century. In a time when little other significant work on fossil angiosperms was taking place, MacGinitie produced a monograph that was comprehensive, accurate, and inspired. His work not only clarified the taxonomy and systematics of the fossil flora, it also provided important information concerning the age, depositional setting, and estimates of temperature, moisture, and paleoelevation of the "Florissant Lake Beds."

In 1994, Emmett Evanoff and Kathryn Gregory-Wodzicki (then Gregory) organized a symposium and field trip during the Rocky Mountain Section meeting of the Geological Society of America. This meeting revealed that a number of researchers were working on different aspects of the Florissant Formation and that there was sufficient interest and new data to generate a collection of papers. This volume represents a portion of the papers presented at that symposium, particularly those dealing with aspects of the vegetation. These papers represent the first major addition to the study of the flora since MacGinitie's effort in 1953.

Unlike most floras in the Rocky Mountain West, which are located in sedimentary basins adjacent to uplifted mountain blocks, the Florissant deposit lies in a paleovalley cut into the Precambrian Pikes Peak Granite on top of the Colorado Front Range. There is ongoing debate concerning the timing of the uplift that caused the present high elevations of the Rocky Mountains of Colorado. This debate made the Florissant deposits the obvious place to undertake a study of paleoelevation. From a regional tectonic perspective, the Florissant area either had its present elevation when the flora was growing in the late Eocene or it achieved that elevation much later. If fossil plants can be used to accurately estimate paleotemperature, a lapse rate can be applied and an estimate made of the paleoelevation at the time of growth. For this reason, the Florissant flora has recently been lofted back into prominence and has become the center of controversy over the utility of plants in estimating paleoelevation.

In this volume, the contributions of Emmett Evanoff, William C. McIntosh, and Paul C. Murphey set the stage by formally describing the stratigraphy of the Florissant fossil beds and naming them the Florissant Formation. The detailed stratigraphic analysis demonstrates the complexity of the formation and shows how the fossil forest levels relate to the leaf- and insect-bearing levels. Assessment of the sparse but time-diagnostic vertebrate fauna supports a Chadronian Land Mammal age. The radioisotopic age for the formation of 34.07 ± 0.10 Ma is in agreement with the faunal determination and places the formation at the very end of the Eocene Epoch. The fossil beds had earlier been considered to be of Oligocene age, but that was when the Chadronian was considered to be Oligocene rather than spanning the Eocene-Oligocene boundary.

Significant advances have been made in the field of palynology since MacGinitie's time. Two papers in this volume utilize palynology to assess the flora and climate of the lakebeds within the Florissant Formation. Estella B. Leopold and Scott T. Clay-Poole recognize 150 pollen and spore taxa and relate them to the leaf flora as described by MacGinitie. In addition,

they use the climatic tolerances of the nearest living relatives of the fossil pollen taxa to broadly circumscribe the paleoclimate of the Florissant area as warm temperate to subtropical. This interpretation is more in line with MacGinitie's assessment than it is with more recent analyses based on leaf physiognomy. F. H. Wingate and D. J. Nichols present a parallel, but more stratigraphic, palynological study. They recognize 130 taxa and place their results within the broad context of the Paleogene palynostratigraphy of the Rocky Mountain region. Wingate and Nichols also discuss evidence of the response of the flora to the volcanic eruptions that are an integral part of the history of the Florissant area. Together, these papers provide a thorough and modern assessment of the palynoflora of the fossil beds.

Steven R. Manchester assesses the fruit, flowers, leaves, and seeds of Florissant and updates Mac Ginitie's floral list. While it is recognized that MacGinitie was ahead of his time, nearly fifty years have passed since his monograph was published. That time has seen a profound change in the manner in which plant megafossils are studied. Significant in this change is the recognition by Manchester that a number of the Florissant taxa represent extinct genera. The biogeographical affinities of the flora are predominantly Laurasian with little or no input from Gondwana. These observations are in agreement with the conclusion of Leopold and Clay-Poole.

The petrified trees of Florissant are the most obvious remnant of the ancient ecosystem, but they have received comparatively little study. Two papers in this volume address the fossil wood. Kathryn M. Gregory-Wodzicki presents an innovative study of the dendrochronology of the large sequoia-like trunks. She is able to demonstrate that the Florissant sequoias were growing in conditions more favorable than that of the modern redwoods of coastal California. In addition, she shows that at least two of the studied trunks grew contemporaneously. E. A. Wheeler provides an anatomical description of five different angiosperm woods including a new extinct genus. Late Eocene woods are poorly known and the presence of angiosperm woods at Florissant, while predictable from the leaf and pollen floras, have not been previously documented. Since Evanoff and others document that the leaf floras and petrified

wood layers occur at different levels within the formation, Wheeler's paper demonstrates that conifers and angiosperms formed mixed stands throughout the deposition of the formation.

Herbert W. Meyer provides a review of the recent discussions about the paleoelevation of the Florissant flora. Fossil floras have long been used to address the difficult problem of estimating paleoelevation. Recently, quantitative estimates based on leaf physiognomy and lapse rates have placed Florissant as high as 1700 to 4100 m above sea level. This is a far cry from MacGinitie's estimate of 300 to 900 m, which was based on the habitats of the nearest living relatives of Florissant taxa. This debate is of more than local significance because Florissant has been a primary battlefield for the testing of different methodologies. Its position high in the Colorado Front Range has serious implications for the extent and timing of uplift associated with the Laramide orogeny. Based on Meyer's review and the contribution by Leopold and Clay-Poole, it is clear that this is an ongoing debate with no clear resolution from the realm of paleobotany. This is significant because Florissant is such a well-collected and well-studied flora. The fact that there remains so much disagreement about its paleoclimatic, and thus paleoelevational, status argues that techniques for such analyses need further refinement, and the prognosis for making paleoelevational estimates from smaller and less well-collected floras is not good.

Collectively, these papers build on the work of MacGinitie and provide a very clear and thorough view of a Rocky Mountain flora at the end of the Eocene Epoch. By combining the studies of pollen and spores, wood, fruits, flowers, seeds, and leaves, this volume represents a rare effort to assess all of the preserved organs of the fossil flora. In this sense, the volume is unique. The mutual insights gained from combining all organs are significant and they allow for a much fuller and complete estimate of the diversity and paleoclimate of the flora. Despite this, a considerable debate remains about the paleoclimate and serious differences exist between estimates based on nearest living relatives and leaf physiognomy.

—Kirk R. Johnson and Emmett Evanoff

1.

STRATIGRAPHIC SUMMARY AND ^{40}AR/^{39}AR GEOCHRONOLOGY OF THE FLORISSANT FORMATION, COLORADO

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ABSTRACT—The Florissant Formation is a heterolithic accumulation of shale, tuffaceous mudstone and siltstone, tuff, and arkosic and volcaniclastic sandstone and conglomerate. The name Florissant Formation redefines the former designation of the Florissant Lake Beds. The formation is divided into six informal units, including, from bottom to top: the lower shale, lower mudstone, middle shale, caprock conglomerate, upper shale, and upper pumice conglomerate. Fossil mammals include the co-occurrence of the horse *Mesohippus* and large brontotheres, indicating that the age of the formation is Chadronian.

Single-crystal ^{40}Ar/^{39}Ar analyses of sanidine from pumice in sandstone and debris flow deposits of the upper Florissant Formation yield a mean age of 34.07 ± 0.10 Ma. Although the pumice fragments are reworked and do not represent a primary volcanic deposit, their abundance and the unimodality of sanidine ages suggest that 34.07 ± 0.10 Ma is a good estimate for the depositional age of the Florissant Formation. The sanidine age data do not support derivation of the Florissant Formation pumice fragments from any of the catastrophic caldera eruptions that produced ignimbrite deposits in the region. Possible sources for the pumice fragments include early eruptive phases of the 33.5 Ma Mount Aetna caldera or late eruptive phases of the 34.3 Ma Grizzly Peak caldera in the Sawatch Range of central Colorado.

KEY WORDS: Florissant Formation, lithostratigraphy, biostratigraphy, ^{40}Ar/^{39}Ar geochronology

The Florissant "Lake Beds" contains one of the most important fossil flora and insect fauna of the western United States. It has been known as an important fossil location since the 1870s, but the details of its stratigraphy and radiometric age have been uncertain until recent findings. The only previously published radiometric age is a K/Ar analysis of sanidine from the formation by Epis and Chapin (1975) that yielded an age of 34.9 Ma (adjusted to modern decay constants of Steiger and Jaeger 1977). The present report redefines the Florissant Lake Beds as the Florissant Formation, summarizes the lithostratigraphy and biostratigraphy of the formation, and documents new single-crystal ^{40}Ar/^{39}Ar dating of several units within the formation. The area of study includes Florissant Fossil Beds National Monument and outcrops near the town of Florissant, Colorado (Fig. 1).

Methods

The new stratigraphic interpretations are a result of the mapping of four formations and six subdivisions of the Florissant Formation in an area extending from the town of Florissant to the monument. The outcrops of the formation are scattered and discontinuous; therefore, the stratigraphic sequence and the estimate of 74 m for the total thickness of the formation were determined from careful mapping and section measuring. Thirteen stratigraphic sections were described, eleven in the monument and two outside the monument. The distribution of the stratigraphic units and locations of important outcrops and dated rock samples are shown in Figure 1 and Table 1.

For ^{40}Ar/^{39}Ar dating analyses, samples of unweathered, unaltered pumice-rich sandstone or debris

FIGURE 1. Bedrock geologic map and geographic features of the area surrounding Florissant Fossil Beds National Monument. The margins of the Florissant Formation outline the original paleovalley.

flow materials were collected from four localities in the Florissant Formation (Table 2). Sanidine separates were prepared from each sample and irradiated in the Ford Reactor at the University of Michigan. Single-crystal laser-fusion analyses were performed at the New Mexico Geochronology Research Laboratory at New Mexico Tech, Socorro, New Mexico. Details of sample preparation procedures, irradiation, ⁴⁰Ar/³⁹Ar analyses, and age calculations are provided in the footnote to Table 2. Table 2 summarizes weighted mean ages obtained from the five samples, and analytical data from individual crystals are given in Table 3.

Geologic Setting

There are four formal stratigraphic units represented by the rocks in the Florissant area. These include the Pikes Peak Granite, the Wall Mountain Tuff, the Florissant Formation, and breccias of the Thirtynine Mile Andesite. A fifth informal unit, herein assigned to Tertiary boulder conglomerate, occurs in the paleovalley. These units are in the composite section shown in Figure 2.

The oldest rocks in the monument are part of the Pikes Peak Granite, a pink to reddish-tan, medium to coarse-grained, biotitic or biotite-hornblende granite and quartz monzanite (Wobus and Epis 1978). The radiometric age of this granite is 1080 Ma (Wobus 1994). Late Eocene streams cut a long dendritic valley into this granite in which volcanic rocks and sediments later accumulated. Local relief on this unconformity is as great as 300 m near the southern end of the paleovalley. The granite is exposed as boulders, tors, and ridges on the flanks of the paleovalley.

TABLE 1. Locations of measured sections and radiometrically dated sanidine samples in the Florissant Formation.

Map. Loc.#	Name	Features	Public Land Survey Location	UTM Location, NAD 27, Zone 13S
1	Florissant road cut	Complete sequence of the lower shale unit, base of lower mudstone unit.	SW¼ SW¼ NE¼ SW¼ sec. 1, T. 13 S., R. 71 W.	475532mE 4310802mN el. 8223 ft
2	Monument N	Thickest sequence of the lower mudstone unit, capped by the middle shale.	N½ SW¼ NW¼ sec. 12, T. 13 S., R. 71 W.	475204mE 4309757mN el. 8301 ft
3	big stump	Thickest section of the caprock conglomerate, complete sequence of the middle shale unit.	SW¼ NW¼ SW¼ sec. 13, T. 13 S., R. 71 W.	475241mE 4307547mN el. 8321 ft
4	Gregory trench	Complete sequence of the middle shale unit. Site of paleobotanical work of Gregory (1994) and palynological work of Wingate and Nichols (2001).	Center, E½ SW¼ SW¼ sec. 19, T. 13 S., R. 70 W.	476920mE 4305596mN el. 8501 ft
5	lower Boulder Creek	Complete sequence of the upper shale unit, sanidine samples TF3 and TF4.	NW¼ SW¼ SE¼ sec. 14, T. 13 S., R. 71 W.	474395mE 4307349mN el. 8364 ft
6	upper Boulder Creek	Exposures of the upper pumice conglomerate unit, sanidine sample TF5.	NW¼ SW¼ SW¼ sec. 14, T. 13 S., R. 71 W.	473636mE 4307281mN el. 8479 ft
7	nm782	Sanidine sample nm782 from the lower part of the upper pumice conglomerate unit. From ledge halfway up the slope.	NE¼ SE¼ SW¼ sec. 14, T. 13 S., R. 71 W.	474118mE 4307328mN el. 8399 ft

TABLE 2. Summary of ^{40}Ar/^{39}Ar single-crystal laser-fusion results from Florissant Formation sanidines.

Sample	Unit	n	K/Ca	±2s	Age	±2s
TF5	tuff in upper pumice conglomerate unt	19	43.5	17.4	34.01	0.13
nm782	pumice-rich facies of upper pumice conglomerate unit	10	42.8	9.4	34.07	0.09
TF4	tuff in upper shale unit	19	45.1	5.9	34.14	0.08
TF3	sanidine crystals in caprock conglomerate unit	18	47.0	11.3	34.03	0.09
mean of samples		4			34.07	0.13
mean of all crystals		66			34.07	0.10

NOTES: n = number of individual crystals analyzed (SCLF); K/Ca = molar ratio calculated from K-derived ^{39}Ar and Ca-derived ^{37}Ar.

METHODS: Sample preparation of sanidine-crushing, LST heavy liquid, Franz, HF.

IRRADIATION: Five hours in vacuo, H-5 position, Ford Nuclear Reactor, University of Michigan.

NEUTRON FLUX MONITOR: Sample FC-1 of interlaboratory standard Fish Canyon Tuff sanidine with an assigned age of 27.84 Ma (Deino and Potts 1990), relative to Mnhb-1 at 520.4 Ma (Samson and Alexander 1987); samples and monitors irradiated in alternating holes in machined Al discs.

LABORATORY: New Mexico Geochronology Research Laboratory, Socorro, NM.

INSTRUMENTATION: Mass Analyzer Products 215-50 mass spectrometer on line with automated, all-metal extraction system.

HEATING: 10W continuous CO^2 laser.

REACTIVE GAS CLEANUP: SAES GP-50 getters operated at 20 °C and ~450 °C; 1 to 2 minutes.

ERROR CALCULATION: All errors reported at ± 2 sigma, mean ages calculated using inverse variance weighting of Samson and Alexander (1987).

DELAY CONTRANT AND ISOTOPIC ABUNDANCES: Steiger and Jaeger (1977).

ANALYTICAL PARAMETERS: Electron multiplier sensitivity = 1 to 3 x 10^{-17} moles/pA; typical system blanks were 470, 3, 0.6, 3, 3.0 x 10^{-18} moles (laser) and at 470, 3, 0.6, 3, 3.0 (furnace) at masses 40, 39, 38, 37, 36, respectively; J-factors determined to a precision of ± 0.2 percent using SCLF of 4 to 6 crystals from each of 4 to 6 radial positions around irradiation vessel. Correction factors for interfering nuclear reactions, determined using K-glass and CaF$_2$ (^{40}Ar/^{39}Ar) K = 0.00020 ± 0.0003; (^{36}Ar/^{37}Ar) Ca = 0.00026 ± 0.00002; and (^{39}Ar/^{37}Ar) Ca = 0.00070 ± 0.00005.

The Wall Mountain Tuff is the oldest Tertiary rock within the monument. This tuff is a rhyolitic ignimbrite that weathers into brownish-gray to dark gray, subangular blocks. It rests unconformably on the irregular erosion surface cut into the Pikes Peak Granite. The tuff mantles the sides of the paleovalley because it was emplaced by a thick pyroclastic flow that draped the welded tuff over the local topography. The tuff was also eroded prior to the deposition of the other Tertiary units. Accordingly, the thickness of the tuff varies considerably, with a maximum preserved thickness being about 15 m. The age of the Wall Mountain Tuff is 36.73 Ma ± 0.07 (average of two ^{40}Ar/^{39}Ar ages reported by McIntosh and Chapin 1994).

A limited exposure of Tertiary boulder conglomerate overlies the Pikes Peak Granite and the Wall Mountain Tuff on the southeast side of the monument (NE¼ NW¼ sec. 30, T. 13 S., R. 70 W., Fig. 1). This conglomerate contains huge boulders of granite as large as 5.8 m in maximum diameter. The largest boulders are typically near the top of the exposures, suggesting a crude inverse grading. The conglomerate contains cobbles and boulders of granite, gneiss, schist, welded tuff derived from the Wall Mountain Tuff, and scattered fragments of silicified wood. Niesen (1969) and Wobus and Epis (1978) did not recognize the volcanic clasts in this boulder conglomerate and mapped these conglomerates as Echo Park Alluvium. The Echo Park Al-

TABLE 3. ^{40}Ar/^{39}Ar single-crystal sanidine laser-fusion analytical data for Florissant samples.

TF5, J = 0.000773567 ± 0.13%, D = 1.0066 ± 0.0019, NM-17, Lab# = 1671
TF5, J = 0.000773567 ± 0.13%, D = 1.0073 ± 0.0015, NM-17, Lab# = 2045

ID	^{40}Ar/^{39}Ar	^{37}Ar/^{39}Ar	^{36}Ar/^{39}Ar (x 10^{-3})	^{39}Ar$_{K (x 10^{-15} mol)}$	K/Ca	%^{40}Ar*	Age (Ma)	±2s (Ma)
05	24.47	0.023	0.1487	8.94	41.4	99.7	33.75	0.15
01	24.50	0.0119	0.1011	12.5	43.0	99.8	33.81	0.15
07	24.52	0.0107	0.1494	8.11	47.6	99.7	33.81	0.15
02	24.54	0.0111	0.2029	19.9	46.1	99.7	33.82	0.15
13	24.51	0.0107	0.0948	8.96	47.6	99.8	33.82	0.15
04	24.53	0.0119	0.1481	6.56	42.7	99.7	33.83	0.16
17	24.61	0.0127	0.1256	10.00	40.2	99.8	33.95	0.13
03	24.62	0.0114	0.1466	10.0	44.8	99.8	33.96	0.15
09	24.63	0.0111	0.1055	8.16	45.8	99.8	33.98	0.15
06	24.64	0.0122	0.1418	4.29	41.9	99.8	33.98	0.15
11	24.70	0.0119	0.2910	2.54	42.9	99.6	34.00	0.17
18	24.68	0.0122	0.1765	3.94	41.8	99.7	34.02	0.15
19	24.72	0.0386	0.3181	6.89	13.2	99.6	34.02	0.15
08	24.67	0.0122	0.1322	13.4	41.9	99.8	34.03	0.15
20	24.76	0.0104	0.0865	10.8	49.1	99.8	34.17	0.13
15	24.82	0.0107	0.0663	9.41	47.6	99.8	34.26	0.15
12	24.86	0.0094	0.1155	4.61	54.1	99.8	34.29	0.14
16	24.85	0.0089	−0.0577	3.29	57.2	100.0	34.35	0.18
14	24.90	0.0134	−0.1451	2.58	38.1	100.1	34.45	0.16
Weighted mean ± S & A err (n = 19)					43.5 ± 17.4		34.01	0.13

nm782, J = 0.000788491 ± 0.13%, D = 1.0066 ± 0.0019, NM-17, Lab# = 1669

ID	^{40}Ar/^{39}Ar	^{37}Ar/^{39}Ar	^{36}Ar/^{39}Ar (x 10^{-3})	^{39}Ar$_{K (x 10^{-15} mol)}$	K/Ca	%^{40}Ar*	Age (Ma)	±2s (Ma)
05	24.12	0.0114	0.2680	11.4	44.7	99.6	33.86	0.15
03	24.16	0.0123	0.1457	12.9	41.6	99.7	33.96	0.15
01	24.27	0.0156	0.4179	6.77	32.6	99.4	34.00	0.16
06	24.22	0.0108	0.1457	12.5	47.1	99.7	34.04	0.15
02	24.26	0.0113	0.2558	11.8	45.3	99.6	34.05	0.15
10	24.25	0.0108	0.1733	12.8	47.4	99.7	34.07	0.15
07	24.27	0.0114	0.1587	3.51	44.7	99.7	34.11	0.16
04	24.29	0.0116	0.1918	12.8	43.8	99.7	34.13	0.15
09	24.31	0.0115	0.1285	12.6	44.4	99.8	34.17	0.15
08	24.43	0.0139	0.2479	13.9	36.6	99.6	34.29	0.15
Weighted mean ± S & A err (n = 10)					42.8 ± 9.4		34.07	0.12

TF4, J = 0.000775805 ± 0.13%, D = 1.0066 ± 0.0019, NM-17, Lab# = 1670
TF4, J = 0.000775805 ± 0.13%, D = 1.0073 ± 0.0015, NM-17, Lab# = 2046

ID	^{40}Ar/^{39}Ar	^{37}Ar/^{39}Ar	^{36}Ar/^{39}Ar (x 10^{-3})	^{39}Ar$_{K (x 10^{-15} mol)}$	K/Ca	%^{40}Ar*	Age (Ma)	±2s (Ma)
04	24.54	0.0117	0.2360	5.13	43.7	99.6	33.90	0.16
17	24.55	0.0109	0.1949	12.6	46.9	99.7	33.94	0.13

(Table 3 continued)

ID	$^{40}Ar/^{39}Ar$	$^{37}Ar/^{39}Ar$	$^{36}Ar/^{39}Ar$ (x 10⁻³)	$^{39}Ar_{K (x 10^{-15} mol)}$	K/Ca	% $^{40}Ar^*$	Age (Ma)	±2s (Ma)
18	24.57	0.0112	0.1837	8.89	45.5	99.7	33.97	0.14
09	24.57	0.0111	0.1568	10.5	45.9	99.7	33.98	0.15
07	24.55	0.0110	−0.0417	3.00	46.6	100.0	34.04	0.16
01	24.60	0.0117	0.0797	15.2	43.7	99.8	34.05	0.15
02	24.60	0.0117	0.0432	11.5	43.7	99.9	34.06	0.15
08	24.61	0.0111	0.0639	8.84	46.1	99.8	34.07	0.15
06	24.63	0.0112	0.0543	4.96	45.7	99.9	34.10	0.16
05	24.67	0.0114	0.0888	1.99	44.7	99.8	34.07	0.15
13	24.70	0.0099	0.0927	6.83	51.4	99.8	34.18	0.14
12	24.71	0.0115	0.1135	12.3	44.3	99.8	34.19	0.14
20	24.81	0.0135	0.4028	3.90	37.7	99.4	34.21	0.15
14	24.71	0.0118	0.0503	10.4	43.2	99.9	34.21	0.13
03	24.74	0.0111	0.0573	9.54	46.2	99.9	34.25	0.16
10	24.75	0.0105	0.0810	7.09	48.6	99.8	34.26	0.16
19	24.81	0.0115	0.2445	8.28	44.3	99.6	34.28	0.14
15	24.80	0.0106	0.0080	5.38	48.3	99.9	34.35	0.14
11	24.96	0.0127	0.1256	4.03	40.3	99.8	34.53	0.15
Weighted mean ± S & A err (n = 19)					45.1 ± 5.9		34.14	0.12

TF3, J = 0.000787189 ± 0.13%, D = 1.0066 ± 0.0019, NM-17, Lab# = 1672
TF3, J = 0.000780139 ± 0.13%, D = 1.0073 ± 0.0015, NM-17, Lab# = 2044

ID	$^{40}Ar/^{39}Ar$	$^{37}Ar/^{39}Ar$	$^{36}Ar/^{39}Ar$ (x 10⁻³)	$^{39}Ar_{K (x 10^{-15} mol)}$	K/Ca	% $^{40}Ar^*$	Age (Ma)	±2s (Ma)
09	24.06	0.0112	0.4452	3.00	45.4	99.4	33.64	0.22
10	24.02	0.0118	0.1549	4.26	43.4	99.7	33.71	0.16
01	26.37	0.0117	8.009	30.0	43.5	91.0	33.75	0.19
06	24.14	0.0115	0.3195	4.52	44.4	99.5	33.81	0.25
03	24.12	0.0115	0.1377	29.4	44.2	99.8	33.85	0.15
17	24.42	0.0112	0.1196	14.9	45.4	99.8	33.98	0.13
08	24.28	0.0107	0.3463	11.4	47.6	99.5	33.98	0.21
18	24.46	0.0111	0.1926	19.0	46.1	99.7	34.00	0.14
02	24.33	0.0111	0.4597	13.4	46.0	99.4	34.01	0.18
05	24.28	0.0112	0.2243	8.54	45.7	99.7	34.03	0.19
04	24.25	0.0112	0.1320	23.2	45.5	99.8	34.04	0.16
12	24.53	0.0114	0.3178	14.2	44.6	99.5	34.04	0.13
07	24.32	0.0107	0.2913	34.6	47.5	99.6	34.07	0.16
11	24.58	0.0110	0.3468	11.3	46.5	99.5	34.10	0.13
13	24.56	0.0087	0.1370	2.25	58.6	99.8	34.16	0.19
16	24.63	0.0106	0.2848	3.81	48.3	99.6	34.19	0.15
19	24.64	0.0128	0.2427	15.1	39.9	99.6	34.23	0.14
14	24.81	0.0080	0.3457	6.72	64.2	99.5	34.42	0.15
Weighted mean ± S & A err (n = 18)					47.0 ± 11.3		34.03	0.13

Isotopic ratios corrected for blank, radioactive decay, and mass discrimination, not corrected for interfering reactions.
Individual analyses show analytical error only; mean age errors also include error in J and irradiation parameters.
Analyses in italics are excluded from mean age calculations.
Correction factors:

$(^{39}Ar/^{37}Ar)_{Ca} = 0.00067 \pm 0.0000$ $\qquad (^{38}Ar/^{39}Ar)_k = 0.0119$

$(^{36}Ar/^{37}Ar)_{Ca} = 0.00026 \pm 0.0000$ $\qquad (^{40}Ar/^{39}Ar)_k = 0.0260 \pm 0.0020$
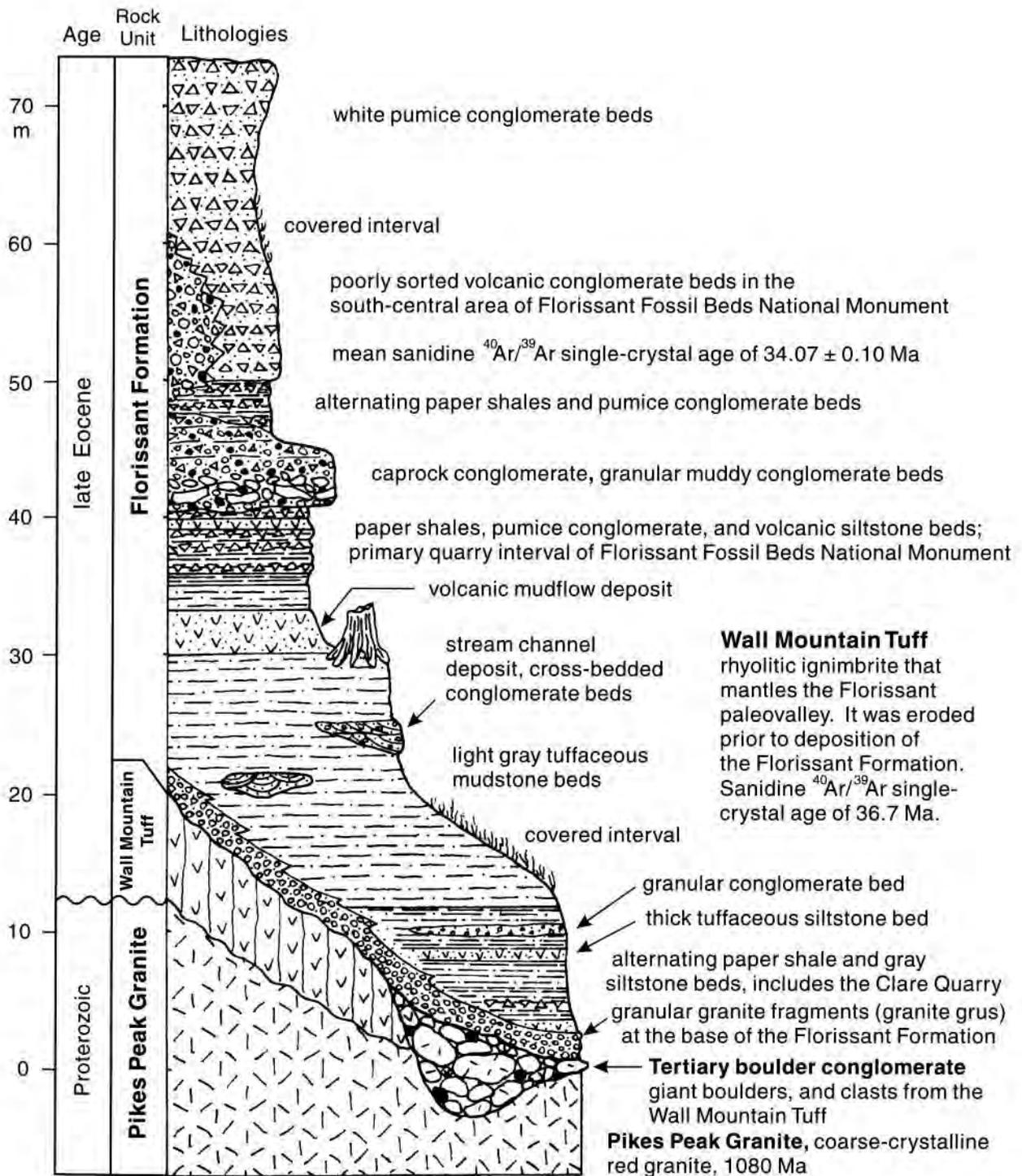
FIGURE 2. Generalized sequence of rock units in the Florissant paleovalley.

Age / Rock Unit / Lithologies

70 m
60
50
40
30
20
10
0

late Eocene

Florissant Formation

Wall Mountain Tuff

Proterozoic

Pikes Peak Granite

white pumice conglomerate beds

covered interval

poorly sorted volcanic conglomerate beds in the south-central area of Florissant Fossil Beds National Monument

mean sanidine ^{40}Ar/^{39}Ar single-crystal age of 34.07 ± 0.10 Ma

alternating paper shales and pumice conglomerate beds

caprock conglomerate, granular muddy conglomerate beds

paper shales, pumice conglomerate, and volcanic siltstone beds; primary quarry interval of Florissant Fossil Beds National Monument

volcanic mudflow deposit

stream channel deposit, cross-bedded conglomerate beds

Wall Mountain Tuff rhyolitic ignimbrite that mantles the Florissant paleovalley. It was eroded prior to deposition of the Florissant Formation. Sanidine ^{40}Ar/^{39}Ar single-crystal age of 36.7 Ma.

light gray tuffaceous mudstone beds

covered interval

granular conglomerate bed

thick tuffaceous siltstone bed

alternating paper shale and gray siltstone beds, includes the Clare Quarry

granular granite fragments (granite grus) at the base of the Florissant Formation

Tertiary boulder conglomerate giant boulders, and clasts from the Wall Mountain Tuff

Pikes Peak Granite, coarse-crystalline red granite, 1080 Ma

luvium is older than the Wall Mountain Tuff and does not contain clasts of welded tuff (Epis and Chapin 1975). However, the boulder conglomerate beds in the monument are equivalent to the Tallahassee Creek Conglomerate, which also contains clasts of the Wall Mountain Tuff. A small exposure of the Tertiary boulder conglomerate also occurs near the bottom of the paleovalley along Twin Creek (NE¼ NW¼ sec. 3, T. 13 S., R. 71 W., Fig. 1).

The Florissant paleovalley was episodically dammed by volcaniclastic debris flows (lahars) derived from the Thirtynine Mile volcanic field to the southwest (Fig. 3). These lahar deposits are poorly sorted, brown to purple, muddy breccias that contain intermediate volcanic clasts and granite fragments. They are part of the Thirtynine Mile Andesite of Wobus and Epis (1978). Their margins progressed northward in the paleovalley, reaching the south end of the monument by the end of lacustrine deposition of the Florissant Formation. These lahar deposits acted as dams to the Florissant valley drainage, creating the ancient Florissant lakes. The upper andesitic breccias from the Thirtynine Mile volcanic field covered the paleovalley sequence, and are preserved at the top of the butte south of the monument (SE¼ sec. 25, T. 13 S., R. 71W.)

Lithostratigraphy of the Florissant Formation

The primary fossil-bearing unit in the area is the Florissant Formation. This unit was named the Florissant Lake Beds by Cross (1894) and this designation has been used by subsequent workers (Niesen 1969; Wobus and Epis 1978). However, the unit contains many mudstone, sandstone, and conglomerate beds that were deposited by streams. The name Florissant Lake Beds does not conform to the modern criteria set forth by the North American Commission on Stratigraphic Nomenclature (1983, Article 22d) that states depositional environments should not be used in the definition of a lithostratigraphic unit. Thus, we redefine the name of the formation as the Florissant Formation.

The Florissant Formation contains a wide variety of lithologies, including arkosic granule conglomerate, volcaniclastic conglomerate, pumice conglomerate, sandstone, tuffaceous mudstone and siltstone, carbonaceous shale, and papery diatomaceous shale (McLeroy and Anderson 1966). The formation includes sediment derived from upstream sources (indicated primarily by metamorphic clasts), local sources (indicated by granite

clasts), and volcanic sediments primarily derived from the Thirtynine Mile volcanic field. The formation was deposited on an erosional surface that cut the Pikes Peak Granite and the Wall Mountain Tuff. The formation contains six informal units (Fig. 4), which include (from bottom to top) the lower shale, the lower mudstone, the middle shale, the caprock conglomerate, the upper shale, and the upper pumice conglomerate. Previous stratigraphic work in the monument by Murphey (1992) and Evanoff and Murphey (1994) referred to the lower mudstone, middle shale, caprock conglomerate, upper shale, and upper pumice conglomerate by the alphanumeric designation Tf^1, Tf^2, Tf^3, Tf^4, and Tf^5, respectively. These alphanumeric unit names were used for classification of mapped outcrops in the monument, and were not intended to be used outside the monument.

The lower shale unit is characterized by alternating tuffaceous siltstone and paper shale beds. The paper shales consist of alternating laminae of diatomite and volcanic ash altered to smectite clays (O'Brien et al. 1998). Thin pumice conglomerate, pumiceous sandstone, and granular conglomerate with granite and volcanic clasts are also scattered throughout the unit. This unit is exposed only near the base of the paleovalley sequence north of the monument. It is exposed in the road cut east of the town of Florissant and at the Clare Quarry south of the town (Fig. 1). The greatest thickness of the lower shale unit is 11.4 m as exposed in the Florissant road cut (Fig. 1, Table 1, Locality 1) where the unit overlies a thin sequence of granular arkosic conglomerate beds and a tuffaceous mudstone containing pumice and granite granules (Fig. 4). The shale beds not only contain plants and insects, but most of the fish and almost all of the bird fossils known from the Florissant Formation. The pollen of the lower shale unit from the Florissant road cut has been described by Leopold and Clay-Poole (2001). The lower shale unit represents deposition in an early expansion of the Florissant lake.

The lower mudstone unit is a sequence of gray tuffaceous mudstone beds, muddy pumiceous conglomerate beds, and rare cross-bedded sandstone and conglomerate ribbons, overlain by a thick, structureless to weakly horizontally bedded, tuffaceous sandy mudstone. The fossilized *Sequoia* and angiosperm stumps (see Gregory-Wodzicki 2001; Wheeler 2001) in the "petrified forest" area of the monument are at the base and are surrounded by these upper sandy mudstone beds. Most of the fossil mammals of the Florissant Formation occur in the mudstone beds below the level of the bases of the stumps. The thickest exposed sequence of
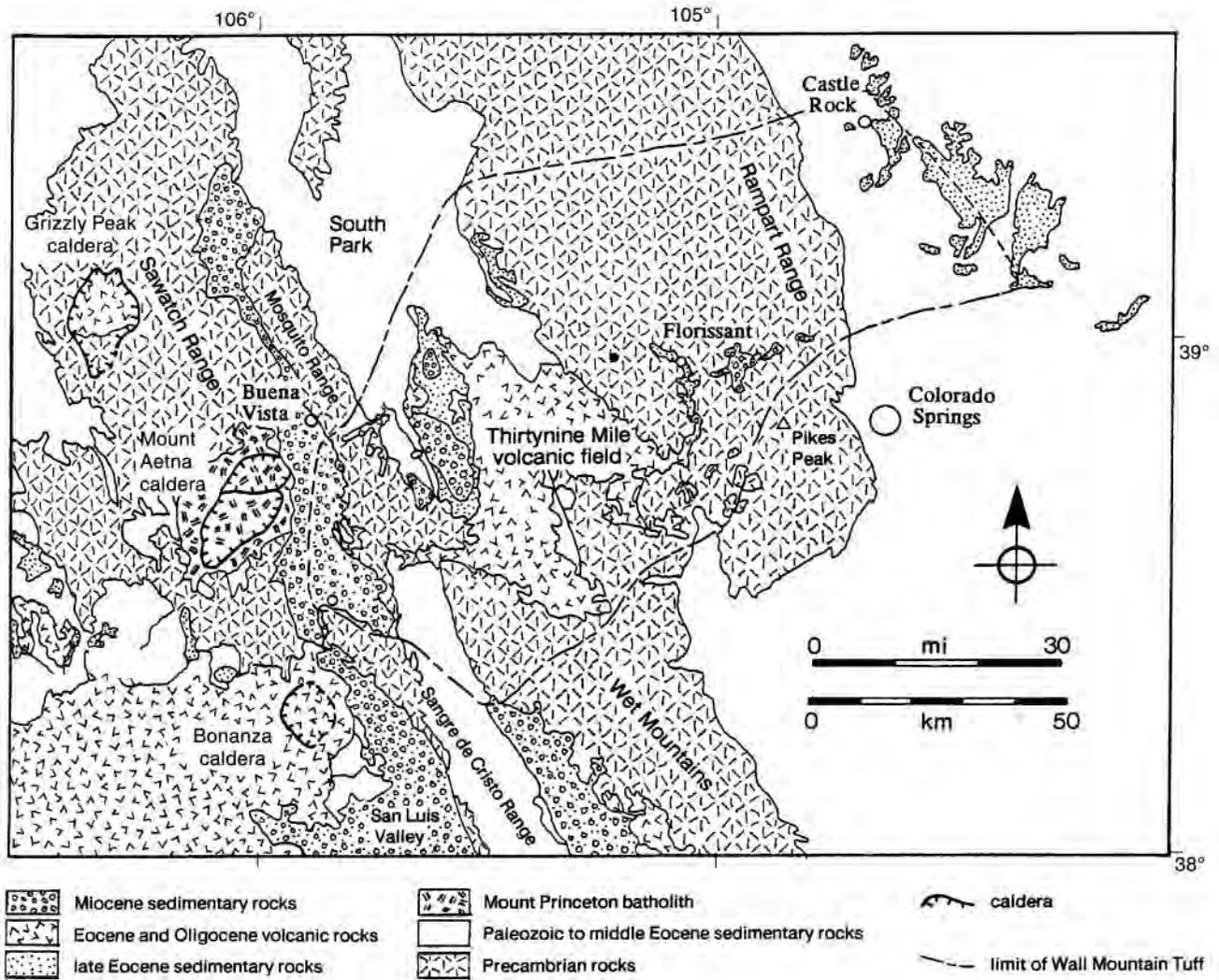
FIGURE 3. Regional map of central Colorado emphasizing Cenozoic geologic features.
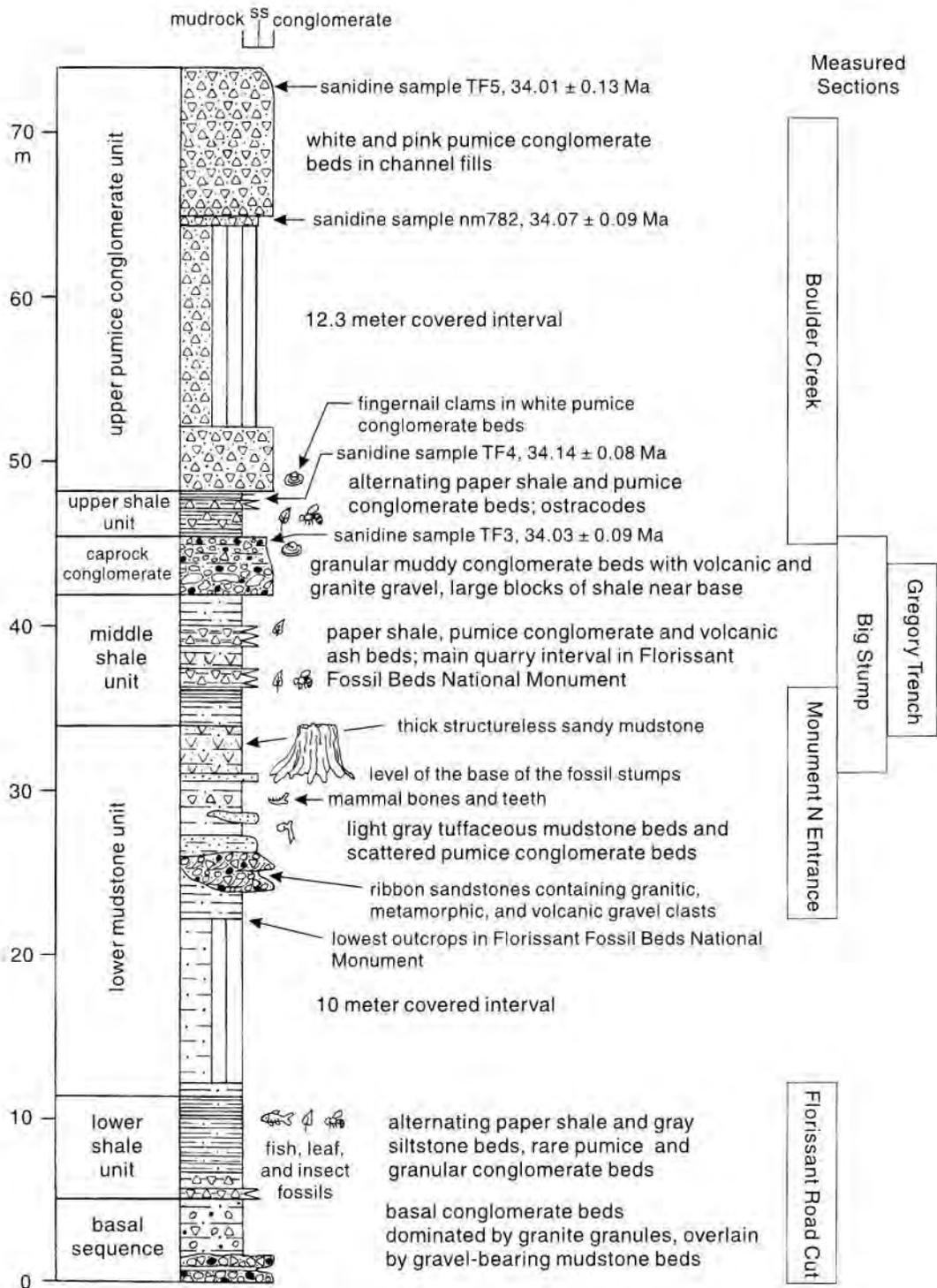
FIGURE 4. Informal subdivisions of the Florissant Formation. This sequence is compiled from the various measured sections at Localities 1–5 as shown in Figure 1 and listed in Table 1. The vertical bars on the right show the vertical range of the stratigraphic sections listed in Table 1.

the lower mudstone unit is 10.4 m near the north entrance road of the monument (Figs. 1, 4, Table 1, Locality 2). The base of the mudstone unit is not exposed in the monument, but is exposed near the top of the Florissant road cut section (Fig. 1, Locality 1). The elevation differences and regional dips of the formation suggest that the unit has an additional thickness of about 10 m. Trough cross-bed sets in the rare sandstone ribbon bodies in this unit show paleocurrent flow directions to the south within a trunk stream flowing down the axis of the main valley. The upper structureless sandy mudstone was deposited as a mudflow that buried the forest in the valley. Its upper part was reworked into horizontal beds by the redevelopment of the Florissant lake.

The middle shale unit (Fig. 4) is characterized by platy to papery shale beds interbedded with thin pumiceous conglomerate beds. The shale beds are also interbedded with scattered blocky to platy tuffaceous mudstone and siltstone beds, tuffs, and pumiceous sandstone beds. McLeroy and Anderson (1966) and O'Brien et al. (1998) studied the laminations in the papery shale beds and found them to be composed of alternating laminae of diatomite and smectite clay. The middle shale unit has a maximum thickness of 9 m in the center of the paleovalley axis. It is best exposed around the hill near the "big stump" (Fig. 1, Table 1, Locality 3) and at the mouth of the Grape Creek arm of the paleovalley (Fig. 1, Table 1, Locality 4). The transition from shale to granitic granular conglomerate beds on the edge of the paleovalley occurs at the mouth of the Grape Creek arm. Rare bones of mammals occur in the granite conglomerate lateral to the middle shale unit south of the Grape Creek arm. Most of the famous fossil plant and insect localities in the monument are from within this unit, but fish, mollusks, and ostracodes are very rare. Gregory (1994) studied the leaves and Wingate and Nichols (2001) studied the pollen in the middle shales at the mouth of Grape Creek (Fig. 1, Locality 4). The middle shales are lacustrine and record an episode of volcanic activity with the addition of pumice beds in the upper two thirds of the unit (see Wingate and Nichols 2001).

A widespread tuffaceous volcaniclastic conglomerate overlies the middle shale unit. This conglomerate is known in the monument as the "caprock" because it caps ridges and benches above the main fossil-producing shale beds (Figs. 2, 4). The clasts in the caprock conglomerate include abundant granite granules and numerous pebbles to granules of intermediate volcanic rocks. It is crudely graded, with pebbles and scattered cobbles or boulders at the base and muddy sandstone at the top. Bedding changes from primarily structureless at the base to horizontally bedded at the top. Vertical tubes representing water-escape structures occur in the middle part of this unit. Freshwater fingernail clams locally occur in the upper half of the unit. The unit is thickest in the central axial valley in the monument, but thins toward the north and northeast in the axial valley and up the tributary valleys. Just north of the monument, the caprock conglomerate pinches out. The thickest exposure of the caprock conglomerate is on the "big stump" hill (Fig. 1, Table 1, Locality 3) where it is 7.3 m thick. This conglomerate was initially a lahar deposit that entered the Florissant lake and was later reworked by lacustrine processes.

The upper shale unit (Fig. 4) is composed primarily of brownish-gray paper shale and secondarily of blocky mudstone and pumice conglomerate. Fossils are locally abundant in the shale, and include plants, insects, fish scales, and ostracodes. In the monument, the upper shale unit is thickest in the mouths of the western tributary valleys where it ranges from 3.6 to 5.6 m thick. The most complete exposures are along the Boulder Creek (Fig. 1, Table 1, Locality 5). Wingate and Nichols (2001) studied the pollen of this unit at this location. In the northwest corner of the monument where the caprock conglomerate is not present, the upper shale unit overlies the middle shale unit. Lithologically, the upper and middle shale units are similar, but the upper shale unit typically contains abundant ostracodes and numerous fingernail clam shells, unlike the middle shale unit. The upper shales represent lacustrine deposition after the influx of the caprock lahar deposits.

The upper pumice conglomerate unit (Fig. 4) consists of pumice-rich, white sandstone and conglomerate that are structureless near the base and cross-bedded near the top. The pumice fragments are typically granular and white with scattered pink clasts. The pumice conglomerate beds are exposed only at the head of the western tributary valleys of the main paleovalley, where they are as much as 22.8 m thick. Where the contact between the upper shales and the pumice conglomerate beds is exposed, the two units interfinger. The best exposures of the upper pumice conglomerate are north of the Boulder Creek (Fig. 1, Table 1, Localities 6, 7). The lower part of the pumice conglomerate unit was deposited in the Florissant lake, as indicated by locally abundant fingernail clam shells. The upper cross-bedded conglomerate beds represent deposition by streams flowing down the tributary valleys.

Mammalian Biostratigraphy of the Florissant Formation

The mammal fossils of the Florissant Formation provide biostratigraphic correlation with upper Eocene deposits of the Great Plains (Evanoff and deToledo 1999). The lower mudstone unit contains the mandible of the horse *Mesohippus* sp., the bones of a small artiodactyl (*Leptomeryx*? sp.), and the tooth fragments of large brontotheres. The arkosic conglomerate adjacent to the middle shale unit has produced the bones of oreodont artiodactyls and brontotheres. Other mammals reported from the formation include the oreodont *Merycoidodon* sp. (MacGinitie 1953), an unidentified rhinoceros, and the mouse opossum (*Peratherium*). Of these, only the mouse opossum has been described in detail (as *Peratherium* near *P. huntii*; Cope, see Gazin 1935). The co-occurrence of a large brontothere, *Mesohippus*, and *Merycoidodon* indicates a Chadronian age for the formation (Wood et al. 1941). These mammals indicate that the Florissant Formation correlates with the Chadron Formation of the White River Group of the Great Plains.

^{40}Ar/^{39}Ar Geochronology of the Florissant Formation

Laser-fusion analyses of a total of sixty-six individual sanidine crystals from four pumiceous samples of the upper Florissant Formation (Fig. 5, Table 3) yielded high-precision single-crystal ages ranging from 33.64 ± 0.22 Ma to 34.53 ± 0.15 Ma (all errors reported at ±2 sigma). Radiogenic yields generally ranged from 99.5 to 100 percent, indicative of minimal alteration or adhering matrix. K/Ca values (calculated from K-derived ^{39}Ar and Ca-derived ^{37}Ar) cluster tightly near a value of 45, suggesting minimal compositional variation among the crystals. Weighted mean ages calculated for each of the four samples (Table 2) all agree within error, and do not show a systematic variation with stratigraphic sequence, suggesting that the sanidine-bearing pumice was derived from a single eruption or closely spaced series of eruptions. The weighted mean of the four sample ages (34.07 ± 0.12 Ma) agrees closely with the weighted mean age of all sixty-six sanidine crystals (34.07 ± 0.10 Ma); we consider the latter to be the best estimate for the eruption age of silicic pumice in the Florissant Formation. The range in ages shown by the entire population of sixty-six individual crystals is somewhat greater than that typically observed in sanidine crystals from individual ignimbrites (e.g., McIntosh and Chamberlin

1994), but the distribution of ages is unimodal and approximately Gaussian (Fig. 5). This age variation among crystals may be related to minor effects of melt inclusions in the sanidine crystals, but may also reflect some small variation in age of eruptions that produced the pumice clasts.

It is considered likely that the Florissant Formation was deposited soon after eruption of the 34.07 ± 0.10 Ma pumice clasts. Although the Florissant Formation lacks definite primary volcanic deposits, such as ignimbrites or pyroclastic fall deposits, several features are consistent with deposition penecontemporaneous with eruption. This interpretation is supported by the close agreement in age of the four stratigraphically distributed samples, the abundance of sanidine-bearing pumice of this age, the unimodal distribution of the single-crystal ages and K/Ca ratios, and the lack of any significantly older or younger pumice fragments.

Eruptive Source of Pumice and Ash in the Florissant Formation

The eruptive source of the silicic pumice and ash in the Florissant Formation is uncertain. Lithologically similar nonwelded pumiceous ignimbrites and reworked sedimentary deposits are present in the Antero Tuff, erupted from the Mount Aetna caldera and exposed in the Thirtynine Mile volcanic field to the south and west of Florissant (Fig. 3). However, sanidine from Antero Tuff has a measurably younger age (33.78 ± 0.09 Ma) than the Florissant Formation sanidine, and significantly higher K/Ca ratios (68.1 ± 16.4) per McIntosh (unpubl. data). The Grizzly Peak caldera (Fig. 3) is another potential source for the Florissant Formation pumice, but no outflow ignimbrites have been identified, and sanidine from samples of the Grizzly Peak intracaldera ignimbrite are older (34.31 ± 0.09 Ma) than the Florissant Formation sanidine, and also have higher K/Ca ratios (84.4 ± 6.2 Ma) per McIntosh (unpubl. data). Given available data, three possible sources for the 34.07 ± 0.10 Ma Florissant Formation pumice can be suggested: (1) early, pre-ignimbrite eruptions from the 33.8 Mount Aetna caldera, (2) late, post-ignimbrite eruptions from the 34.3 Ma Grizzly Peak caldera, or (3) eruption of local rhyolite domes in the vicinity of Florissant. Geologic mapping in the Florissant area has not identified any rhyolitic domes in the appropriate 34 Ma age range, although it is possible that such domes were present but are now eroded or covered.
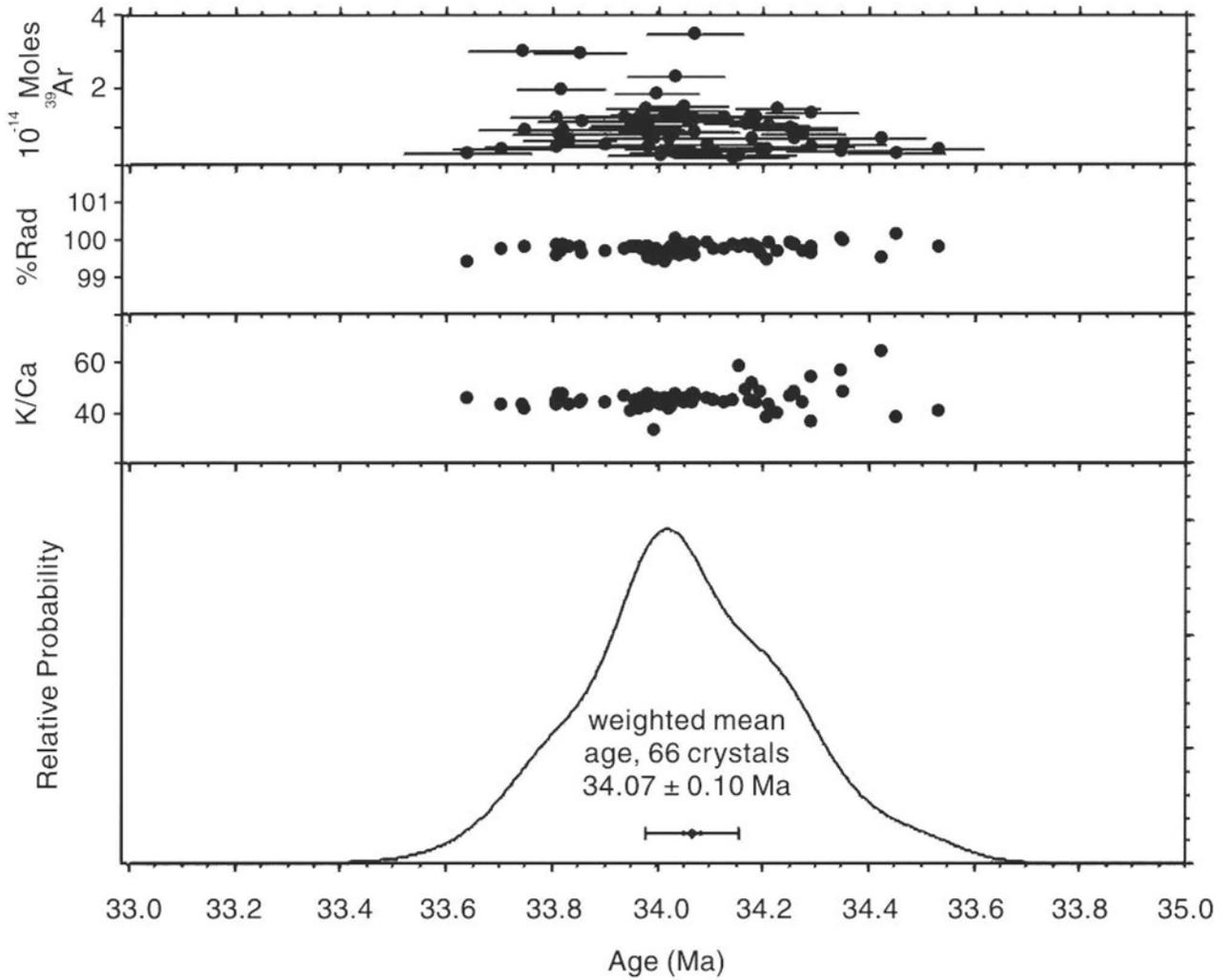
FIGURE 5. Ideogram (age probability diagram; Deino and Potts 1992) of single-crystal laser-fusion results of sanidine from the Florissant Formation.

Conclusions

The Florissant Formation is a heterolithic assemblage of shale, tuffaceous mudstone and siltstone, arkosic and volcaniclastic sandstone, and conglomerate. The formation was deposited within a valley that drained to the south. The valley was episodically blocked by lahar deposits, which eventually extended at least to the monument. The Florissant Formation records two episodes of lake formation. The first lacustrine episode is represented by the lower shale unit. These lower lacustrine deposits were separated from the middle lacustrine shale beds by a fluvial unit (the lower mudstone unit). The caprock conglomerate divides the upper lake sequence into two shale sequences within most of the monument area. The lacustrine deposits were eventually buried first by pumice gravel and then by additional laharic breccias from the Thirtynine Mile volcanic field. Post-Oligocene erosion has exposed the formation such that much of its present distribution reflects the original extent of the paleovalley fill.

The $^{40}Ar/^{39}Ar$ age of 34.07 ± 0.10 Ma of the Florissant Formation places its age within the latest Eocene. The current widely accepted age of the Eocene/Oligocene boundary is at 33.7 Ma ± 0.5 Ma, based on the age of the boundary stratotype in the northern Apennine Mountains of Italy (Montanari et al. 1988). McIntosh et al. (1992) have suggested a younger age for the boundary (near 33.4 Ma) based on calibrating the geomagnetic polarity time scale using $^{40}Ar/^{39}Ar$ dated ignimbrites in Colorado, New Mexico, and west Texas. Both ages for the boundaries place the Florissant Formation in the latest Eocene. The presence of large brontotheres also suggests a latest Eocene age for the formation because brontotheres became extinct at or very near the Eocene/Oligocene boundary in the Great Plains (Obradovich et al. 1995).

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2.

FLORISSANT LEAF AND POLLEN FLORAS OF COLORADO COMPARED: CLIMATIC IMPLICATIONS

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ABSTRACT—The rich leaf flora of Florissant dated at 34.1 Ma, and identified by Harry D. MacGinitie's classic work, is well represented by our data from fossil pollen and spores. The diversity of the flora is indicated by the 114 species that MacGinitie identified from leaves and fruits, and the more than 150 phenotypes found among the pollen and spores. Pollen identifications from various parts of the Florissant Formation corroborate the generally warm paleoclimate indicated by fossil leaves. The pollen further adds a number of additional warm-temperate to subtropical taxa to the flora: *Cyclocarya*, *Engelhardtia/Alfaroa*, *Juglans*, *Platycarya* of the walnut family, and *Eucommia*. Others such as *Fagus* (beech), *Pterocarya*, and *Pteroceltis* represent warm-temperate taxa that do not range into subtropical climate areas. All of these types, which are generally associated with humid, summer-moist climates in eastern Asia, North America, and Mexico, undoubtedly grew together in the humid lowland habitat surrounding Lake Florissant. Of special importance is our collection of a fossil palm leaf that indicates a relatively frost-free climate, with cold month average temperatures no lower than 5 to 7 °C. Several additional taxa, including *Sarcobatus* (greasewood) and other salt bushes, *Datura*, *Elaeagnus*, and two woody taxa of northern Mexico (aff. *Xylonagra* and *Semeiandra*), were probably associated with local dry environments. Diverse conifers and shrubs probably belonged to dry woodland habitats above the lake.

Twenty-six of the fifty-two families of identified vascular plants from fossil leaves are corroborated by pollen and spores and ten new ones have been added. Of the ca. ninety-eight genera of vascular plants that MacGinitie and Manchester (2001) have described in the leaf flora, some twenty-three have been identified in the microfossil record. The twenty-five genera we add to the flora by microfossil evidence include several new families not previously identified at Florissant, including Selaginellaceae, Schizaeaceae, Elaeagnaceae, Rhoipteleaceae, Ericaceae/Pyrolaceae, Onagraceae, Chenopodiaceae, Eucommiaceae, Apocynaceae, and Solanaceae. Further, a member of the Fremontodendreae has verified the family Sterculiaceae. We found three new conifer taxa (*Pseudotsuga/Larix*, *Cedrus*-type, and *Tsuga*). Related pollen groups represent the main fossil wood taxa (Wheeler 2001).

Our pollen identifications corroborate many of the reported leaf taxa, especially among those plant groups that are wind-pollinated and are prolific pollen producers (86 percent of these can be identified). By contrast, among those groups that are moderately low to low pollen producers, including many insect-pollinated types, we can corroborate only 27 percent of the leaf taxa.

Samples from a measured section in the lower part of the Florissant Formation indicate that Taxodiaceae (TCT) pollen types are common (10–35 percent of the tally), Pinaceae are less common (5–25 percent), Ulmaceae-types range from 5 to 15 percent, and Fagaceae and Juglandaceae pollen are less common, ranging from 1 to 10 percent of the total counts. *Fagopsis*-type pollen reaches ~10 percent in some samples.

The evidence from the microfossils accords with conclusions from fossil leaves, fruits, and fossil insects that the climate in the vicinity of the lake was relatively equable, moderate rainfall in summer, warm-temperate to subtropical, with mild, dry winters. Forty percent of the nearest living relatives (NLR) of the new genera range into subtropical climate zones, and the others are mainly warm-temperate. Several taxa suggest a mean annual temperature no lower than ~17.5 °C, a climate that is on the borderline between warm-temperate and subtropical. This estimate of mean annual temperature is 4 to 6.8 °C warmer than CLAMP or multiple regression (MR) estimates of other authors. The discrepancy between estimates may reflect the fact that the NLR data emphasize conditions around the lake itself, and take into account the limiting factors for warm-temperate and subtropical plants.

If the paleolapse rate in Colorado was the same as the present lapse rate of 5.9 °C/km, then the paleoflora indicates a relatively low elevation, perhaps below 984 m (<3000 feet) as suggested by MacGinitie at the Florissant site for the Eocene/Oligocene transition. If the paleolapse rate was lower, the present temperature requirements of the plants involved still indicate a mean annual temperature (MAT) of at least 17.5 °C (not 10–12 °C of some authors). The floral data do not accord with a cool-temperate flora of high elevations as postulated by other authors.

Much has been written recently about the proposed environment and topography of the Florissant basin of Colorado at the time the famous fossil-bearing sediments accumulated in ancient Lake Florissant, but the interpretations conflict. How and when did the basin get to its present elevation (Trimble 1989)? How warm was the climate? Paleoclimatic evidence comes primarily from the fossil plants. The present report on pollen and spores adds new plant genera, several of which are warm-temperate to subtropical in distribution, and corroborates many taxa from the identified leaf flora.

The monograph by MacGinitie (1953) on the Florissant fossil leaves stands as a model of careful work that all contributors to this volume build upon. The care with which MacGinitie studied the taxonomy and modern affinities of the flora becomes apparent when one notes how few assignments have been changed over the years since his publication.

The pollen work reported in this volume, begun by the first author while working at the U.S. Geological Survey in Denver, Colorado, is designed to compare the fossil pollen and spore types with modern ones of the groups that MacGinitie and Manchester (2001) identified at Florissant. Questions of special interest include: How well do the microspore types corroborate the megafossil identifications? What biases do we face in the pollen record? What can the pollen flora add to the understanding of the conditions at Florissant? Do pollen grains provide the same ecological and climatic picture of the flora as megafossils?

Background

The leaf flora of the Florissant lake beds identified by MacGinitie included some 114 species of plants, one of the larger leaf and fruit floras of Tertiary age in the western United States. Manchester's taxonomic review (2001) of the megafossils shows the number of Florissant taxa to be still about 110 to 120, including ca. 98 genera. The chief families represented by leaves are the legumes (nine genera), the rose family (seven genera), and the Sapindaceae (six genera). The pollen flora that we can identify shows a different spread of taxa, especially of gymnosperms and dicotyledonous groups known to be prolific pollen producers.

The fossil vegetation at Florissant (MacGinitie 1953) was chiefly of woody, warm-temperate groups with many summer-moist types and some subtropical types, in contrast with the present flora of Florissant, which contains an abundance of herbs and the subarid shrub community of the *Pinus ponderosa* woodland (Edwards and Weber 1990).

MacGinitie determined that the nearest modern analog of the flora is in Central America's northernmost cloud forest—a rare area of extreme biodiversity on the eastern slope of the Sierra Madre Oriental in northeastern Mexico. There the rich subhumid mixed deciduous and conifer vegetation occurs in central Tamaulipas Province (lat 23°N) as described by Martin (1958), and lies about 50 km south of Ciudad Victoria. Because of its scientific value, the Mexican government declared 145,000 hectares of lands in this area to be

saved as the Reserva de la Biosphera El Cielo (now a part of the Man and the Biosphere Program of the United Nations).

El Cielo represents a transition zone between tropical and temperate forests that has produced four basic ecosystems. Above a lowland thorn forest is a tropical caducifolia jungle in the eastern one-third of the reserve. Above this area is the cloud forest (*bosque de niebla*, 800–1400 m), an area that receives rainfall six months of the year (May–October). Above 1400 m, a pine-oak forest exists; and on the Sierra's lower western slopes is a chaparral-matorral of dwarf oaks and heaths.

The caducifolia jungle and cloud forest (Puig 1976; Puig et al. 1983) include a wide array of genera such as may have grown in low moist areas around the Lake Florissant. Some of the hardwoods are closely related to riparian species that now occur in lowland environments of the Edwards Plateau of central Texas (MacGinitie 1953). On the high flanks of the Sierra Madre Oriental stands a dry forest dotted with pines and evergreen oaks. The oaks grow stunted and gnarled with spreading crowns, usually less than 25 m (~82 feet) tall. The vegetation is more sparsely distributed than in the cloud forest, and some elements of the pine-oak woodland may be a good analog of the highland vegetation above and around the Florissant basin.

Presently the climate of Florissant (elevation 2453 m or 8047 feet) in Teller County is summer-moist and cool-temperate with heavy freezing in winter. The mean annual temperature (MAT) is only 3.3 °C and the cold month average is −9.3 °C (Table 1). The seasonal range between the coldest and the warmest month (MART) is quite large: 25.4 °C with a mean annual precipitation of 32.2 cm, falling mostly between May and July. The National Weather Service records are from Lake George, 10 miles northwest of Florissant (elevation 2560 m or 8397 feet).

However, the general climate of the hill region south of Ciudad Victoria, Mexico, (MacGinitie 1953) is different by being warm-temperate to subtropical with rare, if any, frosts. For example, the mountain area of the eastern Sierra Madre piedmont at lat 23°N (Rancho del Cielo; Table 1) has a MAT of 19.5 °C; a low range of monthly mean temperature (7 °C); and a local precipitation of 2.54 m/year (summer-wet; Larry Lof, unpubl. data; Koeppen 1948; Puig 1976). Regional rainfall is less, with ca. 650 mm/year (World Meteorological Organization 1979). Heavy fog hangs over the area for long periods, alleviating the stress of drought during winter and early spring. Below 1175 m the climate is frost-free, though a brief and rare freezing event occurred in the cloud forest under northern winds in 1951 (Martin 1958, 1999).

In the Florissant basin today, ponderosa pine (*Pinus ponderosa*) woodland with aspen extends down to ca. 2438 m (8000 feet) and does not grow on the lake

TABLE 1. Temperature and rainfall characteristics of Lake George, near Florissant, Colorado, and of Rancho del Cielo cloud forest on the east slope of the Tamaulipas highlands, Sierra Madre Oriental, northeastern Mexico (Appendix 1, World Meteorological Organization 1979; Martin et al. 1998). Rainfall mean for El Cielo Biosphere Reserve is listed in right-hand column (World Meteorological Organization 1979).

	Lake George, CO	*Rancho del Cielo Tamaulipas Province, NE Mexico*
Latitude	39°N	23°N
Elevation	2560 m (8396 ft)	1175 m (3854 ft)
Mean annual temperature	3.3 °C	19.5 °C
Warm month mean	16.6 °C	23 °C*
Cold month mean	−9.3 °C	16 °C*
Mean annual range temperature	25.9 °C	7 °C*
Mean annual precipitation	325 mm (mainly spring and summer)	2000–2540 mm** (mainly May–October)

* Cold month, warm month, and mean annual range (MART) data for 1953–1955 after Martin 1958.
** Larry Lof, 22-year rainfall record, unpublished.

deposits in the center of the basin. Colorado blue spruce (*Picea pungens*) occurs where the granite bedrock is close to the surface, and blue spruce along with Douglas-fir (*Pseudotsuga menziesii*) grows in the draws, north-facing slopes, and cool stream valleys. Piñon and bristlecone pine are found on dry summit ridges (Edwards and Weber 1990). Outside the Florissant Fossil Beds National Monument, Engelmann spruce (*Picea engelmannii*) becomes dominant above 3048 m (10,000 feet), and altitudinal tree line is approximately 3444 m (11,300 feet). The modern pollen rain at Florissant is overwhelmingly dominated by pine, but is mixed with sagebrush (*Artemisia*), grass, and pollen of other herbs.

Previous work on Florissant lake bed sediments includes the study of laminae by McLeroy and Anderson (1966) by which they estimated the length of time that might have been involved for the deposition of the lake deposits. Early identifications reported by Leopold (1965) and shown in photographs of Florissant pollen for the book edited by Tschudy and Scott (1969, Plate 16.6) established some of the key taxa. A comprehensive thesis with pollen counts by Hascall (1988) documented pollen and spores from the section that Cross and Taggart describe (unpubl. data). A review of Eocene floras of the central Rocky Mountains displays a clear decline of Old World tropical taxa, which were replaced by New World tropical types (Leopold and MacGinitie 1972). Florissant is a benchmark flora because it comes at the end of the tropical period of the Eocene. The pollen diagram from the lower part of the Florissant deposits shows relatively little vegetative change within this section (Leopold et al. 1992).

Location and Age of Deposits

The outline and topography of the old Florissant basin were similar to those that we see today (Epis and Chapin 1968, 1975). The extent of the Florissant sediments, based on walking the margin of the outcrops (Wobus and Epis 1978; Leopold and Lind, Natl. Park Serv., unpubl. report, 1964), seems generally to be delineated by the treeless area on topographic maps (Lake George Quadrangle, U.S. Geological Survey 1956 1:24,000). The isotopic age of the Florissant Formation, 34 Ma, was originally established from K/Ar dating on volcaniclastic rocks that overlie the lake sediments (Evanoff et al. 2001; Epis and Chapin 1975). Newer evidence from ^{40}Ar/^{39}Ar single-crystal laser-fusion dating shows that the Florissant Formation is bracketed by an

age of 34.07 ± 0.10 Ma (Evanoff et al. 2001) on the overlying volcanics and 36.7 Ma from the underlying Wall Mountain Tuff. Based on the association of Chadronian mammals and using the revised age of the Eocene/Oligocene boundary, the Florissant is latest Eocene in age (Evanoff 1994; Evanoff and Doi 1992).

The sites from which sediment samples were prepared for our fossil pollen studies come from areas in the north and central parts of the Florissant basin (Fig. 1). The first sediments prepared, U.S. Geological Survey Paleobotany localities D1095 and D1083, were from hand samples received from other sources, and the locality information for these is lacking. The long section (13 m; see Appendix 3) is University of Washington paleobotanical locality W-1 from the road cut ½ km east of the Florissant townsite. The top of this section is what Cope (1875) called the Amyzon beds. In the list of collection localities shown in Appendix 2, the D numbers refer to U.S. Geological Survey Paleobotanical Localities (data available at the U.S. National Museum).

Our samples analyzed for pollen were collected by Leopold, and were chiefly from lacustrine sediments, many of which were laminated paper shales with graded bedding (fining upward) suggesting sequential ashfalls. Laminae are 2 mm to 9 m thick; the lower parts of each lamina were typically of silt or fine sand, grading upward into silt and clay. At one section (D1177) we sampled a thick massive silt and clay bed that contained abundant green algae and occasional pollen. Evanoff remeasured our section W-1 in detail in 1993 and has made the results available (see Appendix 3). The thickness of the lithologic units and the position of the pollen samples are shown in Figure 2. Based on field examination of D1177 and W-1 sections (Evanoff et al. 1994), these northern localities represent the lower part of the Florissant sedimentary sequence.

Methods

The first author carried out the photography and taxonomic research, and both authors shared the counting of pollen and spores for the pollen diagram. Identifications were based on modern pollen reference slides that cover a wide number of taxa from east Asian and New World tropics and temperate zone. The reference slides are housed at the U.S. Geological Survey Climate Program at the Denver Federal Center in Denver, Colorado, and at the Pollen and Seed Laboratory, Department of Botany, University of Washington, Seattle.

Preparation methods followed Doher (1980), starting with careful cleaning of fresh sediment blocks,
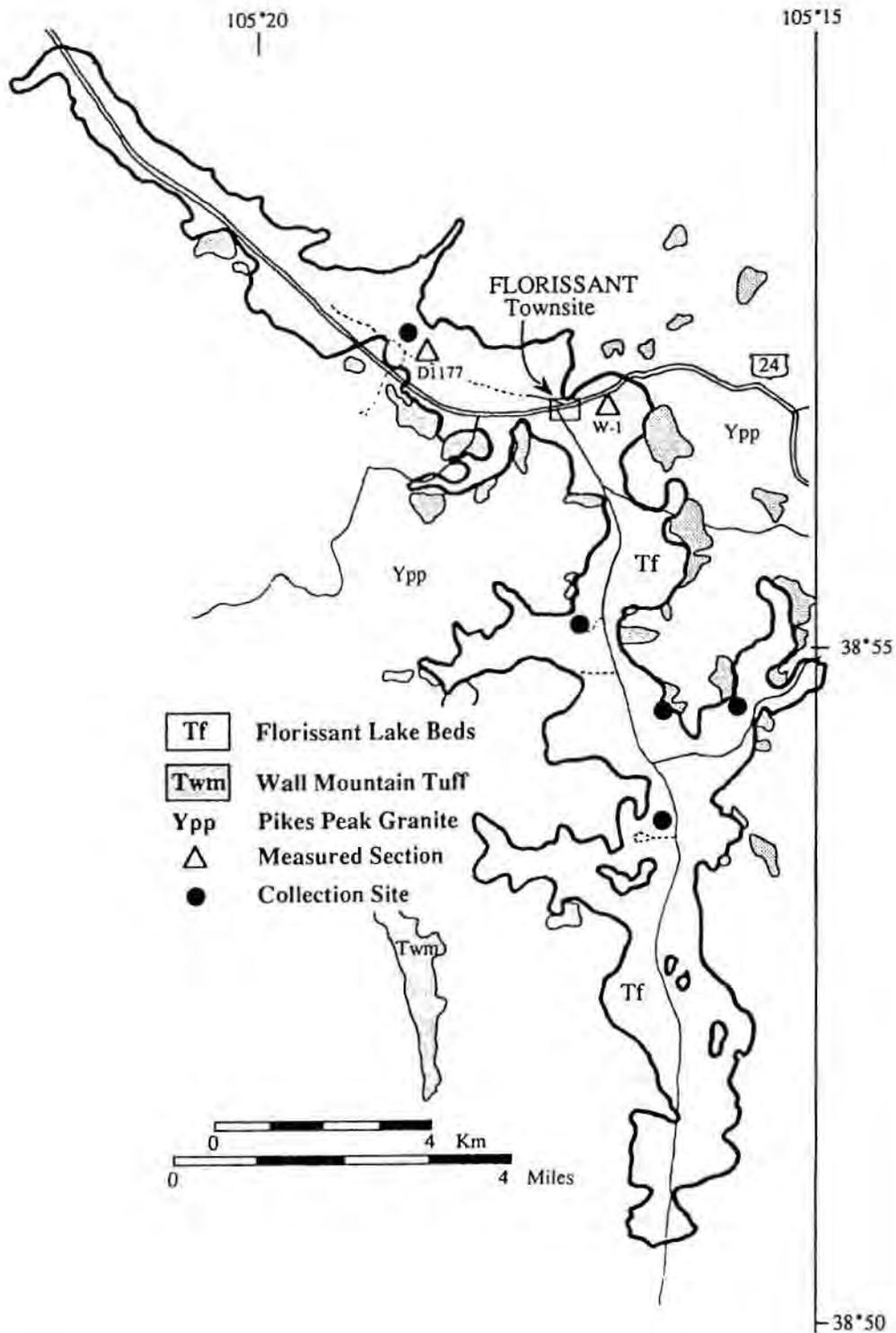
FIGURE 1. Map of Florissant basin showing outline of the Florissant Lake Beds and localities where samples were taken. Measured section W-1 east of the town site is the location of the pollen histogram of Figure 3.
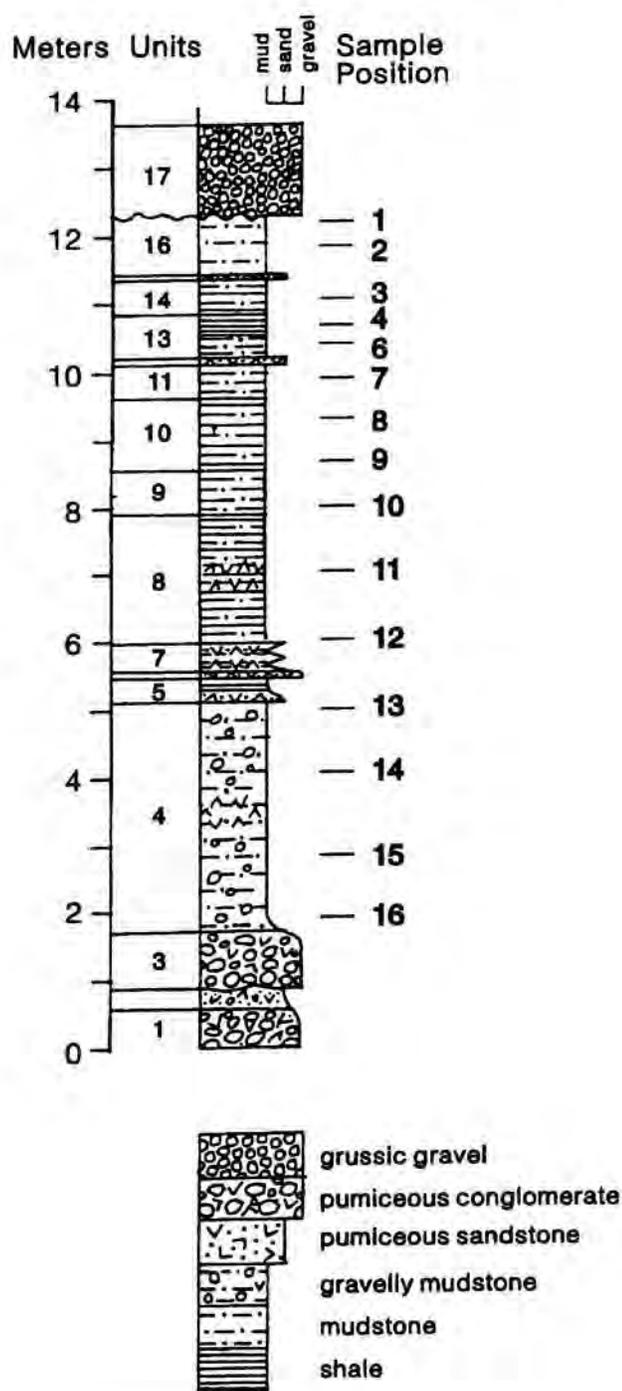
FIGURE 2. Measured section W-1 showing lithologic units and pollen-sampling levels; meters above base of section (description in Appendix 3; Evanoff et al. 2001) are rounded off here.

crushing with mortar and pestle to pea-sized chunks, and initial treatment with 10 percent HCl to dissolve carbonates present in some samples. Hydrofluoric acid treatment was utilized, ranging from several hours to overnight periods at room temperature. Acetylation of sediments was followed by a swirling and panning treatment used to clean the residue of unwanted fragments. Fossil pollen were mounted in glycerin jelly with safranin O as a light stain. Cover slips were sealed with plastic. Slides and extra samples are stored at the U.S. Geological Survey Climate Program laboratory at the Denver Federal Center in Lakewood, Colorado. Counts of fossil pollen included 200 to 400 grains per slide.

Results

Composition of the Pollen Flora Related to the Megafossils

The plant taxa identified from spores and pollen (Table 2) are compared taxonomically with the megafossil record in Table 3. The spore data add at least two fern allies to the flora, and pollen of gymnosperms indicates the presence of at least three additional genera of Pinaceae. Pollen of angiosperms provides evidence of one additional monocot, and add six genera of Hamamelids, one genus of Caryophyllidae, and five Rosidae-types. Of the ninety-eight identified leaf genera, about twenty-three are found from microfossil evidence (genus or subfamily level) and twenty-five generic types are new additions to the flora. Of the fifty-two families identified from vascular remains, some twenty-three are corroborated by pollen and spore evidence, and ten new families have been added. Algal types that are locally abundant, such as *Pediastrum* and *Botryococcus*, are described by other authors (Wingate and Nichols 2001; Cross and Taggart, unpubl. data). The pollen diagram (Fig. 3) shows relative numbers of pollen and spores in the tallies for section W-1. The classification of Juglandaceae follows Cronquist (1981).

FERNS AND FERN ALLIES

Among the spores of vascular plants, several represent *Selaginella*. One type is an excellent match for the spores of *Selaginella densa* (Plate 1, Figs. 2, 3), a herbaceous groundcover plant that is common on dry exposures in the Rocky Mountains. Trilete spores of this type with a flange along the equatorial plane are also commonly seen in Miocene deposits of western North America. Several other types are *Selaginella* cf. *S. longipila* (Plate 1, Fig. 1), cf. *S. sanguinolenta* (Plate 1, Fig. 4),

TABLE 2. List of Florissant pollen and spore identifications. Taxa added to the flora by microfossil identifications are marked with an asterisk (*). Classification of Juglandaceae follows Cronquist (1981).

Group	Genus		Common Name
Pteridophyta and Gymnospermae:			
Selaginellaceae*	Selaginella*	cf. S. densa	Lesser clubmoss
		cf. S. longipila	
		cf. S. mairei	
		cf. S. sanguinolenta	
Polypodiaceae			Polypody fern–types
Schizaeaceae*	Lygodium*	cf. L. kaulfussi	
Pinaceae	Abies	cf. A. venusta	Fir
	Pseudotsuga/Larix*		Douglas-fir or Larch
	Picea spp.		Spruce
	Tsuga spp.*		Hemlock
	Pinus spp.		Pine
	Cedrus* extinct type		Deodar Cedar–type
Taxodiaceae-type	TCT pollen type		Sequoia-type
	Also Sequoia affinis		in situ prepared pollen
Gnetaceae	Ephedra,	cf. E. nevadensis	Mormon's tea
		cf. E. torreyana*	
Angiospermae:			
Liliopsida			
Arecaceae (Palmae)			Palmae-type pollen
Poaceae (Gramineae)			Grass pollen
Typhaceae/Sparganiaceae	Typha/Sparganium		Cattail or rush
Magnoliidae			
Nymphaeaceae*	Nuphar*		Water lily
	(not figured)		
Berberidaceae	Mahonia/Berberis		Oregon grape–type
	(not figured)		
Eucommiaceae*	Eucommia*	cf. E. ulmoides	
Ulmaceae	Pteroceltis		Asian relative of Celtis
	Ulmus-Zelkova		Elm
Hamamelidae			
Betulaceae	Ostrya-Carpinus (Ostrya-type)		Hornbeam–type
Fagaceae	Castanea		Chestnut
	Fagopsis in situ pollen prepared		Extinct genus
	Fagus*		Beech
	Quercus		Oak
	Quercoid, long-axial pollen		(extinct genus of Fagaceae)*
Juglandaceae	Carya	cf. C. cordiformis	Hickory
	Cyclocarya*	cf. C. paliurus	Asian hickory
	Engelhardtia/Alfaroa*	cf. E. spicata	
	Juglans		Walnut
	Pterocarya*		Wingnut
	Platycarya*	cf. P. strobilacea	
Moraceae	Morus-type		Mulberry-type
Rhoipteleaceae*	aff. Rhoiptelea*		
Caryophyllidae			
Caryophyllaceae	Stellaria or Silene-type		Chickweed*
Chenopodiineae*	Amaranthus or Chenopodiaceae		Saltbush group

(continues)

(Table 2 continued)

Group	Genus		Common Name
Chenopodiaceae*	Sarcobatus*	cf. S. vermiculatus	Greasewood
Dilleniidae			
Salicaceae	Populus		Poplar, cottonwood
	Salix		Willow
Sterculiaceae	Florissantia-type		
	Fremontodendreae		Extinct
Rosidae			
Anacardiaceae	Astronium-type		
Elaeagnaceae*	Elaeagnus*	cf. E. argentea	Buffalo berry
Ericales*	Ericaceae or Pyrolaceae		Heath
Euphorbiaceae	Croton*		
Fabaceae		cf. Petalostemon*	Prairie clover
Rosaceae	Malus/Pyrus		Crabapple/Apple
Onagraceae*	Semeiandra*	cf. S. grandiflora	Evening primrose
	aff. Xylonagra*	cf. X. arborea	
Rutaceae	? Ptelea	cf. P. amygdalina (not figured)	
	aff. Evodia*		
Sapindaceae	Acer	cf. A. glabrum	Maple
	Cardiospermum	cf. C. halicacabum	
	Koelreuteria		Varnish tree
Thymeliaceae	Daphne		
Vitaceae	Parthenocissus/Cissus		Five-finger vine group
Asteridae			
Apocynaceae*	Tabernaemontana*	cf. T. coronaria	Dogbane group
Caprifoliaceae	Viburnum*	cf. V. lentago	Sheepberry, Nannyberry-type
	Sambucus	cf. S. formosana	Elderberry group
Malvaceae*	Malvaceous pollen*		Mallow family
Oleaceae	Fraxinus-type		Ash-type
Solanaceae*	Datura*	cf. D. discolor	Jimson weed
Uncertain			
Asteraceae/Compositae?			
Aquifoliaceae?	Ilex-type		
Haloragidaceae?	Myriophyllum-type		

* New taxa from pollen evidence

TABLE 3. Corroboration of leaf and fruit taxa by identifications of pollen/spore flora. Megafossil list includes corrections and corroboration by Manchester (2001), except where pollen data do not support the correction.

Manchester's identifications = †
Wheeler's additions from fossilwood = ‡
Counterparts if found from microfossils = right-hand column
New pollen/spore additions to flora = right-hand column*

MICROFOSSIL CORROBORATION OF MEGAFOSSIL TAXA

Leaf/Fruit/Wood		*Pollen/Spores*
Bryophyta:	2 spp.	liverwort, undet.
Sphenopsida:		*Selaginellaceae *Selaginella* 4 spp.
Equisetaceae	*Equisetum*	
Pteropsida:		
Polypodiaceae		Polypodiaceae-type spores
	Dryopteris	
		*Schizaeaceae, *Lygodium*
Gymnospermae:		
Pinaceae	†*Abies*	
	Abies longirostris	*Abies* cf. *A. venusta*
		Cedrus-type, extinct
	Picea	*Picea*
		Pseudotsuga/Larix
	†*Pinus*	*Pinus*
		Tsuga
Taxodiaceae	†*Sequoia affinis*	*S. affinis* pollen
Taxaceae	†*Torreya*	
Cupressaceae	†*Chamaecyparis*	TCT pollen
Gnetaceae	*Ephedra*	*Ephedra,* 2 spp.
Angiospermae:		
Liliopsida		
Cyperaceae	†*Cyperacites*	
Potamogetonaceae	†*Potamogeton*	
Liliaceae	*Smilax*	Liliales-types
Arecaceae (Palmae)	†*Palmacites*	Palmae-type pollen
Poaceae(Gramineae)	†*Stipa*	Grass pollen
Typhaceae	*Typha*	Typhaceae or Sparganiaceae *Typha /Sparganium*
†Dioscoreaceae	†*Dioscorea*	
Magnoliidae		
Aristolochiaceae	*Aristolochia*	
Berberiaceae	†*Mahonia*	*Mahonia/Berberis*
Eucommiaceae	†*Eucommia*	*Eucommiaceae *Eucommia*
†Lauraceae	*Sassafras, Persea* *Lindera*	
		*Nymphaeaceae
Ulmaceae	†*Cedrelospermum*	
	Celtis	*Celtis* *Pteroceltis*

(continues)

(Table 3 continued)

Leaf/Fruit/Wood		Pollen/Spores
	†*Ulmus*	
	‡cf. *Zelkova*	*Ulmus-Zelkova*
	‡cf. *Hemiptelia*	cf. *Hemiptelia*
Hamamelidae		
Betulaceae	†*Paracarpinus*	*Ostrya-Carpinus*
	†*Asterocarpinus*	
Fagaceae	*Castanea*	*Castanea*-type
	†*Fagopsis*	*Fagopsis in situ* pollen
	†*Quercus* 9 spp. lvs	*Quercus* 2 spp.
Juglandaceae	†*Carya*	*Carya*
		*Cyclocarya
		*Engelhardtia/Alfaroa
		*Juglans
		*Platycarya
		*Pterocarya
Moraceae	*Morus*	*Morus*-type
Platanaceae	†*Platanus*	*Platanus*-type
		*Rhoipteliaceae cf. *Rhoiptelia*
Caryophyllidae		*Chenopodiineae
		*Chenopodiaceae
		*Sarcobatus
Dilleniidae		
Salicaceae	†*Populus*	*Populus*
	†*Salix*	*Salix*
†Sterculiaceae	†*Florissantia*	*Sterculiaceae
		*Fremontodendrae
Styraceae	*Halesia*	
Tiliaceae	*Tilia*	
Rosidae		
Anacardiaceae	*Astronium*	
	Cotinus	
	†*Rhus*	
	Schmaltzia	
†Araliaceae	*Oreopanax*	
Burseraceae	*Bursera*	
Celastraceae	*Celastrus*	
		*Ericales tetrads
		*Elaeagnaceae, *Elaeagnus*
Euphorbiaceae	*Euphorbia*	
		*Croton
Fabaceae (Leguminosae)	*Cercis* (and 6 living genera	cf. *Petalostemon*
	and 3 organ genera)	
Grossulariaceae	*Ribes*	
Hydrangeaceae	*Hydrangea*	
	Philadelphus	
†Meliaceae	†*Cedrela* or *Toona*	
	Trichilia	
Myrtaceae	*Eugenia*	
†Onagraceae flower		*Onagraceae pollen
		*Semeiandra cf. *S. grandiflora*
		*aff. *Xylonagra*

(continues)

(Table 3 continued)

| Leaf/Fruit/Wood		Pollen/Spores
Rhamnaceae	*Colubrina*	
	Rhamnites	
	Zizyphus	
Rosaceae	†*Amelanchier*	
	†*Cercocarpus*	
	†*Crataegus*	
	†*Holodiscus*	
	†*Malus*	*Malus, Pyrus*
	†*Prunus*	
	†*Rosa*	
	†*Rubus*	
	†*Vauquelinia*	
Rutaceae	†*Ptelea*	cf. *Ptelea*
		Evodia-type
Sapindaceae	†*Acer*	*A. glabrum*–type
	†*Dipteronia*	
	Athyana	
	Cardiospermum	*Cardiospermum*
		cf. *C. halicacabum*
	Dodonaea	
	†*Koelreuteria*	*Koelreuteria*
	Sapindus	
	Thouinia	
Simaroubaceae	†*Ailanthus*	
Staphyleaceae	*Staphylea*	
Thymelaeaceae	*Daphne*	*Daphne*
Vitaceae	*Parthenocissus*	*Parthenocissus/Cissus*
	Vitis	*Vitis?*
Asteridae		
†Apocynaceae	†*Apocynospermum*	Apocynaceae
		Tabernaemontana
Caprifoliaceae	†*Sambucus*	*Viburnum* cf. *V. lentago*
	†*Diplodipelta*	
Convolvulaceae	*Convolvulites*	
		*Malvaceae
Oleaceae	*Osmanthus*	*Fraxinus*–type
		*Solanaceae; *Datura* cf. *D. discolor*
Verbenaceae	*Petrea*	
Other:		Asteraceae/Compositae?
Uncertain		Haloragidaceae *Myriophyllum*–type
		Ilex-type
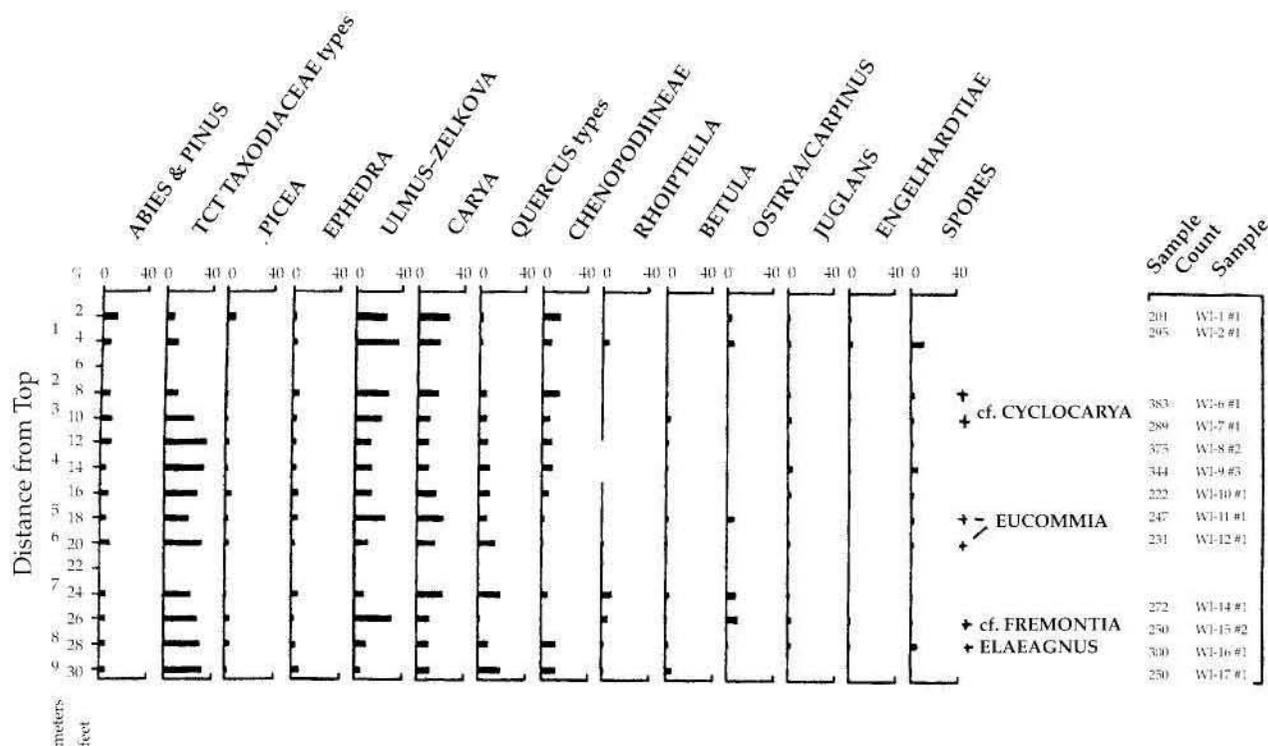
FIGURE 3. Pollen diagram showing selected pollen types; percent total pollen and spores.

and cf. *S. mairei* (Plate 1, Figs. 5, 6). Though the genus is cosmopolitan, the resemblance to these *Selaginella* species is striking.

Large, smooth, thick-walled trilete spores (Plate 1, Fig. 10) look very much like the large spores that we extracted from a fertile leaf fossil of *Lygodium kaulfussii* (Schizaeaceae). This species is common in other middle and late Eocene deposits in the Rocky Mountain region (MacGinitie 1974:53, Plate 36, Fig. 10). We report similar Eocene spores in Love et al. (1978). *In situ* spores of *L. kaulfussii* are illustrated by Manchester and Zavada (1987, Fig. 12) from the late Eocene Bridger Formation of Wyoming. They show that *L. kaulfussii*, with its peculiar nonlaminar, highly dissected foliage, is related to *L. palmatum* of warm-temperate distribution in the eastern United States. The living genus has twenty-five species that are tropical and subtropical, with one American and one Japanese species that range northward along the eastern seaboard, both of which grow in summer-wet climates. Genera of the family Schizaeaceae are primarily tropical taxa. Several monolete spore types suggest the family Polypodiaceae, which leaf evidence indicates is a common group of the flora.

GYMNOSPERMS

We found pollen representation for three of MacGinitie's five gymnosperm families, as well as six of his seven megafossil conifer genera, and have added several new genera. MacGinitie compared the seeds of fossil *Abies* or true fir (*A. longirostris*) with *A. venusta* (now *A. bracteata*), the Santa Lucia fir that is endemic to the Santa Lucia Mountains, Monterey County, California. Our pollen data agree and support this assignment. The *Abies* pollen at Florissant is highly distinctive. It is unusually large in size (140–180 μm in length; Plate 3, Fig. 2; Plate 4, Fig. 1), and has distinctive morphology among Pinaceae. We compared this fossil type with many *Abies* species in our herbarium collections, and find it to be an excellent match with modern pollen of *A. bracteata*, a unique type, the sole member of the most primitive section of the genus *Abies* (Liu 1971). In our reference collections *A. bracteata* has the largest pollen in the genus and in the family. MacGinitie's *A. longirostris* Knowlton is an important identification, especially as the present-day *A. bracteata* is so isolated and has a restricted range. No other representatives of this section of *Abies* now live in the New World. Manchester indicates

that a similar form of *Abies* occurs in the Oligocene flora at Creede, Colorado, and indeed we have seen this same pollen type in Creede deposits also.

Picea pollen (Plate 2, Figs. 1, 2; Plate 3, Fig. 1; up to 160 µm in length) is hard to assign to a subgenus but generally resembles *P. engelmannii* and/or *P. pungens* (Engelmann spruce and Colorado blue spruce). MacGinitie had identified two species of spruce from seeds, one of which he compared with *P. noeveitchii* of the mountains of China and Japan. The Florissant spruce pollen is also similar to a Sierra Madre species, *P. chihuahuana*, that is like *P. breweriana* of the Pacific Northwest.

Pinus pollen in these sediments may represent several species, but because of the difficulty in separating even subgenera of pine, we can only cite a small type (Plate 2, Fig. 4) and a large type (Plate 2, Fig. 3; Plate 5, Fig. 2); aperture details are not preserved. The latter may be similar to *Pinus ponderosa* (see Hansen and Cushing 1973), as MacGinitie compared *Pinus florissantii* to that species.

To the Pinaceae we have added *Cedrus*-type (Plate 5, Fig. 1), based on the thick, smooth cappus and compact bladders; this taxon seems to be an extinct form. We have also added *Pseudotsuga/Larix* (Plate 4, Fig. 2) and *Tsuga* spp. (Plate 1, Figs. 7, 8). These pollen types are uncommon at Florissant. Although the genus *Tsuga* is known from the middle Eocene (pollen records in Wodehouse 1933; Leopold and MacGinitie 1972; winged seeds in Wehr and Schorn 1992), *Pseudotsuga* and/or *Larix* represent an early pollen occurrence in the western United States, and are not yet recorded in earlier sediments elsewhere (Hermann 1985). *Cedrus* pollen types are occasional in Miocene sediments in Alaska (Leopold and Liu 1994) and were widespread in Oregon (Gray 1964:29).

From a fertile hand fossil of *Sequoia affinis*, Leopold removed a male cone and obtained thousands of Taxodiaceae pollen grains. We noted that a few of these are characterized by a small papilla (germinal aperture) about 5 µm in length, but most have no papilla at all, in contrast with the pollen of extant *Sequoia* in which most grains are distinctly papillate. The gemmate surface sculpture is similar to that of *Sequoia* and *Sequoiadendron*. It may be difficult to discern the papillate grains from pollen of *Torreya*, or the nonpapillate grains from *Chamaecyparis*, both having been reported by MacGinitie. In our counts we lump all the Taxodiaceae, Taxaceae, and Cupressaceae into one group (TCT; Plate 4, Fig. 3), and these grains comprise up to 30 percent of the count. Because of the abundance of *Sequoia* remains in the leaf and wood record, we assume that a lot of these belong to that genus.

We are able to corroborate one other important gymnosperm found by MacGinitie, *Ephedra* (Ephedraceae), which he thought was related to *E. nevadensis*. Indeed, pollen of the unique *Ephedra* cf. *E. nevadensis*–type (Plate 4, Fig. 4) appears in almost every sediment sample. We also find *E. torreyana*–type pollen (not figured; Steeves and Barghoorn 1959) regularly here. *Ephedra* pollen comprises 2 to 6 percent of the count and is always present in Florissant samples.

Wingate and Nichols (2001, Plate 3) suggest that the family Podocarpaceae may be present at Florissant.

MONOCOTYLEDONS

Arecaceae (Palm family): A palm leaf fossil found by Leopold and students near locality D1496 (*Palmacites*, Manchester) is an important addition to the flora. Though Lesquereux (1874) assigned two fruits to *Palmocarpon*, Knowlton (1916) doubted these could be palms, partly because the family was unknown at Florissant. Our palm leaf, which was identified by MacGinitie (pers. commun., 1975), is figured and described by Manchester (2001). Some of our smooth, monosulcate pollen likely represents this group and other monocots (not figured). The palm leaf adds a tropical to warm-temperate element to the flora, and implies a frost-free environment (cold month mean >5 to 7 °C; Wing and Greenwood 1993).

Poaceae (Gramineae): Pollen of the grass family (Plate 8, Figs. 1, 2) is occasional and rare at Florissant. The sediments have also yielded excellent macrofossils, which MacGinitie identified from a single fruiting body as *Stipa*. This is one of the earliest known identified grass macrofossils according to Thomasson (1980). The identification is important because it represents an extinct member of the Stipae, a subfamily that became dominant during the Miocene in deposits of the Great Plains (Elias 1942; Thomasson 1986). The group is known for its primitive C_4 photosynthetic pathway. Agnes Chase once identified well-preserved Florissant fruits related to *Muhlenbergia* (Knowlton 1916:250). Grass pollen appears occasionally in middle Eocene and Oligocene deposits in the western United States (Leopold and Denton 1987; Leopold et al. 1992), but grass macrofossils are not abundant until the Miocene in the western United States.

Typhaceae (cattail family) or Sparganium: Though not abundant, monoporate pollen monads representing the Typhaceae (cattail; *Typha* cf. *T. angustifolia*, Plate 8, Fig. 3) suggest lakeside emergent aquatics. This monad is so similar to pollen of *Sparganium* (bur reed)

that we could not decide which is which, so we lumped them together. MacGinitie found both narrow- and wide-leafed cattails in the flora. Leaf and fruit remains of another aquatic, *Potamogeton,* are figured by Manchester (2001).

Liliales: A lily or amaryllis-type (Plate 5, Fig. 3) is rare. We did not find pollen of the *Smilax*-type, a monocot identified by MacGinitie. Water lily of the Nymphaeaceae, *Nuphar*-type, is a floating aquatic and an addition to the flora, though not a common pollen type (locality W-1; not figured). Monosulcate pollen may include bromeliad-types (epiphytic plants).

Wingate and Nichols (2001, Plate 9, Fig. 6) report pollen that suggests *Scirpus* of the Cyperaceae.

DICOTYLEDONS

MAGNOLIIDAE

Ulmaceae (elm family): Pollen of Ulmoidae includes abundant three-, four-, and five-pored fossulate elm types. Though at one time we assumed the predominantly four-pored pollen was that of *Zelkova* (Asian elm), Manchester (1987a, 1989) indicates that the abundant *Zelkova* leaves are probably the extinct type, *Cedrelospermum,* based on the attached fruits. Fossulate, a five-pored *Ulmus*-type pollen, is especially common in the lower part of section W-1. At Florissant, we have occasionally seen six-pored pollen that has low verrucae and thickened pore areas. This is reminiscent of *Hemiptelia,* an Asian ulmaceous genus. Wheeler (2001) reported from her study of wood remains a cf. *Zelkova* (Ulmoidae suggestive also of *Hemiptelia*) and *Zelkovoxylon chadronensis* that is characteristic of *Zelkova.* Pollen of *Ulmus-Zelkova* represents up to 35 percent of the tally.

Pollen related to that of *Celtis* is identified with two types: (1) an orb-shaped grain with three pores resembling *Celtis* (not figured), and (2) a multiporate grain that has four to five equatorial rough-edged pores with slightly thickened rims (*Pteroceltis;* Plate 9, Figs. 4, 6). This latter type of pollen is seen regularly at Florissant, and we have seen it in the mid- and late Tertiary of Oregon. Pollen of *Pteroceltis* adds a new identification for western Tertiary floras. In eastern China the genus is represented by one species, *Pteroceltis tatarinowii,* that ranges from warm-temperate to cool-temperate areas from lat 23°N to lat 40°N, between elevations of 200 and 800 m. This plant has leaves and fruits quite different from the endemic *Mirandoceltis* of northeastern Mexico described by Sharp (1958). Wingate and Nichols (2001; Plate 7, Figs. 15, 16) figure a similar zonoporate form. A fossil fruit of *Petroceltis* is

reported from the Eocene Republic beds of Washington (Wes Wehr and Kathleen Pigg, oral commun., 2001).

Eucommiaceae: The family, with its monotypic genus *Eucommia,* is another new addition to the flora. Manchester reports finding a *Eucommia* fruit (2001) confirming the identification. *Eucommia* is a deciduous warm-temperate tree with limited distribution in Southeast Asia (Fig. 4). Its pollen (Plate 5, Fig. 5) is smooth, tricolpate with infolded furrows and orate apertures at the equator. *Eucommia* is a regular member of the middle Eocene forests in the Rocky Mountain region (Leopold and MacGinitie 1972; MacGinitie 1974), and at Florissant its pollen is an occasional but consistent element. It endured much longer in western Europe (Pliocene) than in western North America.

Berberidaceae (barberry family): A few pollen grains suggest *Mahonia,* also reported by MacGinitie (similar to Oregon grape). Manchester verifies that two to three species of *Mahonia* may be present based on its evergreen leaflets at Florissant. *Mahonia* is also present in the Marshall Pass flora (3.29 Ma) of Colorado. While *Mahonia* and laurels have evergreen foliage, the diverse laurels found in the leaf record are not apparent in our pollen assemblage, probably because their delicate pollen is poorly preserved in sediments.

HAMAMELIDAE

The subclass Hamamelidae (or witchhazel group), which is chiefly wind-pollinated, is especially well represented in the pollen record. We added a new family (Rhoipteleaceae), and found several new genera for the Juglandaceae.

Juglandaceae (walnut family): Leaves and fruits of *Carya* (hickory) have been reported at Florissant (MacGinitie 1953:96). Manchester identified (1987b) a locule cast of *Juglans* (black walnut–type). Leopold figured Juglandaceae pollen in Florissant sediments in Penny (1969, Plate 16.6). Fossil pollen of this family includes not only *Carya,* but new to the flora are *Juglans; Pterocarya* (wing nut), an Asian warm-temperate group; and the tropical group Engelhardtiae; the pertinent genera are *Engelhardtia* and *Alfaroa* (*Oreomunnea* pollen does not resemble the Florissant pollen). Engelhardtiae are tropical and subtropical genera. *Engelhardtia* has five species in Southeast Asia and *Alfaroa* has species in Central America (as shown on Rzedowski's map, Fig. 5). *Engelhardtia*-types have long records in the Tertiary of the Northern Hemisphere (Nichols 1973). The American taxa have somewhat larger pollen than the existing east Asian species, and the Florissant fossil may be related to *Alfaroa.* Living members of Engelhardtiae are reported

Eucommia
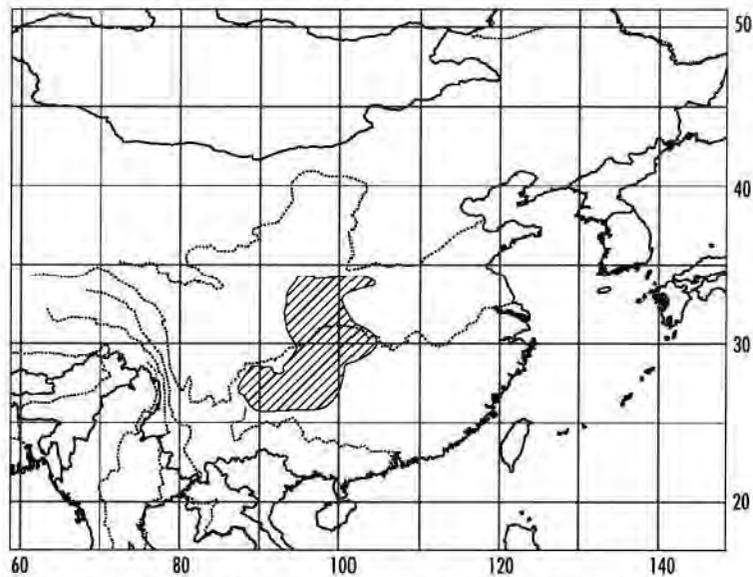
FIGURE 4. Map showing the distribution of *Eucommia ulmoides* in China (after Guo 2000).

Engelhardtiae
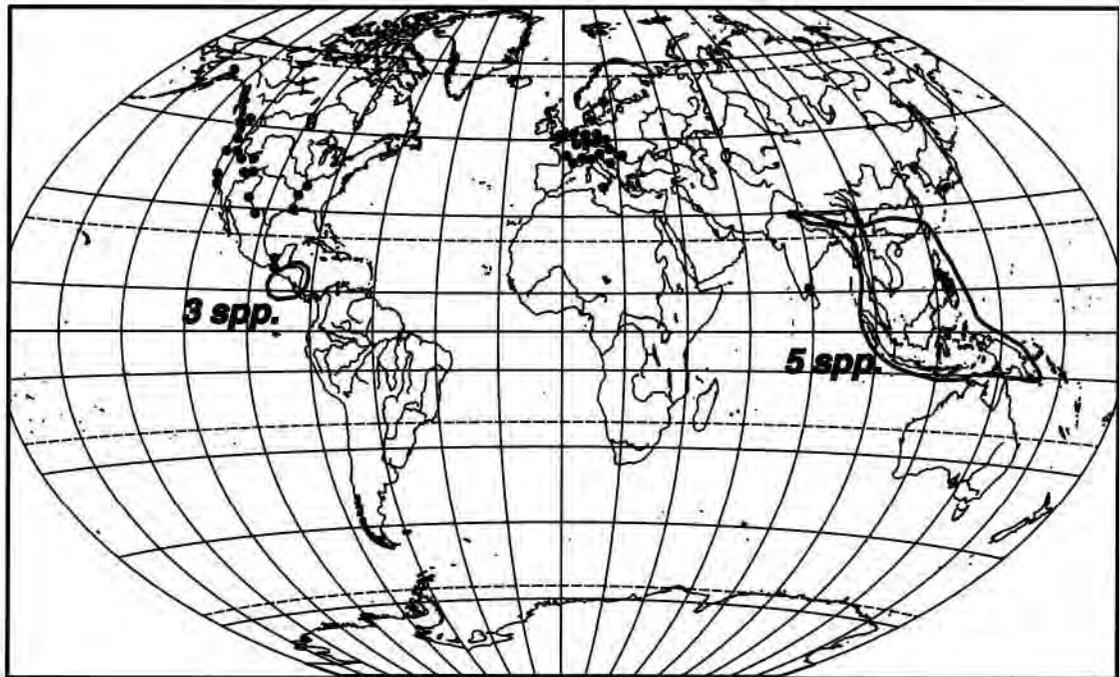
FIGURE 5. Map showing known world distribution of Engelhardtiae of the walnut family. Line-outlined areas show that the present distribution of Engelhardtiae is strictly tropical (Rzedowski 1978), with three species in Central America and five species in Southest Asia. Fossil records (shown as dots) of Tertiary occurrences reveal a broad distribution in North and Central America and Europe, with some occurrences also in Southeast Asia.
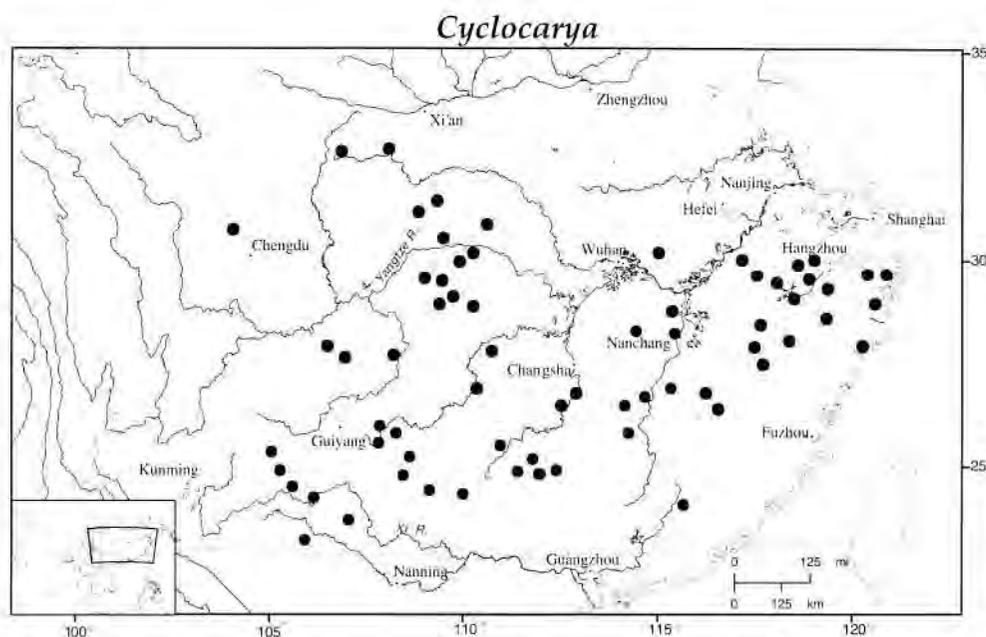
Cyclocarya

FIGURE 6. Map showing distribution of *Cyclocarya* (Ying et al. 1993). This genus grows between the elevations 450 and 1830 m mainly south of the Yangtze River in China. ● = *Cyclocarya paliurus* (Batalain) Iljinskaja.

south of lat ~20°N in Mexico, but grow as far north as lat ~27°N in Southeast Asia. A species of *Engelhardtia* had been reported but not figured by Lesquereux (1874) at Florissant. Wingate and Nichols (2001, Plate 8, Figs. 1, 2) verify the presence of Engelhardtiae pollen under the organ genus *Momipites*.

We also report another new taxon, *Platycarya* (Plate 8, Fig. 9), a monotypic genus found chiefly in the mixed mesophytic forest in southeastern China (Wang 1961; Wing and Hickey 1984). The genus is usually restricted to lower and middle Eocene strata in the Rocky Mountains, at which time it had a very wide distribution in the middle latitudes of North America (Leopold and MacGinitie 1972, Plate 1, Fig. 12). *Platycarya* at Florissant is also confirmed by Wingate and Nichols (2001, Plate 8, Fig. 3).

In addition to the aforementioned, a most unusual member of the walnut family is *Cyclocarya* (Manchester 1987b). Its four-pored pollen is quite characteristic as a new minor element of the Florissant flora (Plate 8, Figs. 13, 14), and we have seen it in other late Eocene floras of the Rocky Mountains. This monotypic genus (*C. paliurus*) grows between elevations of 450 and 1830 m in forests along streams in southeastern China (see distribution map, Fig. 6). It occurs mostly south of lat 30°N, so it is very warm-temperate to subtropical in distribution. While *Carya* is the most abundant pollen of the walnut family, and represents from 10 to 25 percent

of the tally, *Juglans* and *Pterocarya* are in every pollen sample in amounts of 1 to 3 percent; and *Cyclocarya* and *Engelhardtia/Alfaroa* are present in a few samples as trace elements (ca. 1 percent; Fig. 3).

Rhoipteleaceae: A first in the Eocene pollen record may be the monotypic family Rhoipteleaceae, which is another member of the Southeast Asian subtropics and warm-temperate, summer-moist forest. Pollen assigned to this family (Plate 8, Figs. 7, 8, 10–12) shows strong arci between the three apertures, and its pores are simple and oblong. The wall has a thick ektexine with a tectum (tegillate) and the sculpture is faintly microreticulate. Rhoipteleaceae comprises up to 6 to 8 percent of the pollen tally in section W-1 and appears in about half of our samples. Wolfe (1973) has reported *Rhoiptelea* pollen from the Upper Cretaceous sediments of the eastern United States.

Betulaceae (birch family): The Betulaceae is represented in the leaf and fruit flora of Florissant by Coryleae (*Carpinus*) types, now considered to be the extinct genera *Asterocarpinus* and *Paracarpinus* (Manchester and Crane 1987; Manchester 2001). Our betulaceous pollen seems to be consistently three-pored and of the *Ostrya*-type that also includes *Carpinus* (Plate 8, Figs. 4, 5). Affinity with *Carpinus*, which has three- to four-pored pollen, cannot be excluded. Our betulaceous pollen assigned to *Ostrya-Carpinus* reaches 5 percent near the top and base of section W-1.

Fagaceae (beech family): An important group is the Fagaceae, especially the extinct genus *Fagopsis* (Manchester and Crane 1983), which is the most abundant leaf fossil at several localities; hence this plant is presumed to grow along shorelines (MacGinitie 1953). Pollen of *Fagopsis*, which Leopold extracted from flowering male aments, yielded hundreds of tricolpate smooth pollen with indistinct pores, similar to the type shown in Plate 6, Figure 7. *Fagus* pollen (Plate 6, Fig. 11) may be related to a western beech, *Fagus mexicana*, which grows locally in cloud forests of the Sierra Madre Oriental. Its distribution described by Fox and Sharp (1954) is shown on their map as Figure 7, including its occurrence at Rancho del Cielo at ~1175 m. *Fagus* is a new addition to the fossil flora.

Fossil leaves of *Quercus* (oak) are diverse (about nine spp. that MacGinitie said are difficult to distinguish), and they all are probably evergreen oaks. Among the oak-type pollen we found, one is assigned to *Quercus*, as it is tricolpate with furrows bent at the equator, with scabrate sculpture found in many deciduous oaks today (Jarvis et al. 1992a, 1992b; Plate 5, Fig. 6). A second is a mystery-type with a longer polar axis, tricolpate with inrolled furrow margins and fagaceous scabrate sculpture (Plate 5, Fig. 7). Almost everything about the latter suggests *Quercus,* but we know of no modern Quercoid or Fagaceous species whose pollen has such a long polar axis. Crepet (1989) has described a number of extinct genera in the Fagaceae of Oligocene and Eocene age, and this prolate grain may well be a Fagaceous pollen.

In addition to *Fagus* and the quercoid-types, we have recorded several diagnostic-looking pollen grains of *Castanea/Castanopsis* (not figured), which support MacGinitie's determination of *Castanea* (chestnut) leaves, though Manchester did not find the leaves convincing. Quercoid pollen reaches 20 percent of the pollen count and is present in every sample, while *Castanea*-type and *Fagus* are rare.

Moraceae: MacGinitie identified leaves of *Morus* (mulberry). We found rare two-pored pollen of the *Morus*-type (not figured). Manchester (2001) has rejected the leaf identification.

Platanaceae: Leaves of the genus *Platanus* have a possible counterpart here in the pollen record (cf. *Platanus*) that looks very similar to platanoid pollen from
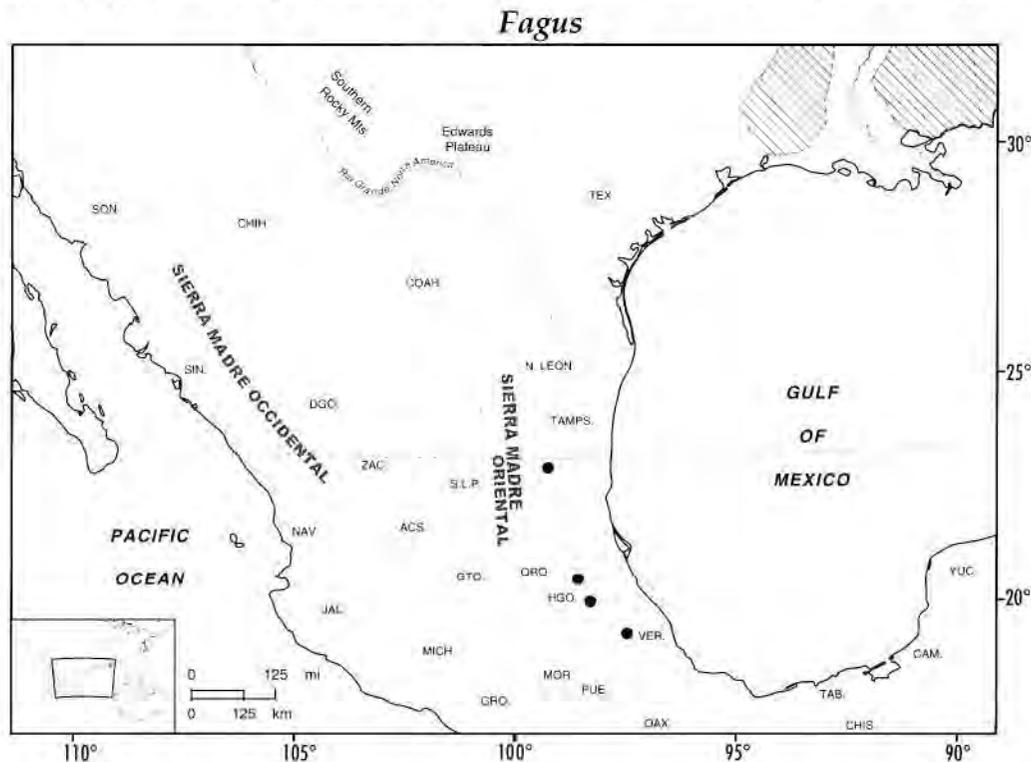
Fagus

FIGURE 7. Map showing distribution of *Fagus* in Mexico (dots; Fox and Sharp 1954). These isolated sites are of *Fagus mexicana* located in the Sierra Madre Oriental, and the northernmost occurrence is the location of Ranço del Cielo cloud forest above Gomez Farias in Tamaulipas. *Fagus grandifolia* of eastern United States occurs in Texas (shaded area).

earlier Eocene sites (Leopold in MacGinitie 1974; Plate 39, Figs. 23, 32, 33).

CARYOPHYLLIDAE

The subclass Caryophyllidae, which does not appear in the leaf record here, has at least two families represented by their pollen. Chenopodiaceae (saltbush family) or *Amaranthus*-type of the Amaranthaceae (together called Chenopodiineae) pollen are common or present in every sample. Most of the Chenopodiineae grains appear identical to *Sarcobatus* (greasewood; Plate 9, Figs. 11–14), which today ranges from the Great Basin southward into Mexico, and is a common pollen type throughout the Rocky Mountain lowland Eocene. Other grains (Plate 9, Fig. 15) may represent either Chenopodiaceae or *Amaranthus*-type.

Another member of this subclass is a pollen grain of Caryophyllaceae (chickweed family; not figured) and resembles the herb *Silene* or *Stellaria*. If in place (e.g., if not a contaminant), this is an early record for Caryophyllaceae, which generally is not known at middle and high north latitudes before the Miocene (Leopold and Denton 1987; Leopold and Liu 1994; Liu and Leopold 1994; White and Ager 1994).

DILLENIDAE

Of the four Dillenid families reported, the pollen evidence corroborates two—the Salicaceae (willow family; *Populus, Salix*, not figured) and the Sterculiaceae. We have no evidence of Styracaceae (*Halesia*) and no certain records of Tiliaceae (*Tilia*). However, Wingate and Nichols (2001) figure a suggestive Tiliaceous form (their Plate 7, Fig. 12) as well as a Bombacaceae-type (their Plate 7, Fig. 7).

Sterculiaceae: The Sterculiaceous pollen (Plate 6, Fig. 15) looks similar to *Tilia*, except that it lacks strong thickenings under/around the pore. In this feature our specimens do not fit with Bombacaceae pollen types. Manchester (1992) has found similar pollen taken from the flower of the extinct genus *Florissantia*, which he placed tentatively in the Sterculiaceae. Our fossil pollen closely resembles the pollen Manchester extracted from *Florissantia* flowers. This pollen type strongly resembles the section Fremontodendreae of the Sterculiaceae, and supports Manchester's family assignment. Similar small Sterculiaceous grains are typical in middle Eocene floras of the Rocky Mountains (Leopold in MacGinitie 1974; Plate 44, Figs. 14, 16–18).

ROSIDAE

Although by far the greatest numbers of megafossil taxa are rosids, pollen representation is poor. Of the forty-seven genera of this subclass, we find only about thirteen in our microfossil evidence. Four new rosid genera, including three new families, are present in the pollen record.

Euphorbiaceae (euphorb family): *Croton* (Plate 9, Fig. 5) is represented in the pollen record by a few specimens. *Croton* is an important member of the tropical deciduous forest and thorn forest in northeastern Mexico (Martin 1958). Wingate and Nichols (2001, Plate 7, Fig. 23) report a similar form suggesting *Croton*.

Fabaceae (Leguminosae, pea family): Cf. *Petalostemon* pollen (not figured) is occasional. The genus (tentative) is a common perennial herb in the prairie flora of the Black Hills and eastern Great Plains. Admittedly the pollen of legumes is difficult to identify, and in spite of MacGinitie's rich legume leaf flora, we were unable to determine legume pollen types. Wheeler (2001) discusses ring-porous woods of legumes at Florissant.

Rosaceae (rose family): Leaf evidence of ten Rosaceous-types, including *Rosa* and *Malus*, clearly indicate the importance of this family at Florissant. Identified pollen of the rose family includes *Malus* (apple; Plate 5, Fig. 11) and/or *Pyrus*. *Malus* is first recorded from megafossils in the middle Eocene at Republic (Wehr and Hopkins 1994), a montane site in Washington where Wolfe and Wehr (1987) described an early diversification of this family.

Rutaceae: Cf. *Ptelea* (not figured) and cf. *Evodia* are rare pollen types that may belong to this family. *Ptelea* is widespread in the United States and in northeastern Mexico, and the living species that MacGinitie cited grow on rocky slopes or open areas along streams. Fruits MacGinitie assigned to *Ptelea* have been reassigned to Caprifoliaceae, *Dipelta*-like. But Manchester (2001) also reports two new *Ptelea* fruits and the trifoliate leaves confirming that genus. We figured the *Evodia*-type pollen (Plate 6, Figs. 5, 6).

Sapindaceae: Some nine leaf genera are present at Florissant, of which pollen corroborates only a few. Pollen of *Acer* cf. *A. glabrum* (Plate 5, Figs. 8–10) may represent the *Acer* leaves and fruits in the flora. *Cardiospermum*, though not accepted by Manchester, is represented by its pollen, which with its syncolpate breviaxial features and reticulate sculpture is unmistakable (Plate 7, Figs. 3–7). The form genus *Boehlensporis* (Wingate and Nichols 2001, Plate 5, Fig. 23) resembles this taxon. *Cardiospermum* is a herbaceous or woody vine in warm-temperate areas from Missouri into Mexico and in the West Indies. The species this Florissant pollen most closely resembles is *C. halicacabum*, of tropical Mexico, which is the same species that MacGinitie's *Cardiospermum* leaves re-

semble. Pollen, wood, and fruits of *Koelreuteria* are present (pollen on Plate 7, Fig. 1). Other sapindaceous pollen, trisyncolpate reminiscent of *Cupania,* is found at Florissant (see Muller and Leenhouts 1976 for a helpful review of Sapindaceae pollen morphology).

Vitaceae: In the Vitaceae (grape family), *Parthenocissus* (five-finger vine) or possibly *Cissus*-type pollen is occasional in our counts (not figured). *Parthenocissus* is a hardy, adaptable vine common in damp woods. In the western United States it ranges southward from the Rocky Mountains into Mexico and Cuba. Possible *Vitis* pollen is present, and this genus is tentatively accepted by Manchester (2001).

Meliaceae (mahogany family): In the Meliaceae, both MacGinitie and Manchester have described seeds of *Cedrela* or *Toona.* We have not yet discovered the diagnostic pollen of this family at Florissant, though *Melia* pollen occurs in other mid-Tertiary floras of the region, and pollen of this group appears to be present in Wingate and Nichols (2001, Plate 6, Figs. 20, 22).

THE FOLLOWING RECORDS INDICATE FAMILIES OF ROSIDAE NEW TO THE FLORA

Elaeagnaceae: Elaeagnus cf. *E. argentea* (buffalo berry) is a shrub that has ecologically similar species in central China and the western United States. They inhabit open vegetation along waterways on both continents. This is a new family for Florissant, and its pollen is a regular minor element appearing in many samples. The *Elaeagnus* pollen type is recorded in Miocene of Oregon (Gray 1964; Plate 4, Fig. 4), as well as at several Eocene localities in the Rocky Mountains (Leopold in MacGinitie 1974, Plate 42, Fig. 28; Wingate and Nichols 2001, similar form in Plate 6, Fig. 18).

Ericales (heath group): A pollen tetrad represents an unknown taxon that is clearly a member of the Ericaceae or Pyrolaceae (Plate 7, Figs. 10, 11).

Onagraceae (evening primrose family): Two evening primrose pollen types appear as rare elements at Florissant. One is *Semeiandra* cf. *S. grandiflora* (Plate 6, Fig. 3), a woody genus from the eastern Sierra Madre of Mexico, and the other is related to *Xylonagra* (Plate 6, Fig. 4), a shrub of Baja, California. Each of these genera stands out as unique pollen types within the living Onagraceae.

As far as we know these are the earliest records of the evening primrose family in the New World. It may be significant that these early forms are woody in habit. Notice that the preservation is quite wonderful, for the fragile viscin threads hanging out of a pore of the aff. *Xylonagra* pollen on Figure 4 are clearly seen. These

are the sticky threads peculiar to this family that cling to a pollinating insect. Imagine finding these in volcanic ash 34 Ma in age! Recently Manchester (2001) found an Onagraceous flower at Florissant (see also Wingate and Nichols 2001, Plate 7, Figs. 14, 15).

ASTERIDAE

In the pollen record of the highly evolved group Asteridae, we found three genera and three families new to Florissant. The new families are as follows:

Apocynaceae (dogbane family):Tabernaemontana, cf. *T. coronaria*–type. This unusual brevi-tricolporate-type has large pores thickened along their rims within short furrows. The pollen wall has psilate to scabrate sculpture. Though this large pollen is similar to that of *Melia,* it differs by having equatorially oriented, oblong pores, it always has three apertures (instead of four for *Melia*), and it closely resembles the apocynaceous genus. *Tabernaemontana* is a member of the tropical deciduous forest of the Sierra Madre Oriental (Miranda and Sharp 1950).

Solanaceae (nightshade family): The pollen we identify as *Datura* cf. *D. discolor*–type is striate with several pores (not figured). *Datura discolor* (jimson weed) grows in subarid areas of Arizona and northern Mexico, and the genus *Datura* is warm-temperate and subtropical of wide distribution (Avery et al. 1959).

Malvaceae (mallow family; not figured): The pollen is Malvaceous, large, with several brevicolporae and numerous large spines, but the genus is uncertain. Fossil mallow pollen represents a new record of the family at Florissant.

Of the four Asteridae families so far recorded by megafossils we have ascertained pollen types for two:

Caprifoliaceae (elderberry family): A new Florissant genus is *Viburnum* cf. *V. lentago* (Plate 6, Fig. 14). This pollen type regularly appears in the latest Eocene and Oligocene (White River Group) of the Rocky Mountain region. The pollen does not resemble *Sambucus* of this family, which is present in the leaf record here. The outstanding sculptural feature is the graded reticulum, which is very coarse in the intercolpal equatorial regions, and is special in that this reticulum sometimes is deciduous, for we have seen many fossil specimens in which the sculpture is a deciduous net that peels away from the endexine. A similar form may be Wingate and Nichols's Plate 5, Figure 21, *Rhoipites* C (2001), a type we have seen in other Chadronian sediments of the Rocky Mountains.

Oleaceae (olive/ash family): We observed *Fraxinus*-type pollen (ash), which is not similar to pollen of

Osmanthus, a genus that MacGinitie identified in the leaf flora at Florissant.

Haloragidaceae? (millfoil family): Myriophyllum-type. We have a few specimens resembling this millfoil and think it may be a part of the aquatic flora of the lake. Similar forms are figured by Leopold and Liu (1994; Plate 2, Fig. 9).

Asteraceae (Compositae, sunflower family): Pollen of this family include long- and short-spined types that are extremely rare in our preparations. Only a few grains (less than five) have been seen among all our collections. These may not be fossils, as we believe they are contaminants (see following discussion). Wingate and Nichols (2001, Plate 5) in their form Tricolpate D, seems to represent Valerianaceae pollen, a very advanced herbaceous family; they also report a short-spined Compositae type (their Plate 6).

Discussion

Relation of the Leaf and Pollen Floras

Our identifications from pollen and spores (Table 2) provide new information concerning the composition and character of the Florissant flora. Comparison of microfossil and megafossil lists of identifications is shown in Table 3. Within the leaf flora of about 120 species (~100 genera of Manchester) of vascular plants, some sixty-two are now of known modern biogeographic affinity. Of these, at least twenty-three leaf genera have also been found in the pollen record. The twenty-five new genera added to the flora by fossil pollen/spore evidence include about four subtropical types and five warm-temperate to subtropical taxa. Some of these taxa have endemic distributions today in the southwestern United States and some are endemic to Southeast Asia. Several (fourteen) new families and groups have been added to the flora: Arecaceae/Palmae (megafossil), and pollen of Apocynaceae, Chenopodiaceae, Ericaceae/Pyrolaceae, Elaeagnaceae, Eucommiaceae, Malvaceae, Nymphaeaceae, Onagraceae, Rhoipteleaceae, Schizaeaceae, Selaginellaceae, Solanaceae, and Sterculiaceae.

Of special interest are the occasional grains of Asteraceae/Compositae that, if they are stratigraphically in place, are the earliest record of this highly evolved family. However, the grains we have found are either brightly stained or are stained differently, indicating they may be modern contaminants that absorb somewhat more stain than the fossils. A few have evidence of protoplasm and cell contents that would be expected in fresh pollen, denying these as fossils. Further, *Artemisia*, and long- and short-spined Asteraceae, are known in the literature to occur commonly as lab contaminants (e.g. MacGinitie 1974, Plate 42, Fig. 22). Pollen of Valerianaceae suggested by pollen of Wingate and Nichols records a highly advanced Asterid family. The record of a single Caryophyllaceae pollen grain, even though it looks like a fossil, is also in doubt because of its rarity, and as most occurrences of this family are of Miocene or younger age (Leopold and Denton 1987; White and Ager 1994).

Groups within the leaf flora that are wind-pollinated and high pollen producers are most likely to be represented in the pollen flora as well. If we divide the identified leaf groups into the following categories, we can measure the bias in favor of wind pollination in the microfossil record (Fig. 8): (1) high producers of pollen or spores (e.g., Juglandaceae, Chenopodiaceae, Pinaceae); (2) moderate producers of pollen (e.g., *Acer*, Sterculiaceae, Salicaceae); and (3) taxa that are chiefly insect-pollinated and are low pollen producers (e.g., Onagraceae, Berberidaceae, Moraceae, Rosaceae). Within each category the megafossil taxa identified by MacGinitie and Manchester (black bars) are corroborated to some extent by pollen evidence (gray and dotted bars). The corroboration is most evident by the wind-pollinated plants (86 percent; Category 1). Pollen representation for megafossil taxa of the insect-pollinated plants that produce either moderate amounts of pollen (27 percent; Category 2) or low amounts (27 percent; Category 3) is much lower. For the new taxa added to the flora by microfossil evidence (polka-dot pattern), we have found more new taxa from the first group (wind-pollinated; twelve taxa) than from the second (medium pollen production) or the third (low production) group. The ratio of the leaf taxa to pollen/spore types found among the high pollen producers is 7:6, compared to the intermediate group or the low producers, 4:1. Thus we have a measure of the taxonomic representation according to pollen production that is obvious in the Cenozoic pollen record. The bias favors high pollen producers and wind-pollinated plants by about 3:1 (see Fig. 8).

A high numerical representation of pollen in the tallies indicates a local abundance of Ulmoidae (up to 35 percent), *Carya* (up to 24 percent), TCT or Taxodiaceae-types (~35 percent) that probably combine *Chamaecyparis* (white cedar) and the more distinctive *Sequoia* pollen (Fig. 3). From the abundance and location of *Sequoia* megafossils, this group is considered to be riparian or
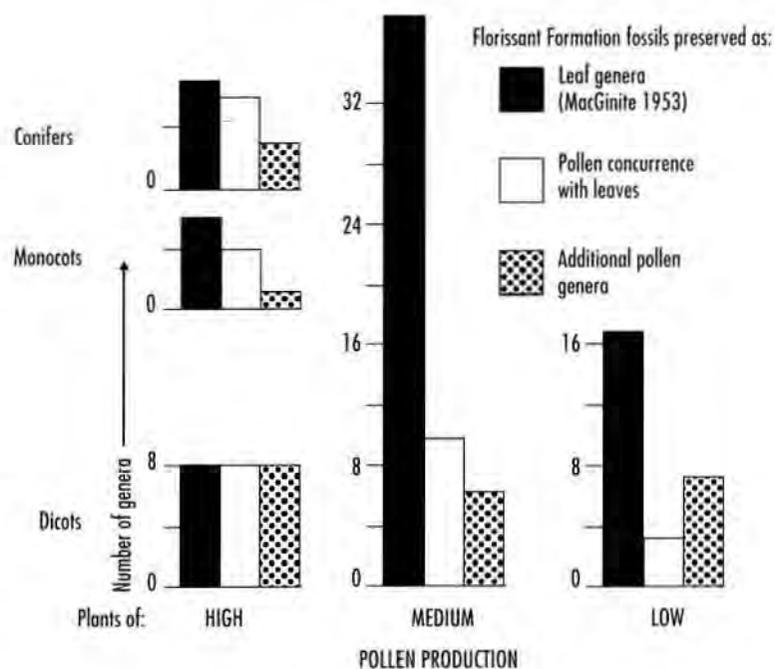
FIGURE 8: Histogram showing number of plant genera in fossil record preserved as megafossils (black bars), corroboration of these by pollen identifications (gray bars), as well as genera new to the flora added by pollen evidence (bars with dots). These are grouped according to taxa that are typically high, medium, or low pollen producers. The diagram demonstrates that pollen evidence has a great potential to add new identifications to a flora where high pollen producers are concerned.

growing near the lake. These taxa are all high pollen producers. The numerically abundant leaves of *Fagopsis*, the extinct beech-type that MacGinitie thought was also a lakeside plant, is only moderately abundant in the pollen record. Perhaps like certain other members of the beech family (such as *Fagus*), it was not a high pollen producer. Other megafossils in the same category include cf. *Typha* (cattail) and *Populus* (poplar/cottonwood). Subarid scrub types, *Sarcobatus* and related saltbush Chenopodiineae and *Ephedra*, are regular minor elements in each sample and represent less than 15 percent of the count.

Elements that MacGinitie considered to be montane taxa, such as *Abies* and *Pinus*, from 2 to 15 percent, and *Picea* plus *Quercus* represent from 3 to 10 percent of the pollen tally at section W-1. Because these taxa are moderate to high pollen producers, their source trees were probably on higher ground some distance from the lake at this time in Florissant history. As Gray (1986) and Spicer (1989) have indicated, the representation in the pollen and leaf records relates strongly to the proximity of the source plant to the site, as well as to other complex factors such as their productivity of pollen and spores and their habitat.

Geographic Floral Elements and Ecological Conditions

The various geographic elements have great significance as they provide impressive evidence that the flora is composed of disparate lineages that once grew together but now are widely separated geographically. Even though separated now, the climatic requirements of their remaining nearest living relatives can tell us much about the climatic scenarios of the past, suggesting a range of niches and microclimates that may have existed at Florissant.

MacGinitie's (1953.38, Table 1) eight geographic groups and his list of most similar living species cite taxa whose relationships can be determined with some degree of certainty. The MacGinitie numbers of megafossil taxa shown in Table 4 for each geographic group take into account the identifications added by Manchester (2001), but where pollen evidence indicates the genus is actually present, the list is corrected by this information. Our new additions to the flora are listed in the lower part of Table 4 for genera where biogeographic affinities are known.

TABLE 4. Geographic groupings citing nearest living relatives.

	Rocky Mountains, S. to Chihuahua (temperate, humid)	Edwards Plateau of Central Texas S. to San Luis Potosi (temperate)	S. Mexico from Jalisco to Vera Cruz (sub tropical)	W. Mexico, from Sinaloa N. into S. Arizona (sub humid scrub flora & tropical)	Ozark Plateau E. to the S. Appalachians (warm temperature, streamside)	Central and S. China, Sichuan to Jiangxi (warm temperate to subtropical, humid)	California, & Great Basin (temperate, seasonally dry)	Middle Latitude, South America (subtropical)
Geographic group no:	1	2	3	4	5	6	7	8
MacGinitie's Summary Data as Altered by Manchester's Review (2001)	26	25	3	8	10	19	8	1
This Report: Additional genera or subgenera added from fossil pollen/spore record:								
Cyclocarya cf. *C. paliurus*						X		
Datura cf. *D. discolor*				X			X	
Engelhardtia/Alfaroa			X			X		
Ephedra cf. *E. torreyana*							X	
Elaeagnus cf. *E. argentea*	X				X			
Eucommia cf. *E. ulmoides*						X		
Fagus		X			X	X		
Juglans		X		X	X	X	X	
Lygodium cf. *L. palmatum*					X			
Platycarya cf. *P. strobiliformis*						X		
Pterocarya						X		
Pteroceltis						X		
Rhoipteleaceae cf. *Rhoiptelea*						X		
Sarcobatus cf. *S. vermiculatus*							X	
Semeiandra cf. *S. grandiflora*			X	X				
Tabernaemontana		X		X				
Viburnum cf. *V. lentago*	X				X			
aff. *Xylonagra*				X				
Subtotal	2	3	2	5	5	9	4	0
TOTAL	28	28	5	13	15	28	12	1

Taxa of broad distribution:

Selaginella	Northern Hemisphere
Nuphar	Northern Hemisphere
Cedrus type (extinct)	
Palmae (fan palm)	Pantropical

MacGinitie's tabulation indicated that the primary affinities of the leaf flora are with Group 1: the Rocky Mountain area of southern Colorado to Chihuahua of central northern Mexico (Fig. 9), and Group 2: the temperate subhumid Edwards Plateau of central Texas southward to San Luis Potosí of northeastern Mexico. His data indicated that an important secondary affinity of the flora is with Group 6: warm-temperate to subtropical taxa of central and southern China, and Group 5: warm-temperate taxa growing in the central and eastern United States. He found minor relationships with subtropical Mexico, the subhumid scrub taxa of southern Arizona, and the seasonally dry areas of northern Mexico and California.

The net effect of the pollen data (itemized in Table 4) is that the primary affinities of the Florissant flora are still with the Edwards Plateau to northeastern Mexico (Group 2), and the Rocky Mountains to Chihuahua (Group 1). Our data especially strengthen the association with plants of central and southeast China

(Group 6) and the Appalachians and the Ozarks (Group 5). A few forms are added to plants now of California (Group 7).

By expanding the flora we add new information, based on affinity with taxa that are limited in their climatic distributions today. The effect is that the pollen data supplement the original geographic affinities cited by MacGinitie, and also our findings add a number of warm-temperate to subtropical forms as the nearest living relatives of the fossils. We discuss here the biogeographic significance of those taxa (Table 4) in order of their geographic affinities.

Edwards Plateau of central Texas south to San Luis Potosí (Group 2): A very wide number of plants recorded by their leaves (twenty-five spp.) and by their pollen (three additional genera) at Florissant have relatives that now occur in the forests and woodlands of San Luis Potosí, central Texas, and Tamaulipas. It is this area that MacGinitie selected as most indicative of conditions he thought occurred at Florissant, based on
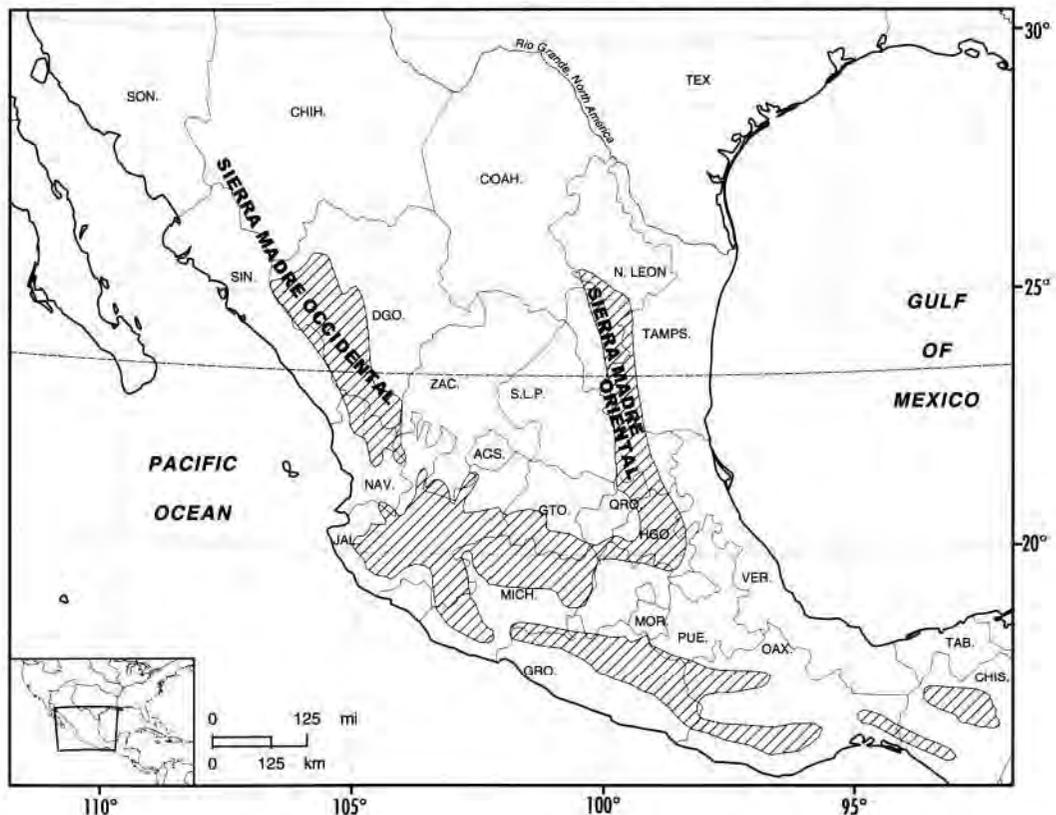

FIGURE 9. Map of Mexico and the southwestern United States. The shaded areas show the distribution of CW climate types (after Rzedowski 1983; based on vegetation types mapped by Leopold 1950). "C" represents humid climates with average January temperature below 18 °C but above 0 °C. "W" type is winter-dry, not more than one-tenth as much rain in driest month as in wettest month.

floristic similarities. With now twenty-eight taxa having near relatives in northeastern Mexico and Texas plateaus, the combined data support the conclusion that this region is the primary geographic affinity of the Florissant flora. (See discussion in vegetation analysis.)

South and central Rocky Mountains to Chihuahua (Group 1; 28 taxa): We have added two taxa to MacGinitie's twenty-six megafossil taxa. We have also extended the geography here to include the Rocky Mountains, accommodating the occurrence of *Elaeagnus* cf. *E. argentea* (buffalo berry), a shrub now common at low elevations in Utah but ranging northward in the northern Rocky Mountains. This genus, as well as *Sarcobatus*, has a long fossil record in the Eocene of the Rocky Mountains.

Central and south China, Sichuan to Kiangsi (Group 6; 28 taxa): Several newly identified genera are now restricted to summer-moist climates of central and eastern China (Engelhardtiae, *Eucommia*, *Platycarya*, *Cyclocarya*, *Pterocarya*, *Pteroceltis*) where they are associated with mixed mesophytic forest or mixed deciduous forest. *Engelhardtia* spp. range southward into full tropical forest environments of Southeast Asia, while its relative, *Alfaroa*, is subtropical in Vera Cruz, Chiapas, Guatemala, and Honduras of Central America (Fig. 5). Though these aforementioned genera have only a few species existing today (four are monotypic), their occurrence together as fossils at Florissant is significant because they are all associated today with climates that are summer-moist, and warm-temperate to subtropical. Their occurrence fits well with other findings of equable warm climates during the mid-continental Eocene (Greenwood and Wing 1995; Leopold and MacGinitie 1972; Manchester 1987b; Wing and Hickey 1984), and the flora has many taxa in common with other Eocene floras of the Rocky Mountain region. Newly discovered pollen taxa such as Rhoipteleaceae (monotypic family of the mixed mesophytic forest in China; Wang 1961) may also represent a moist, warm climate in the past, as it does today.

We are aware of the theoretical danger of extrapolating climate from monotypic genera whose former tolerances may no longer be typical of the remaining monotypic species. But the four monotypic genera (*Cyclocarya*, *Eucommia*, *Platycarya*, *Pteroceltis*) are all east Asian, and fit well with the distributions and climatic preferences of the other fourteen east Asian taxa whose modern geographic affinities are known. They also fit well with the ecological requirements of other lowland elements of the fossil flora. They considerably strengthen the climatic and floristic affinity already established in MacGinitie's (1953) work.

Ozark Plateau east to the southern Appalachians (Group 5; fifteen taxa): Fronds and spores of the fossil fern, *Lygodium kaulfussi* (so far not reported from Florissant), are typically associated with the warm interval of the Rocky Mountain middle Eocene (MacGinitie 1974). The living genus is a tropical and warm-temperate scandent vine. The nearest living relative of the Florissant is ascertained to be *L. palmatum*, which grows in the eastern United States (Georgia to West Virginia) along wetland margins. A type like this probably grew along the lake edge and low ground areas of Lake Florissant.

The fossil hardwoods, *Fagus* and *Juglans*, as well as a wide number of other deciduous hardwoods found in this area, have ranges in warm-temperate, summer-moist areas of the eastern United States, northeasternmost Mexico, and eastern Asia.

California (Group 7; twelve taxa; temperate, seasonally dry): To this group we add *Ephedra* cf. *E. torreyana*, which has a long Tertiary record in the western United States. Other semiarid types include *Sarcobatus* (greasewood) and other Chenopodineae. The black walnut *Juglans* has taxa in central California.

West Mexico, from Sinaloa north into southern Arizona (Group 4; thirteen taxa): We have added three taxa that are members of the subarid scrub flora (southern Arizona to Sinaloa). *Datura* cf. *D. discolor* is now found in warm desert scrub areas, also occurring in Group 7. *Semeiandra* and *Xylonagra* are woody evening primroses that live in warm disturbed environments of northwestern Mexico. These may have occupied dry sites near Florissant.

Southern Mexico, Jalisco to Vera Cruz (Group 3; five subtropical taxa): The Central American members of the Engelhardtiae (*Alfaroa*) grow in the cloud forests of southern Mexico. *Semeiandra* (evening primrose) also occurs in this area.

Middle latitude South America (Group 8; one taxon): In this group we have no additions.

Geographic affinities with plants of central and southern China (Group 6) are now about as important as plants of the Edwards Plateau of Texas south to San Luis Potosí and of the Rocky Mountains south to Chihuahua (Groups 1 and 2). Because of their summer moisture requirements, plants of Groups 5 and 6 may have enriched the streamside/lakeside vegetation described by MacGinitie.

We append several genera that are now chiefly subtropical (*Lygodium*, Engelhardtiae, and *Cyclocarya*). *Engelhardtia* species that occur in the mesic forest of Southeast Asia have very small pollen (e.g., *E. cole-*

brookiana), but the large *Engelhardtia* pollen type here is like *E. spicata*, a tropical species. It does also resemble the large juglandaceous pollen of *Alfaroa* of Central America. These identifications represent three new subtropical elements. They expand MacGinitie's list of about six subtropical taxa at Florissant (adding *Cyclocarya*, Engelhardtiae, *Tabernaemontana*) to a total of nine. Along with the palm frond from Florissant, it is significant that these types are regular participants in the middle Eocene Green River and Kisinger Lake floras of Wyoming.

ASPECTS OF VEGETATION SUGGESTED BY THE FLORA

The fossil association of wetland and streamside plants (*Sequoia* and various deciduous hardwoods), along with dryland types (mountain mahogany, jimson weed, greasewood, mormon tea, *Cercocarpus, Datura, Sarcobatus, Ephedra*), and a modern-looking grass (*Stipa*), may seem strange to the beholder; but many regions of the western United States have these disparate genera where ecological gradients are steep. The canyons of the Edwards Plateau in Texas and in the east-draining side of the Sierra Madre Oriental in northeastern Mexico have a mesic floral belt capped with dry ridges supporting a semiarid vegetation. The same steep gradients occur in California along the coastal ranges. MacGinitie pointed out that in such areas, plants such as *Sequoia*, walnuts, elms, beech, and chestnut are on the edge of their ranges, and in many cases form pockets of mesic forest surrounded by dry uplands, which may have been the case at Florissant.

Many Florissant plants have their nearest living relatives in the highlands of the provinces of Tamaulipas and San Luis Potosí in northeastern Mexico (Table 4). Based on the floristic similarities with this region, MacGinitie cites the Ciudad Victoria and Monterrey, Mexico, forest slopes as having a winter-dry and summer-wet climate similar to that of Lake Florissant (Fig. 9). Paul Martin (1958) described the montane vegetation of Tamaulipas near Gomez Farias south of Monterrey. On east-facing slopes of massifs along the Sierra Madre Oriental, monsoon-laden winds from the Gulf of Mexico provide for rich vegetation above about 300 m in this area. (Dry thorn forest and desert grow on the extensive hot lowlands below ~200 m.) Paul Martin's schematic diagram of vegetation types along altitudinal transects between lat 23°N and lat 23°30"N in southwestern Tamaulipas appears in Figure 10.

In this region of Mexico, tropical deciduous forest, with a warm, subhumid climate, reaches from ca. 200 m to as high as 800 m. Trees are of medium height, widely spaced, with a dense understory of shrubs and small trees. The forest is leafless in winter, and in summer leaves are of medium sizes. Vines, lianas, and genera of Bombacaceae, Burseraceae, Ulmaceae, and Fagaceae are common.

Cloud forest from 800 m to ~1400 m characteristically has a high biomass with dense semi-evergreen forest, the deciduous elements developing leaves in March and April. This forest is rich in epiphytes. Leaves are mesophyllous or middle-sized. Evergreen shrubs are abundant in the understory below the canopy of mainly deciduous trees. Dominant trees are *Quercus* (evergreen), *Magnolia, Carya, Liquidambar*, and *Acer*. *Fagus mexicana* and *Abies* are found in pockets. The cloud forest is not found north of the Gomez Farias region of Tamaulipas. Mean annual temperature here is 19 °C, and winters have only light if any frosts. Fog envelops the area even during the dry spring, minimizing water loss.

Pine-oak forest, and above that pine-oak woodland, occur above the cloud forest and interdigitate with it above about 1300 m. The climate is cool and humid. The structure is much more open, and leaves are sclerophyllous and small. Needle-leafed trees are dominant and grass is abundant. Epiphytes are common on the oaks, but lianas are absent.

The pine-oak forest and woodland along with the cloud forest of Rzedowski (1966, 1978) occupy an area typified by dry-warm winters and summer-wet climate (CW climate type), shown as the hatched area in Figure 9. Some of the Florissant genera seen in these forest zones are listed in Table 5.

Palms grow with the oak and pine vegetation in both the occidental and oriental Sierra Madre at 1300 to 2000 m (Martin 1958). The diversity of evergreen oak taxa of Florissant (nine spp.) is reminiscent of the Sierra Madre Occidental where Paul Martin has seen ten species of oaks growing at a single site (Basaseachic Falls; Paul Martin, pers. commun.) and has noted twenty-nine species of oak in the Rio Mayo region to the west (Burquez et al. 1992; Martin et al. 1998). *Abies* occurs in cool ravines as low as 1300 m in the cloud forest of northeastern Mexico (Martin 1958).

The vegetation of these mountains at middle elevations above Ciudad Victoria and Gomez Farias, Tamaulipas, consists of a mix of temperate species (*Fagus, Acer, Cercis, Fagus*) mixed with tropical species (*Trichilia, Eugenia, Tabernaemontana*, and Burseraceae) as described by Hernandez et al. (1951) and Martin et al. (1998).
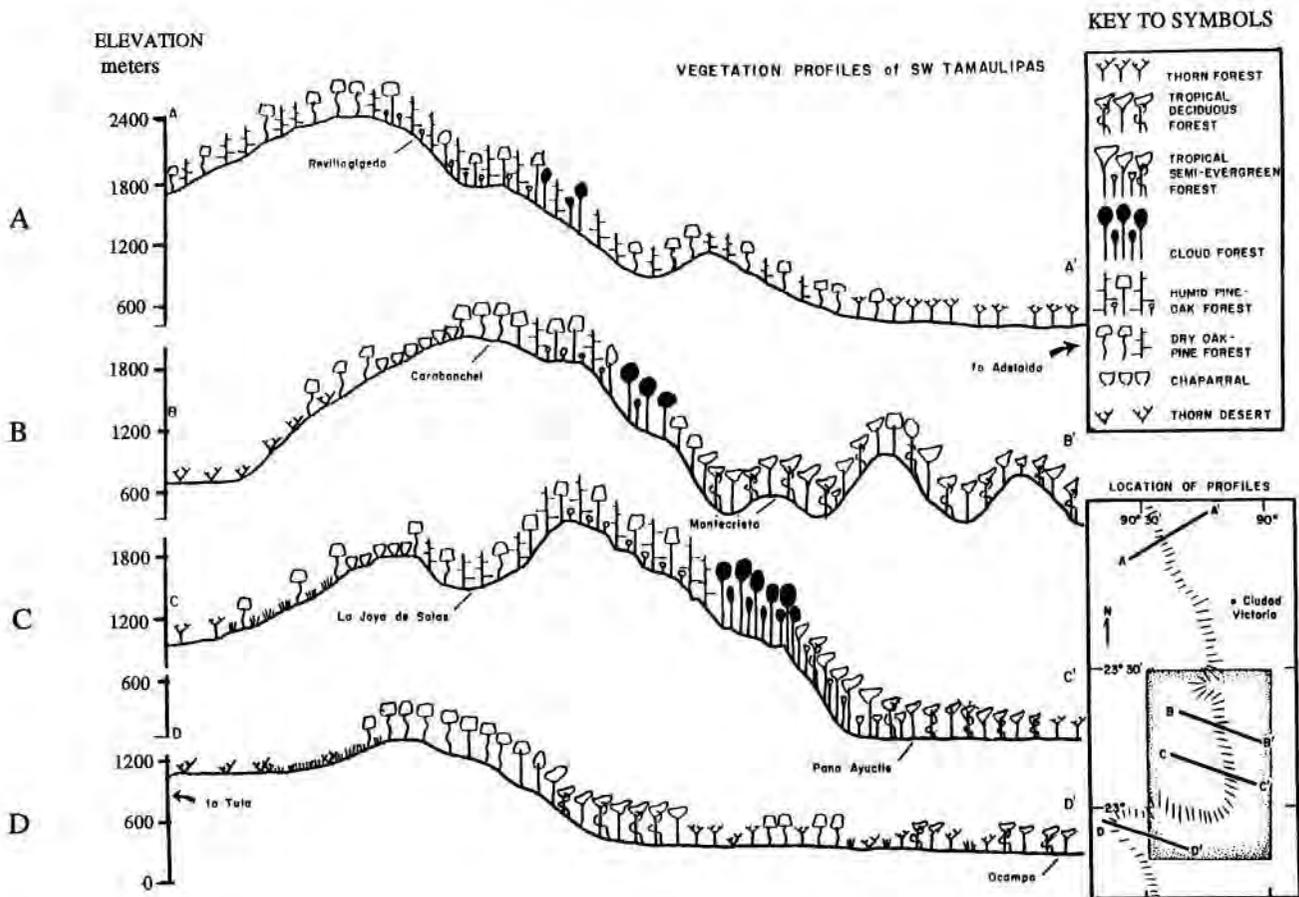
FIGURE 10. Altitudinal profiles of forest and scrub types in Tamaulipas, eastern slope (after Martin 1958). In the shaded box (lower right) Transect C passes through the Rancho del Cielo area cloud forest. The local tropical forests (semi-evergreen, evergreen, and deciduous, in vertical order), characterized by a warm, subhumid climate, range up to ca. 900 m in elevation. The cloud forest with its mild, humid climate occurs between ca. 900 and 1500 m, while the cool humid pine-oak forest lies above, and a dry pine-oak woodland and chaparral above that in some areas. Fieldwork by Hernandez et al. (1951) indicates that many generic elements of the Florissant pollen flora occur today in these vegetation zones, particularly in the cloud forest zone.

Vegetation Types at Florissant

The Florissant flora does not match any particular Tamaulipas vegetation zone, but many genera from this region appear in this Eocene basin of Colorado. The prevalence of deciduous elements that are particularly reminiscent of the cloud forest of northeast Mexico suggests a forest type for vegetation around the lake. With the deciduous trees probably grew *Sequoia affinis* (related to the California redwoods), and Ulmoidae whose stumps are abundant on the lake margin areas. This assemblage suggests a humid environment around the lake. Epiphytes probably included some ferns (e.g.,

Lygodium, Selaginella taxa) and monosulcate pollen may suggest monocot bromeliads. A wide variety of deciduous trees and shrubs that require summer moisture and/or damp ground probably grew in this basin.

Above the *Sequoia* and deciduous forest vegetation, the evergreen oaks and pine most likely represented a woodland on warm-dry slopes and ridge tops. Spruce and fir probably occupied cool forest pockets in the draws. Away from the lake, in drier areas, desertlike scrub vegetation that included *Sarcobatus, Datura,* aff. *Xylonagra,* and *Semeiandra* could be found. Alternatively, gypsum deposits at some levels in the Florissant lake beds indicate periods of drying of the lake, and might have provided habitat for halophytic taxa.

TABLE 5. Plant genera identified in the Florissant flora that now typically grow in the tropical deciduous forest, the cloud forest, the pine-oak forest, or the pine-oak woodland of El Cielo Biosphere Reserve, Tamaulipas (Martin 1955; Hernandez et al. 1951; Sharp et al. 1951). Some other montane genera are found farther south: *Oreopanax, Ostrya, Sambucus, Crataegus,* (Miranda and Sharp 1950). Some overlaps (such as fan palms, *Quercus* spp.) represent taxa that occur in all these forest types. Winter temperature in the Tamaulipas cloud forest area is between 12.5 and 15 °C. July mean temperature is 22.5 °C, and MAT is between 18 and 19 °C. Mean annual range is about 7 to 8 °C (World Meteorological Organization 1979). Rainfall is seasonal and occurs mainly in summer.

Tropical Deciduous Forest	Cloud Forest	Humid Pine-oak Forest	Dry Pine-oak Woodland
Croton	Fagus	Pinus	Pinus
Petrea	Acer	Quercus	Quercus
Burseraceae	Abies	Abies	Palm family
Quercus (evergreen)	Cercis	Viburnum	
	Carya	Carya	
Cedrela	Juglans	Rhus	
Celtis	Prunus	Palm family	
Malvaceae	Carpinus	Juglans	
Tabernaemontana	Eugenia		
Palm family	Palm family		
	Mahonia		
	Persea		
	Quercus		
	Tilia		
	Trichilia		

SIMILARITY TO OTHER EOCENE FLORAS

The fossil flora most similar to that of Florissant is the middle Eocene Green River flora of Wyoming and Colorado, which has eighteen closely similar leaf taxa and four identical species in common with Florissant (MacGinitie 1969). From a pollen perspective, these floras share many forms, including *Lygodium*, Pinaceae genera (*Abies, Picea, Tsuga, Pinus*), *Ephedra, Sequoia*-type, *Sarcobatus, Typha*, palm-types, Poaceae, *Castanea/Castanea, Quercus, Ulmus/Zelkova, Carya, Pterocarya, Cyclocarya, Platanoidites, Platycarya, Engelhardtia/Alfaroa, Ostrya/Carpinus, Eucommia, Morus, Salix, Croton, Dodonea, Elaeagnus,* Rosaceae-types, *Astronium*-type, Sterculiaceae/Fremontodendreae, and Sapindaceae cf. *Cupania* (Cushman 1978; Leopold, unpubl. data). The leaf data indicate a strong tropical aspect to the Green River flora and a chiefly warm-temperate aspect for the Florissant flora. The pollen data show many warm-temperate and some subtropical to tropical elements in common supporting this conclusion. As in the case of most Eocene floras of the mid-continent (Wing and Greenwood 1993), the Florissant flora apparently had an equable climate.

How is it possible for a mix of dry upland and moist lowland types of leaves and/or pollen to occur together, as is the case for both the Green River and Florissant floras? How is it possible for a mix of relatively tropical forms to be found with temperate forms?

It is important to realize that the present vegetation in the mountains of Tamaulipas, Mexico, consists of temperate species (e.g., *Fagus mexicana, Acer Skutchii, Liquidambar styraciflua*) that are growing side by side with tropical species (e.g., *Trichilia havanensis, Turpinia piniapinnata, Croton, Eugenia* sp., palms). The northern outpost of the known range of mixed tropical and temperate vegetation into the Sierra de Guatemala (or Sierra de Cucharas) of Tamaulipas is reported by Hernandez et al. (1951). These forests are unique in floristic composition and in many ways are suggestive of the past when temperate and tropical genera may have grown side by side over large areas of North America (Hernandez et al. 1951).

Another consideration for the diverse mix of ecological types at Florissant concerns the source area for megafossils and for pollen and spores. Spicer (1989), in a taphonomic study of modern aquatic environments, showed that some higher ground types of leaves float down with stream water and occur in lake margins alongside lowland leaf types. This process may account in part for the mixture of ecological types found in the leaf flora. Pollen, of course, has a larger source area than megafossils.

BIOGEOGRAPHICAL IMPLICATIONS OF THE FLORA

The composition of the Florissant flora has many implications for past biogeography. One of these is the presumption from this and other Eocene floras of North America that there have been past biogeographical plant distributions across corridors of the Pacific rim, as have been described by many authors, most recently by Manchester (1999). The primary affinities of the Florissant flora lie with taxa that now occur in the mountains and canyons along the Gulf of Mexico (lat 30°N–lat 20°N). Secondary affinities are in the southern Rocky Mountains and in the region along and south of the Yangtze River in Southeast Asia.

Another implication from Florissant is that there once existed continuous temperate forests between the Appalachian Mountains, the Ozark highlands, and the Sierra Madre Oriental. Remarkable is that vicariant taxa, which were probably once connected around the Gulf of Mexico [such as *Mirandoceltis monoica* and *Celtis* (Sharp 1958); *Fagus mexicana* and *Fagus grandifolia* (Fox and Sharp 1954; Fig. 7)], have diverged so little considering the long separation of these American mountain areas (Hernandez et al. 1951). Some taxa, such as *Illicium floridanum*, now of Florida and the Tamaulipas highlands, seem to have not changed (diverged) at all. While it is not clear when this geographic separation occurred, the floras from the Rocky Mountains and Great Plains suggest that nothing like the rich Florissant mix of warm-loving species has been recorded from midcontinent North America since Florissant time (Leopold and MacGinitie 1972).

CLIMATIC CONDITIONS ESTIMATED FROM THE FLORA

Based on the composition of the flora and the climate tolerances of the present living relatives, MacGinitie estimated that the character of the Florissant climate is as follows (Table 7): mean annual temperature of "… not less than 18 °C (65 °F)," with an absolute minimum temperature of "… probably not below −7 °C (20 °F), and the mean summer temperature of about 26 to 27 °C (80 °F)." (The palm frond we collected at Florissant now confirms this type of warm winter with rare light frosts.) Rainfall would have been confined to the warm season, mostly in late spring and early summer, and was not adequate to support true forest except along streams and lakes. The climate he cites is characteristic in parts of northeastern Mexico between lat 20°N and lat 30°N (Appendix 1, Fig. 9). MacGinitie also estimated the general paleoelevation of the Florissant basin, which he thought was below about 914 m (~3000 feet), based on the geographic occurrence today of plant assemblages with affinities to the Florissant flora.

Within the geographic area cited by MacGinitie as having the most similar floristic associations with Florissant is the example of the Tamaulipas highlands. This region, along the eastern slope of the Sierra Madre Oriental, has a climate type of Cw or winter temperature above 0 °C, but below 18 °C. The driest month has more than 3 cm of precipitation, or one tenth of the rainfall of the summer months (Koeppen 1948). The regional mean annual precipitation is 559 to 600 mm (World Meteorological Organization 1979), but the annual rainfall in the cloud forest at Rancho del Cielo is said to be 2.54 m. On the westerly slope of the Sierra Madre, the dry BS climate has precipitation lower than the evaporation rate. To the north the Edwards Plateau of Texas has fewer of the mesic taxa of the Florissant NLRs and is characterized by the dry BShs regional climate where the January temperature is well above 0 °C (Appendix 1, Fig. 9).

What is subtropical and what is temperate? A mean annual biotemperature of ~18 °C is cited by Holdridge (1967) in his vegetation classification of latitudinal regions as marking the boundary between subtropical and warm-temperate regions. For example, a mean biotemperature between 18 and 24 °C characterizes subtropical vegetation while between 12 and 18 °C is considered warm-temperate. Biotemperature to Holdridge is "… the average monthly temperatures for all months above freezing, divided by 12." So for a climate with warm winters like that of the Edwards Plateau of Texas, or mid-montane Tamaulipas, the biotemperature is the same as the mean annual temperature (MAT). So a MAT of 18 °C is one delineation for the margin of subtropical conditions.

Wolfe's (1979) basic classification of mesic forests of eastern Asia draws the line between subtropical (chiefly evergreen) and temperate (chiefly decidu-

TABLE 6. Showing estimated climatic characteristics of some indicator plant taxa of Florissant. Temperatures are in °C. Asian ranges are roughly estimated from present distributions in Ying et al. (1993) and Wang (1961). American ranges are estimated from Rzedowski (1978) and are precisely given in Thompson et al. (1999a, 1999b), except *Lygodium*, which is estimated, from Gray and Thompson et al. (1999a). Palm data are in part from Wing and Greenwood (1993). None of these plant taxa grow in the Rocky Mountain region today.

	Estimated Climate Characteristics				
	Mean Annual Temp. (°C)	Cold Month Mean (°C)	Warm Month Mean (°C)	Mean Annual Range (°C)	Precipitation Type
Abies venusta	9–11	8–9	12–18	10	Jan.–July
Arecaceae (Palmae)	~17–26	>5–7	~21–33	~5–25	monsoon, seasonally dry
Bursera (Mex.)	13–28	5–25	12–32	~18	various
Carpinus carolinina	11–21	0–10	22–32	~25	all year
Carya (Asian)	~17–24	~6–18	—	~10–24	monsoon
(U.S.)	4–25	–15–17	15–30	—	all year
Cyclocarya	~16–20	~1–6	—	15–20	monsoon
Datura discolor	16–23	~6–25	~20–31	~9–25	semiarid
Engelhardtiae					
(U.S.)	~25	~20–26	~20–30	~2–11	monsoon
(Asian)	~18–26	—	—	—	monsoon
Eucommia ulmoidea	12–20	~2–8	~14–27	15–26	monsoon
Fagus grandifolia	0–19	–15–11	12–28	—	all year
Lygodium palmatum	14–18	0–10	20–26	0–26	monsoon
Platycarya	~13–19	~1–6	—	~14–20	monsoon
Pteroceltis	~10–20	—	—	~9–19	monsoon
Ulmus (U.S.)	–5–22	–25–15	12–30	—	all year

ous) vegetation as having a MAT of 13 °C. The annual range of temperature (MART) for his subtropical sites is from ~10 to 25 °C, while for the temperate sites MART is as high as 40 to 45 °C. However, some details of this important work may have limited application for floras of the northeast Mexico/central Texas region. For example, deciduous forests in the Gomez Farias region range from the warm-temperate areas (1300 m) well into the tropics (600 m) and have a mean annual temperature of ca 20 to 18 °C, which is far warmer (by ~7 °C) than any mesic deciduous east Asian forest mentioned. Perhaps the reason why these tropical Tamaulipas forests are de-

ciduous, and not evergreen, relates to their strongly seasonal rainfall, in contrast to the year-round more mesic climate of the Notophyllous Broad-leaved Evergreen forest in Southeast Asia.

In the case of the fossil flora of Florissant, the strong affinities with present-day Southeast Asian taxa is basically equal to the affinities with modern taxa of northeastern Mexico and central Texas (Table 4). Hence, it is still useful to use Wolfe's east Asian nomogram x and y axes for plotting climate data here (see Fig. 11).

Further climatic information about the ancient Florissant climate comes from some of our key additions

to the Florissant flora that reinforce the warm aspect of this site. For some of these we have plotted the temperature characteristics (Table 6) of key taxa in Figure 11, where the annual temperature (vertical axis) is plotted against the range between the coldest and warmest month for the plant area (horizontal axis). Some of the temperature estimates of Table 6 are rough (east Asian) and some for the United States taxa are well documented (Thompson et al. 1999a, 1999b). Several living plants that are close relatives of the fossil taxa do not grow in areas where mean annual temperature is lower than 15.5 °C (Engelhardtiae, Arecaceae/Palmae, *Datura*) and some are absent where the MAT is lower than 13 °C (*Bursera, Cyclocarya, Lygodium palmatum;* Fig. 11, Table 6). A wide number of hardwood genera that are characteristic of the deciduous forests of Southeast Asia and North America

can be considered warm-temperate in the sense of Holdridge (1967). Their climatic limits chiefly fall in a biotemperature zone or MAT between 10 °C and 18 °C (*Ulmus, Fagus, Pterocarya, Ostrya, Carpinus,* and *Parthenocissus*). A number of these also range into subtropical areas. These plants are chiefly mesic in their requirements and may have grown close to the lake where moisture and rainfall were not as limiting as in the highlands.

Based on the identifications of the Florissant plants and Figure 11, the climate around the Florissant Lake may have had an average annual temperature not lower than ~17.5 °C. Coldest month temperature was above freezing, and probably above 5 to 7 °C, based on the presence of fan palms (Greenwood and Wing 1995). Engelhardtiae may indicate even warmer winters at least in the basin. Summer temperature was probably
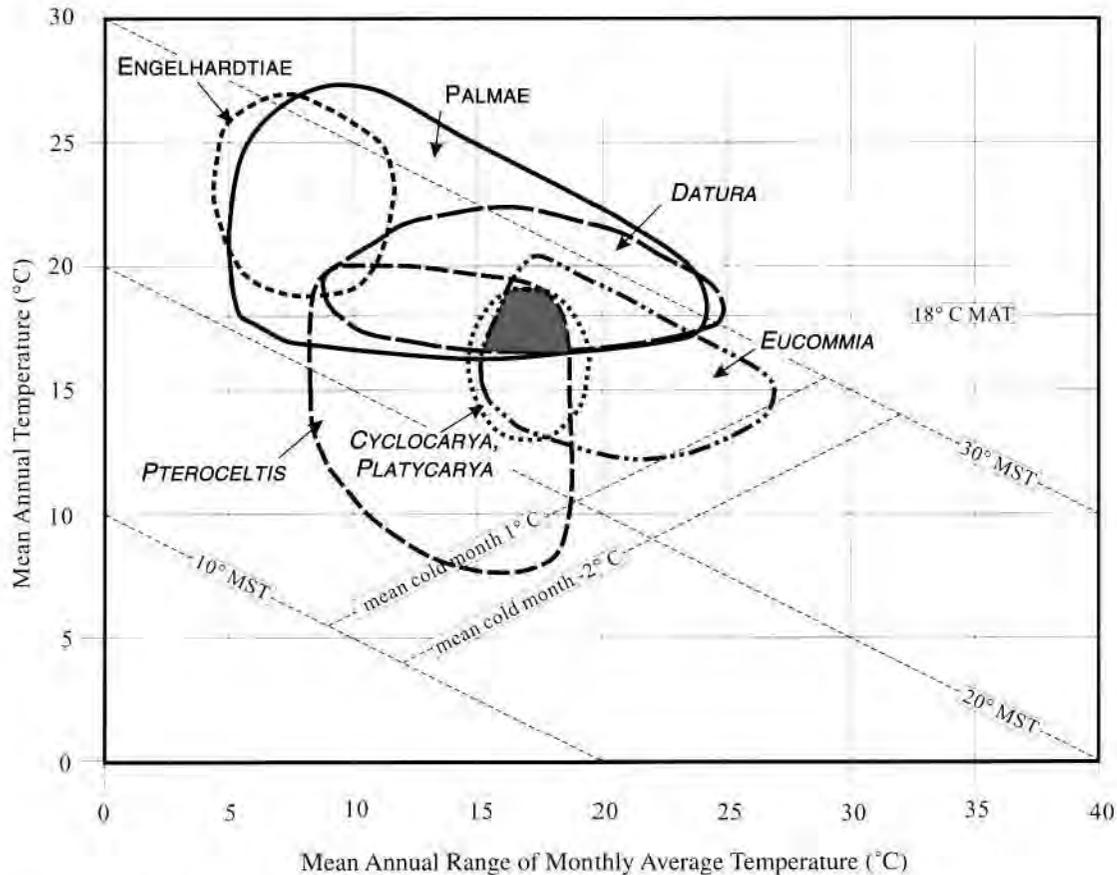
FIGURE 11. Climate nomogram of mean annual temperature with mean annual range and showing estimated ranges of key genera (circles) identified from the pollen assemblage or by our collections. The dashed angular lines are taken from Wolfe's (1979) nomogram based on temperature characteristics of east Asian vegetation types. MST indicates average summer temperature. The 18 °C mean annual temperature (MAT) is used by some authors (e.g., Holdridge 1967) to define the demarcation between subtropical and warm-temperate regions. Note that the six key additions to the flora shown here either are restricted to areas warmer than 18 °C MAT or occur both in warm-temperate and subtropical climates.

TABLE 7. Climate estimates of Florissant conditions by various authors (temperature in °C).

Our estimates using nearest living relatives (NLR) suggest temperature conditions that are considerably warmer than what authors based on leaf architecture (CLAMP and MR methods). We inserted cold month mean temperature in MacGinitie's estimates based on Wing and Greenwood's (1993) data on palms and frost-free climate.

	#Spp. Taxa	Mean Annual Temp.	Cold Month Mean	Warm Month Mean	Mean Ann. Range Temp.	Ppt mm Annual	Method
MacGinitie 1953	112	>18	frost-free, >5–7	27	10	"adequate to support true forest"	NLR
Gregory & Chase 1992	29	10.7					MR
Meyer 1992	112?	14	7.5	20.5	13		Asia Clim.
Wolfe 1993		12–12.5					
Wolfe 1994		10.8	4.6	17.0	12.4		CLAMP
Gregory & McIntosh 1996	29	12.8	>–2	30.0	27.7	570**	MR
	97	13.9	1.3	33.3	29.1	690	
This report	135	17.5	>7	26	17	~1000	NLR

Asia Clim. = Asiatic climate nomogram of Wolfe (1979)

CLAMP = Climate-Leaf Analysis Multivariate Program of Wolfe (1993)

MR = multiple regression technique of Gregory and Chase (1992)

NLR = nearest living relative method

** = Precipitation (MAP) is based on the formula growing season precipitation (GSP) divided by 1 minus seasonality of precipitation (SEASE; Gregory 1994)

above 25 °C, and the range was no greater than 20 °C, and probably no less than 10 °C. Rainfall was concentrated in the summer and annually was probably at least 1000 mm in the lake basin.

CLIMATE INFORMATION FROM FOSSIL INSECTS

The astonishing diversity of well-preserved fossil insects at Florissant (182 families; Evanoff and Doi 1992) lends certain climate information for consideration. A mixture of temperate and tropical taxa in Dipteran families is described by James (1939:47), who mentions that the assemblage was reminiscent of the gulf states. He described fauna that suggests "... the lake lay in an arid region, but with a broad zone of mesophytic vegetation, which produced a local climate around it."

Scudder in his review (1880:35) indicated that the insect fauna represented a climate warmer than today, "similar to that of Georgia." Bequaert (1930) pointed out the climatic significance of the fossil tsetse flies, which do not occur above an elevation of 1525 m (5000 feet), in Africa today. Bequaert and Carpenter (1936) discussed the paleoclimate as having been subtropical with dry-warm summers.

Of the twelve butterflies that have been described from Florissant, two of the Pieridae and seven of the Nymphalidae species "appear to have a neotropical relationship, being especially close to modern northern neotropical species." One taxon is a temperate Northern Hemisphere type that ranges south to Indo-Malaya. The snout butterflies "resemble southeast Asian and perhaps African types" (Emmel et al. 1992).

Hence, from wasps to flies and termites and butterflies, the insect biota of these deposits strengthen the conclusion of a warm-temperate climate that includes subtropical forms.

Estimates of Climate by Other Authors

Wolfe (1994) made paleotemperature estimates of the Florissant assemblage based on the Climate-Leaf Analysis Multivariate Program (CLAMP) method of Wolfe (1992, 1993; Table 7). This innovative method uses the architecture of leaves (e.g., the presence or absence of serrate teeth, drip points, and leaf size) to correlate with local climate stations, and then this datum is applied to estimate paleoclimate. Using multiple regression (MR), Gregory and Macintosh (1996) estimated

paleotemperatures for the Florissant basin. One estimate was 12.8 °C MAT (based on twenty-nine species of fossil leaves), with a cold month mean of >–2 °C and warm month mean of 30 °C and an annual range of 27.7 °C. Growing season precipitation was estimated at 570 mm. Their second sample, based on MacGinitie's leaf figures (ninety-seven taxa), gave warmer values and a wide seasonal range (MAT 13.9 °C; MART 29.1 °C; Table 7). Wolfe (1994) predicted a much cooler mean annual temperature of 10.8 °C (Table 7).

The low MAT and winter temperatures and the wide range for Florissant climate estimated by the CLAMP method are incompatible with the composition of the flora, implying a high frequency of freezing winter temperatures. The presumed paleotemperature of only 10.7 °C MAT or even 12 °C in today's climate represents a cool-temperate climate with freezing winter temperatures characteristic for the northern middle latitudes of the United States. An exception on the West Coast (e.g., Cape Blanco on the shores of Oregon) is a cool-temperate area with a relatively frost-free winter with a MAT of 10.3 °C. Exceptions would also be special areas such as Holdridge's Tropical Montane rainforest (MAT 11 °C) or Christchurch, New Zealand. In general, a cool-temperate climate with prolonged freezing temperatures would be incompatible with subtropical and many warm-temperate taxa. While it is clear from the plant affinities that the Florissant climate was temperate, it was warm-temperate, not cool-temperate, as might be implied by an estimated MAT of 10.7 °C. Hence we have real concerns regarding the relatively cool climates now proposed by the CLAMP and MR investigators, particularly in view of the present lack at this time of a northern Mexican and Texas climate database for the areas thought to represent the general modern counterparts for the paleoflora. Another concern about the method is ecological, as pointed out by Burnham et al. (in press), who indicate that the architecture of streamside plants may distort the regional signal and suggest a cooler temperature by several degrees than the leaves from more distant parts of the forest.

The method developed by Meyer (1986, 1992, 2001) and used by Gregory and Chase (1992) and Wolfe (1992) involves estimating lapse rates (change of temperature with altitude) and an inferred MAT in order to calculate paleoaltitudes for fossil floras of Tertiary age. Wolfe explains that the lower lapse rates in mountainous areas of western United States and of Asia are almost certainly forced by incursions of frigid air masses from the north. One wonders if low lapse rates are a major factor during the Eocene, a period characterized by its lack of an Arctic Front and for its equable subtrop-
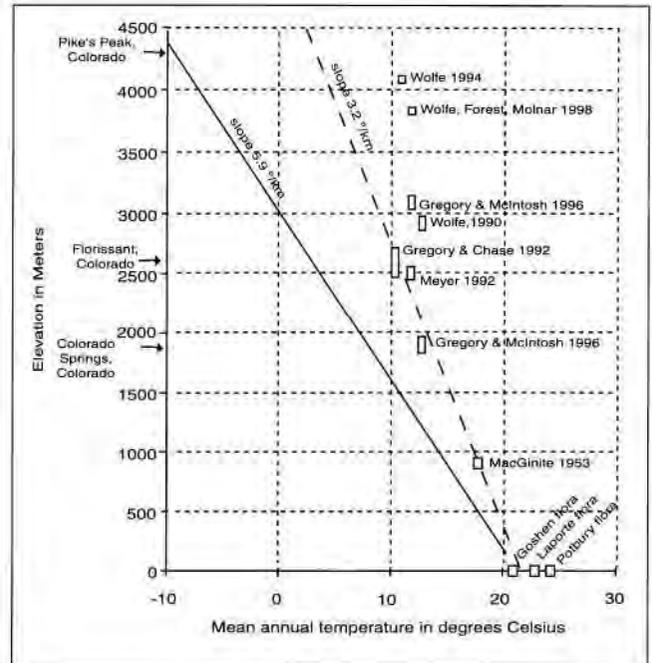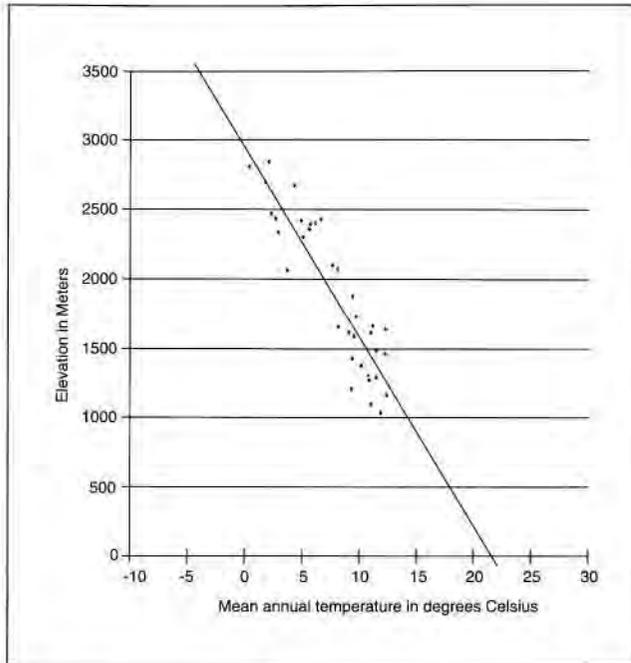
FIGURES 12A and B. Modern variation of surface temperature with altitude in Colorado (A), and presumed Eocene lapse rates (B), plotting mean annual temperature against elevation. Figure 12A utilizes data from present-day Colorado weather stations from a wide range of altitudes. The slope of a regression line is 5.9 °C/km of altitude. Figure 12B contrasts this line with the lower calculated lapse rate of 3.2 °C/km of Gregory and Chase (1992). MacGinite's estimated MAT of >18 °C along with his proposed elevation of <970 m (below 3000 feet) is plotted here, and is in considerable contrast to the estimates of Meyer, Gregory, and Chase and Wolfe. Three tropical Eocene floras from near sea level along the Pacific Coast are shown according to their presumed MAT (after Wolfe et al. 1998).

ical climate over large parts of the world. Frigid air incursions were not hitting the lowland Eocene floras of middle latitudes, for example.

The modern lapse rate estimated from the variation of surface temperature with altitude for central Colorado is about 5.9 °C/km; if we use the present temperature/altitude ratio to plot the various CLAMP temperature estimates (Figs. 12a, b) to estimate paleoelevation, we would see that these points would fall below 1400 m. For example, a MAT of 10.7 °C would represent an elevation of ca. 1400 m, and a MAT of 12 °C would be at ca. 1200 m. MacGinitie's estimate of >18 °C MAT would fall at or below ca. 980 m. On the other hand, if one uses the calculated lapse rate of 3.2 °C/km as Gregory and Chase have done (Fig. 12b), the paleoaltitude (MAT = 10.7 °C) comes out to be quite high, ~2500 m (8200 feet), which is around the present altitude of the basin. Wolfe's 1994 proposed elevation of 4133 m, which is well above present tree line on Pikes Peak, raises the question of how the Florissant basin has physically dropped in elevation. We are not aware of any geologic field evidence that supports this hypothesis. Here

the altitude calculations depend entirely on which lapse rate is used.

The variation of temperature with altitude in stable air—the lapse rate—is about 6 °C/km. Actual ground surface temperatures vary less regularly with altitude because of such factors as coastal currents, continentality, orography, and weather patterns. For example, the temperature/altitude variation for Colorado weather stations, in diverse settings throughout the state, now deviates by only ± 3 °C from, and otherwise statistically fits, the ideal stable-air lapse rate (Fig. 12a). But this line projects to zero altitude at a temperature much warmer than present coastal California at the same latitude. The Colorado ground temperatures approximate the ideal lapse rate. Early Tertiary climates of the western United States were more equable than those of the present. The major extension and great topographic differentiation of Basin-Range deformation had not yet begun and cold coastal currents had yet to chill California. So a closer fit than now of the regional ground temperatures to the ideal lapse rate is to be expected. Nevertheless, Wolfe (1992) and others assumed that in middle Tertiary time,

surface temperatures in the western interior United States differed so greatly from modern ones that both intra-Colorado and regional temperatures fit and effective lapse rate of only 3.2 °C/km. By using this lapse rate they doubled the calculated altitudes.

Another integrative technique for estimating paleoaltimetry comes from the work of Forest et al. (1995, 1999) that makes use of the principle of energy conservation in the atmosphere. These authors use physiognomy of the fossil leaf assemblages to infer enthalpy (heat content of the atmosphere), which varies with, notably, humidity. But to get altitude from it required an estimate of how it varied along the ground surface, rather than how it varied vertically in stable air. Forest et al. (1995, 1999) used ground-surface altitude and calculated lapse rate to predict a paleoaltitude for the Florissant basin of 2700 ± 670 m.

Geologic evidence concerning the history and timing of uplift in the central Colorado area is of critical importance in resolving topographic issues. Were the Front Range and the Florissant basin uplifted considerably after the Eocene, as many field geologists attest? Or did it happen before the late Eocene and then drop in elevation some time later, as Wolfe et al. (1998) suggest? Geologic evidence, for example from Steven et al. (1997), based on physiography, erosional history, and regional deposits, indicates that regional uplift in the Front Range took place after the Miocene and that rifting of the headwaters of the Arkansas River took place in the Miocene but not before. This type of field evidence tends to negate the proposal that the Front Range was at an elevational high during the Eocene.

Conclusions

The diverse pollen and spore flora at the Florissant fossil beds has provided a number of new taxa and new ecological information about the paleoenvironment and flora.

Affinities and vegetation types: Our data have added to the diversity of the lakeside and riparian group of plants that probably represented deciduous forest around the shores of Lake Florissant. Nine of these have their only modern relatives in the warm-temperate zone of central and southern China. Four trees are closely related to eastern United States taxa and to Ozark Plateau species. Because these also require summer moisture, they were probably growing in riparian low areas of the basin. The montane elements are members of the pine family and oak family, fitting well with the macrofossil evidence of upland woodland vegetation described by

MacGinitie, such as from the dry upper slopes of the Tamaulipas highlands in northeastern Mexico. Subarid shrubs such as greasewood and woody evening primrose add to MacGinitie's group of scrub taxa that suggest dry or even saline environments occurred nearby, suggesting steep ecological gradients.

Climate: Our findings establish the warm-temperate to subtropical character of the Florissant plants (MAT 17.5 to 18 °C), and substantiate conclusions drawn by MacGinitie about equable conditions in the basin. Our conclusions from pollen do not support the estimated cool-temperate nature (10–12 °C MAT) of the Florissant basin suggested by other authors because a wide number of taxa require warm-temperate conditions and a few require a subtropical climate. The freezing winters and the seasonal range of temperatures that some authors predict would stress or eliminate subtropical taxa such as the fan palms, now added to the flora. Rainfall, which was probably moderate, fell chiefly in summer.

Taxonomy, biogeography, and other Eocene floras: The pollen evidence in several instances corroborates the subgeneric affinities of megafossils cited by MacGinitie. One of the outstanding examples is the huge pollen resembling *Abies bracteata* (formerly *A. venusta*), an endemic species of fir in the Santa Lucia Mountains of California. The seeds and pollen of *Abies* from Florissant are identified as the *A. venusta*–type. Also from pollen we document the presence of taxa that are not known to occur in the central Rocky Mountains after the Eocene (*Platycarya, Cyclocarya, Pteroceltis,* and *Eucommia*). The Florissant flora has strong resemblances to the mid-Eocene Green River flora and represents to the last interval of equable warm-temperate climate in the central Rocky Mountains during the Tertiary.

The floristic mix at Florissant indicating affinities with plants now occurring in far-flung areas (e.g., Sierra Madre Oriental, Southeast Asia, Ozark Plateau, and Appalachian areas) records tropical and temperate taxa that grew side by side. This, along with a body of paleontological data, suggests that the former geographic ranges of these taxa were once widespread, and that these disparate taxa used to grow together.

Relation to other authors: Most important, the warm character of the pollen flora substantiates the ecological range of types and the climatic diagnosis identified by the plant macrofossils and the insects. Three subtropical types and about ten warm-temperate woody genera are added to the flora. Using the character of the identified flora as a climate indicator, our microfossils fit well with an estimated MAT of ~17.5 °C. In the light of

these results, the estimates of a cool-temperate climate based on the CLAMP and multiple regression models mentioned above are incompatible with the floral composition and the NLRs. The broad uncertainties of the CLAMP method have yet to be fully explained in the literature. A possible reason for the discrepancy may lie partly in the fact that leaf physiognomy data quantitatively embrace the flora, treating upland and lowland types alike, while the estimates from floristics (NLR) take into account the tolerance limits of the warm-temperate and subtropical plant genera, and therefore emphasize the climate of the lower Florissant basin around the former lake.

Acknowledgments

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Plate Descriptions

NOTE: Figures are shown at 1000 magnification, unless otherwise noted.

PLATE 1. Spores of Selaginellaceae, Schizaeaceae; Pollen of Pinaceae
Figures
   1. *Selaginella* cf. *S. longipila*
   2., 3. *S.* cf. *S. densa*
   4. *S.* cf. *S. sanguinolenta*
   5., 6. *S.* cf. *S. mairei*
   7., 8. *Tsuga* spp.
   9. *Pinus* sp.
   10. Schizaeaceae, *Lygodium* cf. *L. kaulfussii*

PLATE 2. Pollen of Pinaceae (scale reduced; 800x)
Figures
   1., 2. *Picea* cf. *P. pungens*
   3., 4. *Pinus* spp.

PLATE 3. Pollen of Pinaceae (scale reduced; 800x)
Figures
   1. *Picea*
   2. *Abies* cf. *A. venusta*

PLATE 4. Pollen of Pinaceae, Taxodiaceae (TCT), and Ephedraceae
Figures
   1. *Abies* cf. *A. venusta*
   2. *Pseudotsuga/Larix*
   3. Taxodiaceae/Cupressaceae/Taxaceae ("TCT type"); pollen resembles that removed from *Sequoia affinis* male cone
   4. *Ephedra* cf. *E. nevadensis*

PLATE 5. Pollen of Pinaceae, Liliales, Eucommiaceae, Fagaceae, *Acer*, and undetermined
Figures
   1. *Cedrus*-type
   2. *Pinus*-type
   3. *Liliopsis*
   4. Fagaceae, quercoid-type
   5. *Eucommia* cf. *E. ulmoides*
   6. *Quercus*
   7. Fagaceae, quercoid-type
   8., 9., 10. *Acer* cf. *A. glabrum*
   11. *Malus/Pyrus*
   12., 13., 14. Brevicolporate, undetermined
   15., 16. Tricolpate, undetermined

PLATE 6. Pollen of Fagaceae, Onagraceae, Rutaceae?, Elaeagnaceae, Apocynaceae, Caprifoliaceae, and Sterculiaceae-type
Figures
   1., 2. *Quercus*
   3. *Semeiandra* cf. *S. grandiflora*
   4. aff. *Xylonagra*
   5., 6. Rutaceae? cf. *Evodia*
   7. *Fagopsis*-type
   8., 9. *Elaeagnus* cf. *E. argentea*
   10. *Fagus*-type
   11. *Fagus*
   12., 13. Apocynaceae *Tabernaemontana* cf. *T. coronaria*
   14. *Viburnum* cf. *V. lentago*
   15. Sterculiaceae aff. Fremontodendrae

PLATE 7. Pollen of Sapindaceae, Rutaceae-type, Ericales, and undetermined
Figures
   1. *Koelreuteria*
   2. Rutaceae-type
   3., 4., 5., 6., 7. *Cardiospermum* cf. *C. halicacabum*
   8., 9. Quercoid tricolpate pollen
   10., 11. Ericales, cf. Ericaceae or Pyrolaceae
   12. Tricolporate, undetermined

PLATE 8. Pollen of Poaceae, Sparganiaceae/Typhaceae, Betulaceae, Rhoipteleaceae, Juglandaceae
Figures
   1., 2. Poaceae (Gramineae)
   3. *Sparganium* or *Typha* cf. *T. angustifolia*
   4., 5. *Ostrya/Carpinus*
   6. Triporate, undetermined
   7., 8. Rhoipteleaceae
   9. *Platycarya*
   10., 11., 12. Rhoipteleaceae cf. *Rhoiptelea*
   13., 14. *Cyclocarya* cf. *C. paliurus*
   15. *Carya*

PLATE 9. Pollen of Engelhardtiae, Ulmoidae, Croton, Juglandaceae, and Chenopodiaceae
Figures
   1. *Engelhardtia/Alfaroa*
   2., 3. *Ulmus/Zelkova*
   4., 6. *Pteroceltis*
   5. *Croton*
   7. Juglandaceae
   8., 9., 10. *Juglans*
   11., 12., 13., 14. Chenopodiaceae, *Sarcobatus* cf. *S. vermiculatus*
   15. Chenopodiaceae undetermined
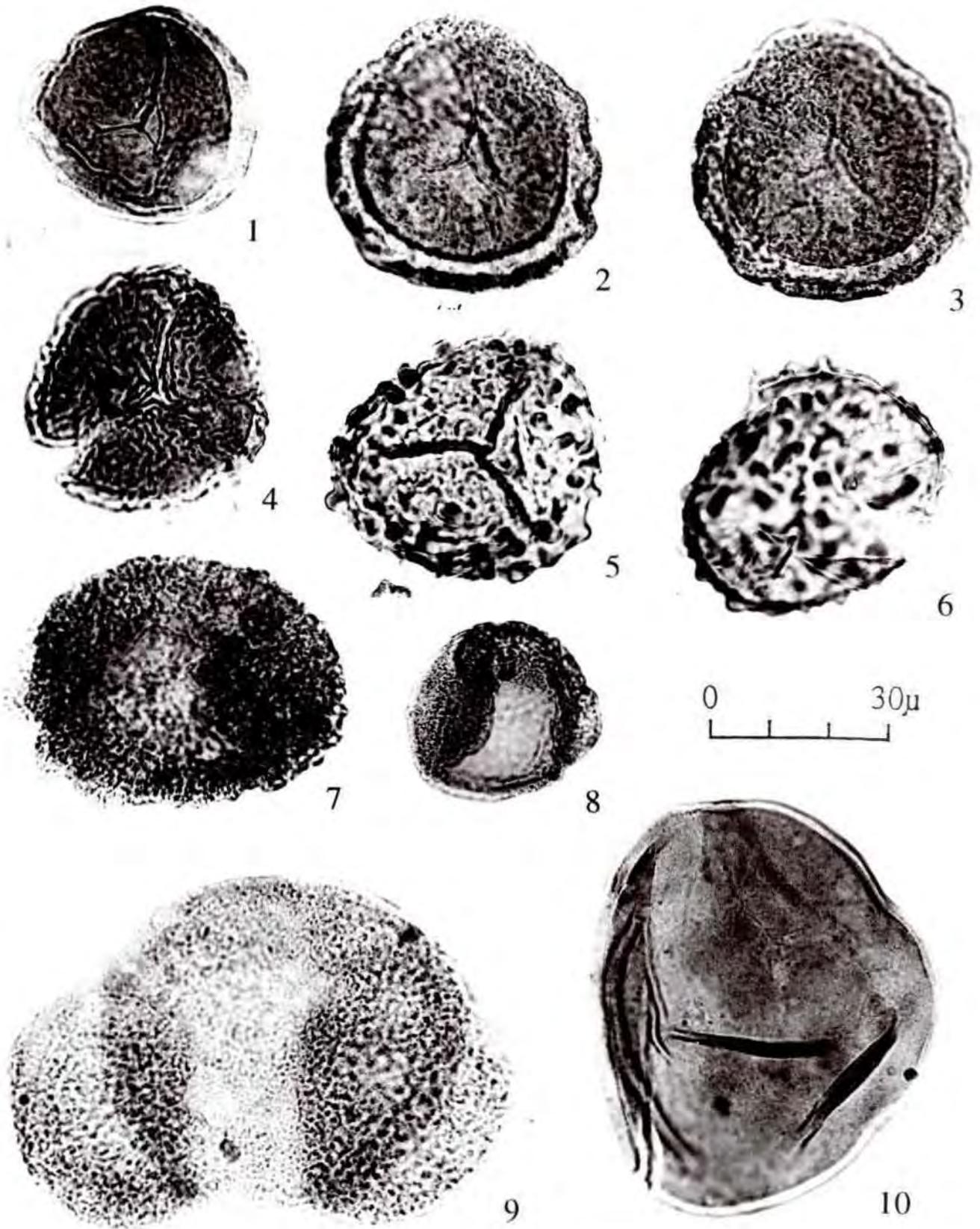
PLATE 1. Spores of Selaginellaceae, Schizaeaceae; pollen of Pinaceae.
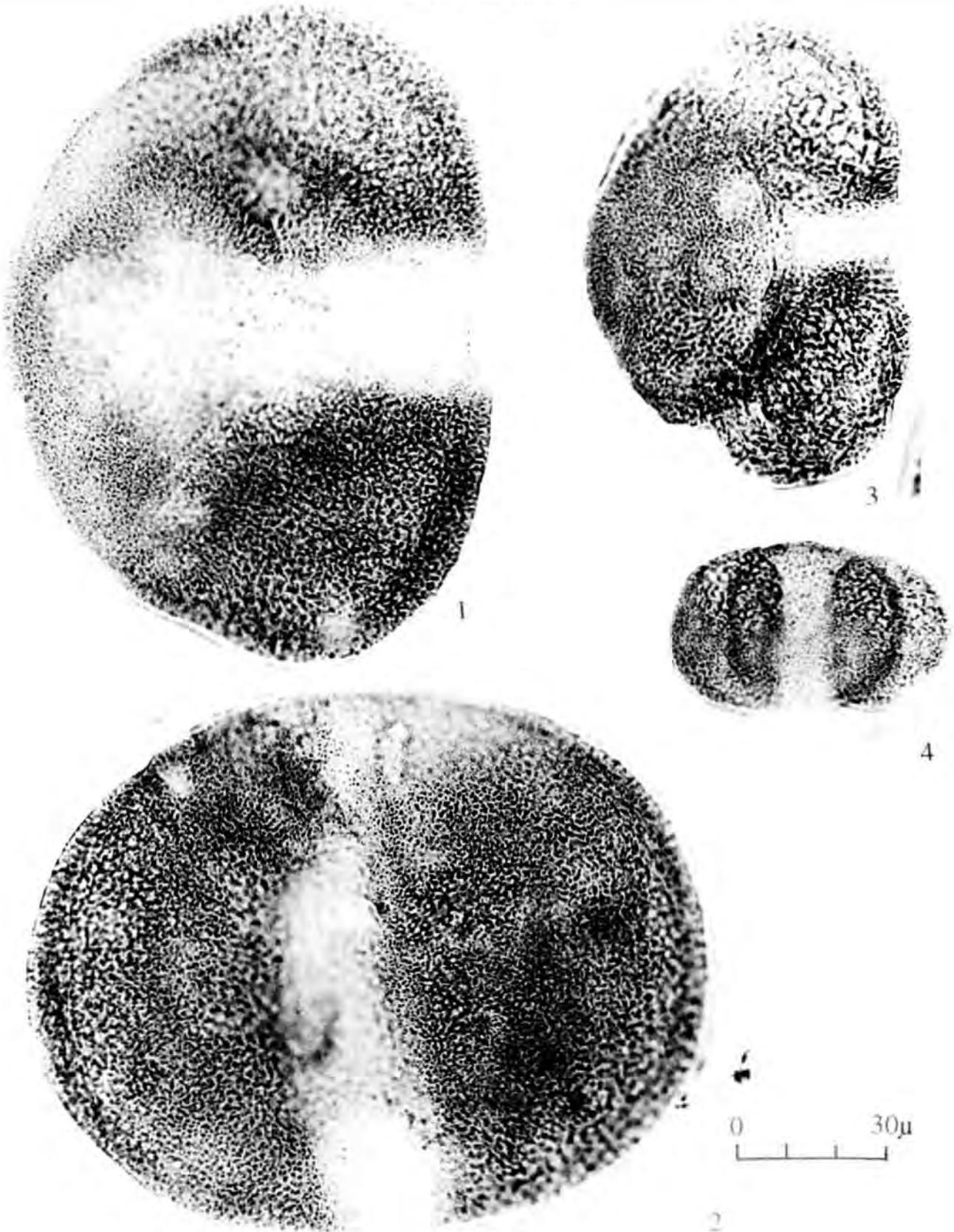
PLATE 2. Pollen of Pinaceae (scale reduced; 800x).
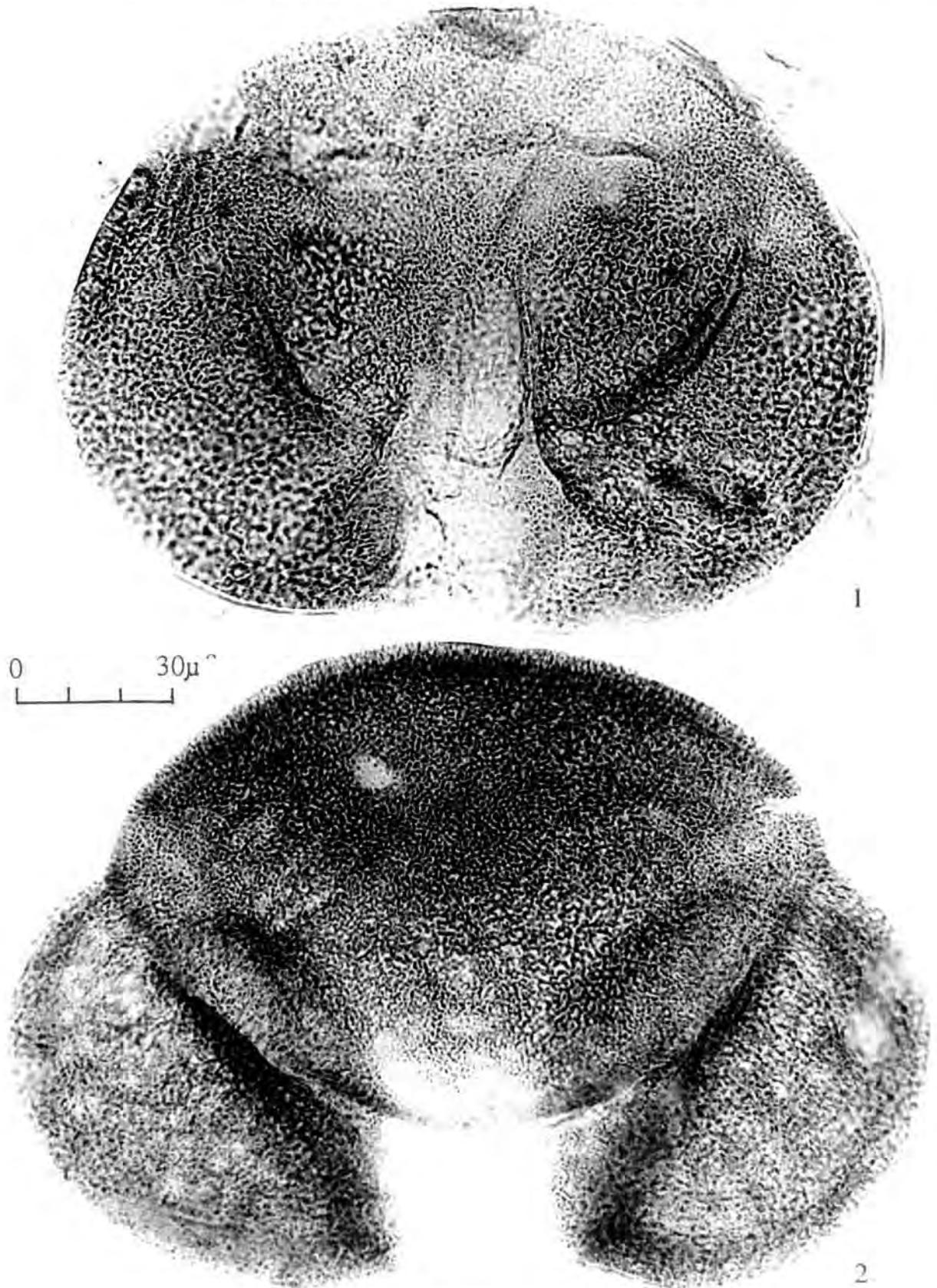
PLATE 3. Pollen of Pinaceae (scale reduced; 800x).
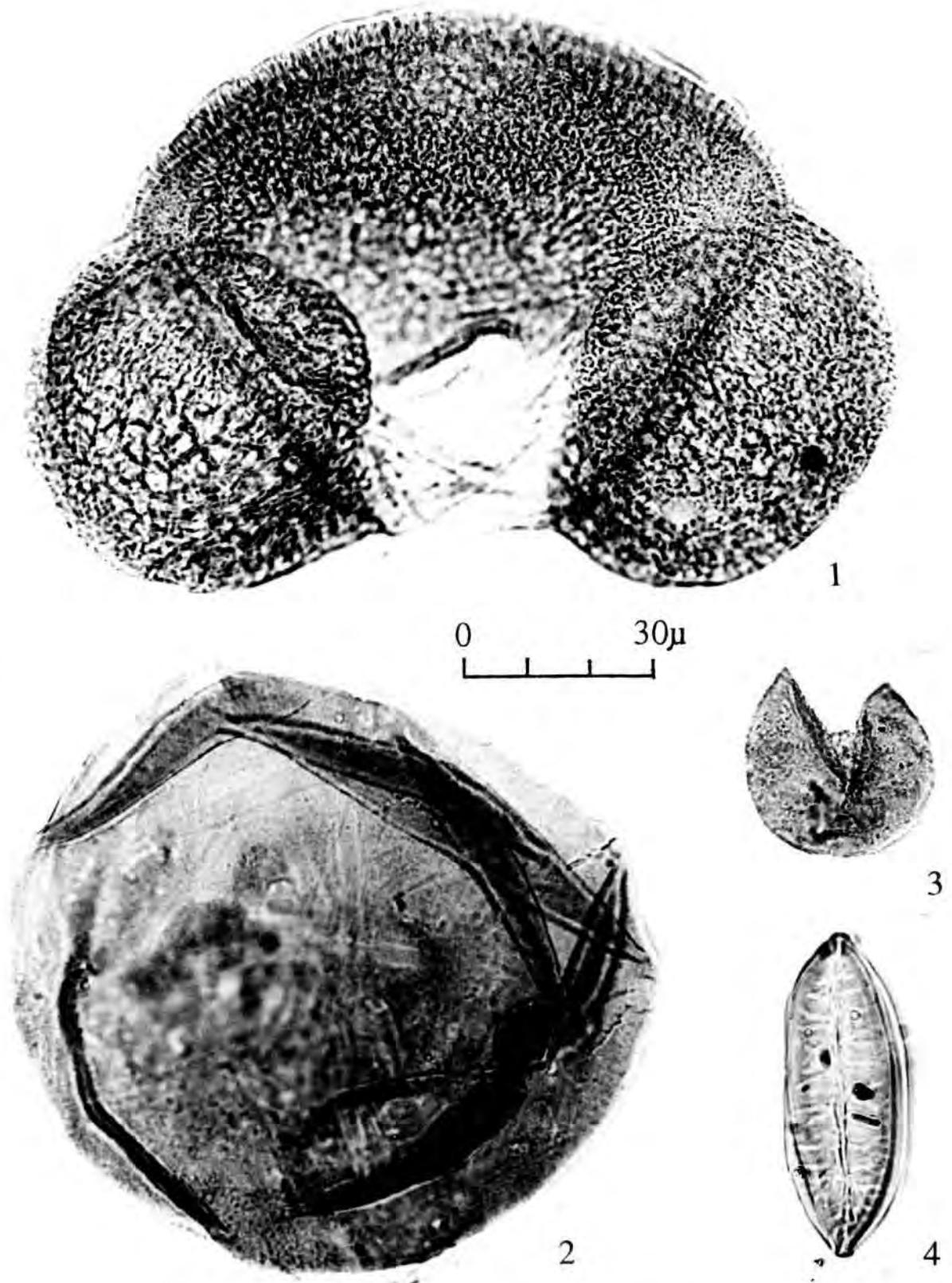
PLATE 4. Pollen of Pinaceae, Taxodiaceae (TCT), and Ephedraceae.
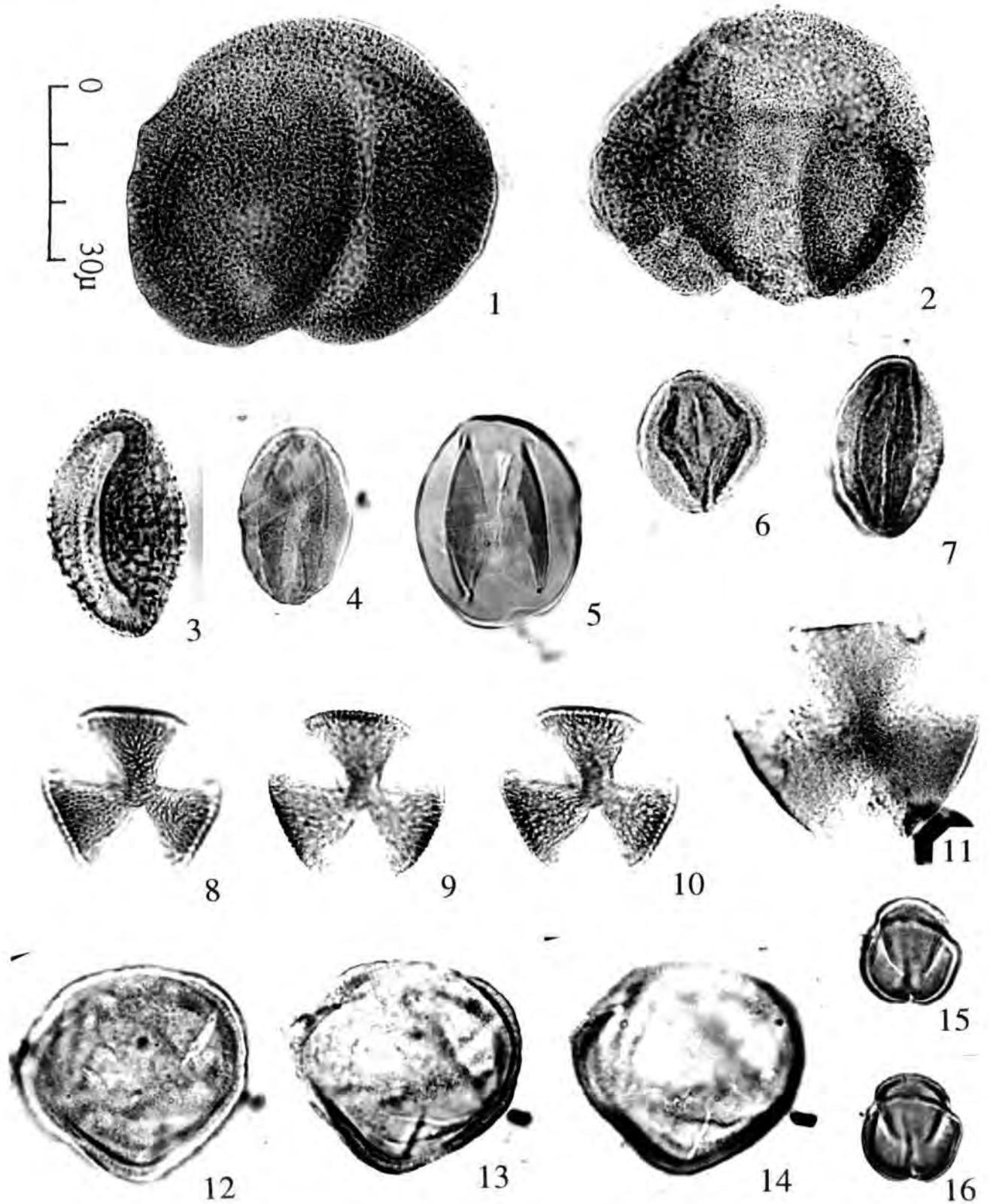
PLATE 5. Pollen of Pinaceae, Liliales, Eucommiaceae, Fagaceae, *Acer*, Rosaceae and undetermined.
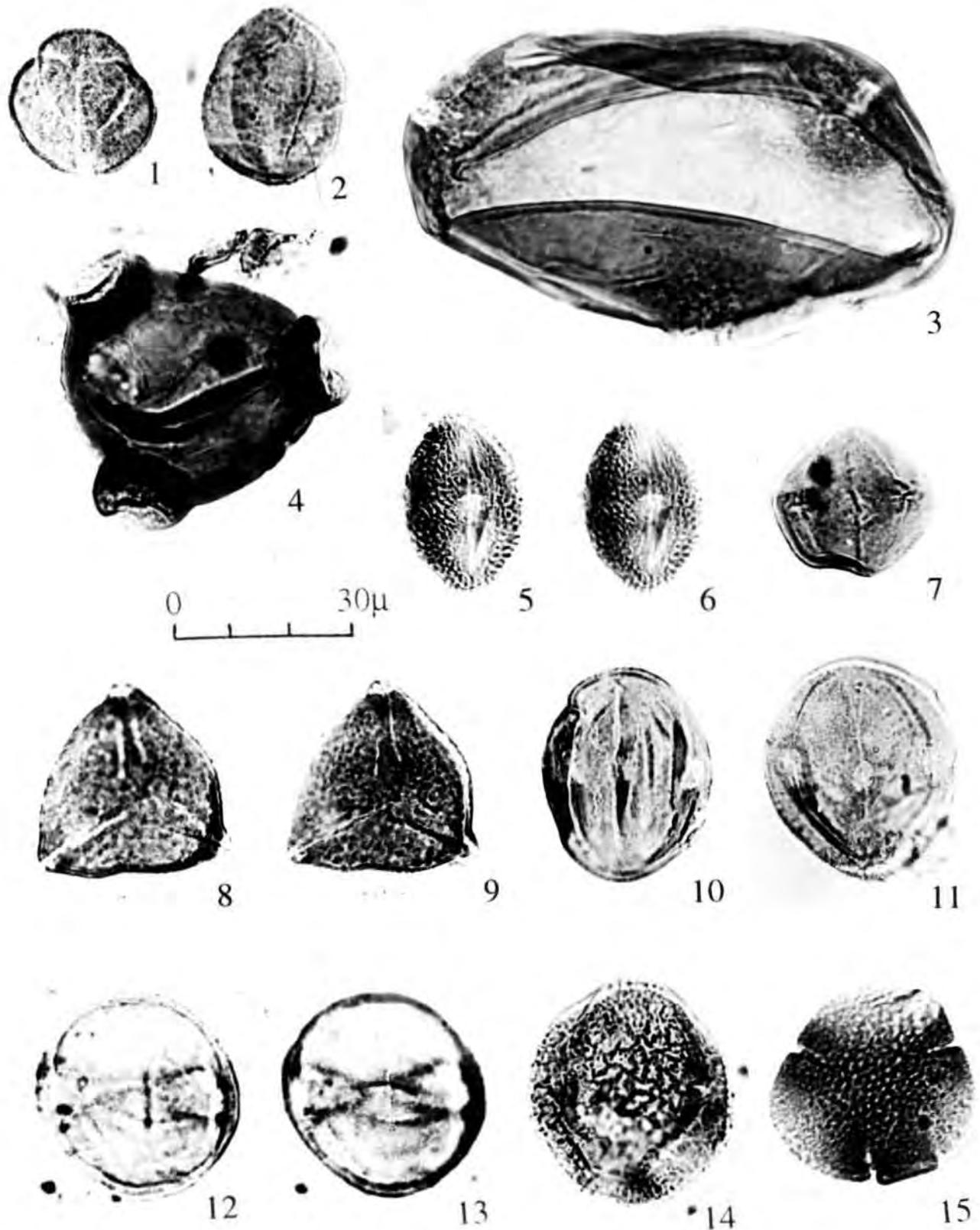
PLATE 6. Pollen of Fagaceae, Onagraceae, Rutaceae?, Elaeagnaceae, Apocynaceae, Caprifoliaceae, and Sterculiaceae-type.

PLATE 7. Pollen of Sapindaceae, Rutaceae-type, Ericales, and undetermined.

0   30µ
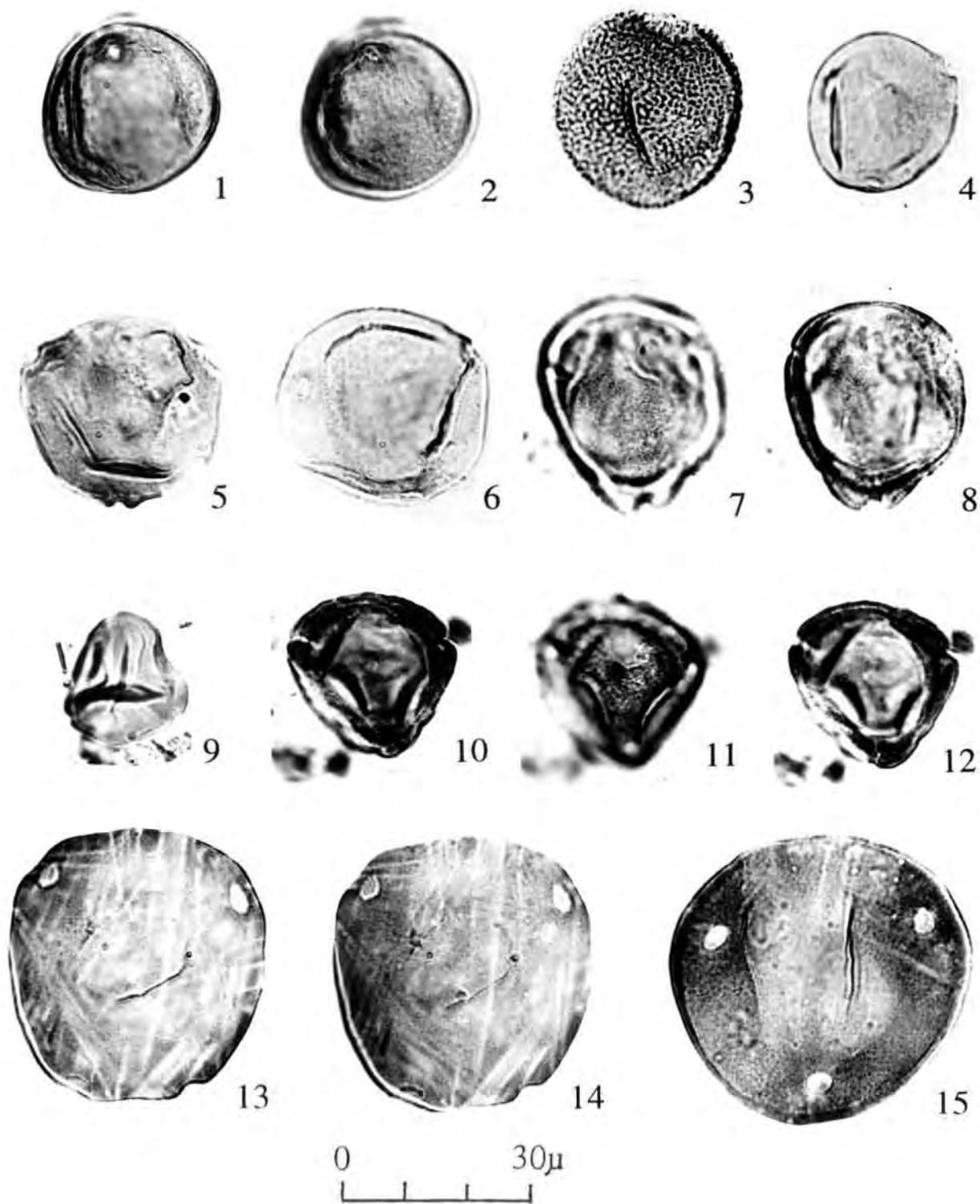
PLATE 8. Pollen of Poaceae, Sparganiaceae/Typhaceae, Betulaceae, Rhoipteleaceae, and Juglandaceae.
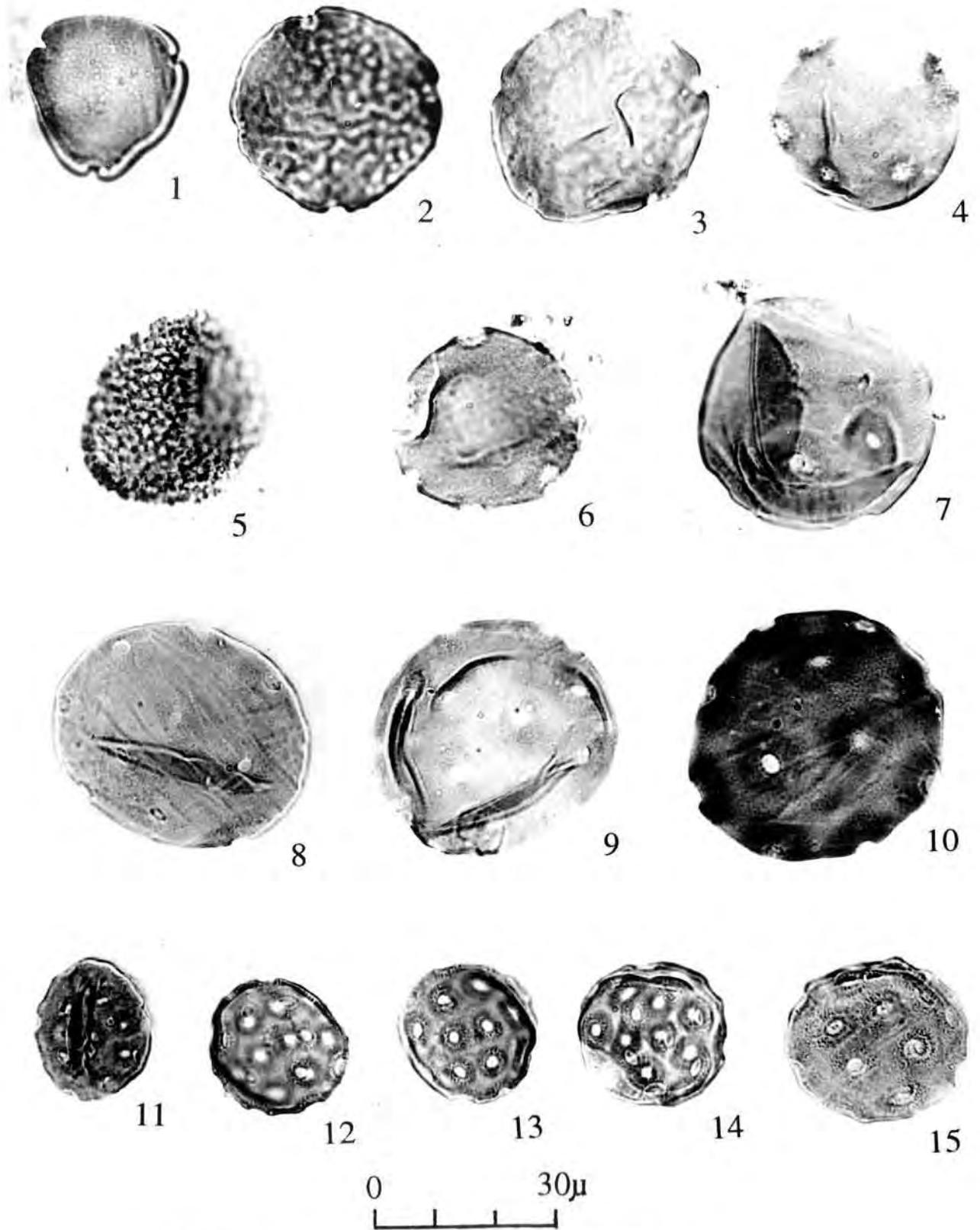
PLATE 9. Pollen of Engelhardtiae, Ulmoidae, *Croton*, Juglandaceae, and Chenopodiaceae.

APPENDIX 1.

Climate data.

	Altitude (m)	MAT (°C)	January Temp. (°C)	July Temp. (°C)	Range (°C)	Annual ppt (mm)
1. San Angelo, Edwards Plateau, Texas	580	18.7	8–10	28	18–20	508–559
2. Guanajuato, San Luis Potosí, Mexico	2000–3000	17.7	12–14	22–26	12–16	254–508
3. Chihuahua, Mexico	1400	18.0	10	25	15	394
4. Mazatlan, Sinaloa, Mexico	78	24.0	18–20	27–29	9–11	880
5. Vera Cruz, Mexico	16	25.0	21	27	6	1787
6. Lake George, Colorado	2560	3.3	−9.33	16.1	25.5	325
7. Lakewood, Colorado	1717	10.2	−0.61	22.5	23.1	385
8. Colorado Springs, Colorado	1874	9.4	−1.77	21.7	23.5	392
9. Lake Moraine, Colorado	3129	2.0	−6.50	12	18.5	632

MAT = mean annual temperature
ppt = precipitation, water equivalent

COLORADO DATA:
Climate Normals for the U.S. (Base: 1951–80). 1983. Detroit: Gale Research Co.

MEXICO DATA:
Conway M, Liston L, editors. 1990. The Weather Handbook. Norcross, GA: Conway Data.

APPENDIX 2.

Locality data for pollen and spore collections prepared and examined for this report.
"D" numbers are USGS paleobotany localities. Teller County, Colorado.

D1177. Road cut east of Stohl's Ranch, NE¼ SW¼ NE¼ sec. 3, T. 13 S., R. 71 W. Leopold measured section. Gray conchoidally fracturing clay beds overlie laminated leaf-bearing shales. This is also Cockerell's locality 7b (1909), and it lies at the north end of the Florissant basin.

W1. Road cut on south side of Highway 24 (north-facing exposure) just east of townsite, W½ NW¼ SW¼ sec. 1, T. 13 S., R. 70 W., at 8200 feet elevation. Leopold collected and measured section, remeasured by Evanoff, with 13 m exposed (see Fig. 2). These are the "Amyzon" fish beds of Cope (1875), on the north end of the Florissant basin. It records an arkosic unit at the base (Unit 2) abruptly overlain by mudstones, pumiceous sands, and clay, with laminated silty clay and pumice to the top of the section.

D1197. Florissant Formation from trench behind the former Singer Ranch buildings, elevation 8400 feet. Includes nine samples from top down, covering 17 feet of section. SW¼ sec. 13, R. 71 W., T. 13 S., middle shale unit.

D1496. MacGinitie's "Fish Bed Locality" field location EL58-43A through -E plus leaf impressions, ca. 8440 feet elevation; Center W½ SE¼ NE¼ sec. 24, R. 71 W., T. 13, S. From Leopold and MacGinitie collections. Site is on a west-facing slope of a terrace about ⅛ mile north of buried aqueduct line that crosses west to east.

D3495. Location at Snare Ranch—one sample; 500 feet NW of gate to Nathan Snare Ranch, elevation 8525 feet, Section 25 R71W T13S.

D3496. Behind school house, Florissant Grange building at base of Crystal Peak Road E½ NW¼ SE¼ sec. 2, R. 71 W., T.13 S.

D5464. South side of Twin Rock Road at 8600 feet elevation, SE¼ SW¼, sec. 19, T. 13, S., R. 70 W. Leopold and Carol Lind collection.

D1175. Elso Barghoorn and Richard Scott's collections at Roland W. Brown's site. Samples A and B, NE¼ SW¼ NE¼ sec. 3, T. 13., S. R. 71 W., Lake George.

D1095. F. S. MacNeil sample; undetermined locality, Florissant.

D1083. Roland W. Brown sample; U.S. National Museum Location. No. 9327, specimens 50323 and 50343.

APPENDIX 3.

Section measured by Evanoff.

Location W1: Florissant road cut, W NW NE SW¼ sec. 1, T. 13 S., R. 71 W. Beds dip 3°W (apparent) lowest part of Florissant Formation, Lake George, Colorado, 7.5 degree quadrangle, 1984 edition. The top of this section represents the Amyzon (fish) beds of Cope (1875). Units 8–11 of Evanoff are summarized.

Unit Number and Thickness in Meters		Meters Above Base of Section	Description
17	1.30	12.30–13.60	Weathered granite grus, Quaternary colluvium. Top of road cut here.
16	0.88	11.42–12.30	Mudstone, blocky with abundant plant fragments, light gray in color. Local top of Florissant Formation.
15	0.03	11.39–11.42	Sharply defined fine-sand pumice bed, yellow in color.
14	0.60	10.79–11.39	Laminated beds of silt grading upward to clay. Brown in color.
13	0.58	10.21–10.79	Silt grading upward to clay at top. Contains fish scales. Sediments brown in color with abundant rusty stain.
12	0.08	10.13–10.21	Sharply defined very fine-sand pumice bed; pumice particles yellow-brown in color. This is a marker bed.
11–8	4.14	5.99–10.13	Silty clay, platy to blocky with layers of silt grading upward into clay. Layers are 9 cm thick at base of unit decreasing to 2 cm thick at top. Scattered fish in top 20 cm. Color brown at top, light brown alternating with gray clay at base. Organic content high except in top 20 cm. Abundant woody material at base. Fossil leaves occur 25 cm below top of unit. Very fine pumice layer at 6.8 m. Basal contact of sedimentary interval at 5.99 m is sharply defined.
7	0.47	5.52–5.99	Silty clay beds with laminae that grade from very fine-sand pumice at base of laminae upward to clay; organic rich.
6	0.03	5.49–5.52	Layer of small gravel-sized pumice, purple-gray in color. Contact at base is diffuse.
5	0.39	5.10–5.49	Pumiceous fine sand at base grading upward to pumiceous clay at top. Every 2 cm has dark organic-rich thick laminae. Contact at base very distinct. Color is gray to medium brown.
4	3.31	1.79–5.10	Mudstone, blocky, massive with fine gravel-sized stones and pumice-rich layer 4 cm thick in middle. Poorly defined layering 2 cm thick at base. Color light gray, pumice beds streaked with subvertical ferric oxide stains. Scattered plant fragments. Contact at base is diffuse.
3	0.90	0.89–1.79	Very fine gravel and pumice with lenses of coarse sandy mudstone. This unit is lenticular, arkosic at base. Largest pumice grains at top. Contact at base is sharply defined.
2	0.29	0.60–0.89	Very fine gravel grading upward to very coarse sand with large boulders of pumice; yellow-olive in color. Arkosic at base of unit. Contact at base is diffuse to distinct.
1	0.60	0–0.60	Fine gravel grading upward to very coarse sand at top; olive-gray in color. Base of unit not exposed (at road level).

APPENDIX 4.

Elevation and mean annual temperature of Colorado sites.

	Elevation (meters/feet)	MAT (°C)
Alamosa	2297/7536	5.1
Aspen	2416/7928	4.9
Bailey	2357/7733	5.6
Boulder	1659/5445	11.2
Buena Vista	2424/7954	6.6
Burlington	1269/4165	10.9
Byers 5 NE	1585/5200	9.6
Cañon City	1628/5343	12.3
Cedaredge	1883/6180	9.4
Cheesman	2095/6875	7.6
Cherry Creek Dam	1721/5647	9.7
Cheyenne Wells	1295/4250	10.8
Cochetopa Creek	2438/8000	2.7
Colorado National Monument	1609/5280	11.0
Colorado Springs	1873/6145	9.4
Cortez	1882/6177	9.3
Crested Butte	2699/8855	1.8
Del Norte	2403/7884	6.2
Eads	1284/4215	11.5
Fruita	1373/4507	10.2
Grand Junction	1479/4855	11.5
Greeley CSC	1418/4658	9.4
Gunnison	2336/7664	2.9
Holly	1034/3393	11.9
John Martin Dam	1162/3814	12.4
Palisade	1457/4780	12.3
Rifle	1645/5400	8.2
Rye	2069/6790	8.1
Silverton	2841/9322	2.1
Steamboat Springs	2063/6770	3.7
Sterling	1200/3939	9.3
Taylor Park	2806/9206	0.4
Telluride	2668/8756	4.3
Walden	2468/8099	2.3
Waterdale	1603/5260	9.1
Westcliffe	2395/7860	5.7
Wray	1089/3575	11.0

3.

PALYNOLOGY OF THE UPPERMOST EOCENE LACUSTRINE DEPOSITS AT FLORISSANT FOSSIL BEDS NATIONAL MONUMENT, COLORADO

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ABSTRACT—Samples collected through two intervals of lacustrine deposits consisting of shale interbedded with mudstone and pumiceous air-fall tuff within the Florissant Formation at Florissant Fossil Beds National Monument yielded rich assemblages of pollen, spores, and algal microfossils. These samples are from the middle shale unit, which overlies the unit containing the well-known petrified stumps, and the upper shale unit, which overlies the caprock conglomerate. The middle and upper shale units also yielded a wide variety of well-preserved fossil leaves and insects. The palynoflora of about 130 species represents the vegetation of Lake Florissant and regional habitats of latest Eocene age. Assemblages from most samples are dominated by pollen of gymnosperms, primarily Pinaceae and Cupressaceae. Angiosperm pollen is diverse—about 100 species—although many species are low in abundance. The numerically most abundant angiosperm pollen species are referable to the anemophilous families Ulmaceae, Juglandaceae, and Fagaceae. Pollen of lake-margin and aquatic angiosperms includes probable representatives of the families Cyperaceae, Nymphaeaceae, Pandanaceae, and Sparganiaceae or Typhaceae; cysts, coenobia, and colonies of aquatic algae are common. Drier habitats are indicated by consistent presence of pollen of Ephedraceae and Chenopodiaceae/Amaranthaceae. Repetitive minor ashfalls recorded in the lake sediments evidently had little effect on the composition of the vegetation, but major fluctuations in relative abundances of certain groups of palynomorphs are inferred to reflect the response of plant communities to major volcanic eruptive phases. The palynoflora of these deposits supplements data from plant megafossils pertaining to the paleoecology and paleoclimate of the region in latest Eocene time. The Florissant Formation has further significance in that it preserves a diverse, well-dated palynoflora that is an important data source for Paleogene palynostratigraphy in western North America. Species of pollen present apparently are the stratigraphically oldest palynological records in either North America or the world of the angiosperm families Aceraceae, Fabaceae, Malvaceae, Polemoniaceae, and Salicaceae, and possibly of the Asteraceae, Eleagnaceae, and Ranunculaceae. Three new nomenclatural combinations are proposed for taxa discussed.

KEY WORDS: Colorado, Eocene, Florissant, palynology, taxonomy

In latest Eocene time, about 34 million years ago, volcanic activity in the Thirtynine Mile volcanic field and perhaps other volcanically active areas in what is now central Colorado caused a remarkable series of depositional events. At that time a small valley existed in the vicinity of the present-day town of Florissant, Colorado, west of Pikes Peak. The valley, which had been eroded into Pikes Peak Granite, had well-vegetated slopes and a southeasterly to southerly flowing stream within it. A major eruption at the Guffey volcanic center,

within the Thirtynine Mile volcanic field to the southwest, blocked the southern end of the Florissant paleovalley, damming the stream and initiating the development of ancient Lake Florissant. Intermittent large and small eruptive events continued during the time that the lake existed. Many of these events involved falls of pumice ash and lapilli that eventually constituted much of the sediment that accumulated in the lake. The vegetation of the lake margin and the valley slopes, and even aquatic algae inhabiting the lake itself, left a unique fossil record in the fine-grained lake sediments. The leaf fossils from the Florissant Formation deposits are world famous, as are delicate fossils of insects in the same beds. Less well known are the microscopic fossil spores, pollen, and algal microfossils that were preserved by the millions in the fine mud and ash settling to the bottom of the lake. These fossils are the subjects of this report.

The complete history of ancient Lake Florissant and its associated deposits is more complex than is suggested by the preceding brief outline, which is based primarily on papers included in a field trip guidebook edited by Evanoff (1994) and Evanoff et al. (2001). His extensive stratigraphic investigations have revealed the presence of three intervals of lacustrine deposits in the area of Florissant Fossil Beds National Monument, two of which are preserved within the monument (Fig. 1). Readers are referred to Evanoff (1994) and Evanoff et al. (2001) for more complete accounts of the stratigraphic and volcanic history of the Florissant area. This report concerns palynologic analyses of two intervals of lacustrine shale within Florissant Fossil Beds National Monument, the middle and upper shale units of the Florissant Formation. These analyses provide an additional set of data and new interpretations pertaining to this important fossil locality. This report provides new insight on the question of how the frequent episodes of volcanism may have affected the flora in the vicinity of ancient Lake Florissant.

Previous Studies

Prior to this study and another in this volume, no comprehensive reports of the palynoflora of Florissant have been published. In contrast, the megafossil flora has received considerable attention. A complete review of previously published reports on the megafossil paleobotany of the Florissant Formation, which are myriad, is beyond the scope of our report. The earliest studies on fossil leaves date back to the late 1800s and extend to the recent, more definitive work of Manchester (2001). Perti-
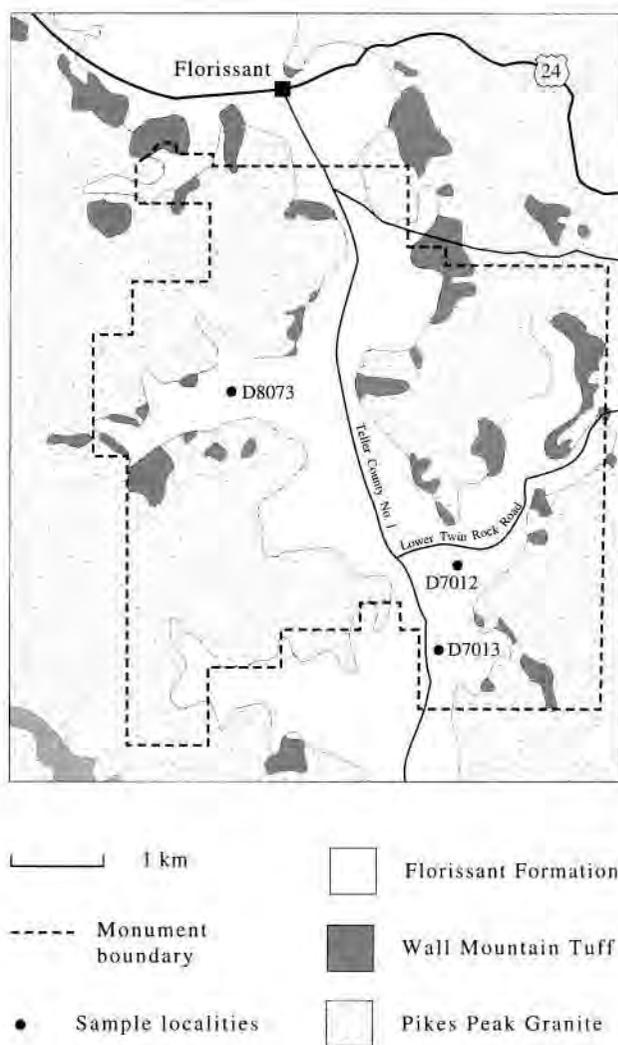
FIGURE 1. Simplified geologic map of Florissant Fossil Beds National Monument and vicinity (after Wobus and Epis 1978), south of the town of Florissant, Colorado, showing positions of localities sampled in this study. Localities D7012 and D7013 are in the middle shale unit, and locality D8073 is in the upper shale unit of the Florissant Formation. Samples discussed in detail in this report are from localities D7012 and D8073.

nent to our discussion are a few of the more recent works briefly noted here; they are cited in chronological order. The few previous studies that concern plant microfossils are of special interest, and some are cited later in detail.

MacGinitie (1953) conducted a comprehensive study of the plant megafossils from the Florissant beds. He concluded that only about one-half of the nearly 258 species described by earlier workers were valid. Manchester (2001) has revised many of the taxonomic determinations of MacGinitie, but he notes that the diversity of the assemblage is similar to that estimated by MacGinitie, with about 100 genera and 120 species.

McLeroy and Anderson (1966), in a study that focused on the origin of laminations in the lacustrine shale at Florissant, included a list of modern genera identified from fossil pollen in the deposits. The pollen identifications were by W. S. Ting. The list included four genera of gymnosperms and ten of angiosperms.

Penny (1969) cited personal communication with E. B. Leopold in discussing that pollen derived from fossil *Sequoia* at Florissant more closely resembles pollen of modern *Taxodium* than that of modern *Sequoia*. He included a plate of photomicrographs of fossil pollen and spores from the Florissant Formation that was provided by Leopold (in Penny 1969, Plate 16-6). Penny also discussed the difficulty of correlating Tertiary megafloras regionally, because they tend to be widely separated and often represent different ecological settings.

Leopold and MacGinitie (1972) discussed numerous fossil floras, including palynofloras, of the Tertiary of the Rocky Mountain region. They referred to the Florissant flora as being warm-temperate to subtropical in character and concluded that it is closely allied with plants living in the highlands of northeastern Mexico today. However, Manchester (2001) questions the validity of several of the identifications that MacGinitie used to draw his floristic comparison.

Manchester and Crane (1983) studied staminate and pistillate inflorescences attached to branches bearing *Fagopsis longifolia* foliage from the Florissant Formation. They concluded that *Fagopsis longifolia*, the most abundant leaf fossil at Florissant, is more closely allied with the Fagaceae than with the Betulaceae, as had been proposed by MacGinitie (1953). Their description and illustration of pollen extracted from the staminate inflorescences provide a basis for determination of occurrences of *Fagopsis longifolia* pollen in our study.

Leopold et al. (1992) mentioned the flora of the Florissant lake beds with special reference to paleoclimatic implications. An abundance of woody xerophytes was seen as indicative of a seasonally dry, savanna-type

climate. Their interpretation, based largely on palynologic evidence, calls for dry hill slopes surrounding lowland riparian and lakeside environments.

Gregory and Chase (1992) and Meyer (1992) interpreted paleobotanical data from Florissant to determine the elevation of the site in late Eocene time. Their results are discussed later under Paleoecology.

Stratigraphy and Age

In his well-known study of the megafossil flora of the Florissant lake beds, MacGinitie (1953) included discussions of the geology of the deposits and the geologic history of the region. Recent work by Evanoff (1994) and Evanoff et al. (2001) has shown many of MacGinitie's geologic interpretations to be incorrect in whole or in part. These accounts are the most complete reviews of previous geologic studies and of the geologic framework of Florissant as currently understood. We concur with the new interpretations. Perhaps most significantly we agree that ancient Lake Florissant always was restricted in area to the valley in which its deposits are now found and did not fluctuate in size appreciably during its history. This view disagrees with that of MacGinitie (1953) and McLeroy and Anderson (1966), but is consistent with geologic mapping and stratigraphic studies (Wobus and Epis 1978). We also adopt the stratigraphy of the Florissant Formation in the monument as revised by Evanoff et al. (2001).

The Florissant Formation is divided into five units within the boundaries of the monument (Fig. 2). The lower mudstone unit is the lowest unit exposed in the monument. It consists of tan to gray tuffaceous mudstone, muddy pumiceous conglomerate, and minor beds of sandstone overlain by massive tuffaceous sandy mudstone. Its maximum thickness is 10.4 m. The lower part of the unit represents stream deposits, and the upper part is a volcanigenic mudflow. The world-famous silicified *Sequoia* stumps are preserved in this unit (Fig. 2). Most of the fossil mammals known from the Florissant Formation have been found in this unit. No samples were collected from this unit in our study.

The middle shale unit of the Florissant Formation is the main interval of lacustrine deposits in which most of the fossil leaves and insects known from the vicinity of the monument have been found (Fig. 2). It consists of platy mudstone and laminated shale and is about 9 m thick. The shale is interbedded with tuffaceous mudstone and siltstone, tuff, pumiceous sandstone, and thin pumiceous conglomerate. These beds grade into arkosic sandstone, which contains mammal bones, at the
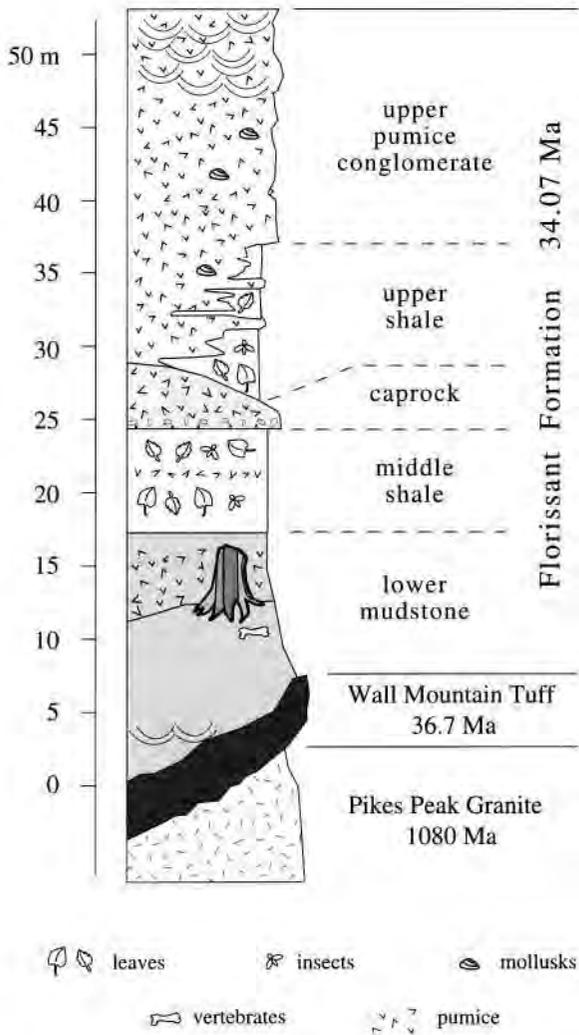
FIGURE 2. Diagrammatic representation of the stratigraphy of the Florissant Formation within the boundaries of the national monument, simplified from Evanoff (1994, Figs. 2–6). Samples discussed in this report are from the middle and upper shale units, lacustrine deposits that preserve abundant palynomorphs (plant microfossils) as well as the better known fossil leaves and insects. The famous petrified stumps on display at the monument are in the lower mudstone unit.

sides of the paleovalley. The tuff and pumice beds represent air-fall volcanigenic deposits (ash). A major eruptive event that occurred during the deposition of the lacustrine deposits is signaled by an increase in pumice beds about halfway up the section within the middle shale unit, and pumiceous conglomerate marks the culmination of this event. The middle shale unit was sampled for palynologic analysis at two localities within the monument (D7012 and D7013, Fig. 1).

The caprock conglomerate of the Florissant Formation is a thick (1.5–7.9 m), tuffaceous, volcaniclastic conglomerate. It was deposited as a lahar that flowed over the lacustrine beds of the middle shale unit. Originally thought to have ended lacustrine deposition in the Florissant area, the caprock conglomerate is now known to have been deposited in the lake and is overlain by more lacustrine deposits. No samples were collected from this unit in this study.

The upper shale unit of the Florissant Formation consists of 3.6 to 5.6 m of shale with secondary mudstone and pumiceous conglomerate. This unit represents lacustrine deposition that took place after the emplacement of the caprock conglomerate. Like the middle shale unit, the upper shale unit is highly fossiliferous and yields well-preserved leaves, insects (Fig. 2), and, unlike the middle shale unit, calcareous microfossils (ostracodes). The upper shale unit also has locally abundant fingernail clams (sphaeriids; Evanoff, written commun., 1996). The upper shale unit is exposed in the northwestern part of Florissant Fossil Beds National Monument, and it was sampled for palynologic analysis in this study (locality D8073, Fig. 1).

The uppermost unit of the Florissant Formation consists of pumiceous sandstone and conglomerate. It overlies and interfingers with the upper shale unit and is up to 22.8 m thick. This unit overwhelmed ancient Lake Florissant, and it represents the final event in the development of the Florissant Formation. Its upper boundary is an erosional unconformity.

McLeroy and Anderson (1966) studied the laminations of the lacustrine deposits from the interval referred to here as the middle shale unit. They determined that the laminations are of three kinds: (1) couplets averaging about 1 mm in thickness that consist of diatomite and sapropel; (2) layers averaging about 8 mm in thickness that consist of graded tuff overlain by one or more diatomite-sapropel couplets; and (3) layers averaging about 1.5 cm in thickness that consist of pumice sporadically interbedded with diatomite-sapropel couplets. The diatomite-sapropel couplets were interpreted as varves representing one year of deposition. On this

basis, McLeroy and Anderson (1966:615) estimated that the lake existed for 2500 to 5000 years. These diatomite-sapropel couplets constitute the lacustrine shale collected for analysis in our study (Fig. 3).

Until just recently, the Florissant flora was regarded as early Oligocene in age, based on MacGinitie's (1953) comparison of the megaflora with other North American Tertiary floras. However, the most recently published radiometric age of the beds at Florissant—34.07 ± 0.10 Ma (Evanoff et al. 2001)—and recent revisions of the Tertiary time scale (Berggren et al. 1992) indicate that these beds are latest Eocene in age. The Eocene-Oligocene boundary currently is established as 34 Ma (Berggren et al. 1992). J. D. Obradovich of the U.S. Geological Survey (pers. commun., 1994) has further refined the date for the Eocene-Oligocene boundary in the Gulf Coast of the United States to 33.6 to 33.7 Ma, based on additional studies. Thus, the age of the fossils described here is latest Eocene.

Materials and Methods

As an aspect of geologic site studies conducted by the National Park Service (Root 1983), several trenches were excavated through the fossiliferous lacustrine deposits preserved at Florissant Fossil Beds National Monument (Fig. 4). In collaboration with Ralph Root, samples were collected for palynologic analysis from each of two of the trenches by one of us (DJN). Samples were processed at the U.S. Geological Survey's palynological laboratory in Denver, and a detailed analysis of the samples from one trench, which completely exposed the middle shale unit, was begun by one of us (FHW). When subsequent stratigraphic studies by Evanoff and Murphey (in Evanoff 1994) revealed the existence of an interval of lacustrine deposits above the caprock conglomerate within the monument, that interval was sampled also for palynological analysis. All localities sampled in our study are within the monument boundaries. The lower shale unit of the Florissant Formation, which is exposed along U.S. 24 east of the town of Florissant, was not sampled in this study, but see Leopold and Clay-Poole (2001).

Samples were collected from the middle shale unit at localities TR-10 and TR-11 of Root (1983) and from an exposure of the upper shale unit. Only lithologies having good potential for preservation of palynomorphs—carbonaceous shale and mudstone—were collected, either at changes in lithology or at regular intervals. Locality D7012 of this report (Fig. 1) is the same as TR-10 of Root (1983) and is also referred to as the Gregory trench

(Evanoff 1994); it is U.S. Geological Survey (USGS) paleobotany locality D7012 (NE¼ SW¼ SW¼ sec. 19, T. 13 S., R. 70 W., Teller Co., Colo.; Lake George 7½ min. quadrangle). Locality D7013 (Fig. 1) is the same as TR-11 of Root (1983) and is also known as Root's gully (Evanoff 1994); it is USGS paleobotany locality D7013 (NW¼ SW¼ NW¼ sec. 30, T. 13 S., R. 70 W., Teller Co., Colo.; Lake George 7½ min. quadrangle). The upper interval of lacustrine deposits was sampled at locality D8073 (Fig. 1), which is USGS paleobotany locality D8073 (NE¼ SW¼ SE¼ sec. 14, T. 13 S., R. 71 W., Teller Co., Colo.; Lake George 7½ min. quadrangle). Because locality D7012 afforded access to the complete thickness of the middle shale unit (in contrast with locality D7013, which exposes only the upper part of this unit), only samples from locality D7012 and those from locality D8073 were analyzed for this report.

Samples were processed according to standard procedures as described by Doher (1980). Following an extensive survey of palynological morphotypes present on the slides, relative abundance counts were made. Counting proceeded in iterative stages, as follows.

Initially 200 specimens were counted from each sample, and percentage relative abundances of taxa were calculated. Most samples were numerically dominated by pollen of coniferous gymnosperms and many by microfossils of freshwater aquatic algae, but many of the botanically most interesting and biostratigraphically most important taxa were present only in low relative abundance. To permit a better assessment of the less common taxa, the more abundant ones were deducted from the total, and successive counts were conducted until a total of 200 specimens was again reached for each sample. The successive counts permitted estimates of relative abundances of less common taxa to be obtained despite the masking influence of the overwhelmingly abundant taxa. Thus, in the first iteration, all taxa were counted. In the second iteration, aquatic algae were omitted, which permitted a better representation of the land flora (vascular plants) of the region. In the third iteration, aquatic algae and coniferous pollen were omitted, which emphasized the relative abundances of pollen of angiosperms and spores of all kinds. Finally, in the fourth iteration, algae, conifer pollen, and fungal spores were omitted. This method produced counts ranging from 323 to 678 specimens per sample. Relative abundance data resulting from most but not all counts are presented in graphic format in this report (Figs. 5–8).

In this study, identifications of palynomorph taxa are based on comparisons with both fossil and modern palynomorphs described in the literature, and the generic and specific nomenclature applied derives
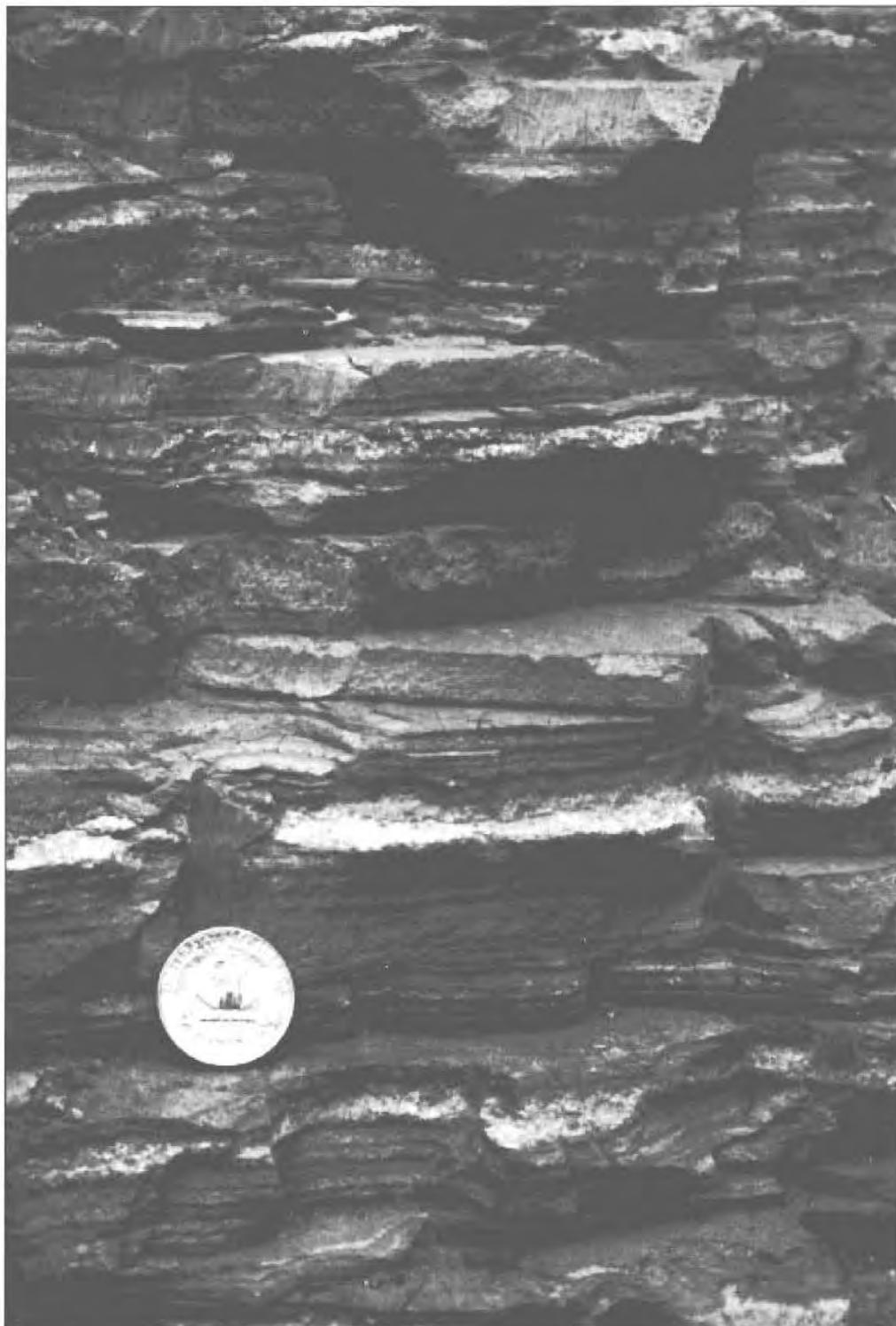
FIGURE 3. Shaly lacustrine deposits (pumiceous couplets of diatomite and sapropel) in the middle shale unit of the Florissant Formation. These beds yielded abundant palynomorphs (fungal spores, bryophyte and pteridophyte spores, gymnosperm and angiosperm pollen, and algal microfossils). The coin is about 2.5 cm in diameter.

FIGURE 4. Locality D7012, the trench excavated through the total thickness of the middle shale unit of the Florissant Formation and sampled in this study. In the foreground is geologist Ralph Root.
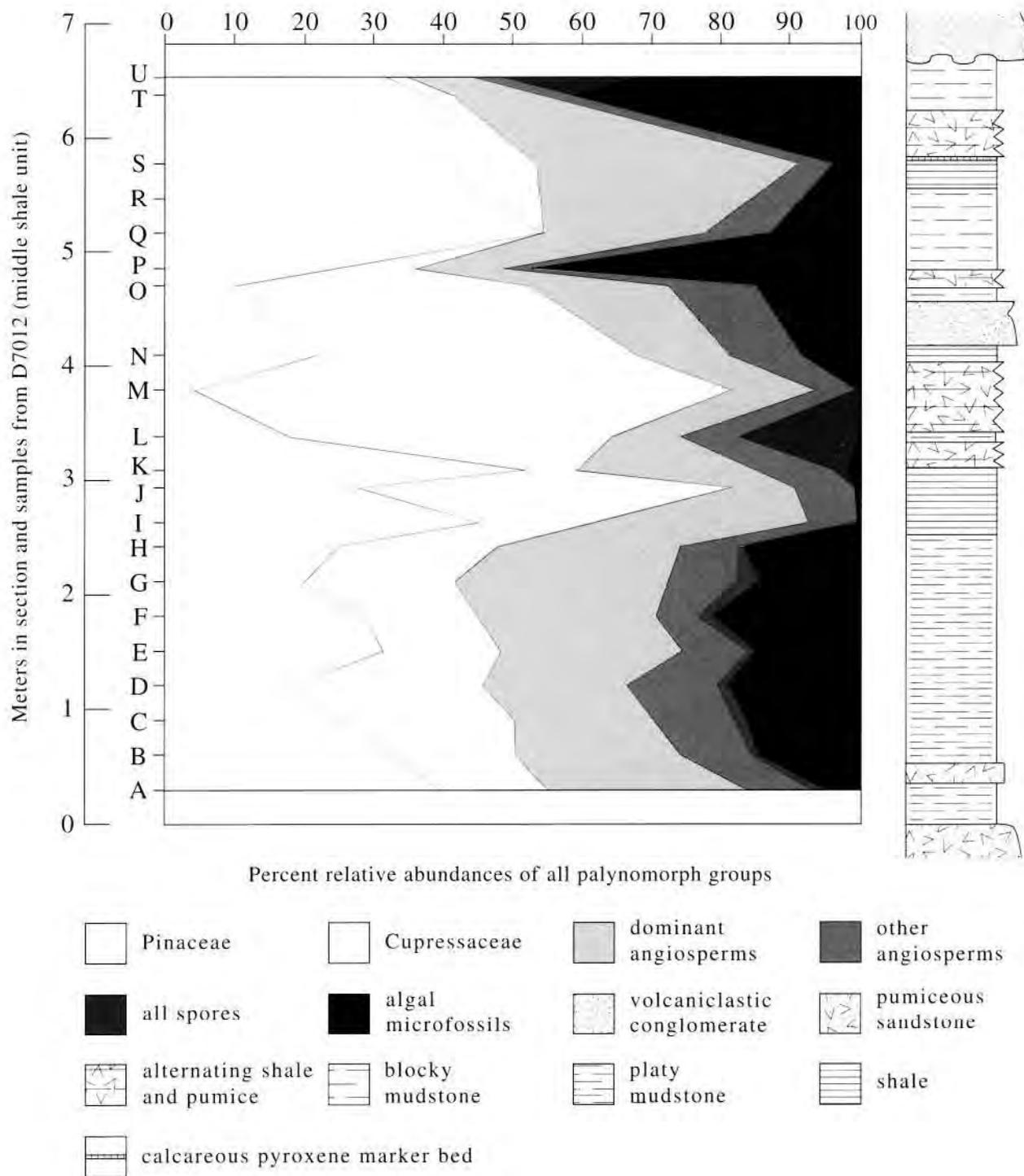
FIGURE 5. Diagram showing relative abundances of all major groups of palynomorphs in samples from the middle shale unit at locality D7012. Letters indicate stratigraphic levels at which samples were collected. Relative abundance data are based on counts of 200 specimens and include all palynomorph taxa present. The lithostratigraphic column is based on data and interpretations provided by Evanoff (pers commun., 1996).
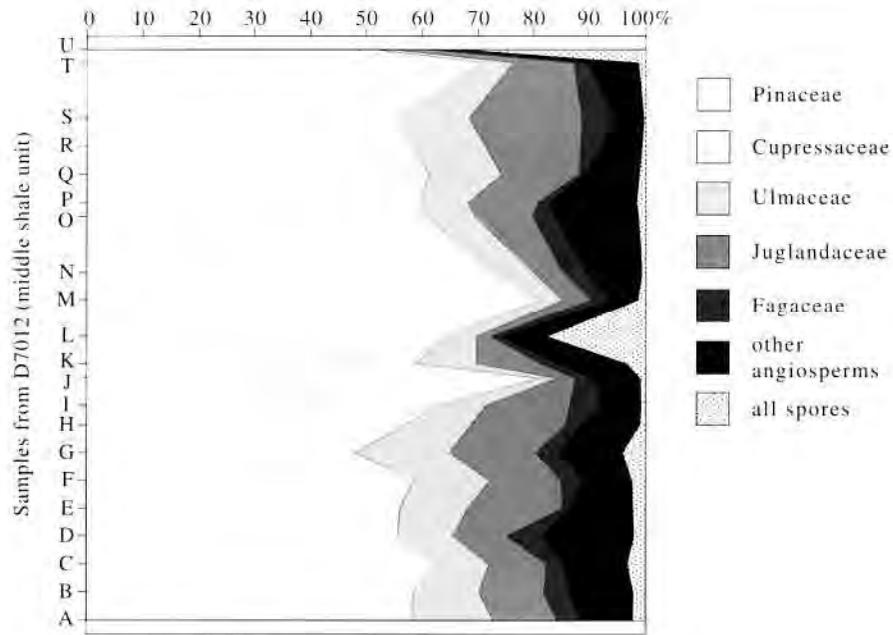
A. Percent relative abundances of land flora

Legend for A:
- Pinaceae
- Cupressaceae
- Ulmaceae
- Juglandaceae
- Fagaceae
- other angiosperms
- all spores
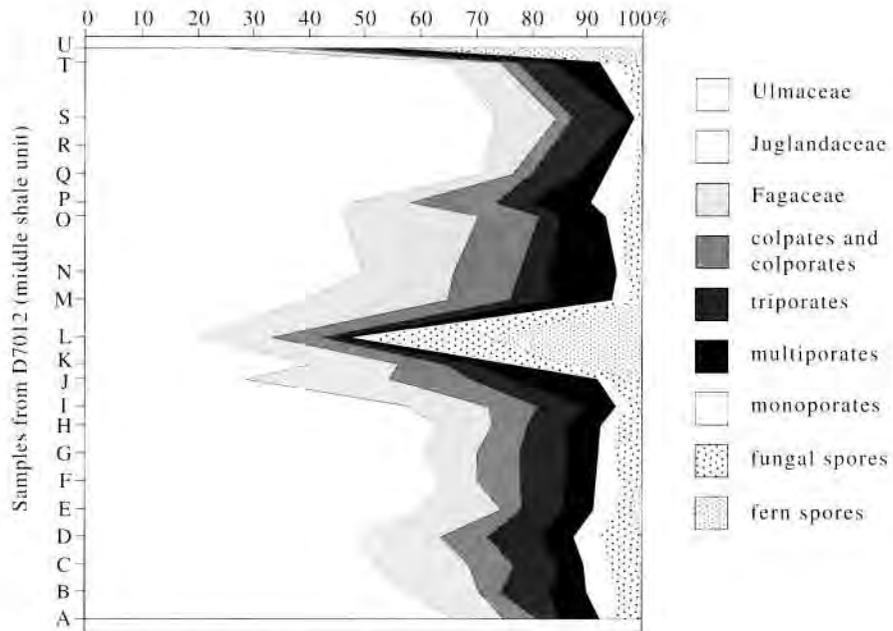
B. Percent relative abundances of angiosperms, ferns, and fungi

Legend for B:
- Ulmaceae
- Juglandaceae
- Fagaceae
- colpates and colporates
- triporates
- multiporates
- monoporates
- fungal spores
- fern spores

FIGURE 6. Diagrams showing relative abundances of selected groups of palynomorphs in samples from the middle shale unit at locality D7012. Letters indicate stratigraphic levels at which samples were collected. (A) Data for the "land flora" only, based on counts of 200 specimens exclusive of aquatic algae. (B) Data based on counts of 200 specimens exclusive of aquatic algae and the numerically dominant pollen of gymnosperms (Pinaceae and Cupressaceae), and thus emphasizing the relative abundances of angiosperms. Ulmaceae, Juglandaceae, and Fagaceae are modern families that include the most commonly occurring species of angiosperms; colpates and colporates, multiporates, and monoporates are morphological groups of angiosperm pollen having various botanical affinities.
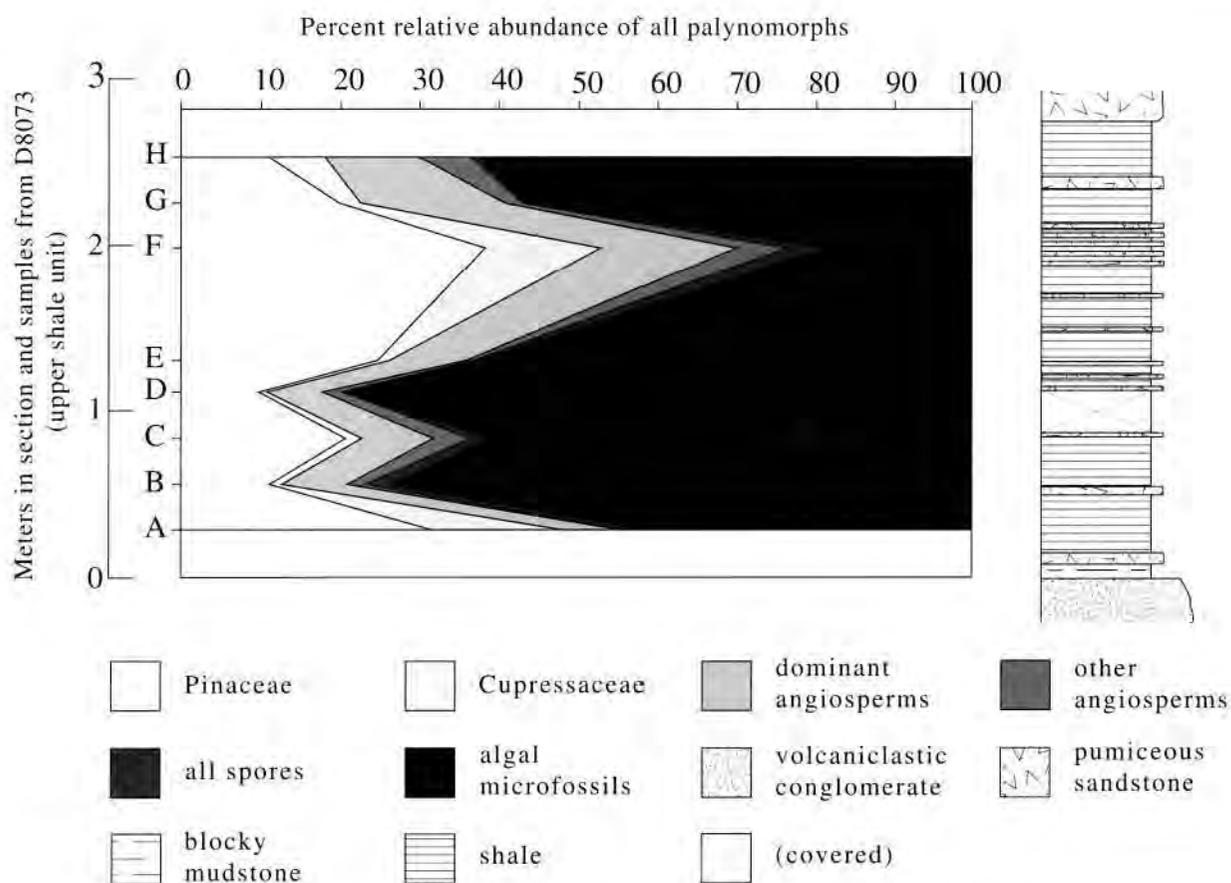
FIGURE 7. Diagram showing relative abundances of major groups of palynomorphs in samples from the upper shale unit at locality D8073. Letters indicate stratigraphic levels at which samples were collected. Relative abundance data are based on counts of 200 specimens and include all palynomorph taxa present. Assemblages from most stratigraphic levels are dominated by microfossils of aquatic algae. The lithostratigraphic column is based on data and interpretations provided by Evanoff (pers. commun., 1996).
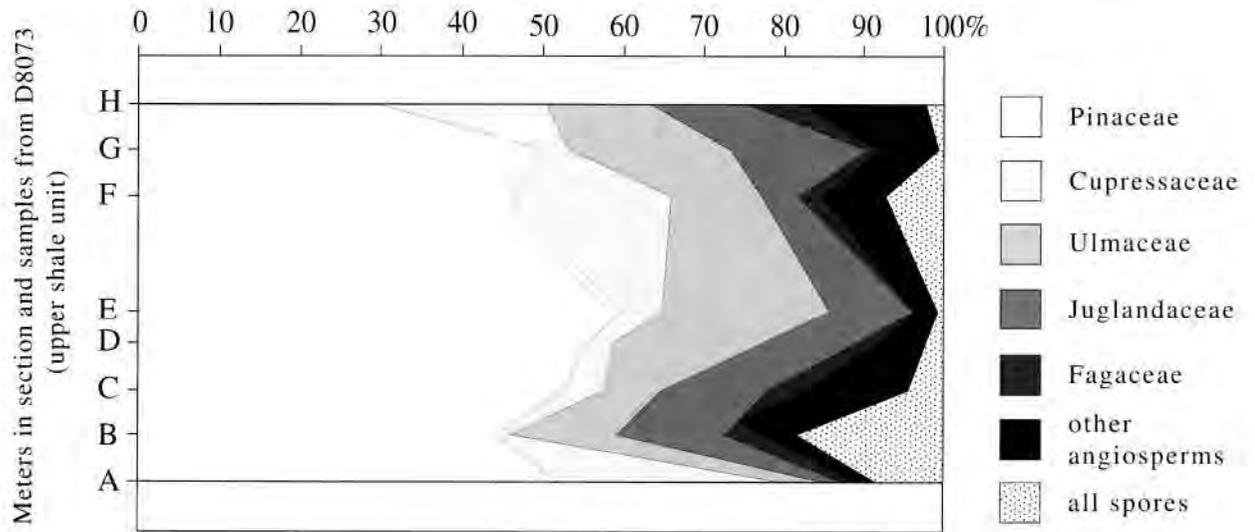
A. Percent relative abundance of land flora
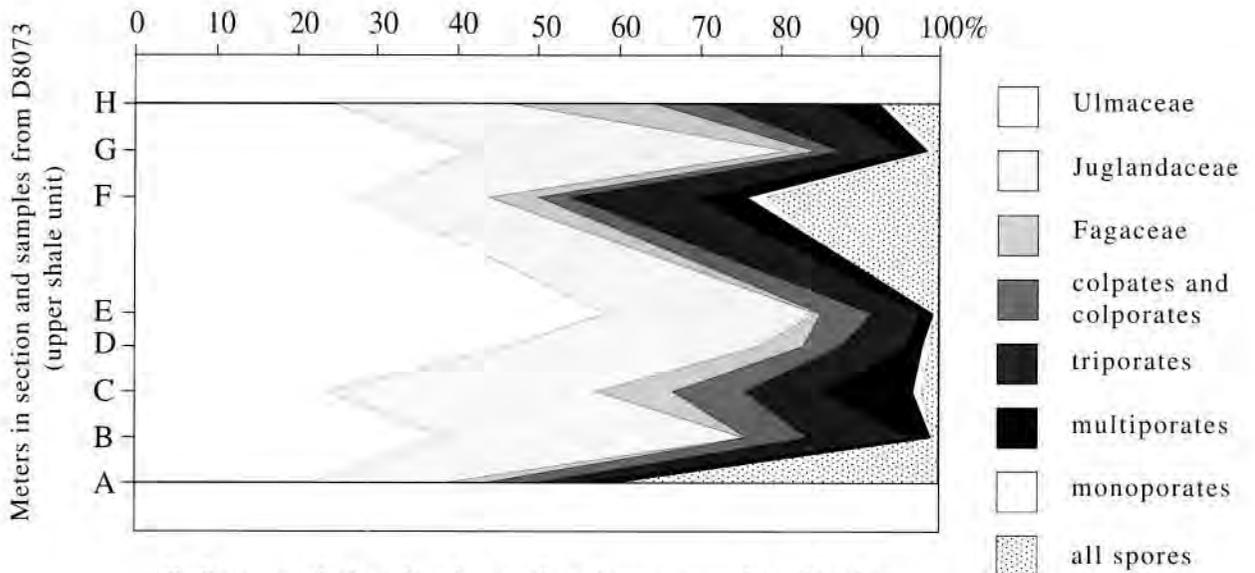
B. Percent relative abundance of angiosperms and pteridophytes

FIGURE 8. Diagrams showing relative abundances of selected groups of palynomorphs in samples from the upper shale unit at locality D8073. Letters indicate stratigraphic levels at which samples were collected. (A) Data for the "land flora" only, based on counts of 200 specimens exclusive of aquatic algae. The category "all spores" includes spores of ferns, fern allies, and fungi. (B) Data based on counts of 200 specimens of angiosperm pollen and pteridophyte spores only, excluding algae and pollen of numerically dominant gymnosperms. Compare with Figure 6B.

from stratigraphic palynology rather than neobotany. Determination of the taxonomic affinities of the spores and pollen is based primarily on their morphology; reference to the megafossil record for verification of identifications is a secondary approach. The objective of this study is to document the Florissant palynoflora, the foremost significance of which centers on its being a diverse, well-dated, latest Eocene assemblage.

Paleofloristics

The Megafossil Record

Plant megafossils offer a detailed, though incomplete, picture of the floristic composition of the vegetation at the time of deposition of the Florissant beds. Palynological and paleobotanical data supplement each other in revealing the nature of the ancient vegetation, but comparisons of microfossil floras with megafossil floras typically exhibit areas of both agreement and discrepancy. Much of this is the result of different factors affecting the fossilization process, particularly with regard to abundance of material and effects of transportation. An indication of the modern affinities of the Florissant flora (Table 1) summarizes some of these differences.

Manchester (2001) agrees with MacGinitie's conclusion that five taxa comprise about 60 percent of the megafossil assemblage, in terms of numbers of specimens. MacGinitie (1953) reported that the dicot angiosperm *Fagopsis longifolia* is the most abundant form (31.4 percent), *Chamaecyparis linguaefolia* is the most abundant conifer (7.5 percent), and there are moderately high abundances of Ulmaceae (approximately 10.9 percent), *Typha* (5.8 percent), and *Populus* (5 percent). Penny (1969) commented on the work of MacGinitie and reported that, in terms of numbers of species, six families are predominant in the megafossil flora and account for approximately 45 percent of the seed-plant species: Pinaceae, Rosaceae, "Leguminosae" (Fabaceae), Fagaceae, Sapindaceae, and Anacardiaceae. (As discussed later, only two of these families are among the most abundant on the basis of the plant microfossil record.) According to MacGinitie (1953), the most common ulmaceous megafossil is *Zelkova drymeja* (9.6 percent); Manchester (1987) reassigned this species to *Cedrelospermum lineatus*. The other ulmaceous species identified by MacGinitie—*Ulmus tenuinervis* and *Celtis mccoshii*—are less common (slightly more than 1.3 percent). Dominance of the flora by individual species is rather different on the basis of fossil pollen, however. Combining these data sets may provide

a more complete picture of the flora than is revealed by considering only one or the other. Certainly a comparison provides some constraints on interpretations.

Abundances of individual taxa are less significant in megafossil studies than in microfossil studies, and often such information is not presented in paleobotanical reports. MacGinitie (1953; Table 2) provided such data for Florissant megafossils, based on a count of 5356 specimens from four localities. Comparison of the percentage abundance values of MacGinitie with palynomorph relative abundances determined in the present study, which are based on a count of 12,162 specimens from two localities, reveals some significant differences. Many but not all of these differences are attributable to the differential production and preservation of megafossils and microfossils characteristic of different species of plants.

The most commonly occurring leaf fossil is *Fagopsis longifolia* (31.4 percent). Manchester and Crane (1983) determined that the pollen of this species is a small, subspherical, tricolporate form with small pores and characteristic quercoid sculpture. Such grains were noted in this study and were assigned to *Quercipollenites* sp. cf. pollen of *Fagopsis longifolia*. These constitute only a small portion of the total fagaceous pollen, which itself accounts for only 0.5 to 6.5 percent of the vascular plants represented in the palynoflora. *Chamaecyparis linguaefolia* (Cupressaceae), the most frequent conifer in the fossil leaf flora (7.5 percent), is not recognized at all in the palynoflora. Pollen grains assignable to the Cupressaceae occur throughout the section but have been assigned predominantly to *Taxodiaceaepollenites hiatus*, which probably represents fossil *Sequoia*. (Assignment of *Taxodiaceaepollenites hiatus* to the family Cupressaceae rather than to the Taxodiaceae, its more traditional placement in palynological studies, conforms with Manchester [2001], who incorporates the genera formerly included in the Taxodiaceae in the Cupressaceae.) *Taxodiacites* sp. cf. *T. verrucosus*, which occurs rarely, is very similar to pollen of extant *Juniperus*. *Populus*, present in the megaflora at about 5 percent according to MacGinitie, is not recognized in the palynoflora. Modern species of this genus, however, produce a simple, thin-walled, spheroidal pollen grain that degrades easily and is not readily fossilized. A fairly high relative abundance of Ulmaceae (approximately 11 percent) in the megaflora closely corresponds to a similarly high relative abundance of ulmaceous pollen in the total palynoflora: 2 to 14 percent in samples from successive stratigraphic levels and averaging 10.6 percent of the palynoflora excluding algae.

TABLE 1. Affinities of the Florissant flora with modern plant families as determined from the palynofloral (P) and megafloral (M) records.

Megafloral data are from Manchester (2001) and Wodehouse (1934). Angiosperm (Anthophyta) families are listed alphabetically. Spores and pollen described in this study whose affinities are undetermined are not included in this list; some questionable megafossil records that lack any supporting evidence from palynology are omitted as well. An "x" denotes presence; a question mark denotes questionable presence; a double "x" indicates that the family is among those having the greatest relative abundance of specimens in the flora; the asterisk signifies that the Aceraceae are included in the Sapindaceae in the megafloral records.

	P	M		P	M
CHLOROPHYTA			ANTHOPHYTA (cont'd)		
Botryococcaceae	x		Eleagnaceae	x	
Hydrodictyaceae	x		Ericaceae	x	
Zygnemataceae	x		Eucommiaceae	x	x
BRYOPHYTA			Fabaceae (Leguminosae)	x	x
Sphagnaceae	x		Fagaceae	xx	xx
LYCOPODOPHYTA			Grossulariaceae		x
Selaginellaceae	x		Hamamelidaceae	?	
PTEROPHYTA			Hydrangeaceae		x
Osmundaceae	x		Juglandaceae	xx	x
Polypodiaceae	x	x	Lauraceae		x
Salviniaceae	x		Liliaceae	x	?
Schizaeaceae	x		Malvaceae	x	
CONIFEROPHYTA			Meliaceae	?	x
Cupressaceae	xx	xx	Myrtaceae	?	?
Pinaceae	xx	x	Nymphaeaceae	x	
Taxaceae		x	Oleaceae	?	?
GNETOPHYTA			Onagraceae	x	x
Ephedraceae	x	x	Pandanaceae	?	
ANTHOPHYTA			Platanaceae	?	x
Aceraceae	x	*	Poaceae (Gramineae)	x	x
Adoxaceae		x	Polemoniaceae	x	
Alangiaceae	x		Polygonaceae	x	
Anacardiaceae		x	Potamogetonaceae		x
Apocynaceae		x	Proteaceae	?	
Araliaceae	?		Ranunculaceae	?	
Arecaceae (Palmae)	x	x	Rhamnaceae	?	?
Asteraceae (Compositae)	x		Rosaceae	?	x
Berberidaceae		x	Rutaceae		x
Betulaceae	x	x	Salicaceae	x	xx
Bombacaceae	x		Sapindaceae	x	x
Buxaceae	x		Sapotaceae	x	
Caprifoliaceae	x	x	Saxifragaceae		x
Cercidiphyllaceae	x		Simaroubaceae	?	x
Chenopodiaceae			Sterculiaceae	x	x
Convolvulaceae	?	x	Tiliaceae	x	?
Cyperaceae	x	x	Typhaceae/Sparganiaceae	x	xx
Dioscoreaceae		x	Ulmaceae	xx	xx

The Microfossil Record

Five families, as interpreted from pollen, account for 74 to 95 percent of the palynomorphs when algal palynomorphs are omitted: Pinaceae, Cupressaceae, Ulmaceae, Juglandaceae, and Fagaceae (Figs. 6A, 8A). Of the angiosperm pollen, the Ulmaceae and Juglandaceae are dominant and nearly equal in relative abundance in the middle shale unit (13.5–38 percent Ulmaceae, 8–35.5 percent Juglandaceae; see Fig. 6B), and dominant and subequal in relative abundance in the upper shale unit (22–58.5 percent Ulmaceae, 8–37 percent Juglandaceae; see Fig. 8B). *Caryapollenites* and *Momipites* are the dominant juglandaceous pollen genera; in fact, together they constitute 7.5 to 35.5 percent of angiosperm pollen in the Florissant palynoflora. *Carya*-type pollen is significantly more common than pollen assigned to other genera of the Juglandaceae. *Juglans*-type pollen is present in all productive samples, although it was not observed in the counts of a few levels. It reaches a maximum of 13.5 percent of the angiosperm pollen in sample D7012-A (middle shale unit). MacGinitie (1953) suggested that *Carya* is the only member of the Juglandaceae present in the leaf flora, and he considered specimens previously referred to *Juglans* to be clearly *Carya*. In contrast, Manchester (2001) recognizes both genera in the megaflora, and both genera are represented by pollen, as is a third fossil genus of the modern family. The Fagaceae (predominantly *Quercus*-like pollen) account for 0.5 to 6 percent of the total palynoflora (Figs. 5, 7) and 0.5 to 26.5 percent of the angiosperms (Figs. 6, 8). As mentioned, this is in strong contrast to the relative abundance of the fagaceous leaf species *Fagopsis longifolia*.

Comparisons

Based on our analysis of the palynoflora in comparison with the analysis of MacGinitie (1953) as modified by Manchester (2001), there are twelve families recognized in the megaflora that are not represented in the palynoflora (Table 1). Some of these families may be represented by pollen that cannot be assigned to a family with certainty; five families confidently recorded in the megaflora are questionably represented by pollen. In contrast, at least twenty-one (and possibly as many as twenty-six) families recognized in the palynoflora are not included in MacGinitie's original list of forty-seven families or the revised list of thirty-six families fully accepted by Manchester. Of these, three are chlorophyte algae and five are pteridophytes. The total of modern families recognized with

certainty on the basis of palynology is forty-three, and thirteen others are questioned. (In addition we describe and illustrate forty-six palynomorph taxa whose modern affinity is indeterminate or unknown; see Table 2.) Interestingly, five families that were reported by MacGinitie but are questioned or rejected by Manchester are possibly represented by pollen, and two others, Liliaceae and Tiliaceae, are recorded in the palynoflora with fairly high degrees of confidence. One family that is represented by rare specimens of pollen, the Asteraceae (Compositae), was tentatively reported by MacGinitie as *incertae sedis*, a category in which he included "species of somewhat doubtful taxonomic value, kept partly in the hope that the subsequent discovery of further material will clarify their taxonomic position" (1953:159). The palynological evidence from our study may constitute such additional material.

Paleoecology

Elevation

MacGinitie (1953:53) suggested that the Florissant flora represents temperate, upland vegetation growing at "probably not more than 3000 nor less than 1000 feet" (300–900 m) elevation, under subhumid conditions. Gregory and Chase (1992) took exception to MacGinitie's interpretation of the original elevation of the Florissant deposits. Using a foliar physiognomic method of interpreting the leaf fossils, they concluded that the Florissant flora grew at an elevation of 2500 m, which is essentially the elevation of the Florissant locality today. Meyer (1992) also cast doubt on MacGinitie's interpretation by reevaluating lapse rates and other variables that affect estimates of elevation from paleobotanical data. He concluded that the elevation of the Florissant area in latest Eocene time was 2450 m. These closely similar conclusions not only differ from MacGinitie's estimate but also have serious implications for the tectonic uplift and erosional history of the southern Rocky Mountains (see Epis and Chapin 1975). Unfortunately, palynological data can contribute little to this debate because pollen morphology is unaffected by climate or elevation and thus can provide no independent evidence beyond the affinities of the flora.

Habitats and Communities

MacGinitie (1953) interpreted the paleoecology of the Florissant deposits as an area of lakes or

TABLE 2. List of taxa in the Florissant palynoflora identified in this study.

Numbers in brackets are keyed to occurrence records in Table 3. Occurrence records of some taxa are composited in Table 3, as indicated by duplicated numbers in this list.

Algal and probable algal microfossils
- [18] *Botryococcus* sp. (Botryococceaceae)
- [19] *Pediastrum* sp. (Hydrodictyaceae)
- [31] *Ovoidites elongatus* (Hunger) Krutzsch 1959 (Zygnemataceae)
- [44] *Ovoidites ligneolus* Potonié ex Krutzsch 1959 (Zygnemataceae)
- [44] *Ovoidites* sp. (Zygnemataceae)
- [122] Algal spores, gen. & sp. indet.
- [107] *Catinipollis geiseltalensis* Krutzsch 1966

Pteridophyte spores: monolete
- [17] *Laevigatosporites ovatus* Wilson & Webster 1946 (Polypodiaceae)
- [116] *Polypodiisporonites afavus* (Krutzsch) Frederiksen 1980 (Polypodiaceae)
- [26] *Polypodiisporonites* sp. cf. *Polypodiidites secundus* (Potonié) Krutzsch 1963 (Polypodiaceae)

Bryophyte and pteridophyte spores: trilete
- [27] *Lygodiumsporites adriennis* (Potonié & Gelletich) Potonié, Thomson, & Thiergart ex Potonié 1956 (Schizaeaceae)
- [11] *Deltoidospora* sp.
- [69] *Baculatisporites* sp. A (Osmundaceae)
- [70] *Baculatisporites* sp. B (Osmundaceae)
- [73] *Biretisporites* sp.
- [101] *Polycingulatisporites* sp.
- [25] *Lusatisporis* sp. cf. *L. perinatus* Krutzsch et al. 1963 (Selaginellaceae)
- [114] *Heliosporites* sp.
- [96] *Foveotriletes* sp.
- [28] *Stereisporites* sp. (Sphagnaceae)
- [46] *Echinatisporis* sp.
- [52] Reticulate trilete, gen. & sp. indet.
- [83] Rugulate trilete, gen. & sp. indet.

Spore massulae
- [100] *Azolla cretacea* Stanley 1965 (Salviniaceae)

Gymnosperm pollen: bisaccate
- [1] ?*Abiespollenites* sp. (Pinaceae)
- [1] *Piceapollis* sp. (Pinaceae)
- [1] *Pristinuspollenites* sp. cf. *P. microsaccus* (Couper) B. D. Tschudy 1973
- [1] *Pityosporites* sp. A (Pinaceae)
- [1] *Pityosporites* sp. B (Pinaceae)
- [1] *Podocarpidites* sp.

Gymnosperm pollen: monosaccate
- [104] *Zonalapollenites* sp. (Pinaceae)

Gymnosperm pollen: inaperturate
- [2] *Taxodiaceaepollenites hiatus* (Potonié) Kremp ex Potonié 1958 (Cupressaceae)
- [76] cf. *Taxodiaceaepollenites* sp. A of Rouse 1977
- [2] *Taxodiacites* sp. cf. *T. verrucosus* Botscharnikova in Pokrovskaya & Stelmak 1960 (Cupressaceae)
- [2] *Sequoiapollenites* sp. cf. *S. rotundus* Krutzsch 1971 (Cupressaceae)

Gymnosperm pollen: polyplicate
- [20] *Ephedripites claricristatus* (Shakhmundes) Krutzsch 1970 (Ephedraceae)
- [20] *Ephedripites exignus* (Frederiksen 1980) nov. comb. (Ephedraceae)

Angiosperm pollen: monosulcate
- [103] *Arecipites* sp. cf. *A. pertusus* (Elsik) Nichols, Ames, & Traverse 1973 (Arecaceae)
- [118] *Liliacidites* sp. (Liliaceae)
- [90] ?*Nupharipollenites* sp. (Nymphaeaceae)

Angiosperm pollen: tricolpate, sculpture various
- [15] *Cupuliferoidaepollenites liblarensis* (Thomson in Potonié, Thomson, & Thiergart) Potonié 1960
- [106] *Fraxinoipollenites medius* Frederiksen 1973
- [22] *Salixipollenites* sp. A (Salicaceae)
- [22] *Salixipollenites* sp. B (Salicaceae)
- [14] *Salixipollenites* sp. C (Salicaceae?)
- [126] *Rousea araneosa* (Frederiksen) Frederiksen 1980
- [108] *Rousea* sp.
- [7] *Quercoidites microhenricii* (Potonié) Potonié 1960 (Fagaceae)
- [125] *Cercidiphyllites* sp. (Cercidiphyllaceae)
- [60] *Aceripollenites striatus* (Pflug) Thiele-Pfeiffer 1980 (Aceraceae)
- [71] *Aceripollenites* sp. (Aceraceae)
- [121] Tricolpate sp. A
- [94] Tricolpate sp. B (Platanaceae?)
- [82] Tricolpate sp. C (Ranunculaceae?)
- [117] Tricolpate sp. D (Convolvulaceae?)

Angiosperm pollen: tricolporate, psilate to scabrate
- [57] *Tricolpopollenites parmularius* (Potonié) Thomson & Pflug 1953 (Eucommiaceae)
- [55] *Siltaria* sp. cf. *S. scabriextima* Traverse 1955 (Anacardiaceae or Fagaceae)
- [39] *Siltaria* sp. cf. *S. pacata* (Pflug in Thomson & Pflug) Frederiksen 1980
- [37] *Rhamnacidites delicatus* Frederiksen in Frederiksen et al. 1983 (Rhamnaceae?)

Angiosperm pollen: tricolporate, reticulate
- [86] cf. *Araliaceoipollenites profundus* Frederiksen 1980
- [61] cf. *Araliaceoipollenites euphorii* (Potonié) Potonié 1960
- [98] cf. *Horniella brevicolpata* Frederiksen et al. 1983 (Tiliaceae)
- [79] *Horniella* sp. A
- [119] *Horniella* sp. B
- [56] *Margocolporites* sp. cf. *M. vanwijhei* Germeraad, Hopping, & Muller 1968 (Fabaceae)
- [16] *Rhoipites* sp. A
- [38] *Rhoipites* sp. B
- [23] *Rhoipites* sp. C
- [63] *Rhoipites* sp. D
- [95] *Rhoipites* sp. E (Tiliaceae?)
- [81] *Rhoipites* sp. F
- [36] Tricolporate sp. A (Fabaceae)

(continues)

(Table 2 continued)

[45] Tricolporate sp. B
[88] Tricolporate sp. C

Angiosperm pollen: tricolporate, striate
[67] *Ailanthipites berryi* Wodehouse 1933
[68] *Ailanthipites* sp. A
[84] *Ailanthipites* sp. B
[66] *Alangiopollis* sp. (Alangiaceae)
[87] Tricolporate sp. D (Rosaceae?)
[40] cf. Tricolporate sp. D
[123] Tricolporate sp. E

Angiosperm pollen: tricolporate, verrucate
[6] *?Quercipollenites* sp. cf. pollen of *Fagopsis longifolia* (Lesq.) Hollick (Fagaceae)
[89] *Verrutricolporites* sp. A
[97] *Verrutricolporites* sp. B
[59] *Slowakipollis hippophaëoides* Krutzsch 1962 (Eleagnaceae)

Angiosperm pollen: tricolporate, echinate
[127] Asteraceae pollen sp. A (Asteraceae)

Angiosperm pollen: tetracolporate
[42] *Tetracolporopollenites brevis* Frederiksen 1980 (Sapotaceae)
[80] *Tetracolporopollenites* sp. (Sapotaceae)
[115] *?Meliapollis* sp. (Meliaceae or Sapotaceae)

Angiosperm pollen: syncolporate
[10] *Boehlensipollis* sp. cf. *B. granulata* Frederiksen et al. 1983 (Eleagnaceae or Sapindaceae)
[65] *Myrtaceidites parvus* Cookson & Pike 1954 (Myrtaceae?)
[47] *Cupanieidites* sp. A (Sapindaceae or Myrtaceae)
[62] *Cupanieidites* sp. B (Sapindaceae)

Angiosperm pollen: tribrevicolporate
[32] *Bombacacidites* sp. aff. *B. reticulatus* Krutzsch 1961 sensu Frederiksen 1988 (Sterculiaceae)
[41] *Bombacacidites* sp. cf. *B. nanobrochatus* Frederiksen et al. 1983 sensu Frederiksen 1988 (Sterculiaceae)
[35] *Bombacacidites* sp. A (Bombacaceae)
[51] *Bombacacidites* sp. B (Sterculiaceae)
[124] *Lonicerapollis* sp. A (Caprifoliaceae or Symplocaceae)
[113] *Lonicerapollis* sp. B (Caprifoliaceae)
[102] *Lonicerapollis* sp. C (Caprifoliaceae)
[48] *Intratriporopollenites* sp. cf. *I. instructus* (Potonié) Thomson & Pflug 1953 (Tiliaceae)

Angiosperm pollen: triporate
[4] *Caryapollenites veripites* (Wilson & Webster) Nichols & Ott 1978 (Juglandaceae)
[99] *Corsinipollenites oculus-noctis parvus* (Doktorowicz-Hrebnicka) Krutzsch 1968 (Onagraceae)
[74] *Corsinipollenites parviangulus* Frederiksen et al. 1983 (Onagraceae)
[53] *Cricotriporites intrastructurus* (Krutzsch & Vanhoorne) nov. comb. (Ulmaceae)
[105] *?Cricotriporites* sp.
[21] *Momipites coryloides* Wodehouse 1933 (Juglandaceae)
[113] *Momipites microfoveolatus* (Stanley) Nichols 1973 (Juglandaceae)

[21] *Momipites triradiatus* Nichols 1973 (Juglandaceae)
[21] *Momipites ventifluminis* Nichols & Ott 1978 (Juglandaceae)
[8] *Triatriopollenites subtriangulus* (Stanley) Frederiksen 1979 (Myricaceae or Betulaceae)
[93] *Nudopollis* sp.
[91] *Trivestibulopollenites betuloides* Pflug in Thomson & Pflug 1953 (Betulaceae)
[43] Triporate sp. A
[85] Triporate sp. B
[109] Triporate sp. C

Angiosperm pollen: zonoporate
[120] *Alnipollenites verus* Potonié ex Potonié 1931 (Betulaceae)
[54] *Reevesiapollis triangulus* (Mamczar) Krutzsch 1970
[112] *?Reevesiapollis* sp.
[3] *Ulmipollenites undulosus* Wolff 1934 (Ulmaceae)
[24] Zonoporate sp. A
[24] Zonoporate sp. B
[72] Zonoporate sp. C (Polemoniaceae?)

Angiosperm pollen: pantoporate, psilate
[5] *Juglanspollenites nigripites* (Wodehouse) nov. comb. (Juglandaceae)
[12] *Chenopodipollis* sp. (Chenopodiaceae or Amaranthaceae)

Angiosperm pollen: pantoporate, reticulate
[30] *Erdtmanipollis procumbentiformis* (Samoilovitch in Samoilovitch & Mtchedlishvili) Krutzsch 1966 (Buxaceae)
[92] *Persicarioipollis* sp. cf. *P. welzowense* Krutzsch 1962 (Polygonaceae)
[75] *?Persicarioipollis* sp. A (Polygonaceae?)
[34] *?Persicarioipollis* sp. B (Polygonaceae?)

Angiosperm pollen: pantoporate, echinate
[78] *Malvacipollis* sp. A (Malvaceae)
[77] *Malvacipollis* sp. B (Malvaceae)
[128] *Malvacipollis* sp. C (Malvaceae)
[58] *Malvacipollis* sp. D (Malvaceae)
[110] *?Periporopollenites* sp. cf. *P. stigmosus* (Potonié) Pflug & Thomson in Thomson & Pflug 1953 (Hamamelidaceae or Polemoniaceae)

Angiosperm pollen: monoporate
[64] *Cyperaceaepollis* sp. cf. *C. neogenicus* Krutzsch 1970 (Cyperaceae)
[49] *Graminidites crassiglobosus* (Trevisan) Krutzsch 1970 (Poaceae)
[50] *?Pandaniidites* sp. (Pandanaceae?)
[9] *Sparganiaceaepollenites sparganioides* (Meyer) Krutzsch 1970 (Sparganiaceae or Typhaceae)

Angiosperm pollen: diporate
[111] Diporate pollen cf. *Trema* Lour. (Ulmaceae?)

Angiosperm pollen: tetrad
[33] *Ericipites* sp. cf. *E. longisulcatus* Wodehouse 1933 (Ericaceae)

Angiosperm pollen: genus and species indeterminate
[29] *?Triporate* sp. cf. *?Ruellia laxa* (Frederiksen) Frederiksen et al. 1983 (Proteaceae?)

ponds bordered by stands of *Sequoia*, with understory shrubs and small trees. The leaf flora is mostly characterized by riparian vegetation, particularly *Fagopsis*, and to a lesser extent, *Cedrelospermum* (*Zelkova* of MacGinitie) and *Chamaecyparis*. MacGinitie offered the opinion that "fossil floras, almost without exception, are streamside or lakeside floras, with selection in favor of the woody plants bearing resistant leaves and winged fruits. Fossil floras have a deceptively mesic character" (1953:43–45). Several species were interpreted as representing riparian border transitions between streamside and higher ground and were likened to elements of the shrubby flora of modern chaparral associations found from eastern Nebraska south to Mexico. In a paleoecological sense, the Florissant palynoflora agrees quite well with MacGinitie's interpretation of the megafossil flora; differences that are evident provide some further insights.

The patterns of abundance of pollen of the Ulmaceae, Juglandaceae, and Fagaceae likely reflect riparian and nearshore vegetation growing in close proximity to the lacustrine site of deposition of the middle shale and upper shale units. Several other families suggestive of riparian and nearshore vegetation are represented by low abundances of pollen: Salicaceae, Aceraceae, Rosaceae, Sapindaceae, Betulaceae (primarily *Carpinus*-like pollen), Tiliaceae, Eucommiaceae, and ?Hamamelidaceae. The aggregate angiosperm pollen counts, excluding the dominant families Ulmaceae, Juglandaceae, and Fagaceae, range from 5 to 13 percent of the palynoflora in samples from successive stratigraphic levels (Figs. 5, 7). With algae omitted, the range is from 5 to 17 percent (Figs. 6A, 8A). Low abundances of pollen of predominantly herbaceous families were noted. Most common among these are grains assigned to the Chenopodiaceae or Amaranthaceae (up to 4 percent; see multiporates in Figs. 6B, 8B) and the Typhaceae or Sparganiaceae (monads, up to 3 percent; see monoporates in Figs. 6B, 8B).

Various aquatic habitats are suggested by algae, water ferns, and aquatic or semiaquatic angiosperms. The algal forms are assigned to *Pediastrum*, *Botryococcus*, *Ovoidites*, and a category of small spheroidal algal cysts of unknown affinity. *Pediastrum* and *Botryococcus* attain relatively high abundances in various levels within the middle shale unit; in the upper shale unit, *Pediastrum* ranges from absent to 20 percent; *Botryococcus* ranges from absent to 2 percent; *Ovoidites* was not observed in any of the samples. (Abundances of all algal palynomorphs are composited in Figs. 5, 7, but individual taxa are distinguished in Table 3.) *Pediastrum* and *Botryococcus* suggest a lacustrine facies deposited in fresh to slightly brackish

water. *Ovoidites* is believed to be derived from the green alga *Spirogyra*, which indicates the presence of freshwater and is suggestive of marshy conditions. MacGinitie (1953) reported a possible megafossil of *Nitella* (Charophyceae), which is a calcareous alga that grows attached to lake and pond bottoms, often in somewhat acidic water, but *Nitella* does not have a fossil record among palynomorphs. *Azolla* is a free-floating fern found in slow-moving freshwater; fragmentary remains of spores of *Azolla* were observed in two levels within the middle shale. MacGinitie (1953) noted that the ubiquity of *Typha* (corresponding to extant *T. latifolia*) indicated the prevalence of wet soil or extensive, marshy, shallow ponds and lakes; pollen attributable to either the Typhaceae or Sparganiaceae (*Sparganiaceaepollenites*) occurs throughout the middle shale and is also present in the upper shale (see Table 3). Manchester (2001) verified the presence of *Potamogeton*, an aquatic angiosperm common in freshwater lakes of glaciated regions, in the megaflora, but we do not recognize *Potamogeton* in the palynoflora.

MacGinitie (1953:22) reported a deposit of gypsum within the lake sediments, which he interpreted as indicating that the ponds or lakes were rather saline (and subject to desiccation), speculating that this would account for "the entire absence of any fossils of the Nymphaeaceae or Hydrocaryaceae." Although rare, pollen of the Nymphaeaceae (*Nupharipollenites*) is present in the middle shale, and the presence of Nymphaeaceae pollen indicates open freshwater during the deposition of the lake beds. Furthermore, Evanoff (1994) found the "gypsum" layer described by MacGinitie to be fibrous calcite, which negates MacGinitie's interpretation of lake chemistry—and history—as based on the supposed presence of this mineral.

Several of the families represented by pollen but not megafossils are suggestive of dry habitats and probably represent vegetative zones some distance from the lacustrine depositional site. These include Chenopodiaceae (or Amaranthaceae), Malvaceae, Eleagnaceae, and Asteraceae, plus possibly Selaginellaceae, Osmundaceae, and Schizaeaceae. Dry habitats are suggested also by pollen of the Onagraceae and Ephedraceae, families that do have megafossil records in the Florissant flora. Pollen of the Ephedraceae (*Ephedripites*) occurs consistently throughout both the middle and upper shale units (see Table 3).

The relative abundance plots of the palynologic assemblages are indicative of the strong influence of both wind and water transport on the composition of the palynoflora. When algae and fungi are omitted, gymnosperms account for 46.5 to more than 80 percent

TABLE 3. Occurrences of palynomorph taxa in samples of the middle and upper shale units of the Florissant Formation. Taxon numbers are keyed to the list of taxa in Table 2.

| Sample (middle shale unit) | | | | | | | | | | | | | | | | | | | | | Sample (upper shale unit) | | | | | | | | Taxon |
A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	A	B	C	D	E	F	G	H	
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	1
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	2
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	3
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	4
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	5
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x			x		x	x	x	?	6
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x		x	x	x	x	7
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	8
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	?		x	?		9
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x		x	x	x	10
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x					x		11
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	12
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x				x		13
x	x	x	x	x	x	x	x	x		x		x	x					x	x	x								x	14
x	x	x	x	x	x	x	x	x		x	x	x	x	x	x			?	x	x	x	x	x	x	x	x	x	x	15
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			?		x									16
x	x	x	x	x	x	x	x	x	x	x	x	x	x					x	x	x	x	x				x		x	17
x	x	x	x	x	x	x	x	x	x					x			x	x	x	x	x	x	x	x	x	x	x	x	18
x	x	x	x	x	x	x	x	x		x		x			x			x	x	x	x	x	x	x	x	x	x	x	19
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x	x		x		x			x	x	x	20
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	?		x	x		?		x						21
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x	x		?	?	?		?	?	x		22
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x				x	x			x	x						23
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	?				x	x	x	x	x	x	x	24
x	x	x	x	x	x	x	x	x	x	x	x	x					x	x											25
x	x	x	x	x	x	x	x	x	x	x	x	x				x		x			x					x			26
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x	x	x		x	x	x	x			x	x	27
x	x	x	x	x	x	x	x	x	x	x	x	x		x			x												28
x			x	x	x	x	x	x			x	x	x	x	x		x	x			x					x			29
x	x	x				x				x									x		x	x	x	x			x	x	30
x		x		x	x	x	x						?						x		x					x			31
x	x	x	x		x	x	x	x	x	x	x	x			x	x		x									x		32
x	x	x	x	x	x	x	x	x	x	x	x			x	x	x	x	x			?							x	33
x		x	x	x	x	x	x	x	x				x	x		?		x											34
x		x	x	x	x	x	x	x				x		x	x														35
x	x	x	x	x	x	x	x	x					x	x		x													36
?	x	x	x	x	x	x	x	x						x							?						x		37
x	x	x	x	x	x	x	x	x			x	x	x																38
x	x	x	x	x	x	x	x		x		x		x																39
x		x		x	x		x	x			x			x															40
x	x	x		x			x			x			x														x	x	41
x	x	x	x			x	x		x																				42
x	x	x	x	x		x		x																					43
x	x	x			x	x															x								44
x			x		x																								45
x	x	x	x																								?		46
x	x		x																										47
x																													48

(continues)

(Table 3 continued)

| Sample (middle shale unit) | | | | | | | | | | | | | | | | | | | | | Sample (upper shale unit) | | | | | | | | Taxon |
A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	A	B	C	D	E	F	G	H	
x	x	x	x	x	x	x		x	x	x		x	x	x	x	x	x		x	x						x	x		49
x			x	x	x	x			x			x		x			x	x	x	x									50
x			x	x	x	x					x	x			x					x	x				x		x		51
x	x			x	x	x		x												x	x					x		x	52
x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x		x	x		x		x	x	x	x	x	53
x		x		x		x					x	x	x				x											x	54
x		x	x	x	x	x	x	x			x	x		x				x										?	55
?			x	x	x	x	x		x	x		x	x	x				x										x	56
x	x		x	x	x	x	x	x	x	x		x	x	x	x			x	x		x	x	x	x	x	x	x	x	57
x				x				x				x						x											58
x	x	x	x	x	x	x	x				x	x	x	x															59
x	x	x	x	x	x	x	x				x	x	x																60
x				x		x					x	x	x								x								61
x												x																	62
x	x			x		x					x																		63
x											x													?						64
x		x	x			x	x	x													x		x					x	65
x	x	x	x			x	x	x																					66
?			x				x																						67
x	x				x						x																		68
x	x				x																							x	69
x			x																										70
x		x																											71
x	?																												72
		x	x	x	x	x		x	x			x					x				x	x	x	x		x		x	73
		x	x	x	x	x	x							x	x		x					x	x			?	?		74
		x		x	x	x	x	x	x			x		x			x									x			75
		x	x	x	x	x	x				x	x	x				x				x								76
		x		x	x	x								x	x														77
		x			x	x			x								x												78
		x															x												79
		x	x	x	x	x	x	x			x	x	x	x	x														80
		x	x			x			x	x	x	x	x		x						x								81
		x		x					x	?				x															82
		x	x	x	x				x		x		x													?			83
		x										x	x																84
		x											x																85
		x							x			x	x															?	86
		x		x								x																	87
		x	x	x					x			x																	88
		x							x				x																89
		x		?					x																				90
		x																						?					91
		x																											92
			x		x	x	x	x									x												93
			x			x								x									x						94
			x	x		x					x		x													x			95
			x		x	x			x		x										x							x	96
			x		x			x																					97
			x																										98
			x	x		x												x			x								99

(Table 3 continued)

| Sample (middle shale unit) | | | | | | | | | | | | | | | | | | | | | Sample (upper shale unit) | | | | | | | | Taxon |
A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	A	B	C	D	E	F	G	H	
				x	x																								100
				x	x																								101
				x											x														102
					x	x	x		x			x																	103
					x	x	x	x								x													104
						x	x	x	x	x	x	x	x	x				x	?		x		x	x	x	x	x	x	105
						x	x	x	x			x	x		x													x	106
						x	x			x	x				x											x			107
							x	x				x			x			x											108
							x						x	x				x											109
							x	x	x			x	x	x															110
							x	x																					111
								x											x										112
								x																					113
									x		x		x																114
									x				x																115
											x								x		x							x	116
											x		x																117
											x																		118
												x	x																119
													x																120
												x	x	x														x	121
												x	x	x		x	x	x			x	x	x	x	x	x	x	x	122
													x																123
													x																124
													x																125
																x													126
																x													127
																		x											128

of the palynoflora (see Figs. 6A, 8A; fungi are omitted in Figs. 6B, 8B). Both bisaccate pollen of the Pinaceae (predominantly *Pinus*-type, with much less *Abies* and *Picea*) and the nonsaccate *Taxodiaceaepollenites hiatus* (Cupressaceae) occur in great numbers in various levels of the sampled intervals of both shale units. The Cupressaceae generally exceed the Pinaceae in the middle one-third of the middle shale, whereas the reverse is true of the lower and upper thirds of that unit (Fig. 6A). The Pinaceae greatly exceed the Cupressaceae throughout the upper shale, except the uppermost level, where the difference is only moderate (Fig. 8A). There is a strong likelihood that this cupressaceous pollen represents shoreline stands of *Sequoia*. The Pinaceae, on the other hand, probably represent montane forests more removed from the depositional site, including the higher mountain slopes. Pine pollen characteristically is transported by wind far from the trees that produce it and similarly would tend to be transported by water downslope to the site of deposition. Some rarely occurring pollen types also may have been transported to the site of deposition and may not represent plants that were growing in the immediate area.

Effects of Volcanic Activity

An important conclusion of this study is that there is little or no evidence of mass destruction of vegetation, followed by periods of ecologic succession of plant communities, during most of the main phase of lacustrine deposition of the Florissant Formation (the middle shale unit), despite periodic influxes of volcanic ash. There is a gradual introduction of new palynological species throughout the middle shale, and there are only minor disappearances of taxa that might reflect extinctions, extirpations, or dispersals. Although evidence from this study indicates that repetitive, small-scale eruptive events marked by minor ashfalls did not appreciably affect the composition of vegetation of the area, it does indicate that major volcanic events caused significant changes in local and regional vegetation.

Primary evidence of a significant change in regional vegetation is the reversal in dominance of pollen of Pinaceae versus pollen of Cupressaceae in the middle third of the middle shale, a shift that coincides with a major, sustained volcanic eruption (see Fig. 9). Initiation of the strong shift in relative abundances of the dominant kinds of pollen coincides with the introduction of abundant pumice in the lake beds, which signaled the onset of a major and sustained eruptive event in the

Thirtynine Mile volcanic field or perhaps other volcanically active areas nearby. A pumiceous conglomerate unit about 1 m higher in the section marks the culmination of that event. The volcanic event evidently disrupted the regional vegetation, causing a temporary change in dominance of certain plants in the area. That forest trees were affected is shown by reversals in abundances of gymnosperm pollen. The decrease in Pinaceae pollen relative to Cupressaceae pollen suggests that pines growing on slopes were reduced in number relative to *Sequoia* trees growing nearer to Lake Florissant. The pumice-rich interval is marked also by an excursion in abundance of fern spores, suggesting that ferns temporarily increased in abundance in the understory, relative to flowering plants. Spicer et al. (1985) found that ferns were the first plants to recolonize the landscape devastated by pyroclastic surges and air-fall ash deposition following the eruption of El Chichón volcano in Mexico. The increase in abundance of fern spores in the Florissant deposits may be indicative of a similar effect. In lacustrine beds of the middle shale unit above the pumiceous conglomerate, relative abundances of gymnosperm pollen return to the levels attained in the lower part of the middle shale interval, and fern spores return to their former low abundances as pollen of angiosperms increases again, evidently reflecting reestablishment of plant communities.

Subsequent major volcanic eruptions also affected Lake Florissant and vicinity. The volcaniclastic conglomerate composing the caprock unit is a lahar deposit that temporarily overwhelmed the lake. Such an eruptive event presumably would have had a destructive effect on vegetation of the area, and there is some palynologic evidence that it did. Lacustrine deposition resumed after the emplacement of the lahar, as represented by the deposits of the upper shale unit. Although the numerically dominant palynomorph species are the same in the lacustrine depositional intervals below and above the caprock congomerate, in the upper shale unit there is a significant reduction of the total number of taxa. This reduction in species diversity is coincident with a significant reduction in fossil yield per unit volume of sediment. Reduced recovery of palynomorphs from the lacustrine beds of the upper shale unit may reflect floristic changes that were a consequence of the caprock conglomerate depositional event. Pollen of Pinaceae is dominant among palynomorphs of the land flora throughout the upper shale, and no reversal in the relative abundance of pollen of Cupressaceae took place that would correspond to the pattern described for the middle shale, perhaps because the caprock event was
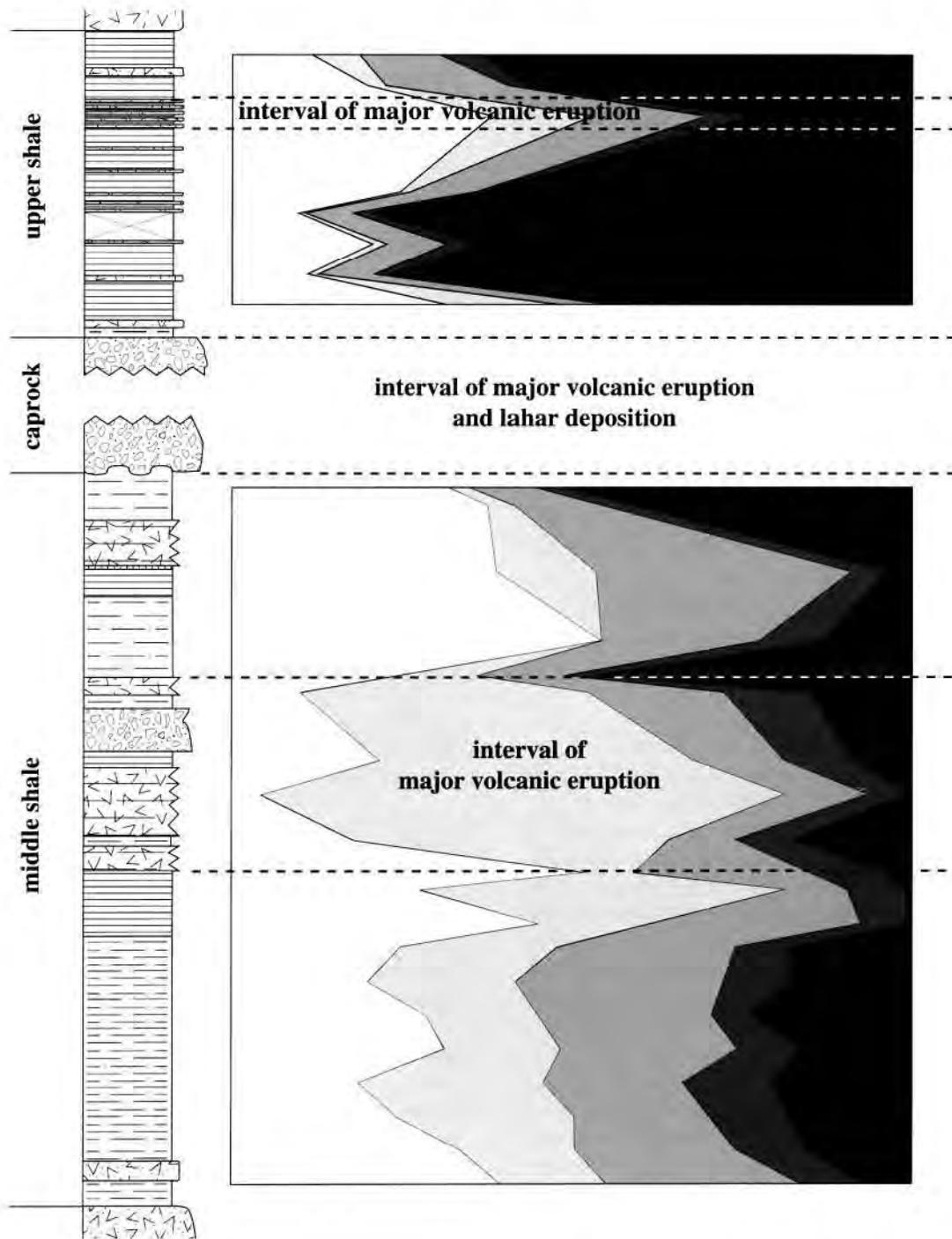
FIGURE 9. Diagram comparing the lithostratigraphic sections at localities D7012 and D8073 and fluctuations in relative abundances of major groups of palynomorphs in samples from the middle and upper shale units of the Florissant Formation (same lithologic and palynologic data as in Figs. 5, 7; patterns and shading are the same as those in keys to Figs. 5, 7). Reversals in dominance of pollen of Pinaceae versus pollen of Cupressaceae, an abrupt increase in abundance of spores, and strong changes in abundance of algal microfossils were coincident with major influxes of pumice and other volcaniclastic debris into Lake Florissant, suggesting that sustained eruptive events affected the flora of the Florissant region.

brief, if violent. Interestingly, algal palynomorphs are conspicuously more common in the upper shale than they are in the middle shale, suggesting that a change in lake chemistry took place, possibly as a consequence of the caprock event. Finally, pumice beds near the top of the upper shale unit mark yet another major eruptive event that is correlated with a striking but temporary reduction in the abundance of algal microfossils (Fig. 9).

Florissant Palynoflora

Species of palynomorphs identified from samples analyzed in this study are discussed in this section. Taxa are grouped as algal microfossils, spores, pollen of gymnosperms, and pollen of angiosperms, and then subdivided within each of those major categories according to their morphology. Table 2 is a summary list of taxa so classified. Discussions of each taxon are brief and are limited to essential comments on morphology and comparisons with similar species. Nomenclatural synonymies and records of occurrence elsewhere have been omitted because of space limitations. Records of occurrence of the taxa in our samples are summarized in Table 3; taxon names are keyed to the numbers listed in Table 2. Especially noteworthy occurrence data are mentioned under Remarks.

Although botanical affinities are noted for many species discussed, all species are assigned to form genera; names of modern taxa are not used (*Botryococcus*, *Pediastrum*, and *Arolla* are exceptions). This practice is in keeping with our view that the Florissant palynoflora represents a uniquely well-preserved and well-dated assemblage of value to Tertiary palynostratigraphy. The use of nomenclature widely applied in other palynostratigraphic studies thus will enhance the utility of these records in future applications.

Algal and Probable Algal Microfossils

Genus *Botryococcus* Kützing 1849

Botryococcus sp.

PLATE 1, FIGURE 1

Description: Spherical to ellipsoidal/colonial aggregates of small cuticular cups, often arranged in a radial pattern. Fragments of colonies range from 23.5 µm to 115 µm.

Remarks: *Botryococcus* belongs to the Chlorophyta (Chlorococcales, Chlorococcaceae) and has a very long geologic history extending back to the Precambrian. It was widespread in the Tertiary. Extant *Botryococcus* is

tolerant of a wide variety of conditions, such as a range of pH 4.5 to 8, and it may thus be abundant where conditions do not allow other algae to grow. Thick, oily, gelatinous, and highly decay-resistant algal deposits of *Botryococcus* may accumulate on lake bottoms, sometimes forming boghead coals (Tappan 1980). *Botryococcus* sp. is present in nearly all samples of the middle shale unit and in all samples of the upper shale unit.

Genus *Pediastrum* Meyen 1829

Pediastrum sp.

PLATE 1, FIGURE 2

Description: Coenobia of flat, platelike cells, with the peripheral cells differing from the interior ones in having one or two blunt projections. Maximum diameter of the coenobia, including projections, ranges from 53 µm to 96.5 µm.

Remarks: Extant species of *Pediastrum* tolerate a broad range of aquatic ecological conditions: temperatures from zero to 34 °C, pH from 4.9 to 9.8, and both eutrophic and oligotrophic water (Greeson 1982). The genus belongs to the Chlorophyta (Chlorococcales, Hydrodictyaceae) and includes both fluviatile and lacustrine plankton. It ranges from the Lower Cretaceous to the Holocene and is widespread geographically (Tappan 1980). *Pediastrum* sp. occurs in nearly all samples of the middle shale unit and in all samples of the upper shale unit.

Genus *Ovoidites* (Potonié) Krutzsch 1959

Ovoidites elongatus (Hunger) Krutzsch 1959

PLATE 1, FIGURE 3

Description: Spores elongate ovoid with a longitudinal line of dehiscence along the maximum dimension. The wall appears psilate in transmitted light and is 1 to 1.5 µm thick. Length 60 to 89 µm; width 25.5 to 43 µm.

Remarks: Much confusion exists over the taxonomic status of *Ovoidites* (see Rich et al. 1982). Forms appearing to be equivalent to *Ovoidites elongatus* and other species of *Ovoidites* were assigned to the genus *Schizosporis* by Cookson and Dettmann (1959), to *Ovoidites* by Krutzsch (1959), and to *Schizophacus* by Pierce (1976). We regard these genera as synonymous, and *Ovoidites* has priority.

Most Florissant specimens are identified as *Ovoidites elongatus* (Hunger) Krutzsch 1959. *Ovoidites elongatus* Nakoman 1966 is a homonym; the Florissant specimens are not this species. *Ovoidites* has been shown to have affinity with the green alga *Spirogyra* (Oedogoniales, Zygnemataceae) in several papers by Dutch workers (van Geel 1976, 1978; van Geel and van der Hammen 1978; Pals et al. 1980; van Geel et al. 1981).

Ovoidites ligneolus
Potonié ex Krutzsch 1959

PLATE 1, FIGURE 4

Description: Same as *O. elongatus* except for wall sculpture. The wall of *O. ligneolus* is rugulate to reticulate. The sculpture may be within the spore wall or may be an artifact produced by the close association of a perispore with the spore wall (Rich et al. 1982). Length 68 to 89 µm; width 42 to 43 µm.

Remarks: *Ovoidites ligneolus*, type species of the genus, has a similar geologic range as *O. elongatus*.

Ovoidites sp.

PLATE 1, FIGURE 5

Description: Spores with a circumscribing line of dehiscence, as in other species of *Ovoidites*. The wall sculpture is more strongly reticulate than *O. ligneolus*. This form differs from both *O. ligneolus* and *O. elongatus* in being nearly spherical rather than ovoid. It is similar to *Schizosporis rugulatus* Cookson and Dettmann 1959. Diameter 67 to 74.5 µm.

Remarks: This morphotype is similar to the form illustrated by van Geel and van der Hammen (1978, Plate 5, Figs. 53, 54) as *Zygnema*-type. This species is combined with *O. ligneolus* in Table 3.

Algal spores, gen. & sp. indet.

PLATE 1, FIGURE 6

Description: Thin-walled, more or less spherical palynomorphs with finely granular wall and usually a dark-staining spot at the approximate center of each spheroid. These objects most commonly occur in small aggregates, sometimes surrounded by very thin-walled tissue. Diameters range from 18 x 22 µm to 33 x 36 µm.

Remarks: The suggestion that these palynomorphs are of algal origin is based on their simple form, lack of obvious germinals, and tendency to occur in aggregates. These algal spores were observed in most samples of the middle shale unit and in all samples of the upper shale unit.

Genus *Catinipollis* Krutzsch 1966
Catinipollis geiseltalensis Krutzsch 1966

PLATE 1, FIGURE 7

Description: More or less spherical palynomorphs without apparent germinal apertures. The most characteristic feature is the closely spaced projections of the wall. These projections are flattened and broad-

ened distally, somewhat like flat-topped pila. Maximum diameter 24 to 31 µm.

Remarks: See Frederiksen et al. (1983) for discussion of various authors' interpretations of this morphotype, which is interpreted to be an algal cyst.

Pteridophyte Spores: Monolete

Genus *Laevigatosporites* Ibrahim 1933
Laevigatosporites ovatus Wilson & Webster 1946

PLATE 1, FIGURE 8

Description: Psilate, monolete spores. Length 26 to 33 µm; width 21 to 24 µm.

Remarks: These are fern spores of probable polypodiaceous affinity. *Laevigatosporites ovatus* occurs in most samples of both units.

Genus *Polypodiisporonites* Potonié 1931
Polypodiisporonites afavus (Krutzsch) Frederiksen 1980

PLATE 1, FIGURE 9

Description: Verrucate, monolete spores. Length 19.5 to 28 µm; width 15.5 to 21 µm.

Remarks: The smaller size of *Polypodiisporonites afavus* distinguishes it from *Polypodiisporonites* sp. cf. *Polypodiidites secundus*.

Polypodiisporonites sp. cf. *Polypodiidites secundus* (Potonié) Krutzsch 1963

PLATE 1, FIGURE 10

Description: Monolete spores characterized by broad verrucae. The positive verrucae do not protrude significantly beyond the spore outline and the intervening spaces form a distinct negative reticulum. Length 42 to 65 µm; width 29 to 45 µm.

Remarks: These are fern spores of probable polypodiaceous affinity.

Bryophyte and Pteridophyte Spores: Trilete

Genus *Lygodiumsporites* Potonié, Thomson, & Thiergart ex Potonié 1956 emend. Singh 1964
Lygodiumsporites adriennis

(Potonié & Gelletich) Potonié, Thomson, & Thiergart ex Potonié 1956

PLATE 1, FIGURE 11

Description: Trilete spores with rounded triangular to subcircular amb. Laesurae extend one-half to two-thirds of the radius and are surrounded by a distinct torus. Wall psilate. Diameter 39 to 51 μm.

Remarks: The transfer of this species to *Deltoidospora* by Frederiksen et al. (1983) is not accepted here. *Deltoidospora* is here considered to be restricted to small trilete spores with straight to slightly concave sides and lacking a torus. Singh (1964:67) emended *Lygodiumsporites* to include "all the smooth to subgranulose species morphologically similar to the spores of *Lygodium*." *Lygodiumsporites adriennis* is present in almost all levels at both localities. Affinity is with the Pterophyta, family Schizaeaceae.

Genus *Deltoidospora* Miner 1935

Deltoidospora sp.

(NOT ILLUSTRATED)

Description: Small trilete spores with psilate wall and triangular amb.

Remarks: *Deltoidospora* sp. was recovered from most samples of both the middle and upper shale units. Affinity is with the Pterophyta (ferns), but the family is uncertain.

Genus *Baculatisporites* Pflug & Thomson in Thomson & Pflug 1953

Baculatisporites sp. A

PLATE 1, FIGURE 12

Description: Trilete spores with circular amb and densely spaced baculate sculpture. Diameter 34.5 to 59 μm.

Remarks: These are spores of ferns. *Baculatisporites* sp. A is rare in occurrence at both localities. Affinity is with the Pterophyta, probably the family Osmundaceae.

Baculatisporites sp. B

(NOT ILLUSTRATED)

Description: Small trilete spores with subcircular amb and dense bacula (some approaching clava) over both proximal and distal surfaces. Diameter 23.5 to 27 μm (two specimens).

Remarks: Only two specimens of *Baculatisporites* sp. B were observed, both in the middle shale unit. Affinity is probably with the family Osmundaceae.

Genus *Biretisporites* Delcourt & Sprumont 1955

Biretisporites sp.

PLATE 1, FIGURE 13

Description: Spores psilate with circular amb. Laesurae bordered by raised lips and extending nearly to the equator. Diameter 29 to 36 μm.

Remarks: Florissant specimens assigned to *Biretisporites* sp. may be conspecific with forms included by Frederiksen et al. (1983, Plate 1, Figs. 9, 10) in *Deltoidospora microadriennis* (Krutzsch) Frederiksen et al. 1983, although the Florissant specimens are slightly smaller. The circular amb and raised lips along the laesurae would seem to exclude this morphotype from *Deltoidospora*. The specimen illustrated as *Leiotriletes microadriennis* by Krutzsch and Vanhoorne (1977, Plate 3, Fig. 3) is significantly larger, has laesurae less than one-half the spore radius, and does not clearly show lips. Affinity: Pterophyta.

Genus *Polycingulatisporites* (Simoncsics & Kedves) Playford & Dettmann 1965

Polycingulatisporites sp.

PLATE 1, FIGURE 14

Description: Trilete spores characterized by two or three concentric rings of exine thickening on the distal surface. Exine sculpture verrucate. Size 30 μm and 38 μm (two specimens).

Remarks: Only two specimens of *Polycingulatisporites* sp. were observed, both in the middle shale unit.

Genus *Lusatisporis* Krutzsch et al. 1963

Lusatisporis sp. cf. *L. perinatus* Krutzsch, Sontag, & Pacltová 1963

PLATE 2, FIGURE 1

Description: Spores rounded triangular with a verrucate, perinous outer wall. The illustrated specimen is focused on the proximal surface through the distal surface, showing several broad folds in the "perine" over the distal surface, suggesting that the outer wall is attached to the inner wall primarily on the proximal surface. Laesurae extend to the equator of the inner body. Diameter of inner body 20 to 34.5 μm; total diameter, including perispore, 33 to 49 μm.

Remarks: This taxon was previously reported from the Florissant locality as *Selaginella* sp. cf. *S. densa*, an extant species (Penny 1969, Plate 16-6, Fig. 3). Frederiksen

(1980a) transferred *Lusatisporis perinatus* to the extant genus *Selaginella*, noting its occurrence near the boundary of the middle and upper Eocene of Mississippi and western Alabama. This species was present in most levels of the middle shale unit. Affinity is believed to be with the Selaginellaceae.

Genus *Heliosporites* Schulz emend.
Srivastava 1972
Heliosporites sp.

PLATE 2, FIGURE 2

Description: Trilete spores with a psilate to finely verrucate proximal surface and an outer wall that is cavate over the equator and distal surface. The outer wall is densely verrucate with sparse, blunt-tipped spines, which are expanded at their bases. Overall diameter 29 to 40 μm.

Remarks: Similar forms were illustrated by Frederiksen (1980a, Plate 4, Figs. 7–10) as *Selaginella* sp. Spores of this type have a long geologic range, extending back to at least the Lower Cretaceous (Albian). See Wingate (1980) and Srivastava (1972) for further discussion. This species is rare in occurrence.

Genus *Foveotriletes* Van der Hammen
ex Potonié 1956
Foveotriletes sp.

PLATE 2, FIGURE 3

Description: Trilete spores with rounded triangular amb and foveolate exine. Laesurae two-thirds the spore radius. Diameter 29 to 33 μm.

Remarks: *Foveotriletes* sp. is rare in occurrence.

Genus *Stereisporites* Pflug in
Thomson & Pflug 1953
Stereisporites sp.

PLATE 2, FIGURE 4

Description: Spores rounded triangular with a narrow cingulum and rugulate sculpture. Laesurae one-half to two-thirds the spore radius. Diameter 16.5 to 23.5 μm.

Remarks: *Stereisporites* sp. is present in most levels of the middle shale unit. Probable affinity is with the genus *Sphagnum* (Sphagnaceae).

Genus *Echinatisporis* Krutzsch 1959
Echinatisporis sp.

PLATE 2, FIGURE 5

Description: Trilete spores with circular amb and finely verrucate to scabrate exine. Both proximal and distal surfaces bear sparse, large spines, which may be bifurcate or trifurcate at the distal ends. Body diameter 18.5 to 27 μm; spines 3.5 to 5.5 μm long.

Remarks: This morphotype is characterized by its large, sparsely distributed spines. Both *Acanthotriletes* and *Apiculatisporis* have small spinules or coni densely distributed over the exine.

Reticulate trilete, gen. & sp. indet.

PLATE 2, FIGURE 7

Description: Trilete spores with high-standing, coarse reticulum over both the proximal and distal surfaces, and a broad equatorial zona. The zona broadens noticeably at the radii. Diameter, including zona, 45.5 to 59 μm.

Remarks: Spores similar to the ones described here have been reported under the names *Lycopodium*, *Lycopodiumsporites*, and *Retitriletes* by various authors. Both *Lycopodiumsporites* and *Retitriletes* lack the zona and proximal sculpture observed in the Florissant specimens, however. These specimens appear to have closer affinity with some species of *Riccia* (see van Campo 1978, Plate 7) than with *Lycopodium*.

Rugulate trilete, gen. & sp. indet.

PLATE 2, FIGURE 6

Description: Small trilete spores with subcircular to rounded triangular amb. Exine covered with broad, high rugulae, giving the margin a thick and crenulate appearance. Diameter 24 to 27 μm.

Remarks: This species rather closely resembles *Muerrigerisporis oderensis* Thiele-Pfeiffer (1980, Plate 4, Figs. 6–9). However, *Muerrigerisporis* Krutzsch 1963 is defined as having a spinose cingulum, which precludes placing the Florissant specimens in this genus.

Spore Massulae

Genus *Azolla* Lamarck
Azolla cretacea Stanley 1965

PLATE 2, FIGURE 8

Description: Massula spherical to ovoid, appearing internally amorphous with a few large spheroidal cells discernible. Glochidia discernible only where they extend outward from the periphery of the massula. Glochidia taper distally to the characteristic anchor-shaped tip. Massula 76.5 x 115 μm to 135 x 144 μm; glochidia up to 36 μm long.

Remarks: *Azolla* is known from the Upper Cretaceous to the Holocene. Modern *Azolla* (Salviniaceae) is a small,

free-floating fern found in freshwater ponds and lakes. Three specimens were noted, all in the middle shale unit.

Gymnosperm Pollen: Bisaccate

Morphotypes comparable to pollen of extant *Abies*, *Picea*, and *Pinus* are present throughout both the middle and upper shale units. They are grouped for purposes of counting and tabulating occurrence under Pinaceae, as in Figure 5 and Table 3. This treatment results from difficulties encountered in distinguishing these genera in many instances where specimens are badly folded or fragmented.

Genus *?Abiespollenites* Thiergart in Raatz 1938
?Abiespollenites sp.

PLATE 3, FIGURE 1

Description: Large, bisaccate, conifer pollen with relatively small sacci that attach to the corpus at a distinct angle. Exine on proximal surface thins slightly from the pole to the point of attachment of the sacci but does not form a distinctive polar cap. Length of corpus 100 to 138 μm.

Remarks: An inadequate diagnosis of the genus *Abiespollenites* was given by Thiergart (in Raatz 1938), referring only to the large size of the grains. Thomson and Pflug (1953) transferred the type species of *Abiespollenites*, *A. absolutus*, to *Pityosporites* Seward 1914. The description of *Pityosporites*, especially as emended by Manum (1960), is most suggestive of the morphology of modern *Pinus*. Manum suggested *Pinuspollenites* may be a junior synonym of *Pityosporites*, which is the current usage in most palynological studies. As *Abiespollenites* is considered a valid genus by Jansonius and Hills (1976), it may be useful to emend the genus to circumscribe the *Abies*-type morphology and to distinguish it from *Pityosporites*. *?Abiespollenites* sp. is present in most samples of both units. Affinity: Pinaceae.

Genus *Piceapollis* Krutzsch 1971
Piceapollis sp.

PLATE 4, FIGURE 1

Description: Large bisaccate pollen characterized by sacci that attach to the corpus with no appreciable indentation, the amb in equatorial view being smooth and continuous. The reticulation of the sacci decreases toward the junction with the corpus and becomes essentially indiscernible with the reticulation of the corpus. Overall length in polar view 93 to 138 μm.

Remarks: Krutzsch (1971) noted that the type of *Piceaepollenites*, *P. alatus*, shows structure that is like that of pine pollen rather than that of spruce pollen, and he therefore considered *Piceaepollenites* to be a junior synonym of *Pityosporites* Seward 1914, and he established *Piceapollis* for fossil spruce pollen. *Piceapollis* sp. was noted throughout both units. Affinity: Pinaceae.

Genus *Pristinuspollenites* Tschudy 1973
Pristinuspollenites sp. cf. *P. microsaccus* (Couper) Tschudy 1973

PLATE 2, FIGURE 9

Description: Bisaccate pollen with more or less spherical corpus and highly reduced sacci that join the corpus without any noticeable line of attachment or significant angle. Reticulation of sacci very fine and only slightly coarser than that of the corpus. Diameter of corpus 51 to 62 μm.

Remarks: *Pristinuspollenites microsaccus* was described by B. D. Tschudy (1973). A similar morphotype, *Phyllocladidites* Cookson ex Couper 1953, differs in having conspicuously thickened exine at the proximal root of each saccus and prominent proximal tubercles on the corpus. This species is tallied with the Pinaceae in Table 3.

Genus *Pityosporites* Seward 1914
Pityosporites sp. A

PLATE 2, FIGURES 10–11

Description: Pollen with sacci nearly as broad as the corpus and more coarsely reticulate. Sacci and corpus meet distally at a high angle. A narrow zone of coarse verrucae often (but not always) occurs on the corpus along the more proximal lines of attachment of the sacci. Total length, including sacci, ranges from 43 to 53 μm.

Remarks: Pollen grains assigned to this species closely resemble pollen of modern pine of the *Pinus sylvestris* type in morphology, and the Florissant specimens probably represent fossil species of the genus *Pinus*. *Pityosporites* sp. A occurs in all samples of both units and is one of the numerically dominant palynomorphs in the lake beds. Affinity: Pinaceae.

Pityosporites sp. B

PLATE 2, FIGURE 12

Description: This species is similar to *Pityosporites* sp. A but has a coarsely rugulate polar cap with even coarser rugulae adjacent to the juncture with the sacci. Length 51 to 67 μm (including sacci).

Remarks: Specimens assigned to this species also are distinctly pinelike in morphology and probably represent

fossil species of *Pinus. Pityosporites* sp. B was observed in most samples of both the middle and upper shale units.

Genus *Podocarpidites* Cookson ex Couper 1953
Podocarpidites sp.

PLATE 3, FIGURE 2

Description: Bisaccate pollen with small corpus, ovoid to circular in polar view, and large sacci. The corpus is two-thirds to three-fourths as broad as the sacci. Thickened, verrucate exine occurs along the lines of attachment of the sacci (marginal crest). Total length 56.5 to 85 μm (including sacci).

Remarks: Although this species is assigned to *Podocarpidites* on the basis of its large sacci, it may not truly have affinity with the extant genus *Podocarpus*. This species is tallied with the Pinaceae in Table 3.

Gymnosperm Pollen: Monosaccate

Genus *Zonalapollenites* Pflug in Thomson & Pflug 1953
Zonalapollenites sp.

PLATE 3, FIGURE 3

Description: Pollen with a saccus that is highly convolute and attached to the endexine over a small area at each pole. The separation of ektexine and endexine forming the saccus is greatest in the equatorial region. Sculpture verrucate. Diameter 41 to 55 μm.

Remarks: *Zonalapollenites* probably represents ancestral *Tsuga* pollen. Affinity: Pinaceae.

Gymnosperm Pollen: Inaperturate

Genus *Taxodiaceaepollenites* Kremp ex Potonié 1958

Taxodiaceaepollenites hiatus (Potonié) Kremp ex Potonié 1958

PLATE 3, FIGURE 4

Description: Spherical to ovoid inaperturate pollen with psilate to faintly verrucate exine. Most specimens are split along a line extending one-half to two-thirds the pollen diameter, forming two equal, boat-shaped halves attached along one-half to two-thirds their length. Diameter 20 to 31 μm.

Remarks: Krutzsch (1971) considered *Taxodiaceaepollenites* to be a junior synonym of *Inaperturopollenites* Pflug in Thomson & Pflug 1953. Potonié (1966) combined the genera *Laricoidites, Laricoipollenites,* and *Laevigatasporites* with *Inaperturopollenites,* in which case *Laevigatasporites* would have priority, but Krutzsch and Vanhoorne (1977) interpreted *Laevigatasporites* as being algal (freshwater plankton).

Florissant specimens here assigned to *Taxodiaceaepollenites hiatus* resemble pollen of modern *Taxodium* (Cupressaceae), but no vegetative remains of *Taxodium* have been found in the Florissant beds. Leopold (cited by Penny 1969:362) noted that pollen removed from the strobili of *Sequoia affinis* bears a closer resemblance to pollen of modern *Taxodium* than to that of modern *Sequoia* (Cupressaceae). The most distinctive morphological feature that characterizes pollen of *Sequoia* is a relatively large and prominent ligula or papilla. This feature is not evident on specimens here assigned to *Taxodiaceaepollenites hiatus*. It is therefore likely that the common occurrence of *T. hiatus* in the Florissant deposits does represent *Sequoia*—a common constituent of the megaflora—but a distinctive late Eocene species of the modern genus. *Taxodiaceaepollenites hiatus* occurs throughout both units and is the dominant palynomorph in some samples in the middle shale unit.

Inclusion of *Taxodium* and *Sequoia* in the family Cupressaceae follows Manchester (2001), who incorporates the genera formerly included in the family Taxodiaceae in the Cupressaceae. Thus, the affinity of *Taxodiaceaepollenites hiatus* is considered to be with the Cupressaceae.

cf. *Taxodiaceaepollenites* sp. A of Rouse 1977

PLATE 3, FIGURE 6

Description: Subspherical palynomorphs with no visible aperture and a densely pilate exine. Maximum diameter 29 to 47 μm.

Remarks: This morphotype appears to be identical with that illustrated by Rouse (1977, Plate 1, Fig. 1). The assignment to the genus *Taxodiaceaepollenites,* however, seems highly speculative. The affinity of the Florissant specimens is here considered unknown.

Genus *Taxodiacites* Botscharnikova in Pokrovskaya & Stelmak 1960

Taxodiacites sp. cf. *T. verrucosus* Botscharnikova 1960

PLATE 3, FIGURE 7

Description: Inaperturate pollen that characteristically splits along approximately one-half the diameter, forming a gap appearing as a widely open beak. Exine

densely covered with high verrucae or low baculae. Diameter 22 to 38 µm.

Remarks: This pollen type is very similar to that of extant *Chamaecyparis* and *Juniperus* (Cupressaceae). MacGinitie (1953) stated that foliage and cones he assigned to *Chamaecyparis* were among the most abundant megafossils in the Florissant beds, but *Taxodiacites* sp. cf. *T. verrucosus* is rare at most stratigraphic levels. Occurrences of this species are included together with *Taxodiaceaepollenites hiatus* in Table 3 because these species were difficult to distinguish during counting.

Genus *Sequoiapollenites*
Thiergart 1938

Sequoiapollenites sp. cf.
S. rotundus
Krutzsch 1971

PLATE 3, FIGURE 5

Description: Spherical pollen with distinct papilla and finely verrucate exine. Diameter 18 to 29 µm.

Remarks: This morphotype is similar to pollen of extant *Sequoia*, *Sequoiadendron*, and *Cryptomeria* (Cupressaceae). Inclusion of *Sequoia* in the family Cupressaceae follows Manchester (2001). *Sequoiapollenites* sp. cf. *S. rotundus* is rare in occurrence. Occurrences of this species are included together with *Taxodiaceaepollenites hiatus* in relative abundance counts and in Table 3.

Gymnosperm Pollen: Polyplicate

Genus *Ephedripites*
Bolkhovitina ex Potonié 1958

Ephedripites claricristatus (Shakhmundes)
Krutzsch 1970

PLATE 3, FIGURE 8

Description: Elongate oval pollen with few, alternating costae and furrows. Numerous short tears or lines of thin exine extend along the furrows and are arranged perpendicularly to the long axis of the furrow. Exine psilate. Length 36.5 to 60 µm.

Remarks: Although the genus name *Ephedripites* is used here, fossil ephedralean pollen is more correctly assigned to the genus *Equisetosporites*. *Equisetosporites* Daugherty emend. Pocock & Jansonius (in Pocock 1965) was originally thought to represent spores of *Equisetum* but was later shown to be based on ephedralean pollen. The emended description by Pocock and Jansonius (in Pocock 1965) is essentially the

same as that for *Ephedripites*. *Equisetosporites* has priority over *Ephedripites* and therefore is the correct name for fossil ephedralean pollen, despite the unfortunate history of the name. The name *Ephedripites* is currently in broad usage, however, and it is employed here, although we acknowledge that it is incorrect. *Ephedripites claricristatus* is present in low relative abundance in almost all samples of both units.

This pollen undoubtedly has affinity with extant *Ephedra* (Ephedraceae), and it closely resembles pollen of the modern species *E. nevadaensis*. A fossilized stem of *Ephedra* from the Florissant beds was described by Wodehouse (1934), who stated that it matched most closely the modern species *E. nevadensis*. Interestingly, although he published no studies of fossil pollen from Florissant, a year earlier Wodehouse (1933) had published the first report on fossil pollen of Tertiary age in North America.

Ephedripites exiguus
(Frederiksen 1980)
nov. comb.

PLATE 3, FIGURE 9

Basionym: *Ephedra exigua* Frederiksen (1980a:37, Plate 7, Fig. 1).

Description: This species of ephedralean pollen differs from *Ephedripites claricristatus* in being smaller and more ovoid in outline, and in having more prominent lateral tears along the furrows. Size 20 x 29 µm and 19 x 26.5 µm (two specimens).

Angiosperm Pollen: Monosulcate

Genus *Arecipites* Wodehouse emend.
Nichols, Ames, & Traverse 1973

Arecipites sp. cf. *A. pertusus* (Elsik)
Nichols, Ames, & Traverse 1973

PLATE 3, FIGURE 10

Description: Monosulcate pollen with sulcus extending the length of the grains. Shape elongate ellipsoidal. Sculpture foveo-reticulate. Length 27 to 33 µm.

Remarks: The Florissant specimens are very similar to those illustrated by R. H. Tschudy (1973, Plate 2, Figs. 16, 17) as *Calamuspollenites pertusus* (now assigned to *Arecipites*). Affinity is with the Arecaceae (palms). Leopold (pers. commun., 1994) collected a rare palm frond from the middle shale unit within the monument boundary; the specimen is illustrated in Manchester (2001). The presence of both pollen and leaves of palms

confirms the presence of these climatically sensitive plants in the Florissant area during latest Eocene time.

Genus *Liliacidites* Couper 1953
Liliacidites sp.
PLATE 4, FIGURE 2

Description: Pollen ellipsoidal, monosulcate, with the sulcus extending the length of the grain. Sculpture reticulate, with lumina decreasing in size toward the ends of the grain. Length 33 μm (one specimen).

Remarks: A single specimen was observed in the middle shale unit. Affinity is with the Liliaceae.

Genus *Nupharipollenites* Nagy 1969
?Nupharipollenites sp.
PLATE 4, FIGURE 3

Description: Large spheroidal pollen with widely spaced, coarse spines. Probably monosulcate, although the aperture is not readily discerned in the specimens observed. Body diameter 53 μm and 57 μm; spine length 4.5 to 7.5 μm.

Remarks: The Florissant specimens are closely comparable to the illustrations of *Nuphar lutea* in Erdtman (1969, Plate 49, Figs. 1, 2). *Nupharipollenites* Nagy 1969 is defined as being oval in shape, which is one of the features used to distinguish it from *Nymphaeacidites* Sah 1967. *Nymphaeacidites* Sah 1967 and *Nymphaeapollenites* Thiele-Pfeiffer 1980 are spheroidal, but they differ from *Nupharipollenites* in being zonosulcate, psilate to densely baculate, "reticuloid," and of smaller size. The Florissant specimens would be readily accommodated in *Nupharipollenites* if the circumscription were expanded to include spheroidal forms. *Nupharipollenites echinatus* (Krutzsch) Mohr as described by Mohr (1984:65, Plate 9, Figs. 1, 2) is similar to the Florissant forms but is smaller and distinctly ovate (although this latter feature appears to be somewhat affected by compression and folding). This species is rare; only two complete specimens and one fragment were noted. Affinity is with the Nymphaeaceae.

Angiosperm Pollen: Tricolpate, Sculpture Various

Genus *Cupuliferoidaepollenites* Potonié, Thomson, & Thiergart ex Potonié 1960

Cupuliferoidaepollenites liblarensis (Thomson in Potonié, Thomson, & Thiergart) Potonié 1960
PLATE 4, FIGURE 4

Description: Prolate tricolpate pollen characterized by psilate exine and small size. Length 20 to 22 μm.

Remarks: The transfer of this species to *Tricolpopollenites* by Thomson and Pflug (1953) is here rejected on the basis that *Tricolpopollenites* is considered to be tricolporate (see remarks under *Tricolpopollenites parmularius*). *Cupuliferoidaepollenites liblarensis* was noted in most samples of the middle shale unit and in all samples of the upper shale unit.

Genus *Fraxinoipollenites* Potonié 1960
Fraxinoipollenites medius Frederiksen 1973
PLATE 4, FIGURE 5

Description: Prolate tricolpate pollen with colpi nearly reaching the poles. Exine tectate, the bacula distinct and giving the appearance of finely verrucate sculpture with an indistinct negative reticulum. Polar axis 34.5 to 38 μm; equatorial axis 21 to 28 μm.

Remarks: Frederiksen (1980a:48) noted that the affinity of this species is "unknown, probably not *Fraxinus* (Oleaceae)." Closely similar forms were illustrated as *Aceripollenites microrugulatus* Thiele-Pfeiffer 1980 by Thiele-Pfeiffer (1980:146, Plate 11, Figs. 26–28, 29–31) and by Mohr (1984:82, Plate 13, Figs. 9.1, 9.2). Both Thiele-Pfeiffer and Mohr described the sculpture as finely rugulate and made no mention of the reticulate, locally striate sculpture that characterizes *Aceripollenites* Nagy 1969.

Genus *Salixipollenites* Srivastava 1967
Salixipollenites sp. A
PLATE 4, FIGURE 6

Description: Prolate tricolpate pollen with reticulate exine. The colpi extend nearly to the poles and are fairly narrow and deep. Reticulation more or less coarse, the lumina decreasing in size over the poles. Length 20 to 23.5 μm.

Remarks: Srivastava (1967:529) remarked that this genus was instituted to accommodate fossil pollen that is comparable to the pollen of the modern genus *Salix* (Salicaceae). He also noted that *Salixipollenites* differs from *Tricolpites* Cookson ex Couper 1953 in being smaller in size and deeply trilobed and having a coarser reticulate sculpture. These characters have questionable value in distinguishing morphotypes at the generic level. N. O.

Frederiksen (written commun., 1995) noted that *Tricolpites* is generally oblate. *Salixipollenites* sp. A is combined with other *Salix*-type pollen in records of occurrence.

Based on consideration of records cited by Muller (1981) and accepted by Collinson et al. (1993), these specimens from Florissant constitute the stratigraphically oldest palynological record of the family Salicaceae. The previous oldest record is that of Graham and Jarzen (1969) from the Oligocene of Puerto Rico. Megafossils of the family are known from Florissant (MacGinitie 1953) and from lower Eocene rocks elsewhere (Collinson et al. 1993).

Salixipollenites sp. B

PLATE 4, FIGURE 7

Description: Similar to *Salixipollenites* sp. A, but larger and more barrel-shaped. Polar axis 29 µm; equatorial axis 26 µm (single specimen).

Remarks: *Salixipollenites* sp. B is combined with other *Salix*-type pollen in records of occurrence. See remarks about stratigraphic records of the family Salicaceae under *Salixipollenites* sp. A.

Salixipollenites sp. C

PLATE 4, FIGURE 8

Description: Subprolate, tricolpate pollen with colpi about two-thirds as long as the polar axis. Reticulate, with prominent pila supporting the muri and lumina of variable size and shape. Length 18.5 to 24 µm.

Remarks: *Salixipollenites* sp. C is comparable to *Salixipollenites* sp. 1 of Frederiksen et al. (1983). It should be noted that this morphotype is similar to pollen of extant *Viburnum* (Caprifoliaceae) and *Cardamine* (Brassicaceae), as well as to that of *Salix*. This species is present in most samples of both units.

Genus *Rousea* Srivastava 1969

Rousea araneosa (Frederiksen)
Frederiksen 1980

PLATE 4, FIGURE 10

Description: Prolate, tricolpate pollen with colpi approximately four-fifths as long as the polar axis. Coarsely reticulate, the lumina being much finer adjacent to the colpi and over the poles than in the mesocolpal areas. The colpi are rounded at the ends. Polar diameter 35 µm; equatorial diameter 24.5 µm.

Remarks: Only two specimens were observed, both in the middle shale unit.

Rousea sp.

PLATE 4, FIGURE 9

Description: The reduction of the mesh of the reticulation adjacent to the colpi and in the polar areas is the criterion used to assign this species to *Rousea*. Polar axis 22 to 27 µm.

Remarks: *Rousea* sp. is rare in occurrence.

Genus *Quercoidites*
Potonié, Thomson & Thiergart
ex Potonié 1960

Quercoidites microhenricii
(Potonié) Potonié 1960

PLATE 4, FIGURES 11–12

Description: Prolate, tricolpate pollen with long colpi (four-fifths of the polar axis, or greater). Exine verrucate, the verrucae being low and sometimes merging into rugulae. Polar axis 20 to 29 µm; equatorial axis 20 to 22 µm.

Remarks: Potonié (1960) noted the presence of a geniculus in the colpi of the type species of *Quercoidites*, *Q. henricii*. Frederiksen (1980a:48) commented that "some specimens of *Q. microhenricii* are pseudo-orate, that is, they have a slit or ragged tear in the floor of each colpus and thus the colpus looks orate in side view. Such phenomena are common in modern *Quercus* grains." The geniculate or pseudo-orate condition was not observed in the Florissant specimens. Probable affinity is with extant *Quercus* (Fagaceae). *Quercoidites microhenricii* is present in almost all samples of both shale units.

Genus *Cercidiphyllites*
Mtchedlishvili in
Samoilovich & Mtchedlishvili 1961

Cercidiphyllites sp.

PLATE 5, FIGURE 1

Description: Tricolpate pollen with short, very broad colpi, rounded at the ends. Polar axis much shorter than equatorial axis (oblate). Exine finely punctate and may appear very finely reticulate. Equatorial diameter 40 µm (single specimen).

Remarks: Mtchedlishvili (in Samoilovich and Mtchedlishvili 1961) noted the close similarity of *Cercidiphyllites* with pollen of extant *Cercidiphyllum* (Cercidiphyllaceae)

but remarked that the common occurrence of furrows of unequal length in the modern genus has not been observed in the fossil forms.

Genus *Aceripollenites*
Nagy 1969

Aceripollenites striatus
(Pflug) Thiele-Pfeiffer 1980

PLATE 5, FIGURE 2

Description: Prolate tricolpate pollen with colpi two-thirds to three-fourths the length of polar axis. Exine sculpture distinctly striate, the striae being somewhat discontinuous and broadly curved. Polar axis 25.5 to 36 µm; equatorial axis 20 to 34.5 µm.

Remarks: Probable affinity is with extant *Acer* (Aceraceae). Based on consideration of records cited by Muller (1981) and accepted by Collinson et al. (1993), these specimens from Florissant constitute the stratigraphically oldest palynological record of the family Aceraceae. The previous oldest record is that of Piel (1971) from the Oligocene of British Columbia, Canada. Megafossils of the family are known from Florissant (MacGinitie 1953) and from Paleocene and older rocks elsewhere (Collinson et al. 1993).

Manchester (2001) cites a recent botanical study in which the family Aceraceae is suppressed and its member taxa included in the family Sapindaceae, a concept that has been proposed at various times since the late eighteenth century. Evaluation of the merits of this concept is beyond the scope of this palynological study. We have retained the family Aceraceae in this report to facilitate comparison with other palynological studies and to emphasize the distinct differences between the morphology of *Acer*-type pollen and that of pollen typically associated with the Sapindaceae, as reported in most palynological literature.

Aceripollenites sp.

PLATE 5, FIGURE 3

Description: Tricolpate or possibly tricolporate pollen with triangular amb in polar view. Colpi broad, expanding somewhat at equator, which may indicate presence of pores. Exine finely striate. Equatorial diameter 19 to 22 µm (two specimens).

Remarks: The specimens encountered here are very similar to the one illustrated by Penny (1969, Plate 16-6, Figs. 16a, 16b) as *Acer*, although that specimen appears slightly larger. Only two specimens were observed, both in the middle shale unit. See remarks about strati-

graphic records of the family Aceraceae under *Aceripollenites striatus*.

Tricolpate sp. A

PLATE 5, FIGURE 4

Description: Tricolpate pollen, subspherical to slightly oblate. Exine psilate. Colpi broad and covered by thin membrane. Equatorial diameter 20 to 23.5 µm.

Remarks: A similar morphotype was illustrated by Wilkinson and Boulter (1980, Plate 7, Fig. 16) as *Tricolpopollenites* Group F. It is from the middle to late Oligocene of the western British Isles.

Tricolpate sp. B

PLATE 5, FIGURE 5

Description: Oblate to spherical tricolpate pollen with short, broad colpi. Colpal margins apparently ragged, as if torn. Exine finely reticulate. Observed only in polar view. Equatorial diameter 23 to 27 µm.

Remarks: These grains are very similar to *Platanus occidentaloides* Frederiksen, which Frederiksen (1980a:48, Plate 10, Fig. 19) noted compares closely with pollen of extant *Platanus occidentalis* L. (Platanaceae) These grains may be assignable to *Platanoidites* Potonié, Thomson & Thiergart ex Potonié 1960, although that genus was described as having narrow, geniculate colpi.

Tricolpate sp. C

PLATE 5, FIGURE 6

Description: Subspherical pollen with short colpi and sculpture of irregularly spaced short coni. Structure tectate, simplibaculate. Polar axis 31 to 35 µm; equatorial axis 29 to 42 µm.

Remarks: This morphotype agrees quite closely with the description of *Caprifoliacidites* Sah 1967, with the exception that the latter is tricolporate. *Echitricolpites* Da Silva Pares Regali, Uesugui, & Da Silva Santos 1974 is broadly defined as tricolpate pollen with spinose exine. Florissant specimens differ in having long colpi and irregularly spaced coni with bases broader than their length. The Florissant specimens are very similar to pollen of extant *Actaea rubra*, which is suggestive of affinity with the Ranunculaceae. According to Muller (1981), this family has no palynological record older than Miocene, suggesting that the Florissant specimens could be the stratigraphically oldest such record. On the basis of data summarized by Collinson et al. (1993),

however, the Ranunculaceae have no megafossil record older than Oligocene, and neither MacGinitie (1953) nor Manchester (2001) identified any Florissant megafossils as belonging to this family.

Tricolpate sp. D

PLATE 5, FIGURES 7A–7B

Description: Tricolpate pollen, subspherical to prolate, exine thick, distinctly columellate. Structure tectate, sculpture of low coni. Polar axis 35.5 µm and 40 µm; equatorial axis 30 µm and 33 µm (two specimens).

Remarks: For a more detailed description, see Tricolpate genus A, sp. 1, of Frederiksen et al. (1983:53), which this species closely resembles. Frederiksen et al. (1983) suggested possible affinity of his species with the Valerianaceae, Convolvulaceae, or Asteraceae (Compositae). A very similar, and possibly conspecific, form is *"Tricolporopollenites" columelloides crassicus* Krutzsch & Vanhoorne, which was described from the Eocene of Europe (Krutzsch and Vanhoorne 1977:74, Plate 31, Figs. 12–16).

Angiosperm Pollen: Tricolporate, Psilate to Scabrate

Genus *Tricolpopollenites* Pflug & Thomson in Thomson & Pflug 1953

Tricolpopollenites parmularius (Potonié) Thomson & Pflug 1953

PLATE 5, FIGURES 8–9

Description: Pollen weakly tricolporate, often appearing tricolpate, with psilate exine. Amb rounded cylindrical to more or less barrel-shaped in equatorial view. Colpi do not reach poles, and one colpus (the middle one of the three) is slightly shorter than other two. Pores, when visible, large and circular. Length 23 to 29 µm; width 16.5 to 24.5 µm.

Remarks: This species is the type species of the genus *Tricolpopollenites*. It is very similar to pollen of extant *Eucommia* (Eucommiaceae), and it has been referred to the modern genus in works by Leopold (1974) and Frederiksen (1988). Originally described as being tricolpate, the holotype was later noted to be tricolporate by Krutzsch (1959). The transfer of this species to *Tricolporopollenites* by Krutzsch (in Krutzsch et al. 1960) is not accepted here. Frederiksen et al. (1983) recognized the nomenclatural problems associated with this morphotype and

chose to tentatively assign it to the extant genus *Eucommia* (as *E. leopoldae*). Regardless of affinity, we choose not to assign middle Tertiary pollen to extant genera, particularly when a fossil ("form genus") name is available.

Genus *Siltaria* Traverse 1955

Siltaria sp. cf. *S. scabriextima* Traverse 1955

PLATE 5, FIGURE 10

Description: Prolate, tricolporate pollen with tectate exine, heads of bacula giving surface a faintly verrucate to scabrate appearance. Colpi long, three-fourths to four-fifths the length of polar axis, and bordered by thickened exine. Pores circular, distinct. Length 14.5 to 22 µm.

Remarks: *Siltaria* sp. cf. *S. scabriextima* is very similar to pollen described by Traverse (1955) as *Siltaria scabriextima* but is smaller. Frederiksen (1980a:52, Plate 11, Figs. 26–28) illustrated similar forms that he compared with *S. scabriextima*. The Florissant specimens compare closely with Frederiksen's in size and sculpture. Frederiksen (1980a) considered the affinity of his specimens to be with the Anacardiaceae, but Traverse (1955) considered his species to have possible affinity with the Fagaceae, morphologically intermediate between *Castanea* and *Quercus*.

Siltaria sp. cf. *S. pacata* (Pflug in Thomson & Pflug) Frederiksen 1980

PLATE 5, FIGURE 11

Description: Subprolate to subspherical tricolporate pollen. Tectate, the bacula faintly visible in optical section. Pores circular, small, and somewhat hidden by geniculate colpal margins. Exine scabrate. Polar axis 13 to 22 µm; equatorial axis 14.5 to 20 µm.

Remarks: Frederiksen (1980a) transferred Pflug's (in Thomson and Pflug 1953) species *Tricolporopollenites pacatus* to the genus *Siltaria*. The Florissant specimens are similar to Frederiksen's in size and sculpture, but they differ somewhat in having smaller exopores. *Siltaria* sp. cf. *S. pacata* is rare in occurrence.

Genus *Rhamnacidites* Chitaley ex Potonié 1960

Rhamnacidites delicatus Frederiksen in Frederiksen et al. 1983

PLATE 5, FIGURE 12

Description: See Frederiksen et al. (1983:63, Plate 18, Figs. 2–5) for descriptive details. Equatorial diameter 15.5 to 22 µm.

Remarks: Many of the Florissant specimens are slightly larger than those of Frederiksen et al. (1983) but are otherwise closely comparable. Affinity is possibly with the Rhamnaceae.

Angiosperm Pollen: Tricolporate, Reticulate

Genus *Araliaceoipollenites*
Potonié ex Potonié 1960

cf. *Araliaceoipollenites profundus*
Frederiksen 1980

PLATE 5, FIGURE 13

Description: Prolate pollen with colpi two-thirds to three-fourths the length of polar axis and bordered by slight exinal thickening. Pores small and indistinct. Exine sculpture fine, appearing to be microreticulate or finely verrucate. Length 33 to 38 μm; width 25 to 31 μm.

Remarks: Frederiksen (1980a:53) indicated that the sculpture of *Araliaceoipollenites profundus* ranges from "distinctly granulate to coarsely punctate or finely reticulate." The Florissant specimens compare closely with Frederiksen's in sculpture; they fall toward the smaller end of the size range of his specimens.

cf. *Araliaceoipollenites euphorii*
(Potonié) Potonié 1960

PLATE 5, FIGURE 14

Description: Pollen tricolporate with thickened exine bordering the colpi and pores. Exine finely reticulate. Subprolate to prolate with rounded poles. Polar axis 18 to 31 μm.

Remarks: As with *Araliaceoipollenites profundus*, the sculpture of specimens here assigned to cf. *Araliaceoipollenites euphorii* is microreticulate to finely verrucate. The Florissant specimens are comparable to forms described as *Araliaceoipollenites euphorii* by Thiele-Pfeiffer (1980) and Mohr (1984).

Genus *Horniella* Traverse 1955

cf. *Horniella brevicolpata*
Frederiksen et al. 1983

PLATE 5, FIGURE 15

Description: Tricolporate pollen with colpi rather obscured by sculpture, but appearing to be two-thirds or more the length of polar axis. Pores lalongate with parallel sides in the equatorial plane. Sculpture indistinctly reticulate with high, narrow muri supported by long, pilate columellae. Prolate with broadly rounded poles. Polar axis 42 μm and 53 μm (two specimens).

Remarks: This species appears to be identical with the form illustrated by Leopold (Love et al. 1978, Plate 3, Figs. 18–21) as *Triumfetta* (Tiliaceae), which Frederiksen et al. (1983:70) also likened to *H. brevicolpata*. Essentially the same form was illustrated by Rouse (1977, Plate 2, Fig. 36) as *Rhoiipites* [sic] *latus* Frederiksen 1969, which was not formally named until published by Frederiksen (1980a:55), but Rouse's specimen differs significantly from Frederiksen's species. Although Frederiksen et al. (1983) described *H. brevicolpata* as having short colpi (one-fourth to two-thirds the length of the grain), their illustrations suggest that the colpi probably are longer. On this basis, Frederiksen et al. (1983:70) questioned the affinity of this morphotype with *Triumfetta* and suggested an affinity with the "*Grewia* type of Muller (1981:45)." Muller had referenced a report of *Triumfetta-Grewia* type pollen by Leopold (1974, Plate 44, Fig. 1, as *Triumfetta*), and regarded *Triumfetta* and *Grewia* as belonging to the same morphological group, as did Erdtman (1966). These two modern genera are members of the Tiliaceae.

Horniella sp. A

PLATE 5, FIGURE 16

Description: Tricolporate pollen with rounded oval shape in equatorial view. Colpi long and bordered by prominent exinal thickening. Pores lalongate, appearing as narrow slits oriented parallel to the equator. Exine finely reticulate, with long columellae supporting high, narrow muri surrounding small, circular lumina. Polar axis 31 to 35 μm; equatorial axis 16.5 to 25.5 μm.

Horniella sp. B

PLATE 5, FIGURE 17

Description: Prolate tricolporate pollen with long colpi that nearly reach poles. Pores lalongate, large. Exine finely verrucate and thickened along the margins of colpi. Length 36.5 μm and 40 μm (two specimens).

Genus *Margocolporites*
Ramanujam ex Srivastava 1969

Margocolporites sp.
cf. *M. vanwijhei* Germeraad,
Hopping, & Muller 1968

PLATE 6, FIGURES 1–2

Description: This species appears to be identical with the forms illustrated by Truswell et al. (1985:286, Figs.

8A, 8B). The structure of the apertures is somewhat obscured by the surface sculpture and may be inferred as being colpi only in some cases and pores only in others. Some specimens clearly exhibit circular pores with slightly thickened exine bordering them, and in these specimens the colpal areas appear more finely reticulate and tend to stain darker than the rest of the surface. The intracolpal and intercolpal areas are equal in width. These grains are quite large, with equatorial diameter from 37 to 53 µm.

Remarks: Playford (1982:48) noted a possible affinity of this pollen type with the Fabaceae (Leguminosae), remarking on the particular similarity with pollen of extant *Caeasalpinia crista* and *C. coriaria*. This proposed affinity was also suggested by Germeraad et al. (1968) and accepted by Truswell et al. (1985). A closely comparable morphology is seen in the pollen of several other genera of Fabaceae, particularly *Brasilettia*, *Haematoxylon*, *Libidibia*, *Nicarago*, and *Poincianella* (see Tsukada 1964, Plates 17–23).

Based on consideration of records cited by Muller (1981) and accepted by Collinson et al. (1993), these specimens from Florissant constitute the stratigraphically oldest palynological record of the family Fabaceae. The previous oldest palynological record is considerably younger (Pliocene), but megafossils of the family are known from Florissant (MacGinitie 1953; Manchester 2001) and from rocks as old as Paleocene elsewhere (Collinson et al. 1993).

Genus *Rhoipites*
Wodehouse 1933

Rhoipites sp. A

PLATE 5, FIGURE 18

Description: Tricolporate pollen with colpi extending nearly to poles and with thickened margins. Pores circular to slightly lalongate. Exine reticulate; bacula supporting the muri very distinct. Amb subprolate to subspherical. Polar axis 16 to 23.5 µm; equatorial axis 16 to 21 µm.

Remarks: This species is very similar to the form illustrated by Wilkinson and Boulter (1980, Plate 8, Fig. 29) as *"Tricolporopollenites"* group E, which is from the Oligocene of the western British Isles.

Rhoipites sp. B

PLATE 5, FIGURE 19

Description: Grains subprolate, oval. Colpi and pores with strongly thickened margins. Exine reticulate with irregularly shaped lumina and fairly thick muri. Polar axis 23.5 to 29 µm; equatorial axis 18 to 24 µm.

Remarks: *Rhoipites* sp. B differs from *Rhoipites* sp. A in being larger and having a reticulum composed of thicker muri and more angular lumina.

Rhoipites sp. C

PLATE 5, FIGURE 21

Description: Tricolporate pollen with colpi approximately four-fifths the length of polar axis. Colpi with thickened margins; pores indistinct, appearing generally as thin areas in the colpal margins. Exine reticulate with high, simplibaculate muri enclosing lumina of highly variable size and shape. Size of lumina decreases over poles. Polar axis 32 to 47 µm; equatorial axis 28 to 38 µm.

Remarks: This species is distinguished by its large size and strong reticulation. Many of the specimens appear to be tricolpate, as the pores are quite indistinct. Similar forms have been reported from the Eocene of Nevada as *Rhoipites* sp. (Wingate 1983, Plate 3, Figs. 11–13) and the Miocene of southern Germany as *Tricolporopollenites striatoreticulatus* (Thiele-Pfeiffer 1980, Plate 14, Figs. 1–8). *Tricolporopollenites* sp. A of Rouse (1977, Plate 2, Fig. 37) is similar but exhibits a reticulation with much more uniformly sized lumina and lower muri than in *Rhoipites* sp. C.

Rhoipites sp. D

PLATE 5, FIGURE 20

Description: Grains subprolate, ovoid. Colpi long, with thickened margins. Pores circular to slightly lalongate, often interpreted only as interruptions in the colpi. Thick margins border the colpi. Exine strongly reticulate with fairly high muri. Bacula distinct, particularly in optical section. Polar axis 18 to 23.5 µm; equatorial axis 15 to 20 µm.

Rhoipites sp. E

PLATE 6, FIGURE 3

Description: Prolate, tricolporate pollen with colpi extending two-thirds or more the distance to the poles. Colpi and pores bordered by thickened exine. Reticulate, with low, thick muri and irregularly shaped lumina. Pores oval to lalongate. Length 34.5 to 38 µm.

Remarks: This morphotype is quite similar to the form illustrated by Leopold (1978, Plate 3, Figs. 16, 17) as *Luehea* (Tiliaceae). *Rhoipites* sp. E is more prolate and has smaller pores than Leopold's specimen, however.

Rhoipites sp. F

PLATE 6, FIGURE 4

Description: Reticulate, tricolporate pollen with long colpi and rather small, circular pores. Reticulation uniform over surface of exine. Polar axis 29 to 33 μm; equatorial axis 20 to 24 μm.

Remarks: This species is comparable to the forms illustrated by Thiele-Pfeiffer (1980, Plate 13, Figs. 19–22) as *Tricolporopollenites marcodurensis* Thomson & Pflug 1953. *Tricolporopollenites* is a junior synonym of *Rhoipites* Wodehouse, according to Potonié (1960:101).

Tricolporate sp. A

PLATE 6, FIGURE 5

Description: Prolate tricolporate with colpi extending approximately three-fourths the length of grain and bordered by slightly thickened exine. Pores large, oval, somewhat lalongate. Exine finely reticulate, appearing scabrate to faintly verrucate at low to medium magnification. Polar axis 24.5 to 29 μm.

Remarks: This morphotype is quite similar to pollen of extant *Astragalus gracilis* (Fabaceae).

Tricolporate sp. B

PLATE 6, FIGURE 6

Description: Pollen subspherical to slightly oblate (seen only in polar view). Colpi extend nearly to poles and are bordered by narrow bands of thickened exine. Pores bordered by thickened exine and appear to have a shallow atrium. Exine sculpture fine and difficult to resolve, appearing to be microreticulate to scabrate. Equatorial diameter 22 to 23.5 μm.

Tricolporate sp. C

PLATE 6, FIGURE 7

Description: Grains oblate. Colpi indistinct, revealed mostly by staining during processing. Pores bordered by thickened exine. Exine uniformly reticulate over surface of grain. Equatorial diameter 18 to 26 μm.

Angiosperm Pollen: Tricolporate, Striate

Genus *Ailanthipites* Wodehouse 1933

Ailanthipites berryi Wodehouse 1933

PLATE 6, FIGURE 8

Description: Grains tricolporate, subprolate, with colpi approximately four-fifths the length of polar axis. Colpi bordered by thickened exine. Pores lalongate with parallel sides, forming nearly complete transverse furrow. Exine striate-reticulate, muri of reticulation forming short, sinuous, discontinuous striae. Polar axis 26 to 29 μm; equatorial axis 18.5 to 20 μm.

Remarks: Frederiksen (1980a:58) noted that pollen with similar morphology to *Ailanthipites berryi* occurs in the Anacardiaceae, Leguminosae (Fabaceae), Sapindaceae, and Simaroubaceae (genus *Ailanthus*). Frederiksen et al. (1983:81) reported *Ailanthipites berryi* from the middle Eocene of southern California and stated that it is known from the lower Eocene to the lower Oligocene of the Gulf Coast. The species was originally described from the Eocene of Colorado (Wodehouse 1933) and was also reported from the Eocene of Wyoming by Nichols (1987).

Ailanthipites sp. A

PLATE 6, FIGURE 9

Description: This form is smaller and more spherical than *Ailanthipites berryi* but otherwise is very similar. Polar axis 18 to 20 μm; equatorial axis 16 to 17 μm.

Ailanthipites sp. B

PLATE 6, FIGURE 10

Description: Grains subspherical with colpi two-thirds to three-fourths the length of polar axis. Pores large, circular. Both colpi and pores bordered by thickened exine. Exine finely striate, striae forming spiral patterns. Polar axis 20 to 25 μm; equatorial axis 16.5 to 18 μm.

Genus *Alangiopollis* Krutzsch 1962

Alangiopollis sp.

PLATE 6, FIGURE 11

Description: Subprolate to subspherical pollen with strongly circumstriate exine. Colpi extend approximately two-thirds the length of polar axis. Pores large, ovoid. Polar axis 34 to 40 μm; equatorial axis 27.5 to 42 μm.

Remarks: The circumstriate sculpture and large pores distinguish *Alangiopollis* sp. from other tricolporate grains in the Florissant palynoflora. Affinity is with the family Alangiaceae.

Tricolporate sp. D

PLATE 6, FIGURES 12–13

Description: Prolate pollen with colpi extending nearly to poles and lalongate pores. Colpi and pores bordered

by thickened exine. Exine strongly striate, striae oriented parallel to polar axis. Polar axis 23.5 to 37.5 μm; equatorial axis 17 to 30 μm.

Remarks: The larger forms here included in this taxon are essentially identical with the forms described by Krutzsch and Vanhoorne (1977:78, Plate 43, Figs. 22–24, 28) as "*Tricolporopollenites*" *striatopunctatus*, which has a polar axis of 30 to 45 μm. Per Potonié (1960:101), *Tricolporopollenites* is a junior synonym of *Rhoipites*. In this study, smaller specimens were recorded as "cf. Tricolporate sp. D" (Table 3). These specimens could possibly be assigned to a different species, but the continuous range in size makes it difficult to distinguish two forms consistently. Zaklinskaya (1980, Plate 7, Figs. 1–6) illustrated essentially identical forms as *Parthenocissus simicordatiformis* Lyubomirova (*Parthenocissus* is an extant genus of the Vitaceae). Leopold (1978, Plate 3, Figs. 23–27) illustrated similar forms as *Acer* cf. *palmatum* (*Acer* is an extant genus of the Aceraceae). The pollen morphology of this species also suggests affinity with the Rosaceae.

Tricolporate sp. E

PLATE 6, FIGURE 14

Description: Spherical tricolporate pollen grain with relatively short colpi (approximately two-thirds the polar axis) and circular pores. Exine reticulate-striate, muri forming discontinuous striae aligned mostly with equatorial plane. Polar axis 24 μm; equatorial axis 24 μm.

Remarks: This species differs from Tricolporate sp. D in shape and in having small, circular pores. A single specimen was observed in sample D7012-O.

Angiosperm Pollen: Tricolporate, Verrucate

Genus *Quercipollenites* Wolff 1934

?*Quercipollenites* sp. cf. pollen of *Fagopsis longifolia* (Lesq.) Hollick

PLATE 6, FIGURE 15

Description: Tricolporate pollen, subspherical to subprolate. Colpi extending four-fifths or more the length of polar axis. Pores small, circular. Exine finely verrucate. Polar diameter 16 to 25 μm; equatorial diameter 11 to 20 μm.

Remarks: This species appears to be essentially identical with the pollen extracted from the stamens of inflorescences of *Fagopsis longifolia*, the numerically dominant species of the Florissant fossil leaf flora, by Manchester and Crane (1983:1152, Figs. 15–20). Manchester and Crane discussed the different opinions of earlier workers regarding the botanical affinity of *Fagopsis longifolia*, which has been variously assigned to the Ulmaceae, Fagaceae, or Betulaceae. Having studied leaf and stem fossils with attached staminate inflorescences containing pollen, they presented a strong argument for assigning *Fagopsis longifolia* to the Fagaceae. Contrary to the high abundance of fossil leaves of *Fagopsis longifolia* in the Florissant megaflora, ?*Quercipollenites* sp. is rare in the palynoflora. This species, however, is consistent in occurrence and is present at almost every stratigraphic level sampled in the middle shale unit and at several in the upper shale unit.

Genus *Verrutricolporites* van der Hammen & Wijmstra 1964

Verrutricolporites sp. A

PLATE 6, FIGURE 16

Description: Prolate, tricolporate pollen with colpi extending nearly entire length of grains. Colpal margins thickened. Pores small, circular. Exine structure tectate; columellae prominent and producing a coarse surface pattern. Polar diameter 25 to 29.5 μm; equatorial diameter 19 to 20 μm.

Remarks: This species is similar to both *Verrutricolporites cruciatus* Frederiksen 1980 and *V. tenuicrassus* Frederiksen 1980. *Verrutricolporites cruciatus* differs in having lalongate pores and colpi without marginal thickenings, and *V. tenuicrassus* differs in having thicker exine at the poles than at the equator.

Verrutricolporites sp. B

PLATE 6, FIGURE 17

Description: Grains tricolporate with broad colpi extending nearly to poles and large, circular pores. Colpi with slightly thickened margins. Exine finely verrucate. Equatorial diameter 18 to 25.5 μm.

Remarks: This form differs from *Verrutricolporites* sp. A in the size of the pores. *Tricolpopollenites* group F of Wilkinson and Boulter (1980, Plate 7, Figs. 17–18) is very similar.

Genus *Slowakipollis* Krutzsch 1962

Slowakipollis hippophaëoides Krutzsch 1962

PLATE 6, FIGURE 18

Description: Pollen tricolporate to nearly syncolporate, oblate with slightly rounded triangular amb.

Pores protruding, vestibulate. Finely verrucate sculpture. Equatorial diameter 20 to 30 μm.

Remarks: This species was considered to have affinity with extant *Eleagnus* (Eleagnaceae) by Kirchner (1984) and Mohr (1984) and was illustrated as *Eleagnus* by Leopold (in Penny 1969, Plate 16–6, Fig. 36). Leopold (1974, Plate 42, Fig. 28) illustrated an essentially identical form as cf. *Serjania* (Sapindaceae?). Affinity with the Eleagnaceae is the interpretation preferred here.

Slowakipollis hippophaëoides was originally described by Krutzsch (1962) from the Oligocene of Germany. Muller (1981) accepted Krutzsch's record as being the stratigraphically oldest palynological record of the family Eleagnaceae. The specimens from Florissant are stratigraphically older (latest Eocene), and thus they would be the oldest record of the family. Fossil pollen assigned to the genus *Boehlensipollis*, however, which also may have affinity with the Eleagnaceae (Collinson et al. 1993), is known from older rocks. Megafossils of the family are unknown at Florissant (MacGinitie 1953; Manchester 2001) and from elsewhere are no older than Miocene (Collinson et al. 1993).

Angiosperm Pollen: Tricolporate, Echinate

Asteraceae sp. A

PLATE 6, FIGURES 19A–19B

Description: Tricolporate (possibly tricolpate) pollen with regularly distributed broad-based spines. Prolate, with long colpi extending three-fourths to four-fifths the length of grains. Polar axes 16 μm and 18 μm; equatorial diameters 12 μm and 12.5 μm (two specimens). Morphology closely resembles that of fossil and modern pollen of the subfamily Tubuliflorae of the family Asteraceae.

Remarks: These specimens exhibit affinity with the Asteraceae (Compositae), especially with the Tubuliflorae. Their presence may constitute the stratigraphically oldest record of the modern family, but their occurrence is somewhat problematic. They are exceedingly rare in the Florissant palynoflora (only two specimens found, both from the same sample, D7012-Q). Because of their rarity and unexpected occurrence in deposits of this age, the possibility that they might be modern contaminants in the sample must be considered, but the specimens do not appear to be contaminants. They lack cytoplasmic contents, and their exines show the same level of thermal maturity and staining characteristics of other an-

giosperm pollen in this sample. These characteristics indicate that these fossils are in place.

Muller (1981) accepted as the stratigraphically oldest occurrences of pollen of the family Asteraceae several records from the Oligocene in different parts of the world. Collinson et al. (1993) did not accept these records, however, stating that more ultrastructural examination was required. The specimens reported here from Florissant would predate the records cited by Muller, but they also require ultrastructural examination.

Cockerell (1908) identified a leaf from the Florissant flora as *Aster florissantia*. MacGinitie (1953:163) listed this species in his *incertae sedis*, group 2, which includes species he retained in the hope that discovery of further material would clarify their taxonomic position. He commented that it was "improbable" the specimen identified by Cockerell could be the leaf of an *Aster*. Manchester (2001) notes that the leaf that Cockerell named *Aster florissantia* resembles the leaves of *Philadelphus* (Rosaceae), *Colubrina* (Rhamnaceae), and *Abelia* (Caprifoliaceae).

Angiosperm Pollen: Tetracolporate

Genus *Tetracolporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Tetracolporopollenites brevis Frederiksen 1980

PLATE 6, FIGURE 20

Description: Grains subspherical to subprolate with four short colpi and large oval, lalongate pores. Exine psilate, infrabaculate. Polar axis 23 to 29 μm; equatorial diameter 25.5 μm.

Remarks: The Florissant specimens are at the smaller end of the size range given by Frederiksen (1980a:63) for this species. Botanical affinity appears to be with the Sapotaceae (Anderson and Muller 1975; Frederiksen 1980a).

Tetracolporopollenites sp.

PLATE 6, FIGURE 21

Description: Grains subprolate with flattened poles and short colpi. Pores lalongate and appear to merge into a continuous band of exinal thinning about the equator. Exine psilate. Polar axis 16 to 19 μm; equatorial diameter 13 to 14 μm.

Remarks: This species is very similar to the forms illustrated as Sapotaceae by Leopold (1974, Plate 45, Figs. 11, 13, 14) and to *Tetracolporopollenites* sp. of Frederiksen

(1980a, Plate 16, Fig. 6). Affinity is probably with the Sapotaceae.

Genus *Meliapollis*
Sah & Kar 1970
?Meliapollis sp.

PLATE 6, FIGURE 22

Description: Oblate pollen with circular to quadrangular amb. Tetracolporate with colpi that extend about two-thirds the distance to poles and large, ?circular pores. Exine scabrate to psilate. Equatorial diameter 27.5 to 33 μm.

Remarks: This species is morphologically comparable to, but slightly larger than, the form illustrated as Meliaceae, *Cedrela*-type, by Leopold (in Penny 1969, Plate 16-5, Fig. 42). Another comparable but larger form was illustrated by Playford (1982, Plate 7, Fig. 1) as *Tetracolporopollenites* sp., which he assigned to the Sapotaceae. The botanical affinity is probably with either the Meliaceae or Sapotaceae.

Angiosperm Pollen: Syncolporate

Genus *Boehlensipollis* Krutzsch emend. Frederiksen et al. 1983

Boehlensipollis sp. cf. *B. granulata* Frederiksen et al. 1983

PLATE 6, FIGURE 23

Description: See Frederiksen et al. (1983:62) for description. The Florissant specimens tend to be smaller than *B. granulata* (36–48 μm), although there is considerable overlap in the size ranges. Equatorial diameter 27 to 42 μm; polar axis 25.5 to 28 μm (three specimens).

Remarks: Frederiksen et al. (1983) suggested that the probable botanical affinity of *Boehlensipollis* is with the Eleagnaceae. Leopold (in Penny 1969, Plate 16-6, Fig. 18) illustrated a closely comparable form as *Cardiospermum* (Sapindaceae). The true affinity of this fossil pollen type may be with either family. This species is present at most stratigraphic levels in both units.

Genus *Myrtaceidites*
Cookson & Pike emend. Potonié 1960

Myrtaceidites parvus Cookson & Pike 1954

PLATE 7, FIGURE 1

Description: Syncolporate pollen with narrow, simple colpi and generally small pores, which are difficult to distinguish on some specimens. Exine scabrate to finely perforate. Oblate with circular amb. Equatorial diameter 13.5 to 19 μm.

Remarks: Frederiksen et al. (1983) noted that this is a rather heterogeneous species, possibly representing two or three genera of the Myrtaceae or even the Myrsinaceae. A similar form was illustrated by Leopold (1974, Plate 41, Fig. 5) as cf. *Eugenia* (Myrtaceae). The forms assigned to *Tricolpopollenites* group F by Wilkinson and Boulter (1980, Plate 7, Figs. 17–18) may also belong in this species.

Genus *Cupanieidites*
Cookson & Pike 1954

Cupanieidites sp. A

PLATE 7, FIGURE 2

Description: Oblate pollen with rounded triangular amb. Colpi narrow, with or without thickened margins. Pores indistinct to clearly expressed and slightly annulate. Exine scabrate to finely verrucate. Equatorial diameter 13 to 18 μm.

Remarks: This species lacks the triangular polar field characteristic of *Cupanieidites*, but otherwise it is compatible with the morphology of the genus. Muller (1981:71) noted the affinity of *Cupanieidites* with the Sapindaceae but suggested that pollen with indistinct exine sculpture may be better accommodated in the Myrtaceae.

Cupanieidites sp. B

PLATE 7, FIGURE 3–4

Description: Syncolporate pollen with triangular amb in polar view. Colpi with thickened margins and pores atriate. Exine radially striate to striate-reticulate. Equatorial diameter 20 to 22 μm.

Remarks: This species differs from *Cupanieidites* sp. A in exine sculpture, and the affinity with the Sapindaceae is more strongly suggested. Only two specimens were observed, both in the middle shale unit.

Angiosperm Pollen: Tribrevicolporate

Genus *Bombacacidites* Couper 1960

Bombacacidites sp. aff. *B. reticulatus* Krutzsch 1961 sensu Frederiksen 1988

PLATE 7, FIGURE 5

Description: Tricolporate pollen with very short colpi extending poleward only slightly beyond margins of

pores. Grains oblate with subcircular to subtriangular amb. Exine reticulate, mesh of reticulum being coarser at poles than at equator. Equatorial diameter 20 to 28 μm.

Remarks: Leopold illustrated similar forms as Bombacaceae? (1978, Plate 4, Figs. 15–16) and *Fremontia* (in Penny 1969, Plate 16-6, Fig. 39). Pollen grains of *Fremontia* (Sterculiaceae) are characterized by reticulation that is coarser at one pole than at the other, which is not the case in the Florissant specimens. Manchester (1992, Figs. 43–47) illustrated essentially identical pollen from anthers of *Florissantia speirii* from the upper Eocene and lower Oligocene of Oregon. Manchester (1992:1006) attributed *Florissantia* to the Sterculiaceae, although he pointed out the high degree of overlap in pollen morphology and floral characters in the families Bombacaceae, Sterculiaceae, and Tiliaceae. Overlap of morphological characters in fossil pollen variously assigned to these three families was observed also by Wingate (1983:114) in the lower to middle Eocene Elko Formation of Nevada. The close comparison of *Bombacacidites* sp. aff. *B. reticulatus* from Florissant with pollen of *Florissantia speirii* suggests affinity of the dispersed pollen with the Sterculiaceae.

Bombacacidites sp. cf. *B. nanobrochatus*
Frederiksen et al. 1983
sensu Frederiksen 1988

PLATE 7, FIGURE 6

Description: Tribrevicolporate pollen with thickened margins along very short colpi. Grains oblate with very rounded triangular to nearly circular amb. Exine finely and uniformly reticulate. Equatorial diameter 20 to 25.5 μm.

Remarks: Frederiksen (1988:57) distinguished "cf. *B. nanobrochatus*" from *Bombacacidites nanobrochatus* Frederiksen et al. 1983 on the basis of the more triangular amb of the latter. Considerable variation in size, shape, and coarseness of reticulation was indicated by Frederiksen et al. (1983, Plate 20, Figs. 34–38) and Frederiksen (1988, Plate 15, Figs. 13–15, 18–20). Leopold (1974, Plate 44, Fig. 17) illustrated a very similar form as "Sterculiaceae? Section Helictareae." The striking similarity of the Florissant specimens to pollen of *Florissantia speirii* (see Manchester 1992, Figs. 43–47) leads us to consider the botanical affinity of *Bombacacidites* sp. cf. *B. nanobrochatus* to be with the Sterculiaceae.

Bombacacidites sp. A

PLATE 7, FIGURE 7

Description: Tricolporate pollen with planaperturate to sinuaperturate apertures. Colpi extend nearly to poles.

Grains oblate with triangular amb and broadly rounded angles. Exine uniformly reticulate. Equatorial diameter 16.5 to 24.5 μm.

Remarks: *Bombacacidites* sp. A differs from pollen extracted from *Florissantia* (see Manchester 1992, Figs. 43–52) in being more triangular in outline and having much longer colpi. We believe this morphotype is clearly assignable to the Bombacaceae.

Bombacacidites sp. B

PLATE 7, FIGURE 8

Description: Tribrevicolporate pollen with subcircular amb and finely reticulate exine. Colpi with thickened margins. Equatorial diameter 14.5 to 19 μm.

Remarks: This species is similar to *Bombacacidites* sp. 2 of Frederiksen (1988, Plate 14, Figs. 14–18) but has a more circular amb than that species and is smaller than most of the forms Frederiksen (1988) included in *Bombacacidites* sp. cf. *B. nanobrochatus*. *Bombacacidites* sp. B is quite similar to pollen of *Florissantia ashwillii* (see Manchester 1992, Fig. 48). The botanical affinity of this form is therefore most likely with the Sterculiaceae. This species is widely distributed throughout both shale units.

Genus *Lonicerapollis* Krutzsch 1962
Lonicerapollis sp. A

PLATE 7, FIGURE 11

Description: Tribrevicolporate pollen with vestibulate apertures, postvestibulum with thickened exine. Oblate with rounded triangular amb and protruding apertures. Exine with randomly spaced bacula, spinules, and verrucae. Equatorial diameter 35 μm and 44 μm (two specimens).

Remarks: This pollen morphotype is very suggestive of pollen of the Caprifoliaceae, and quite comparable to that of *Lonicera*, but not exclusively to that genus. It closely resembles *Porocolpopollenites rarobaculatus* Thiele-Pfeiffer from the Miocene of Germany (Thiele-Pfeiffer 1980:135, Plate 9, Figs. 18–25). Frederiksen (1980a:60; 1988:55) considered *Porocolpopollenites* Pflug in Thomson & Pflug 1953 to have affinity with the Symplocaceae and probably with *Symplocos*. *Caprifoliacidites* Sah 1967 is more spheroidal and has nonvestibulate apertures. The affinity of this species may be with either the Caprifoliaceae or the Symplocaceae. Only two specimens were observed.

Lonicerapollis sp. B

PLATE 7, FIGURE 9

Description: Pollen tribrevicolporate with vestibulate apertures and long, thickened postvestibulum. Oblate

with rounded triangular amb, apertures strongly protruding at the angles. Exine covered with widely spaced coarse bacula and pila, and slender echinae. Equatorial diameter 36 μm (single specimen).

Remarks: This morphotype probably belongs to the Caprifoliaceae, and it strongly resembles pollen of modern *Wiegelia floribunda*. A similar pollen type from the Oligocene of British Columbia was assigned to *Diervilla echinata* (Caprifoliaceae) by Piel (1971:1916). A single specimen was observed.

Lonicerapollis sp. C

PLATE 7, FIGURE 10

Description: Same as *Lonicerapollis* sp. A, except that the exine sculpture consists of more evenly distributed fine echinae. Equatorial diameter 31 μm and 36 μm (two specimens).

Remarks: This caprifoliaceous species bears close resemblance to pollen of extant *Symphoricarpos* (see Leopold 1969a, Plate 17-2, Fig. 43). Only two specimens were observed.

Genus *Intratriporopollenites* Pflug & Thomson in Thomson & Pflug 1953

Intratriporopollenites sp. cf. *I. instructus* (Potonié) Thomson & Pflug 1953

PLATE 7, FIGURE 12

Description: Brevitricolporate pollen with annulate pores, the annulus broadening at the equator, and very short, obscure colpi. Oblate with rounded triangular amb. Exine finely reticulate. Equatorial diameter 31 μm (single specimen).

Remarks: As illustrated by Thomson and Pflug (1953, Plate 10, Figs. 14–23), *Intratriporopollenites instructus* includes a broad variety of sizes and shapes and has sculpture of variable coarseness. This species is closely comparable to pollen of modern *Tilia*, and the affinity is considered to be with the Tiliaceae. A single specimen was observed.

Angiosperm Pollen: Triporate

Genus *Caryapollenites* Raatz ex Potonié 1960 emend. Krutzsch 1961

Caryapollenites veripites (Wilson & Webster) Nichols & Ott 1978

PLATE 7, FIGURE 13

Description: Triporate, heteropolar pollen with all three pores on one hemisphere and a distinctive circumpolar ring of thin exine. Equatorial diameter 24 to 37 μm. See Wilson and Webster (1946) and Nichols and Ott (1978:106) for detailed descriptions.

Remarks: *Caryapollenites veripites* differs only slightly from pollen of modern *Carya* (Nichols and Ott 1978:106) and certainly belongs with the Juglandaceae. This species is present in almost all samples of both shale units.

Genus *Corsinipollenites* Nakoman 1965

Corsinipollenites oculus-noctis parvus (Doktorowicz-Hrebnicka) Krutzsch 1968

PLATE 7, FIGURE 14

Description: Triporate pollen with large pores with thick, protruding annuli and distinctive viscin threads. Exine scabrate to psilate. Amb rounded triangular. Equatorial diameter 31 to 45.5 μm.

Remarks: The affinity of this taxon is probably with the Onagraceae, because it is quite similar to the pollen of extant *Epilobium* and *Oenothera*, although it is also comparable to pollen of *Humbertodendron* (Trigoniaceae), as illustrated by Lobreau-Callen et al. (1975, Plate 108).

Corsinipollenites parviangulus Frederiksen et al. 1983

PLATE 7, FIGURE 15

Description: Similar to *Corsinipollenites oculus-noctis parvus* but smaller; equatorial diameter 43.5 to 69 μm. See Frederiksen et al. (1983:39) for detailed description.

Remarks: The viscin threads visible on the illustrated specimen are fairly rare on fossil pollen, but they are a characteristic feature of pollen of extant genera of the Onagraceae.

Genus *Cricotriporites* Leidelmeyer 1966

Cricotriporites intrastructurus (Krutzsch & Vanhoorne) nov. comb.

PLATE 7, FIGURES 16–17

Basionym: *Subtriporopollenites intrastructurus* Krutzsch & Vanhoorne (1977:28, Plate 23, Figs. 8–19).

Synonym: *Celtipollenites intrastructurus* (Krutzsch & Vanhoorne) Thiele-Pfeiffer (1980:130, Plate 8, Figs. 32–34).

Description: Oblate to spheroidal pollen with circular amb. Triporate with slightly annulate, circular pores.

Exine scabrate to very finely verrucate. Equatorial diameter 24 to 31 µm.

Remarks: Krutzsch & Vanhoorne (1977:58, Plate 23, Figs. 8–11,15–19) assigned this species to *Subtriporopollenites* Pflug & Thomson in Thomson & Pflug 1953. The pores in *Subtriporopollenites* are subequatorial and displaced slightly to one hemisphere. The species *S. intrastructurus*, which has equatorial pores, was transferred to *Celtipollenites* Nagy 1969 by Thiele-Pfeiffer (1980:130), but *Celtipollenites* is zonoporate and has lalongate pores. *Annutriporites* aff. *A. subrotundus* Frederiksen et al. (1983, Plate 9, Fig. 29) may be conspecific. The Florissant species is best accommodated in *Cricotriporites*. The species is comparable to triporate pollen of extant *Celtis* (*C. occidentalis, C. tenuifolia*) of the Ulmaceae. Its spheroidal shape tends to cause the pores to appear to be displaced from the equator, as in *Subtriporopollenites*, but this is just an artifact of compression during fossilization. *Cricotriporites intrastructurus* occurs in several samples of the middle shale and in all samples of the upper shale.

?*Cricotriporites* sp.

PLATE 7, FIGURE 18

Description: Oblate triporate with circular amb. Pores equatorial and slightly annulate. Exine finely verrucate to scabrate. Equatorial diameter 14.5 to 20 µm.

Remarks: The Florissant specimens seem less clearly verrucate than *Annutriporites microgranulatus* (Frederiksen) Frederiksen 1983 as described and illustrated by Frederiksen (1980b:155, Plate 1, Figs. 23–29), but otherwise they are quite similar to that species. This species occurs in most samples of the upper shale unit. They are smaller and appear to be more oblate than *Cricotriporites intrastructurus* (Krutzsch & Vanhoorne) nov. comb.

Genus *Momipites*
Wodehouse emend. Nichols 1973

Momipites coryloides
Wodehouse 1933

PLATE 8, FIGURE 1

Description: Oblate triporate pollen with triangular amb, interporia convex, pores atriate; exine surface with evenly spaced fine granules, exine of even thickness at both poles and lacking structural modification. Equatorial diameter 27 to 28 µm (two specimens).

Remarks: These specimens are well within the range described for *Momipites coryloides*. They are tallied with

Momipites spp. in Table 3. Affinity of species of the genus *Momipites* is with the Juglandaceae.

Momipites microfoveolatus
(Stanley) Nichols 1973

PLATE 8, FIGURE 2

Description: Oblate triporate pollen with triangular amb. Sides straight to slightly convex or concave. Pores equatorial, small, and circular. Exine sculpture of evenly spaced fine granules (not foveolae). Equatorial diameter 18 to 22 µm.

Remarks: The affinity of this species has been considered to be with the *Engelhardia* group of the Juglandaceae by previous authors (Stanley 1965:300; Frederiksen 1980a:39). *Momipites microfoveolatus* occurs in most samples of both units and is separately listed in Table 3.

Momipites triradiatus
Nichols 1973

PLATE 8, FIGURE 3

Description: Oblate triporate pollen with triangular amb and distinctive triradiate polar thickening. Equatorial diameter 19 to 23.5 µm. See Nichols (1973:108) for detailed description.

Remarks: Florissant specimens of this species bear superficial resemblance to *Platycarya swasticoida* Elsik 1974 but differ in having structural modification of the exine at only one pole. (They have no relationship to pollen of the genus *Platycarya*.) Lengthy discussion of the *Momipites triradiatus* group of morphotypes has been presented by Frederiksen and Christopher (1978:120–126) and by Frederiksen (1979:149), who treated this pollen type under *Plicatopollis* Krutzsch emend. Frederiksen & Christopher 1978. We do not accept that treatment and regard *Momipites* and *Plicatopollis* as morphologically distinct genera. Unlike species of *Plicatopollis*, *Momipites triradiatus* has structural modification of only one polar hemisphere. Many specimens of *Momipites triradiatus* and *M. ventifluminis* are broken or poorly oriented, making it difficult to distinguish them. The two species were therefore combined for counting, and in combination they occur in most levels of the middle shale and also in the upper shale unit. Both species are tallied with *Momipites* spp. in Table 3.

Momipites ventifluminis
Nichols & Ott 1978

PLATE 8, FIGURE 4

Description: Oblate triporate pollen with triangular amb and three spots of thin exine near one pole. Equato-

rial diameter 23 μm (single specimen measured). See Nichols and Ott (1978:102) for detailed description.

Remarks: The structural modification that distinguishes this species—three spots of thinned exine—is present on one polar hemisphere only. Some specimens are difficult to distinguish from *Momipites triradiatus,* and in this study, records are combined with *M. triradiatus* in relative abundance counts and in Table 3.

Genus *Triatriopollenites*
Pflug in Thomson & Pflug 1953
Triatriopollenites subtriangulus
(Stanley) Frederiksen 1979

PLATE 8, FIGURE 5

Description: Triporate pollen with slightly protruding pores. Pores faintly annulate and atriate. Oblate with subcircular amb. Exine psilate to scabrate. Equatorial diameter 17 to 29 μm.

Remarks: Frederiksen (1979) compared this species to pollen of the modern genus *Comptonia* (Myricaceae). However, the Florissant specimens also appear similar to pollen of some species of *Carpinus* (Betulaceae; see *Carpinus caroliniana* in Heusser 1977, Plate 2, Fig. 18). Affinity is with either the Myricaceae or Betulaceae. Thiele-Pfeiffer (1980, Plate 8, Figs. 14–15) illustrated two closely similar forms as *Carpinuspollenites carpinoides* (Pflug) Nagy 1969 and *Triporopollenites rhenanus* (Thomson) Thomson & Pflug 1953. *Triatriopollenites subtriangulus* was observed in all samples of the middle shale and all but one of the upper shale.

Genus *Nudopollis* Pflug in Thomson & Pflug 1953
?*Nudopollis* sp.

PLATE 8, FIGURE 6

Description: Oblate triporate pollen with rounded triangular amb. Pores with thick annulus and long pore canals. Exine scabrate to faintly verrucate. Equatorial diameter 16.5 to 21.5 μm.

Remarks: The genus *Nudopollis* is a member of the Normapolles group of fossil pollen.

Genus *Trivestibulopollenites*
Pflug in Thomson & Pflug 1953
Trivestibulopollenites betuloides
Pflug in Thomson & Pflug 1953

PLATE 8, FIGURE 7

Description: Triporate pollen with protruding, vestibulate pores. Exine psilate. Equatorial diameter 20 μm.

Remarks: This species is closely comparable to pollen of modern *Betula,* and the affinity is here considered to be Betulaceae. A single specimen was observed.

Triporate sp. A

PLATE 8, FIGURE 8

Description: Oblate triporate grains with a circular amb that is notched by the equatorial pores. Pores large and faintly annulate. Exine psilate. Equatorial diameter 14.5 to 16.5 μm.

Triporate sp. B

PLATE 8, FIGURE 9

Description: Triporate pollen with annulate equatorial pores, circular amb, and scabrate to finely verrucate exine. Equatorial diameter 16.5 μm and 19 μm. Only two specimens were noted.

Triporate sp. C

PLATE 8, FIGURE 10

Description: Triporate pollen with fairly large, circular, annulate pores positioned at the equator. Amb circular in polar view. Exine strongly reticulate over entire surface. Equatorial diameter 23.5 to 27 μm.

Remarks: Although this species closely resembles ?*Subtriporopollenites reticulatus* Krutzsch & Vanhoorne 1977, the equatorial position of the pores argues against assigning the species to *Subtriporopollenites,* in which the pores are subequatorial. An essentially identical form was illustrated by Leopold (1974, Plate 42, Fig. 4) as triporate pollen undetermined.

Angiosperm Pollen:
Zonoporate

Genus *Alnipollenites* Potonié 1931
Alnipollenites verus
Potonié ex Potonié 1931

PLATE 8, FIGURE 11

Description: Psilate pollen with four vestibulate pores located at equator. Amb quadrangular with straight to slightly convex sides. Equatorial diameter 20 μm (single specimen).

Remarks: This *Alnus*-type grain may be a modern contaminant, although this species has been reported from the Paleocene to the Holocene. A single specimen was observed. Affinity: Betulaceae.

Genus *Reevesiapollis* Krutzsch 1970

Reevesiapollis triangulus (Mamczar) Krutzsch 1970

PLATE 8, FIGURE 12

Description: Oblate pollen with circular amb and four or five equatorial apertures. The apertures consist of vestibulate pores with very short colpi (zonocolporate). Exine uniformly reticulate. Equatorial diameter 16.5 to 20.5 µm.

Remarks: Thiele-Pfeiffer (1980:132) cites Krutzsch (1970b), and others, as considering the affinity of this species to be with the Sterculiaceae, genus *Reevesia*. Frederiksen (1980a:59) described similar but slightly larger pollen as *Intratriporopollenites stavensis* Frederiksen 1980, and he proposed the affinity to be with the Tiliaceae or possibly Bombacaceae. Tschudy and Van Loenen (1970, Plate 5, Fig. 15) illustrated a comparable form as *Tiliaepollenites* sp., and Rouse (1977, Plate 1, Figs. 21, 22) recorded essentially the same form as *Intratriporopollenites* sp. A. In the lower Tertiary the families Sterculiaceae, Tiliaceae, and Bombacaceae are difficult to distinguish palynologically because of transitional pollen morphologies.

?Reevesiapollis sp.

PLATE 8, FIGURE 13

Description: Essentially the same as *Reevesiapollis triangulus*, but exine sculpture distinctly striate-reticulate; grains slightly larger than *R. triangulus*. Equatorial diameter 24 µm and 29 µm (two specimens).

Remarks: This morphotype is similar in aperture structure and exine sculpture to forms assigned to *Brosipollis* by Frederiksen (1988), although *?Reevesiapollis* sp. is zonoporate rather than triporate. Only two specimens were observed.

Genus *Ulmipollenites* Wolff emend. Srivastava 1969

Ulmipollenites undulosus Wolff 1934

PLATE 8, FIGURE 14

Description: Pollen zonoporate with three to five annulate pores. Arci connecting two or more pores may or may not be present. Oblate with circular to polygonal amb. Exine strongly rugulate. Equatorial diameter 23 to 34.5 µm.

Remarks: The affinity of this species is undoubtedly with the Ulmaceae. Manchester (2001) recognizes two genera of Ulmaceae in the Florissant deposits, *Ulmus* and *Cedrelospermum*. Either or both of these genera may be represented by *Ulmipollenites undulosus*. *Ulmipollen-*

ites undulosus is present in all samples of both units and is one of the most common pollen species in the Florissant palynoflora. Manchester (2001) notes that leaves formerly referred to *Zelkova* are the second most abundant megafossil at Florissant; he (1989) transferred these leaves to *Cedrelospermum lineatus* and presented evidence indicating that *Cedrelospermum* is an extinct genus of the Ulmaceae. The presence of the genus *Ulmus* at Florissant also has been confirmed by Manchester (2001), but the relative abundances of pollen and leaves suggest that they share a common origin; thus, affinity with *Cedrelospermum* is favored. Ulmaceous pollen from the anthers of *Cedrelospermum nervosum* from the Green River Formation in Colorado illustrated by Manchester (1989) is smaller (18–22 µm) than specimens of *Ulmipollenites undulosus* from Florissant.

Zonoporate sp. A

PLATE 8, FIGURE 15

Description: Pollen with five or six annulate pores positioned at the equator. Oblate with circular to polygonal amb. Exine scabrate to psilate. Equatorial diameter 24.5 to 29 µm.

Remarks: Some of the specimens included in this group approach *Pterocarya* in having atriate pores and a polygonal amb. The majority of the specimens are very comparable to those reported by various authors under various names: Leopold (1974), six-pored pollen, undetermined; Leopold (1978), cf. *Trachelospermum*; B. D. Tschudy (1973), *Multiporopollenites* spp.; Tschudy and Van Loenen (1970), *Juglanspollenites* sp.; Wilkinson and Boulter (1980), *Polyatriopollenites* sp. Elsik (1974) assigned similar forms to *Nothofagus tschudyi*. He included those forms reported by Leopold and Tschudy (referenced here and under Zonoporate sp. B) as synonyms of *N. tschudyi*. The porate, slightly atriate apertures and psilate to scabrate exine of these forms argue against their having affinity with *Nothofagus*, pollen of which is distinctly brevicolpate and has echinate to baculate sculpture. Resemblance of Zonoporate sp. A to pollen of *Pterocarya* suggests affinity with the Juglandaceae, as noted by B. D. Tschudy (1973), although Leopold (1978) suggested possible affinity with the Apocynaceae (the genus *Trachelospermum*).

Zonoporate sp. B

PLATE 8, FIGURE 16

Description: Pollen with five to seven annulate pores positioned at equator or on one polar hemisphere. Exine faintly scabrate. Equatorial diameter 26 µm.

Remarks: A closely comparable specimen was illustrated by Leopold (in Penny 1969, Plate 16-6, Fig. 30) as "undetermined dicotyledon." Morphology is comparable to Zonoporate sp. A, but the position of some pores off the equator is similar to *Juglanspollenites nigripites* (Wodehouse) nov. comb. Records of occurrence are combined with those of Zonoporate sp. A in Table 3.

Zonoporate sp. C

PLATE 8, FIGURE 17

Description: Zonoporate pollen with five to six circular pores and distinctly striate exine. Oblate to subspherical with circular amb. Equatorial diameter 35 µm (single specimen).

Remarks: The morphology of this species is strongly suggestive of the Polemoniaceae, particularly with regard to the pollen of some species of *Collomia, Gilia, Ipomopsis,* and possibly others. If indeed Zonoporate sp. C is a fossil of the Polemoniaceae, evidently it is the stratigraphically oldest record of this modern family. Muller (1981) cites as the oldest record of this family certain specimens from the upper Miocene that resemble modern pollen of *Gilia*. A single specimen of Zonoporate sp. C was observed in sample D7012-B, and a possible fragment was observed in sample D7012-C.

Angiosperm Pollen:
Pantoporate, Psilate

Genus *Juglanspollenites*
Raatz 1937

Juglanspollenites nigripites
(Wodehouse) nov. comb.

PLATE 8, FIGURES 18–19

Basionym: *Juglans nigripites* Wodehouse (1933:504, Fig. 31).

Description: Spheroidal pollen with circular to oval amb with widely spaced pores on one hemisphere only. Pores annulate. Exine appearing psilate; sculpture of evenly spaced fine granules. Equatorial diameter 27.5 to 38 µm.

Remarks: The affinity of this species undoubtedly is with the Juglandaceae, but it cannot be placed in the modern genus *Juglans* with certainty (cf. Nichols 1973:104). *Juglanspollenites nigripites* occurs in all but one sample of the middle shale and in all samples of the upper shale.

Genus *Chenopodipollis*
Krutzsch 1966

Chenopodipollis sp.

PLATE 8, FIGURE 20

Description: Pantoporate pollen with rather widely and irregularly spaced annulate pores over entire surface. Annuli wide and distinctly columellate. Exine psilate to scabrate. Grains spheroidal with circular amb. Equatorial diameter 19 to 31 µm.

Remarks: Leopold (in Penny 1969, Plate 16-6, Figs. 32–33) illustrated identical forms from the Florissant as Chenopodiaceae, *Sarcobatus*-type, although pollen of the family Chenopodiaceae is notoriously difficult to distinguish from that of the family Amaranthaceae. *Multiporopollenites* Pflug in Thomson & Pflug 1953 differs in having fewer pores unevenly distributed over the surface of the grain (as in pollen of *Juglans*). Frederiksen (1980a) illustrated a comparable form and assigned it to *Parsonsidites conspicuus* Frederiksen 1973. Couper (1960) described *Parsonsidites* as having few large, irregularly distributed pores and suggested affinity with the Apocynaceae. *Psilaperiporites* Da Silva Pares Regali, Uesugui, & Da Silva Santos 1974 may be synonymous with *Parsonsidites*. We consider the affinity of this species to be with the Chenopodiaceae or Amaranthaceae.

Angiosperm Pollen:
Pantoporate, Reticulate

Genus *Erdtmanipollis* Krutzsch 1962

Erdtmanipollis procumbentiformis
(Samoilovitch in Samoilovitch
& Mtchedlishvili) Krutzsch 1966

PLATE 8, FIGURE 22

Description: See Srivastava (1972:320) for description. Equatorial diameter 31 to 40 µm.

Remarks: The affinity of this species is considered to be with the Buxaceae, with either *Pachysandra* or *Sarcococca*. Only two complete specimens were observed, although fragments were noted in several samples.

Genus *Persicarioipollis* Krutzsch 1962

Persicarioipollis sp. cf. *P. welzowense*
Krutzsch 1962

PLATE 8, FIGURE 24

Description: Pantoporate pollen with tiny, often obscured pores. Pores on floors of many, but not all, lu-

mina of the very coarse reticulum. Muri of reticulum thick and supported by multiple thick baculae (non-simplibaculate). Grains spheroidal to discoid with circular amb. Equatorial diameter 50 x 56 µm (one specimen).

Remarks: The affinity of this species is with the Polygonaceae, possibly *Persicaria* or *Polygonum*. The genus has a record dating from the Paleocene that Muller (1981) accepted as representing the family Polygonaceae. A single specimen was observed in samples from Florissant.

?*Persicarioipollis* sp. A

PLATE 8, FIGURE 21

Description: As with *Persicarioipollis* sp. cf. *P. welzowense*, but significantly smaller. Equatorial diameter 16.5 to 22 µm.

Remarks: Similar forms in size and sculpture were illustrated by Thiele-Pfeiffer (1980, Plate 13, Figs. 14–18) and Mohr (1984, Plate 12, Figs 7.1, 7.2). Both these forms were described as being tricolporate or tricolpate, although Mohr (1984) noted that the colpi are very unclear. Affinity possibly is with the Polygonaceae.

?*Persicarioipollis* sp. B

PLATE 8, FIGURE 23

Description: Pantoporate pollen with widely spaced pores, often difficult to discern within the coarsely reticulate sculpture. Sculpture consisting of densely packed bacula and clavae supporting an incomplete reticulum. Grains spheroidal with circular amb. Diameter 22.5 to 31 µm.

Remarks: This species differs from *Persicariopollis* sp. cf. *P. welzowense* and ?*Persicariopollis* sp. A in size and in the incomplete development of the reticulum. Affinity possibly is with the Polygonaceae.

Angiosperm Pollen: Pantoporate, Echinate

Genus *Malvacipollis*
Harris emend. Krutzsch 1966
Malvacipollis sp. A

PLATE 9, FIGURE 1

Description: Pollen pantoporate, possibly zonoporate. Exine tectate, with stout supratectal coni that are as broad at the base as they are long. Amb circular. Equatorial diameter 28 to 37 µm.

Remarks: This species is quite similar to pollen of extant *Sphaeralcea coccinea* (Malvaceae), although the

pores are not as distinctly annulate as are those of *S. coccinea*. The botanical affinity probably is with the Malvaceae. *Malvacipollis* sp. A occurs in several samples of the middle shale.

This is one of four species in the Florissant palynoflora that evidently constitute the stratigraphically oldest record of the family Malvaceae in North America, based on consideration of records cited by Muller (1981) and accepted by Collinson et al. (1993). Muller (1981) cited the oldest records of the modern family as being from the upper Eocene of Venezuela and Brazil.

Malvacipollis sp. B

PLATE 9, FIGURE 2

Description: Pantoporate to zonoporate pollen with large, densely packed, supratectal spines that are more long than broad. Pores indistinct, mostly hidden by spinose sculpture. Amb circular. Equatorial diameter 44 to 54.5 µm.

Remarks: This form differs from *Malvacipollis* sp. A in having longer, stouter, and more numerous spines, and in being significantly larger. A comparable form was illustrated by Leopold (1969a, Plate 17-2, Fig. 41; 1974, Plate 45, Fig. 16) as Malvaceae. *Malvacipollis* sp. B was observed in several samples of the middle shale unit. It is one of four species in the Florissant palynoflora that evidently constitute the stratigraphically oldest record of the Malvaceae in North America (see remarks under *Malvacipollis* sp. A).

Malvacipollis sp. C

PLATE 9, FIGURE 3

Description: Large pantoporate pollen with annulate pores. Exine infrabaculate with widely spaced supratectal coni. Amb circular. Equatorial diameter 52.5 µm (single specimen).

Remarks: Morphologically this species is closely comparable to *Malvacipollis tschudyi* (Frederiksen) Frederiksen 1980, except for the larger size of *Malvacipollis* sp. C. Particularly comparable in form (but not size) are *Echiperiporites* spp. of R. H. Tschudy (1973, Plate 3, Figs. 13–14), which were included in the synonymy for *M. tschudyi* by Frederiksen (1980a:44). *Malvacipollis spinulosa* Frederiksen in Frederiksen et al. (1983:42, Plate 12, Figs. 14–16; Plate 13, Fig. 1) appears to be conspecific with *M. tschudyi*, although Frederiksen states that *M. tschudyi* has a thicker exine. Forms illustrated by Frederiksen (1988, Plate 5, Figs. 9–14) as *M. tschudyi* and *M.*

cf. *M. tschudyi* have much coarser spines and indistinct pores and probably are referable to a different species. Frederiksen et al. (1983:42) suggested that the affinity of *M. tschudyi* and *M. spinulosa* is more likely with the Euphorbiaceae than the Malvaceae. R. H. Tschudy (1973: B15) suggested a possible affinity with the Picrodendraceae. We refer *Malvacipollis* sp. C to the Malvaceae because it has supratectal coni or spines with broad bases and several annulate pores, features characteristic of modern pollen of the family. *Malvacipollis* sp. C was observed only in sample D7012-S. It is one of four species in the Florissant palynoflora that may constitute the stratigraphically oldest record of the Malvaceae in North America (see remarks under *Malvacipollis* sp. A).

Malvacipollis sp. D

PLATE 9, FIGURE 4

Description: Pollen probably pantoporate to zonoporate, but pores rather indistinct. Exine covered with fairly fine supratectal spines. Amb circular. Equatorial diameter 31 to 40 µm.

Remarks: This species differs from *Malvacipollis tschudyi* (Frederiksen) Frederiksen 1980 in having indistinct, nonannulate pores. It is comparable to the forms illustrated as ?aff. *Nothofagus* by Tschudy and Van Loenen (1970, Plate 3, Figs. 23, 27–28), but morphologically it is much closer to the Malvaceae than to the Nothofagaceae. *Malvacipollis* sp. D occurs in several samples of the middle shale unit. It is one of four species in the Florissant palynoflora that may constitute the stratigraphically oldest record of the Malvaceae in North America (see remarks under *Malvacipollis* sp. A).

Genus *Periporopollenites*
Pflug & Thomson in
Thomson & Pflug 1953

?Periporopollenites sp.
cf. *P. stigmosus* (Potonié)
Pflug & Thomson in
Thomson & Pflug 1953

PLATE 9, FIGURE 5

Description: Pantoporate pollen with irregularly spaced pores that are oval in shape and have somewhat ragged margins. Exine finely reticulate. Amb circular to ovoid. Diameter 27.5 to 40 µm.

Remarks: This taxon is similar to *Periporopollenites stigmosus* (Thiele-Pfeiffer 1980:139; Mohr 1984:72), but the pores are less circular and lack the verrucate pore mem-

brane that is characteristic of *P. stigmosus*. The authors cited considered the affinity of *P. stigmosus* to be with *Liquidambar* (Hamamelidaceae), but the forms encountered in the Florissant Formation differ sufficiently from *Liquidambar* to render the affinity uncertain. Affinity possibly is with the Hamamelidaceae or Polemoniaceae. This species was observed in several samples of the middle shale unit.

Angiosperm Pollen: Monoporate

Genus *Cyperaceaepollis*
Krutzsch 1970

Cyperaceaepollis sp. cf. *C. neogenicus*
Krutzsch 1970

PLATE 9, FIGURE 6

Description: Pollen pear-shaped, thin-walled, with finely infrareticulate exine. Single, nonannulate pore near center of the grains, which may be the result of an oblique view; pore probably positioned at broadest end of grains. Long axis 29 to 31 µm; short axis 23 to 27 µm.

Remarks: This morphotype is comparable to pollen of extant Cyperaceae. *Cyperaceaepollis neogenicus* is defined as having one or more secondary pores along the equator (Krutzsch 1970a:66), but these are probably areas of degradation in the thin pollen wall. *Cyperaceaepollis piriformis* Thiele-Pfeiffer 1980 is similar but much larger (length 32–50 µm). Only two specimens were observed in the middle shale unit, and a questionable one was observed in the upper shale unit.

Genus *Graminidites*
Cookson ex Potonié 1960

Graminidites crassiglobosus (Trevisan)
Krutzsch 1970

PLATE 9, FIGURES 7–8

Description: Monoporate pollen with annulate pore and psilate exine. Grains spheroidal; amb circular. Diameter 18 to 31 µm.

Remarks: This form appears to be conspecific with *Graminidites crassiglobosus* as illustrated by Kirchner (1984:105, Plate 5, Fig. 1), although some of the Florissant forms tend to be somewhat larger. The affinity is considered to be with the Poaceae (Gramineae). *Graminidites crassiglobosus* occurs in most samples of the middle shale and also in the upper shale unit.

Genus *Pandaniidites* Elsik 1968

?*Pandaniidites* sp.

PLATE 9, FIGURE 9

Description: Spheroidal to oval pollen with echinate sculpture. Spines numerous, tapering from a slightly expanded base that appears to lie within the ektexine. Various specimens appear inaperturate, monoporate, or questionably with two or three small pores. Pore(s) small, rather indistinct, and nonannulate. Diameter 17 to 28 μm.

Remarks: Because *Pandaniidites* is characterized by monoporate, spinose pollen with an annulate pore, it is questionable whether the Florissant forms should be assigned to that fossil genus. The lack of a distinct, annulate pore is compatible with modern *Pandanus* (Muller 1981:112), and the Florissant specimens closely resemble forms reported as *Pandanus* by Jarzen (1978, Plate 1, Fig. 9) and Leopold (1969b, Plate 305, Figs. 16–19). A comparable form was illustrated by Leopold (1978, Plate 2, Figs. 17–18) as monoporate pollen undetermined. Hotton et al. (1994) reviewed the ultrastructure and affinities of fossil pollen attributed to the Pandanaceae. The affinity of the Florissant forms is tentatively considered to be with the Pandanaceae.

Genus *Sparganiaceaepollenites* Thiergart 1937

Sparganiaceaepollenites sparganioides (Meyer) Krutzsch 1970

PLATE 9, FIGURE 10

Description: Spheroidal to oval, monoporate pollen. Pore distinct, circular, and nonannulate. Exine tectate, reticulate. Grains occur as individual monads only. Diameter 22 to 27 μm.

Remarks: This morphotype probably represents pollen of either the Sparganiaceae or Typhaceae, which are difficult to distinguish when encountered as individual monads. *Sparganiaceaepollenites sparganioides* was observed at every stratigraphic level of the middle shale and at several in the upper shale unit.

Angiosperm Pollen: Diporate

Diporate pollen cf. *Trema* Lour.

PLATE 9, FIGURE 11

Description: Pollen with two annulate pores positioned on opposite sides of circular amb. Exine scabrate to finely verrucate. Diameter 14.5 x 20 μm and 16 x 16.5 μm (two specimens).

Remarks: This form is quite similar to forms illustrated as *Trema* (Ulmaceae) by Leopold (1978, Plate 2, Figs. 31–32) and to illustrations of extant *Trema* pollen by Tsukada (1964, Plate 28, Figs. 17–18). Frederiksen (1988:48, Plate 1, Fig. 17) assigned a similar form to *Diporites* sp. There is some question as to the validity of the genus *Diporites* Van der Hammen 1954 (see Jansonius and Hills 1976:card 811); thus the Florissant forms are not assigned to that genus. The affinity is possibly with the Ulmaceae.

Angiosperm Pollen: Tetrads

Genus *Ericipites* Wodehouse 1933

Ericipites sp. cf. *E. longisulcatus* Wodehouse 1933

PLATE 9, FIGURE 12

Description: Pollen tetrad with overall rounded triangular shape and slight notches in the amb where the individual grains join. Grains tricolporate, the colpi long and narrow and the pores tiny and indistinct. Exine appears psilate to scabrate. Diameter of tetrad 25 to 31 μm.

Remarks: This form is comparable to *Ericipites longisulcatus* Wodehouse 1933 except that it is somewhat smaller. It also is similar to *E. ericius* (Potonié) Potonié 1960 but again is smaller. It is also similar to *E. callidus* (Potonié) Krutzsch 1970 (as illustrated by Thiele-Pfeiffer 1980, Plate 17, Fig. 2; and Mohr 1984, Plate 19, Fig. 14), but it tends to be slightly larger. Frederiksen (1980a:64) cites Krutzsch (1970c:422) as suggesting that *E. callidus* and *E. ericius* may be synonymous. The affinity of *Ericipites* is with the Ericaceae.

Angiosperm Pollen: Genus and Species Indeterminate

?Triporate sp. cf. ?*Ruellia laxa* (Frederiksen) Frederiksen et al. 1983

PLATE 9, FIGURES 13–14

Description: Pollen probably with three pores that are difficult to observe because of an enveloping reticulum. Reticulum loosely surrounds, and appears detached from, an inner body of triangular shape. One angle broadly rounded; other two tapering and bluntly truncated. Enveloping reticulum very coarse with large, irregularly shaped lumina; inner body appears to be missing

in several specimens. Exine on inner body scabrate to finely verrucate. No specimens were observed that appeared to be just the inner body with the outer reticulum removed. Equatorial diameter 31 to 49 μm.

Remarks: This taxon is comparable to the forms illustrated by Frederiksen et al. (1983:41, Plate 12, Figs. 3–5) and Frederiksen (1980a:40, Plate 7, Figs. 21– 22, as *Proteacidites? laxus*). Frederiksen et al. (1983) compared this form with several extant species of *Ruellia* (Acanthaceae), a genus of tropical and subtropical America. Their illustration of *Ruellia paniculata* (Frederiksen et al. 1983, Plate 12, Figs. 6–7) suggested similarity with *?Ruellia laxa* but does not appear to provide conclusive evidence of affinity with either *Ruellia* or the Acanthaceae (thus their question mark applied to the genus). There is superficial similarity of this taxon to some forms assigned to *Proteacidites*, such as *P. nasus* Truswell & Owen 1988, although the ektexinal reticulum of *Proteacidites* is more closely appressed to the endexine than occurs with *?R. laxa*. Also, *P. nasus* possesses a strongly projecting boss at one pole (Truswell and Owen 1988), which is lacking in *?R. laxa*. We conclude that this palynomorph is of uncertain affinity, possibly Proteaceae or Acanthaceae, and probably warrants a new genus to accommodate it. Placing it in an extant genus, even questionably, seems inappropriate without further evidence of affinity. MacGinitie (1953) identified winged fruits from Florissant as belonging to the genus *Lomatia* (Proteaceae), but Manchester (2001) rejects that identification and assigns these fruits to *Cedrelospermum* (Ulmaceae).

Acknowledgments

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Plate Descriptions

PLATE 1. All illustrations in brightfield illumination unless otherwise noted; all magnifications ca. 900x.
Figures

1. *Botryococcus* sp., D7012-B
2. *Pediastrum* sp., D7012-C (differential interference contrast)
3. *Ovoidites elongatus*, D7012-F
4. *Ovoidites ligneolus*, D7012-F
5. *Ovoidites* sp., D7012-A (800x)
6. Algal spores, gen. & sp. indet., D7012-O
7. *Catinipollis geiseltalensis*, D7012-G (differential interference contrast)
8. *Laevigatosporites ovatus*, D7012-L
9. *Polypodiisporonites afavus*, D7012-L
10. *Polypodiisporonites* sp. cf. *Polypodiidites secundus*, D7012-H
11. *Lygodiumsporites adriennis*, D7012-D
12. *Baculatisporites* sp. A, D7012-C
13. *Biretisporites* sp., D7012-C
14. *Polycingulatisporites* sp., D7012-E

PLATE 2. All illustrations in brightfield illumination unless otherwise noted; all magnifications ca. 1000x.
Figures

1. *Lusatisporis* sp. cf. *L. perinatus*, D7012-F
2. *Heliosporites* sp., D7012-J
3. *Foveotriletes* sp., D7012-G
4. *Stereisporites* sp., D7012-A
5. *Echinatisporis* sp., D7012-C
6. Rugulate trilete, gen. & sp. indet., D7012-C
7. Reticulate trilete, gen. & sp. indet., D7012-G
8. *Azolla cretacea*, D7012-F (differential interference contrast)
9. *Pristunuspollenites* sp. cf. *P. microsaccus*, D7012-B
10. *Pityosporites* sp. A, D7012-B
11. *Pityosporites* sp. A, D7012-B
12. *Pityosporites* sp. B, D7012-E

PLATE 3. All illustrations in brightfield illumination; all magnifications ca. 1,000x.
Figures

1. ?*Abiespollenites* sp., D7012-I
2. *Podocarpidites* sp., D7012-H
3. *Zonalapollenites* sp., D7012-G
4. *Taxodiaceaepollenites hiatus*, D7012-T
5. *Sequoiapollenites* sp. cf. *S. rotundus*, D7012-J
6. cf. *Taxodiaceaepollenites* sp. A of Rouse 1977, D7012-I
7. *Taxodiacites* sp. cf. *T. verrucosus*, D7012-O

8. *Ephedripites claricristatus*, D7012-J
9. *Ephedripites exiguus* nov. comb., D7012-I
10. *Arecipites* sp. cf. *A. pertusus*, D7012-H

PLATE 4. All illustrations in brightfield illumination unless otherwise noted; all magnifications ca. 1,000x.
Figures

1. *Piceapollis* sp., D7012-I
2. *Liliacidites* sp., D7012-L
3. ?*Nupharipollenites* sp., D7012-C
4. *Cupuliferoidaepollenites liblarensis*, D7012-B
5. *Fraxinoipollenites medius*, D7012-I
6. *Salixipollenites* sp. A, D7012-B
7. *Salixipollenites* sp. B, D7012-A
8. *Salixipollenites* sp. C, D7012-D
9. *Rousea* sp., D7012-S
10. *Rousea araneosa*, D7012-Q
11. *Quercoidites microhenricii*, D7012-C (equatorial view)
12. *Quercoidites microhenricii*, D7012-P (polar view; differential interference contrast)

PLATE 5. All illustrations in brightfield illumination unless otherwise noted; all magnifications ca. 1,000x.
Figures

1. *Cercidiphyllites* sp., D7012-O
2. *Aceripollenites striatus*, D7012-J (three specimens of the same species)
3. *Aceripollenites* sp., D7012-D (polar view)
4. Tricolpate sp. A, D7012-N (differential interference contrast)
5. Tricolpate sp. B, D7012-D
6. Tricolpate sp. C, D7012-C
7a–b. Tricolpate sp. D, D7012-N (high- and middle-level focus on same specimen)
8. *Tricolpopollenites parmularius*, D7012-P
9. *Tricolpopollenites parmularius*, D7012-C
10. *Siltaria* sp. cf. *S. scabriextima*, D7012-C
11. *Siltaria* sp. cf. *S. pacata*, D7012-A
12. *Rhamnacidites delicatus*, D7012-B
13. *Araliaceoipollenites profundus*, D7012-J
14. cf. *Araliaceoipollenites euphorii*, D7012-G
15. cf. *Horniella brevicolpata*, D7012-D
16. *Horniella* sp. A, D7012-C
17. *Horniella* sp. B, D7012-N
18. *Rhoipites* sp. A, D7012-C
19. *Rhoipites* sp. B, 7012-B
20. *Rhoipites* sp. D, D7012-F
21. *Rhoipites* sp. C, D7012-C

(continued)

PLATE 6. All illustrations in brightfield illumination unless otherwise noted; all magnifications ca. 1,000x.
Figures

1. *Margocolporites* sp. cf. *M. vanwijhei*, D7012-G
2. *Margocolporites* sp. cf. *M. vanwijhei*, D7012-J
3. *Rhoipites* sp. E, D7012-E
4. *Rhoipites* sp. F, D7012-G
5. Tricolporate sp. A, D7012-A
6. Tricolporate sp. B, D7012-D
7. Tricolporate sp. C, D7012-C
8. *Ailanthipites berryi*, D7012-E
9. *Ailanthipites* sp. A, D7012-B
10. *Ailanthipites* sp. B, D7012-M (differential interference contrast)
11. *Alangiopollis* sp., D7012-E
12. Tricolporate sp. D, D7012-C (large form)
13. Tricolporate sp. D, D7012-A (small form)
14. Tricolporate sp. E, D7012-O
15. ?*Quercipollenites* sp. cf. pollen of *Fagopsis longifolia*, D7012-A
16. *Verrutricolporites* sp. A, D7012-J (equatorial view)
17. *Verrutricolporites* sp. B, D7012-D (polar view; differential interference contrast)
18. *Slowakipollis hippophaëoides*, D7012-J
19a–b. Asteraceae pollen sp. A, D7012-Q (two views in differential interference contrast)
20. *Tetracolporopollenites brevis*, D7012-B
21. *Tetracolporopollenites* sp., D7012-D
22. ?*Meliapollis* sp., D7012-D
23. *Boehlensipollis* sp. cf. *B. granulata*, D7012-B

PLATE 7. All illustrations in brightfield illumination unless otherwise noted; all magnifications ca. 1,000x.
Figures

1. *Myrtaceidites parvus*, D7012-B
2. *Cupanieidites* sp. A, D7012-D
3. *Cupanieidites* sp. B, D7012-B
4. *Cupanieidites* sp. B, D7012-M
5. *Bombacacidites* sp. aff. *B. reticulatus*, D7012-C
6. *Bombacacidites* sp. cf. *B. nanobrochatus*, D7012-B
7. *Bombacacidites* sp. A, D7012-C
8. *Bombacacidites* sp. B, D7012-E
9. *Lonicerapollis* sp. B, D7012-I
10. *Lonicerapollis* sp. C, D7012-E
11. *Lonicerapollis* sp. A, D7012-O (two specimens of the same species)
12. *Intratriporopollenites* sp. cf. *I. instructus*, D7012-A (differential interference contrast)
13. *Caryapollenites veripites*, D7012-B (differential interference contrast)

14. *Corsinipollenites oculus-noctis parvus*, D7012-H (differential interference contrast)
15. *Corsinipollenites parviangulus*, D7012-E
16. *Cricotriporites intrastructurus* nov. comb., D7012-C (differential interference contrast)
17. *Cricotriporites intrastructurus* nov. comb., D7012-P
18. ?*Cricotriporites* sp., D7012-S

PLATE 8. All illustrations in brightfield illumination unless otherwise noted; all magnifications ca. 1,000x.
Figures

1. *Momipites coryloides*, D7012-I (differential interference contrast)
2. *Momipites microfoveolatus*, D7012-G
3. *Momipites triradiatus*, D7012-M
4. *Momipites ventifluminis*, D7012-E (differential interference contrast)
5. *Triatriopollenites subtriangulus*, D7012-C
6. ?*Nudopollis* sp., D7012-D
7. *Trivestibulopollenites betuloides*, D7012-C
8. Triporate sp. A, D7012-E
9. Triporate sp. B, D7012-C
10. Triporate sp. C, D7012-H
11. *Alnipollenites verus*, D7012-N
12. *Reevsiapollis triangulus*, D7012-F
13. ?*Reevsiapollis* sp., D7012-I
14. *Ulmipollenites undulosus*, D7012-B
15. Zonoporate pollen sp. A, D7012-J
16. Zonoporate pollen sp. B, D7012-J (differential interference contrast)
17. Zonoporate pollen sp. C, D7012-B
18. *Juglanspollenites nigripites* nov. comb., D7012-B
19. *Juglanspollenites nigripites* nov. comb., D7012-B
20. *Chenopodipollis* sp., D7012-J
21. ?*Persicariopollis* sp. A, D7012-Q (differential interference contrast)
22. *Erdtmanipollis procumbentiformis*, 7012-H
23. ?*Persicariopollis* sp. B, D7012-E
24. *Persicariopollis* sp. cf. *P. welzowense*, D7012-C

PLATE 9. All illustrations in brightfield illumination unless otherwise noted; all magnifications ca. 1,000x.
Figures

1. *Malvacipollis* sp. A, D7012-F
2. *Malvacipollis* sp. B, D7012-C
3. *Malvacipollis* sp. C, D7012-S (differential interference contrast)
4. *Malvacipollis* sp. D, D7012-S (differential interference contrast)

(continues)

5. ?*Periporopollenites* sp. cf. *P. stigmosus*, D7012-M
6. *Cyperaceaepollis* sp. cf. *C. neogenicus*, D7012-L (differential interference contrast)
7. *Graminidites crassiglobosus*, D7012-G (differential interference contrast)
8. *Graminidites crassiglobosus*, D7012-B

9. ?*Pandaniidites* sp., D7012-E
10. *Sparganiaceaepollenites sparganioides*, D7012-H
11. Diporate pollen sp. cf. *Trema*, D7012-H
12. *Ericipites* sp. cf. *E. longisulcatus*, D7012-B
13. ?Triporate sp. cf. ?*Ruellia laxa*, D7012-J
14. ?Triporate sp. cf. ?*Ruellia laxa*, D7012-E (differential interference contrast)
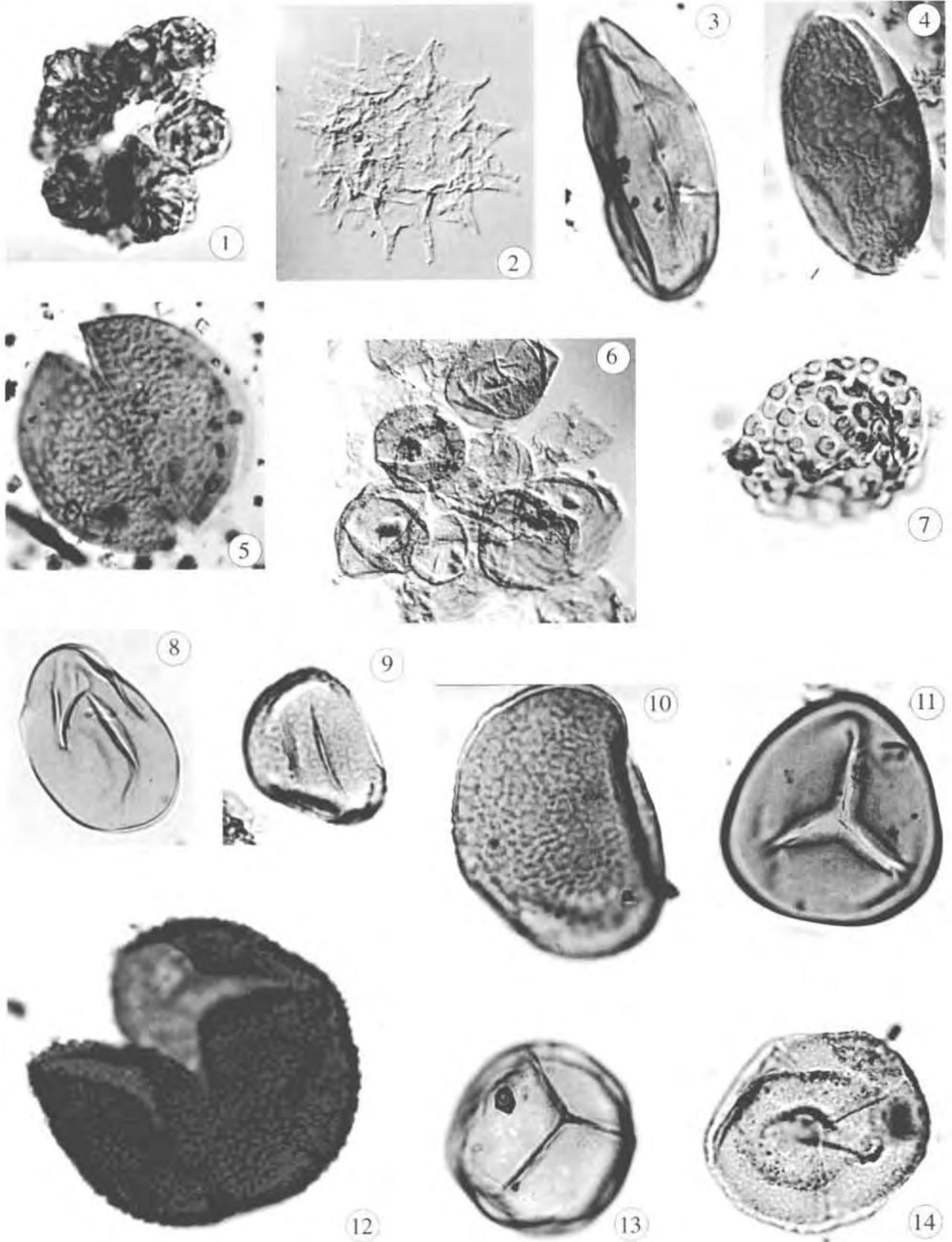
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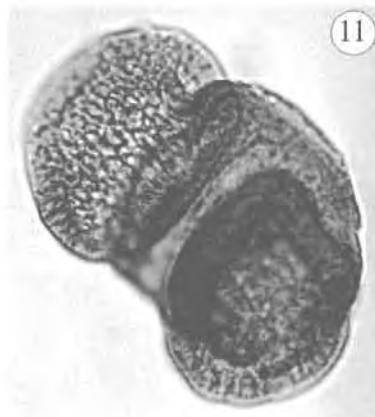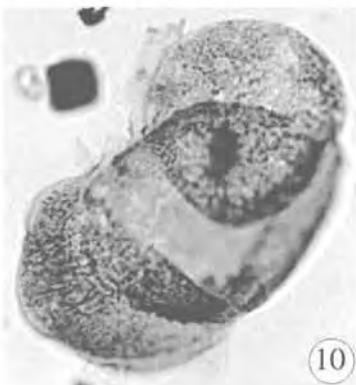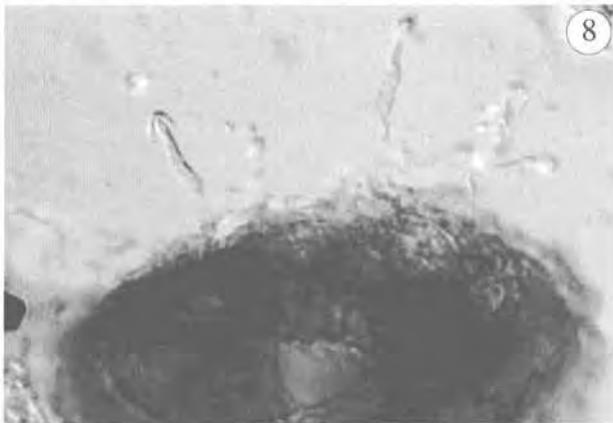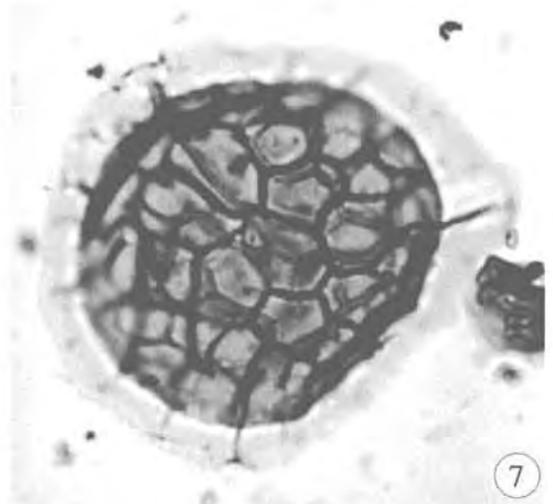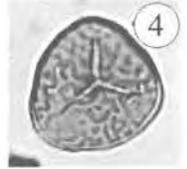
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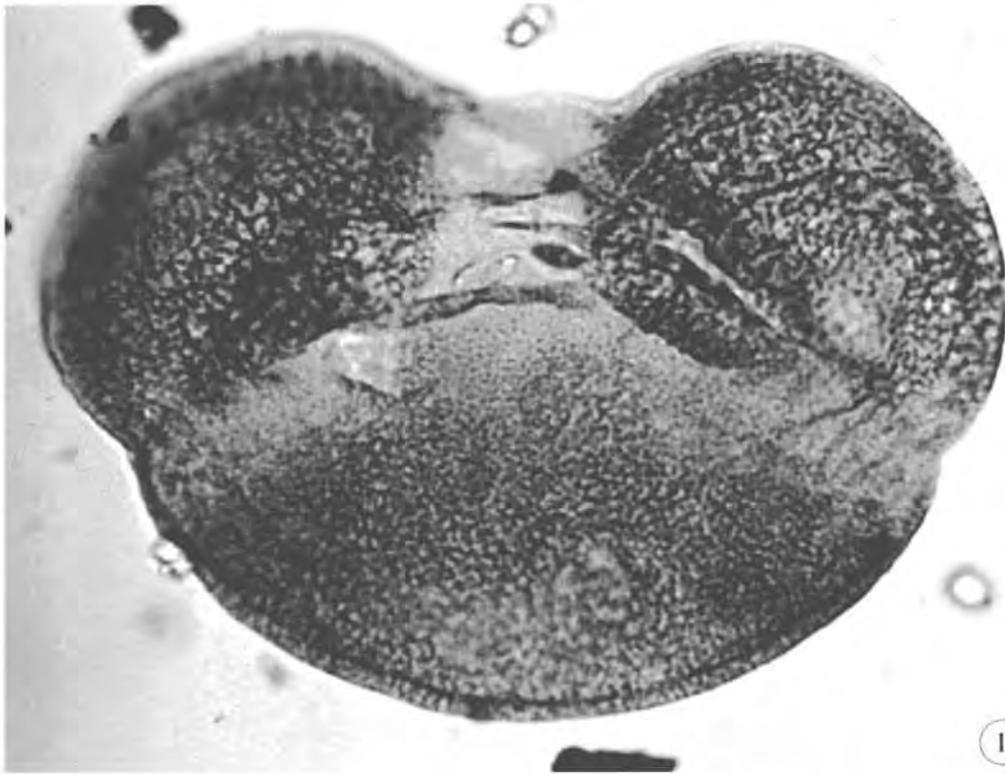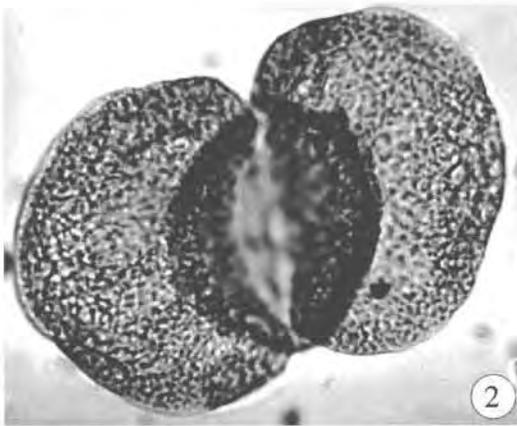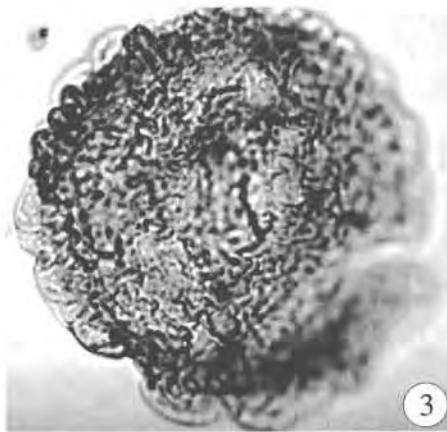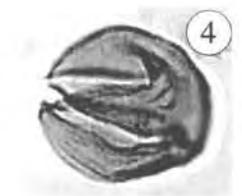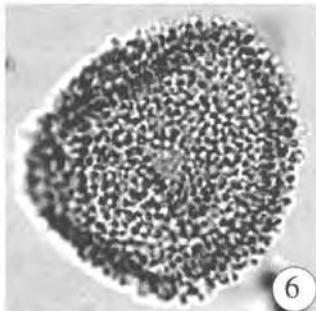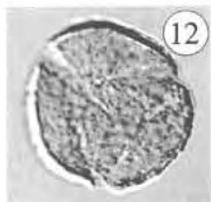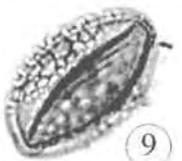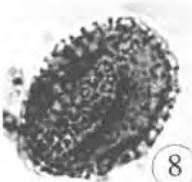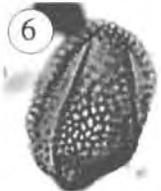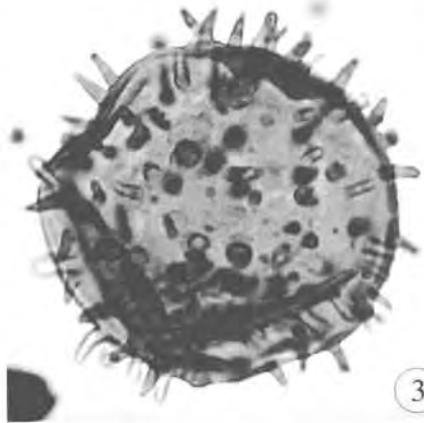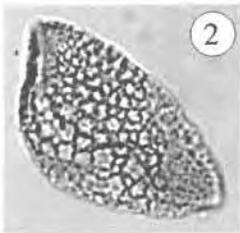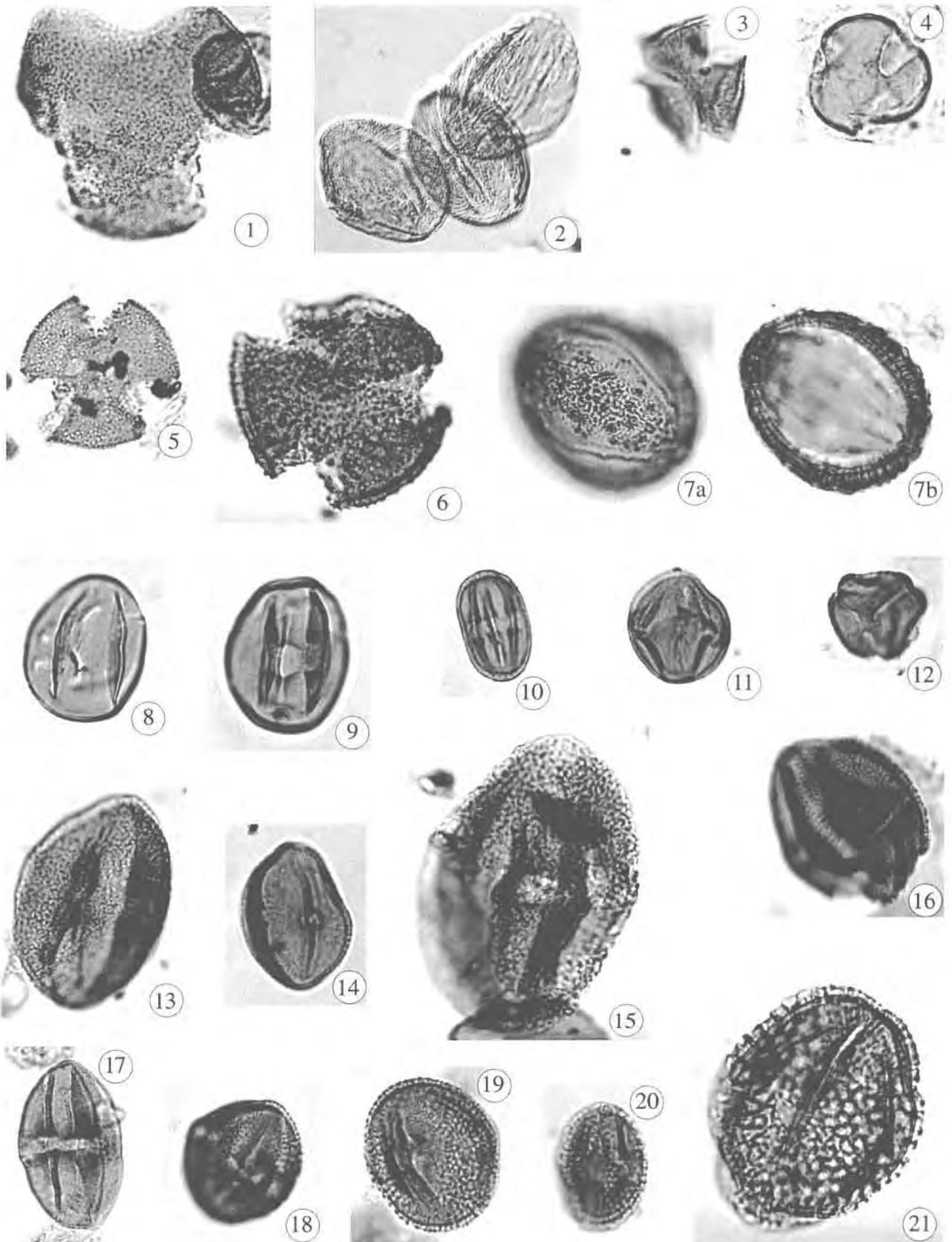
PLATE 3.

PLATE 4.

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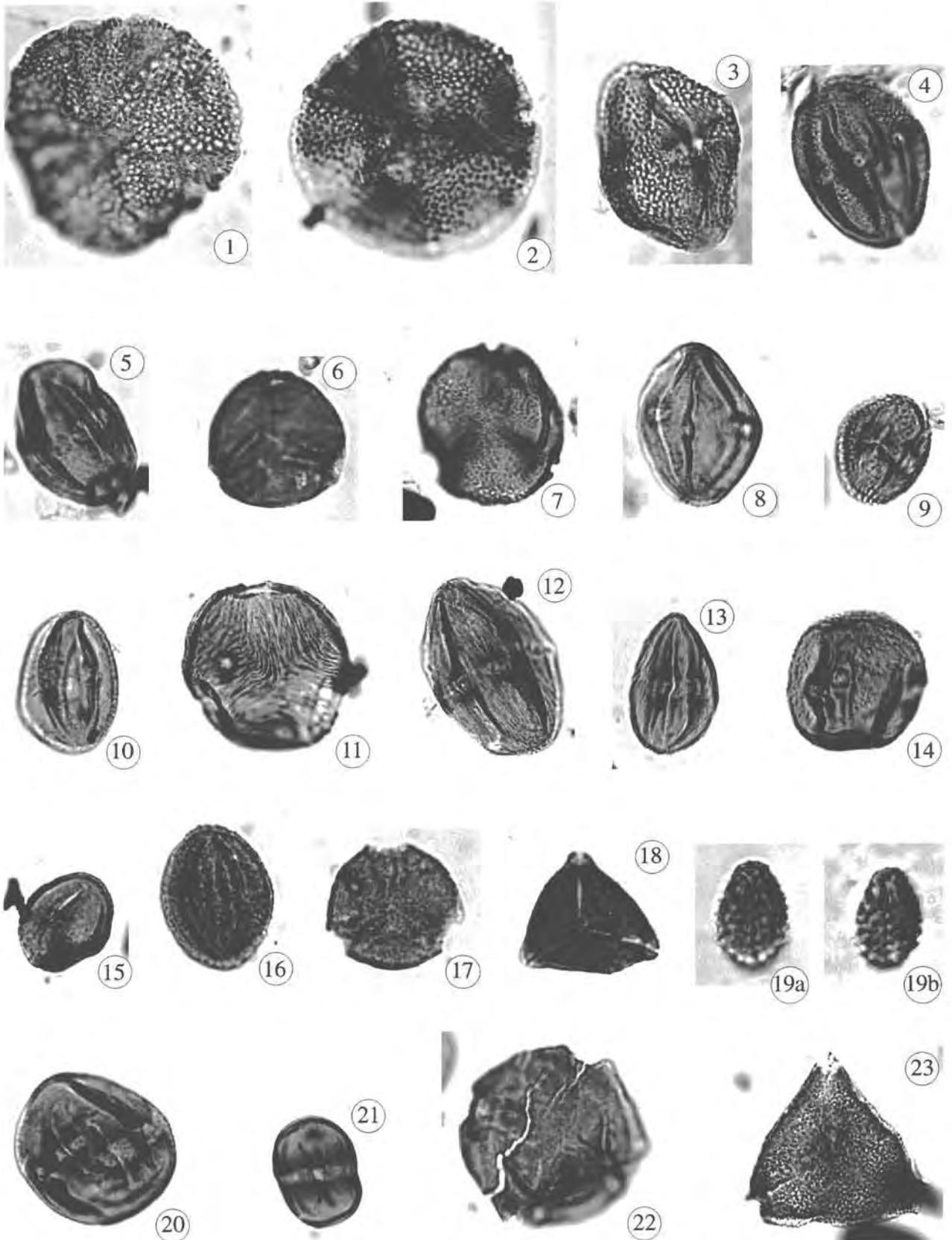
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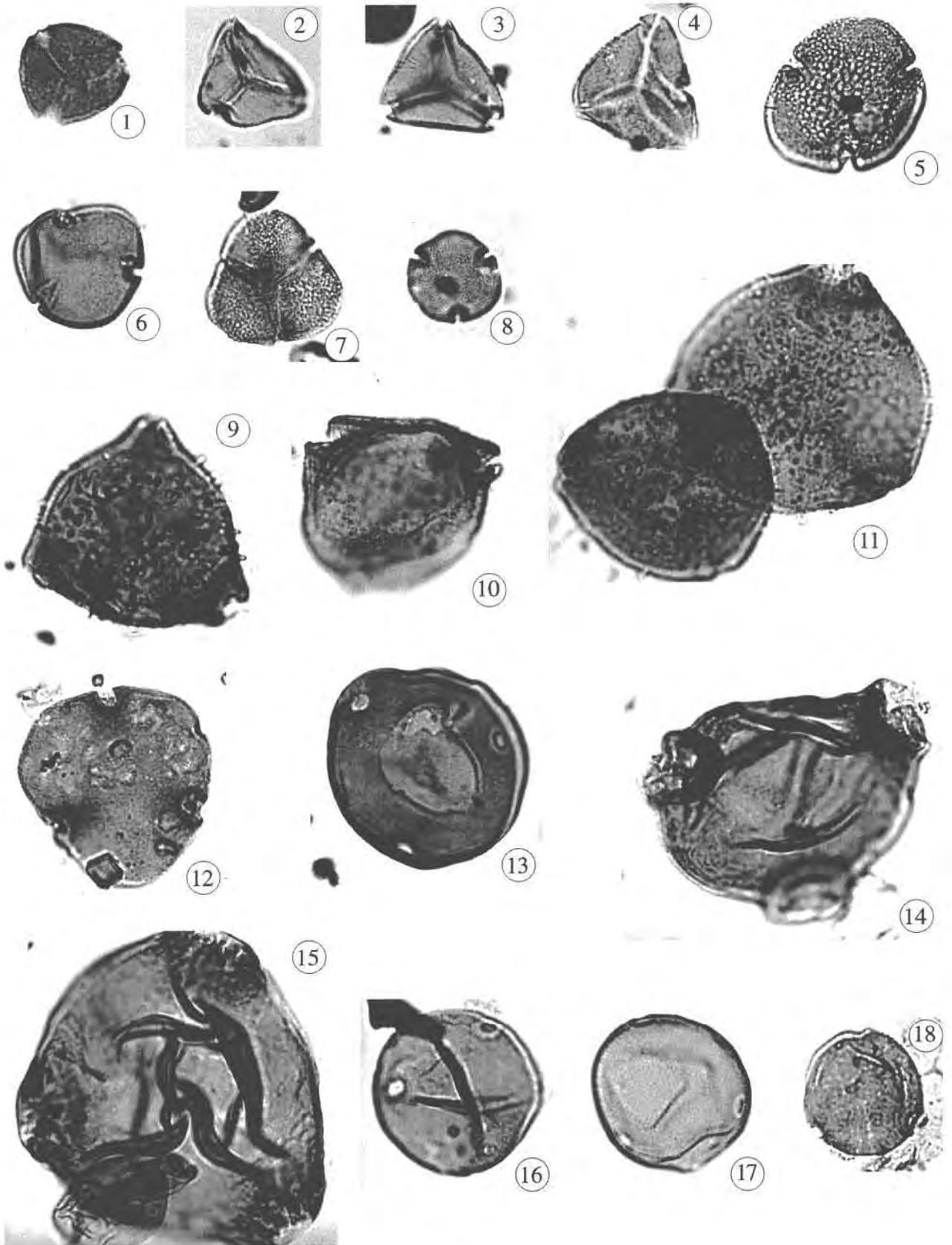
PLATE 7.

PLATE 8.

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4.
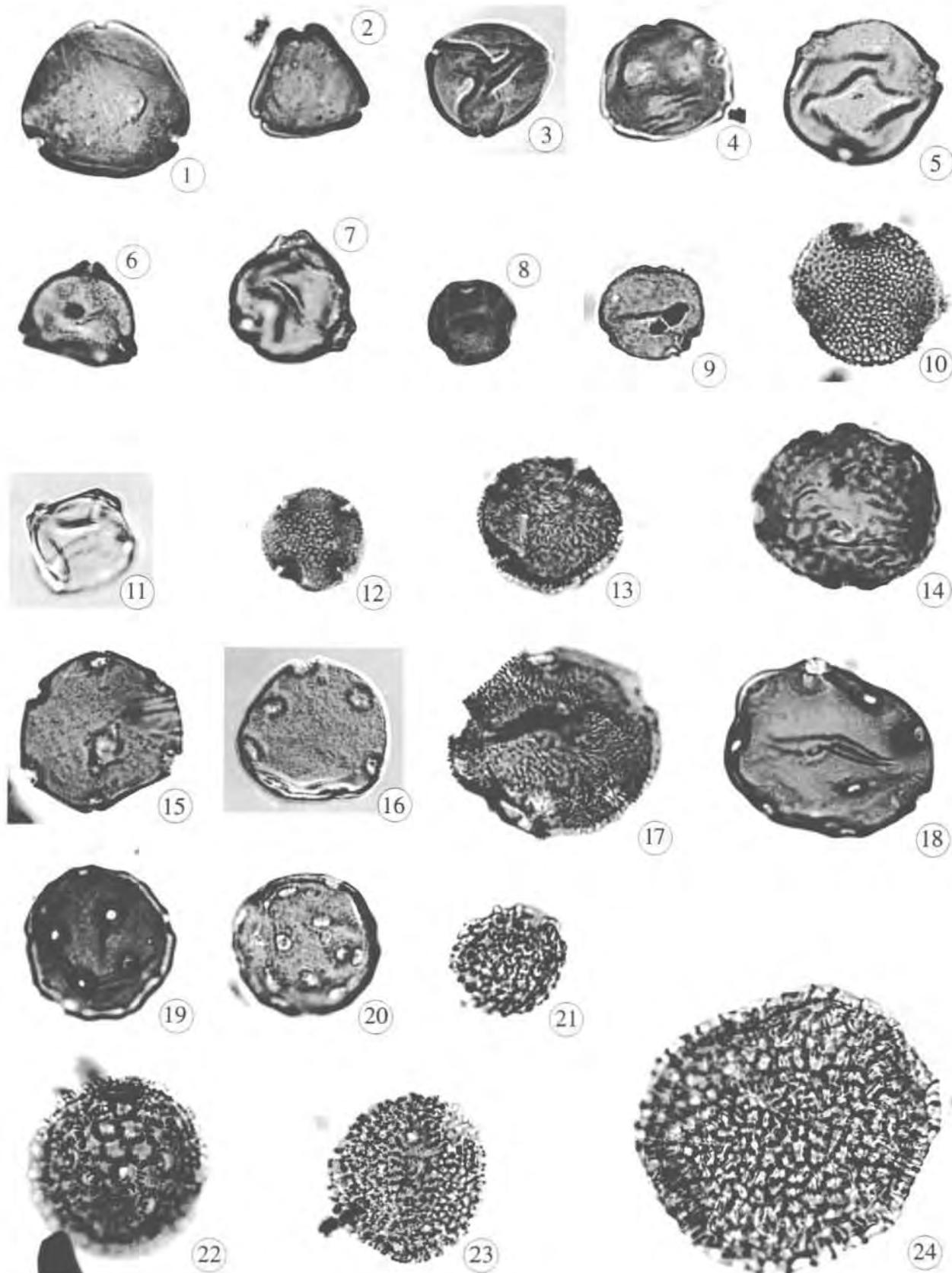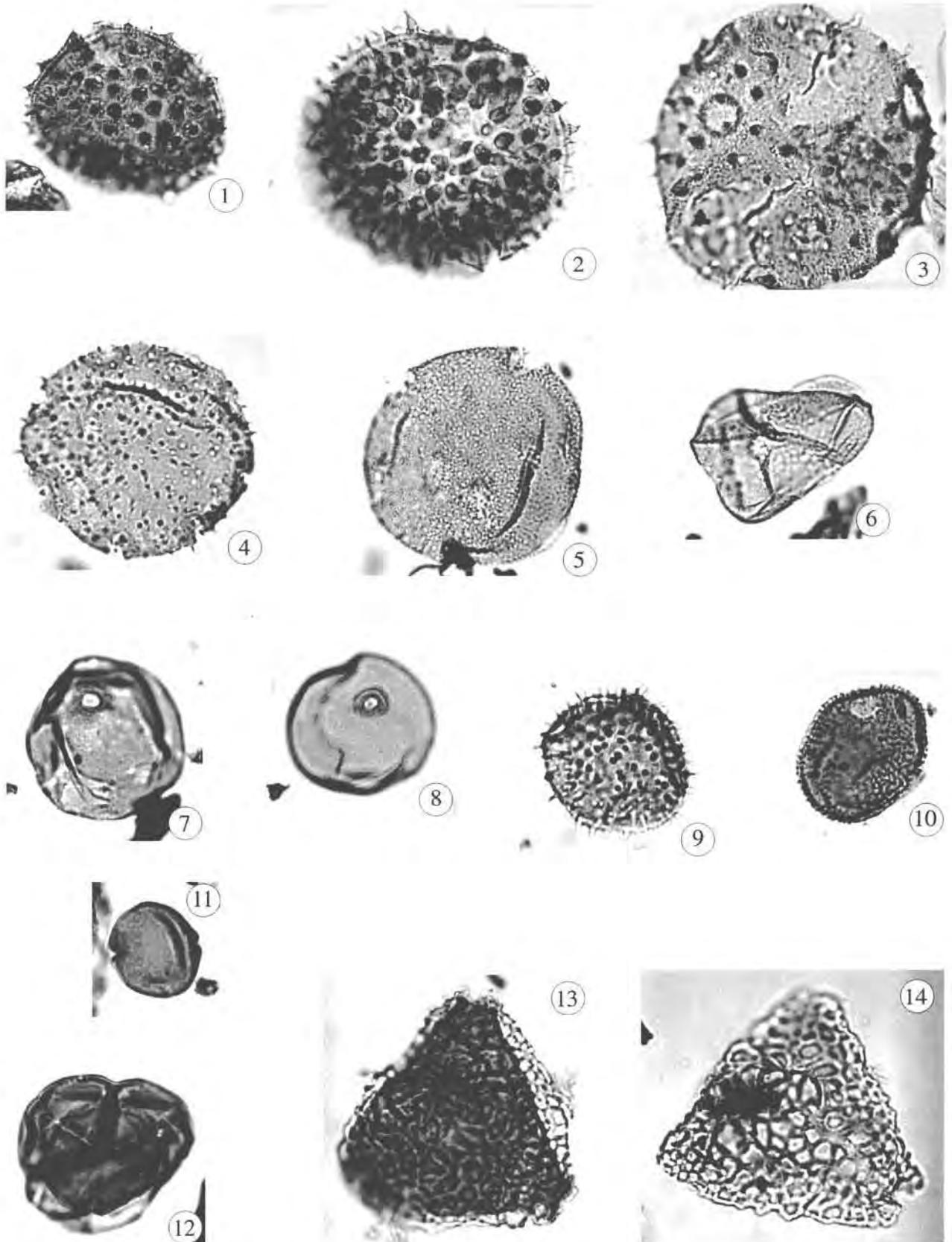
UPDATE ON THE
MEGAFOSSIL FLORA
OF FLORISSANT, COLORADO

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ABSTRACT—The diversity and systematic affinities of the Florissant flora are reviewed taking into consideration research on flowers, fruits, seeds, and leaves that has occurred since the publication of MacGinitie's major monograph in 1953. Overall diversity of the assemblage remains similar to that estimated by MacGinitie, with about 100 genera and 120 species, but some of the generic determinations have been revised, new taxa have been added, and the accuracy of some of the earlier generic assignments remains uncertain. Genera newly recognized over the past five decades include *Cedrelospermum* (extinct Ulmaceae) based on leaves (formerly assigned to *Zelkova*) and fruits (formerly assigned to *Lomatia*), *Asterocarpinus* (extinct Betulaceae), *Florissantia* (extinct Sterculiaceae), *Diplodipelta* (extinct Caprifoliaceae), fruit of *Eucommia*, seeds of *Apocynospermum*, and leaves of *Holodiscus* and *Palmites*. There is a larger proportion of extinct genera than previously recognized. The Florissant flora appears to be composed entirely of Laurasian elements, a small portion of which may have subsequently spread south to Central and South America. Some of the genera—for example, *Dipteronia*, *Eucommia* and *Koelreuteria*—are living today only in eastern Asia and are known to have been widespread in the Northern Hemisphere by the middle Tertiary. There is no current evidence for the presence of Gondwana-derived taxa such as Proteaceae in the Florissant flora. Recent findings from the Tertiary of Mexico, however, indicate that some of the taxa present in the Florissant flora, such as *Cedrelospermum* and *Eucommia*, had spread well into southern North America by the late Tertiary.

KEY WORDS: angiosperms, conifers, Eocene, Florissant, paleobotany, Tertiary

The plant fossils of Florissant have received attention for well over a century and have been the subject of several taxonomic studies, including those of Lesquereux (1883), Kirchner (1898), Cockerell (e.g., 1906a, 1906b), Hollick (1907, 1909), Knowlton (1916), Brown (1937, 1940), and MacGinitie (1953).

The beautiful monograph by MacGinitie (1953) has stood for more than four decades as the primary resource on the Florissant flora, its geologic setting, and the inferred paleoenvironmental conditions. Wolfe (1987) provided a summary of MacGinitie's paleobotanical achievements, giving due praise to the quality of his

treatment of the Florissant flora. It is unlikely that the flora will be monographed again in such a comprehensive sense, but as new specimens are discovered and as individual taxa are studied in greater detail, there continue to be revisions and supplements to our knowledge of the Florissant flora (e.g., MacGinitie 1969; Manchester and Crane 1983, 1987; Manchester 1987, 1989a, 1989b, 1992, 1993; Wolfe and Tanai 1987; Schorn 1998). The purpose of this paper is to bring together taxonomic revisions and additions to the flora that have come to light during the nearly five decades that have elapsed since the publication of MacGinitie's monograph. This paper

deals with the megafossil impression remains, whereas other current papers in this volume address the silicified woods (Wheeler 2001) and the rich fossil pollen record (Leopold and Clay-Poole 2001; Wingate and Nichols 2001). Although leaves are the most abundant megafossils at Florissant, flowers and fruits have attracted increasing emphasis in recent years because of the added systematic resolution available from reproductive structures. The diversity of the flora is recalculated in view of new discoveries and reevaluations of the taxa that MacGinitie recognized, and the biogeographic and evolutionary implications of the flora are reassessed.

Age and Geologic Setting

Interpretation of the age of the Florissant beds has ranged from Miocene to Eocene. MacGinitie (1953) interpreted the age as Oligocene. A Potassium Argon date of 35.0 ± 0.8 Ma (Epis and Chapin 1975, adjusted to new decay constant; not 34.0 as indicated in Manchester 1992), along with a recently obtained $^{40}Ar/^{39}Ar$ date of 34.07 ± 0.10 Ma (Evanoff et al. 2001) indicates that this locality is very near the Eocene/Oligocene boundary, which is currently placed at 34.0 Ma (Swisher and Prothero 1990). Accordingly, the Florissant beds could either be late Eocene or early Oligocene. For this volume, the Eocene assignment is provisionally accepted.

The fossils are preserved in laminated tuffaceous lake sediments of the Florissant Formation (Evanoff et al. 2001). The sediment ranges from siltstone to conglomerate, but the best preserved leaf and fruit remains have been found in the siltstone layers, whereas silicified wood (Wheeler 2001) frequently occurs in the coarser sediment.

Collections

Collections from the Florissant flora are scattered in museums around the world. Significant collections consulted in this study include those of the University of California Museum of Paleontology (UCMP), Berkeley; the U.S. National Museum (USNM), Washington, D.C. (includes the former American Museum of Natural History collection and part of the former Princeton University collection); the Peabody Museum, Yale University (YPM), New Haven, Connecticut (includes the former New York Botanical Garden collection [NYBG] and part of the Princeton University collection); the University of Colorado Museum (UCM), Boulder; the Denver Museum of Nature and Science (DMNS), Denver, Colorado; Department of Geology, Waynesburg College (WC), Waynesburg, Pennsylvania; and Florissant Fossil Beds

National Monument collection (FLFO), Florissant, Colorado. Smaller collections with some significant specimens include those of the Florida Museum of Natural History (UF), Gainesville; the Burke Memorial Washington State Museum, Seattle; the Milwaukee Public Museum (MPM), Milwaukee, Wisconsin; the Swedish Museum of Natural History, Stockholm, Sweden; the Natural History Museum, London; the Field Museum, Chicago, Illinois; and the Royal Ontario Museum, Toronto, Ontario, Canada.

A pervasive problem in many of these collections is the lack of precise field data for each specimen. In most collections, the specimens are simply recorded as being from Florissant. There are many different quarry sites in the Florissant vicinity, some of which were plotted by MacGinitie (1953). Although MacGinitie made field tallies of the taxa found at different quarries, most museum specimens have not been numbered according to their individual sources. The museum specimens are thus all lumped together into a single composite Florissant flora, giving a good sense of the full diversity but precluding the possibility of comparing different sites within the formation.

Diversity of the Flora

Based on a comprehensive and critical survey of all available Florissant paleobotanical collections, MacGinitie (1953) recognized 144 species in the Florissant flora. This number included species identified to his own satisfaction as well as twenty-nine species that he placed in *incertae sedis*. He noted that the *incertae sedis* taxa might include extinct genera as well as specimens too poorly known to identify with confidence. MacGinitie (1953) also provided a list of fifty-eight species from the older literature that he rejected because the type specimens were missing or too poorly preserved for identification. Although many of the taxonomic determinations have changed or are still subject to change, only a few new kinds of megafossil remains have been added to the diversity of the flora, suggesting that 140 to 150 species may be still a reasonable estimate of the diversity in the megaflora. The precise diversity represented in the collections is difficult to assess, however, because we do not know the extent to which species named from reproductive structures may overlap with those named from leaves.

Whenever possible, MacGinitie (1953) attempted to link isolated fruits or flowers with leaves that he considered to represent the same species. For example, he placed both leaflets and pods in the species

Cercis parvifolia, although the foliage and fruits were never found in physical connection. Although several of these hypothetical organ associations still stand uncontested, some of them have since been found to be erroneous. For example, the winged disseminules that MacGinitie (1953) treated as seeds of *Lomatia* were subsequently found attached to twigs of *Cedrelospermum*, rather than the predicted *Lomatia* foliage (Manchester 1989a). In six instances specimens showing actual attachment of fruits on twigs with leaves provide unequivocal proof that the organs are conspecific: *Cedrelospermum lineata* (Manchester 1989a, Figs. 27, 30), *Fagopsis longifolia* (Plate 1, Figs. 1–3), *"Osmanthus" preamissa* (MacGinitie 1953, Plate 70), *Potamogeton geniculatus* (Plate 4, Figs. 4–5), *Palaeopotamogeton florissantii* (Plate 4, Figs. 1–3), and a dicotyledonous plant with opposite leaves and terminal infructescence (Plate 4, Fig. 10).

Because the vegetative and reproductive organs of plants are usually shed separately and have different potential for preservation as fossils, it is useful to give separate diversity estimates for different organs. Based upon MacGinitie's work, with the addition of the newly discovered *Holodiscus* (Schorn 1998), *Potamogeton*, and *Palmites* (Plate 3, Fig. 1), there are at least eighty-four genera and ninety-six species of leaves in the flora. Counting only reproductive structures (flowers, fruits, and seeds), there are about seventy genera and seventy-three species, including twenty-five genera and species that were not considered by MacGinitie. Six types of petrified wood have been recognized (Wheeler 2001). Based on these figures for megafossils, the minimum diversity of the Florissant paleoflora was eighty-four genera and ninety-six species. The maximum diversity of current collections from Florissant can be calculated by assuming minimal taxonomic overlap between reproductive and vegetative species: [ninety-six species of leaves] + [seventy-three species of flowers, fruits or seeds] – [six species where leaves and fruits or flowers are attached, proving conspecificity] = 163 species. Assuming the other extreme—maximal taxonomic overlap among the different organs—the minimum diversity of the flora is ninety-six species (the figure from leaves). The likely diversity represented in present collections thus falls somewhere between 96 and 163 species. In addition, the Florissant shales contain a rich pollen flora, with as many as 150 distinct types (Leopold and Clay-Poole 2001; Wingate and Nichols 2001). The palynological investigations reveal many of the same genera found in the megafossil record but in different abundances, and these studies document some taxa (e.g., Chenopodiaceae, *Ephedra*) that are not convincingly documented in the megafossil record at Florissant.

Systematic Composition of the Flora

Although the current estimate of megafloral diversity is similar to that of MacGinitie (1953), the systematic affinities of many taxa have been revised or remain in need of reevaluation. MacGinitie's stated method of identifying the fossil plants was to compare with as many herbarium samples of modern genera as possible until a morphologically identical modern genus could be found (see MacGinitie 1953:78–79 for his philosophy of taxonomy). In practice, the fossil species were generally assigned to the extant genus providing the closest "match." He applied this approach with good consistency, paying close attention to details of fine venation as well as gross morphology of the leaves. Many of the identifications made in this way appear to be correct, but others are open to question because more than one modern genus may be "identical" to the fossil in features preserved (Dilcher 1974; Wolfe and Schorn 1990) due to convergence and parallelism. In addition, the working assumption for this method—that all of the leaves can be assigned to modern genera—is undermined by the recognition that some of the taxa, such as *Fagopsis*, *Asterocarpinus*, and *Cedrelospermum*, represent extinct genera. By publishing such a thorough monograph on the flora, MacGinitie provided an invaluable resource for those working on the fossil record of particular taxonomic groups.

Table 1 provides a list of families and genera that I accept as valid determinations for the Florissant megafossil flora. In compiling this conservative list I have been hesitant to accept modern generic assignments unless they are supported by clearly defined diagnostic (that is, unique) character sets. This task was made easier by reference to MacGinitie's own discussion of each taxon, in which he provided a subjective evaluation of the reliability of the assignment. For example, under his discussion of *Phaca wilmattae* Cockerell, he states, "The genus must be considered tentative, since there are other legumes in addition to *Phaca* (*Astragalus*) which have very similar pods," (MacGinitie 1953:125). In the case of *Carpinus fraterna*, he states, "These fossils appear to be true *Carpinus* leaves, although it is not always possible to distinguish *Carpinus*, *Ostrya*, and *Acer carpinifolium* Siebold and Zuccarini by means of leaf characters.... The absence of characteristic fruits of *Carpinus*, however, sheds some doubt on this determination," (1953:98). Subsequently, the extinct betulaceous fruit genus *Asterocarpinus* was identified at Florissant, and it is now hypothesized that the *Carpinus*-like leaves

TABLE 1. Florissant families and genera confidently identified from megafossil remains.

This list includes only the taxa accepted as reliable by Manchester. Many genera are not included in this list because of uncertain identity. Families are arranged approximately in the sequence of Cronquist 1981. The more comprehensive systematic list of MacGinitie 1953, annotated to show revisions and level of confidence, is provided in Appendix 1.

Taxaceae
  Torreya leaves
Cupressaceae
  Sequoia leaves, cones
  Chamaecyparis leaves, cones
Pinaceae
  Abies seed
  Picea seeds
  Pinus section *Strobus* leaves, cones, seeds
    (two spp.)
  Pinus section *Pinus* leaves, cone, seeds (three spp.)
Potamogetonaceae
  Potamogeton leaves, fruits
Palmae
  Palmacites leaf
Cyperaceae
  Cyperacites fossil genus of Schimper, leaves
Gramineae
  Stipa (or a similar genus of grass fruits)
Dioscoreaceae
  Dioscorea fruit
Lauraceae
  leaves resembling *Lindera*
  leaves resembling *Persea*
Berberidaceae
  Mahonia leaflets (two or three spp.)
Platanaceae
  Platanus or *Macginitiea* leaf
Eucommiaceae
  Eucommia fruit
Ulmaceae
  Cedrelospermum leaves, fruits
  Ulmus leaves, fruits
Juglandaceae
  Carya leaves, leaflets, staminate
    inflorescences, fruits
Fagaceae
  Fagopsis leaves, inflorescences, fruits, pollen
  Quercus spp. leaves, fruits
Betulaceae
  Asterocarpinus fruits
  Paracarpinus leaves
Sterculiaceae
  Florissantia flowers, fruits

Salicaceae
  Populus leaves, fruits
  Salix leaves
Hydrangeaceae
  Hydrangea calyces
  Philadelphus-like leaves
Grossulariaceae
  Ribes leaves
Rosaceae
  Amelanchier spp. leaves
  Cercocarpus-like leaves, fruits
  Crataegus spp. leaves, fruits
  Holodiscus leaves
  Malus-like leaves
  Prunus-like leaves
  Rosa leaves, leaflets
  Rubus leaves
  Vauquelinia leaves
  leaves formerly called *Lomatia*
Leguminosae
  Caesalpinites leaflets
  Cercis leaves, fruits
  Leguminosites leaflets
Onagraceae
  Onagraceous flower
Sapindaceae
  Acer spp. leaves, fruits
  Dipteronia fruits, perhaps leaves
  Koelreuteria fruits, perhaps leaves
Anacardiaceae
  Rhus leaves
Simaroubaceae
  Ailanthus fruits
Meliaceae
  Cedrela or *Toona* seeds
Apocynaceae
  Apocynospermum seeds
Araliaceae
  Araliaceous fruits
Adoxaceae
  Sambucus leaf, leaflets
Caprifoliaceae
  Diplodipelta fruits

(now called *Paracarpinus fraterna*) were produced by the same taxon as *Asterocarpinus perplexans* (Manchester and Crane 1987).

MacGinitie's treatment included cones, flowers, fruits, and seeds, but with primary attention to the leaves. My bias has been to place stronger emphasis on the reproductive structures, some of which are illustrated in this paper for the first time. These organs have the potential to provide greater systematic resolution than the leaves, and it is noteworthy that the recognition of extinct genera at Florissant has been due to studies of fruits and flowers (Hollick 1909; Manchester and Crane 1983; Manchester 1989a, 1993; Manchester and Donoghue 1995; Wang and Manchester 2000). Investigation of leaves alone gave the impression that all of the taxa belong to modern genera.

Because it includes only the families and genera that I consider to be validly identified, Table 1 does not reveal the full systematic diversity of the Florissant flora. MacGinitie's more comprehensive systematic list is provided in Appendix 1, followed by, in Appendix 2, a list of additional leaf and fruit types not included in MacGinitie's listing. The full diversity of reproductive structures (flowers, fruits, and seeds) from Florissant collections has not been previously considered, but it is interesting to compare with other data. Many of these taxa are still in need of detailed study; some of the more intriguing examples are figured.

Revisions and Additions to the Flora

Many taxa have been revised or added to the Florissant flora since 1953. In this section I summarize these changes in alphabetical order of the relevant families.

Aceraceae. See Sapindaceae.

Adoxaceae. The record of leaves of *Sambucus* is accepted. Based on systematic research on extant genera, *Sambucus* has been transferred from the Caprifoliaceae to the Adoxaceae (Judd et al. 1994).

Anacardiaceae. This family is represented by *Rhus* and other genera in the Florissant flora. The assignment of leaves and fruits to *Astronium,* however, is questioned. On critical evaluation, the fruits that MacGinitie assigned to *A. truncatum* (Plate 2, Fig. 4) cannot represent *Astronium*; the fossil seed body is globose and smooth rather than elongate and striate, and the venation is reticulate rather than dichotomous. The original designation of these fruits as *Porana tenuis* Lesquereux in the Convolvulaceae

(Lesquereux 1883) is also at odds with the fruit morphology. Detailed investigations of well-preserved specimens reveal that the gynoecium consisted of a whorl of five apocarpous ovaries, only one or two of which enlarged at maturity (Wang and Manchester 2000). Thus the similarities of calyx shape and venation between the fossil and both *Astronium* and *Porana* are due to convergence. The species is therefore placed in an extinct genus, *Chaneya* Wang and Manchester, of uncertain familial position.

Apocynaceae. Seeds of *Apocynospermum* having an elongate seed body topped by a plume of elongate dispersal hairs are now recognized in the flora (Plate 2, Fig.1). *Apocynospermum* is a fossil genus established by Reid and Chandler (1926) to accommodate fossil seeds clearly referable to the Apocynaceae that cannot be assigned definitely to a particular living genus. Several living genera of the family have seeds that are difficult or impossible to distinguish from this type of fossil (Reid and Chandler 1926).

Araceae/Lemnaceae. The leaf that Cockerell (1908a) illustrated and described as *Limnobium obliteratum* appears to be conspecific with *Limnobiophyllum scutatum* (Dawson) Krassilov, a species also known from the Paleocene of the Rocky Mountains, the Eocene Green River Formation of Utah, and the Tertiary of Europe (Kvacek 1995). These aquatic plants have been considered to represent an extinct genus of the Araceae with some characters in common with the Lemnaceae (Kvacek 1995). Specimens with attached inflorescences including intact stamens were recently discovered from the Paleocene of Alberta, Canada. Pollen from the anthers is echinate and of the type previously assigned to *Pandaniidites* (Stockey et al. 1997).

Araliaceae. Woody racemes of globose infructescences that were not observed by MacGinitie appear likely to represent Araliaceae. Two specimens are known: one in the Waynesburg College collection (Plate 3, Fig. 2), and one in the Florida Museum of Natural History collection (Plate 3, Fig. 3). The fruits are borne on long pedicels and show epigynous perianth and persistent styles. MacGinitie (1953) described a different kind of structure as "Araliaceous fruits." The fruits described by MacGinitie appear to be composed of five or six achenes. Low oblique lighting reveals a horizontally rugulate surface on each achene (Plate 4, Figs. 6–7). Such morphology is not found among extant Araliaceae; the affinities of this taxon are in need of further investigation.

Betulaceae. *Carpinus fraterna* Lesquereux was transferred to *Paracarpinus fraterna* (Lesquereux) Manchester and Crane (1987) with the recognition that the leaves possess architecture found in more than one genus of Betulaceae. The distinctive four- and five-winged fruits (Plate 2, Fig. 2) formerly called *Petrea perplexans* Cockerell have been transferred to Betulaceae and named to a new genus as *Asterocarpinus perplexans* (Cockerell) Manchester and Crane (1987). Leaves of *Paracarpinus fraterna* and fruits of *A. perplexans* were probably produced by the same biological species (Manchester and Crane 1987). One faintly preserved fruit shows an elliptical nutlet and an asymmetrical wing similar to that of *Carpinus* (Plate 3, Fig. 7). Its affinities remain uncertain.

Fagopsis longifolia was removed from the Betulaceae, in which MacGinitie had placed it, and realigned with the Fagaceae (Manchester and Crane 1983; see "Fagaceae").

Caprifoliaceae. This family is now recognized on the basis of the fruits that MacGinitie attributed to *Ptelea cassiodes* (Lesquereux; Plate 2, Fig. 10). The fossils show an epigynous calyx in conformity with Caprifoliaceae, not a hypogynous calyx as would be expected in *Ptelea*. Details of the winged infructescences indicate that they are most similar to the extant Asian genus *Dipelta* (Manchester 1993). However, the nature of the wing fusion and the presence of two fruits (rather than one) per infructescence indicate that the fossil is distinct from *Dipelta*. The species has been placed in an extinct genus, *Diplodipelta* (Manchester and Donoghue 1995). MacGinitie's identification of *Sambucus*, then considered to belong to Caprifoliaceae, is upheld, but this genus is now treated under Adoxaceae (see aforementioned) following Judd et al. (1994).

Convolvulaceae (not). *Porana tenuis* Lesquereux is rejected. These fruits are now referred to *Chaneya tenuis* (Lesquereux) Wang and Manchester (2000). See discussion under "Anacardiaceae."

Dioscoreaceae. A samaroid fruit of *Dioscorea* was recently identified among the Florissant collections at Berkeley (Plate 2, Fig. 5). The fruit is 18 mm wide and 15 mm long, with at least two wings, apparently three (one hidden in matrix) radiating from the central axis. Like fruits of the extant genus, it has a thick pedicel, perianth persisting at the top of the fruit, and wings that lack venation but possess very fine horizontal striations. Dehiscence occurred by splitting along the central axis, starting at the apex of the fruit, as in extant species.

Eucommiaceae. A single fruit of *Eucommia* has recently been recognized among Florissant collections at the U.S. National Museum. The fruit is an elliptical samara with an asymmetrical wing having a distal stigmatic notch, and an asymmetrically vascularized locule (Plate 2, Fig. 6). It resembles the fruit of *Ulmus*, except that it lacks the reticulate wing venation and strong fimbrial vein, and has distinctive, basally directed pattern of dichotomizing venation over the locule. Although *Eucommia* is endemic to China today, the distinctive fruits of this genus are widely distributed in the Tertiary of North America and Europe (Magallón-Puebla and Cevallos-Ferriz 1994a; Call and Dilcher 1997). The Florissant specimen is small relative to fruits of the extant species but corresponds well with *E. montana*, previously recorded from the early Oligocene of southwestern Montana (Brown 1940). This new report coincides with the recognition of *Eucommia* based on pollen from Florissant (Leopold and Clay-Poole 2001; Wingate and Nichols 2001). It is possible that the genus has been overlooked among leaf fossils from Florissant. Fossil *Eucommia* leaves and fruits from other localities were readily identified in a darkened room with the aid of an ultraviolet light due to the yellow fluorescence of remnant rubber from the laticifers (Call and Dilcher 1997).

Fagaceae. The extinct genus *Fagopsis*, which represents the most abundant leaf type in the flora (MacGinitie 1953), is known from twigs with attached leaves, staminate inflorescences with *in situ* pollen (Plate 1, Fig. 1), pistillate inflorescences (Plate 1, Fig. 2), and infructescences (Plate 1, Fig. 3; Manchester and Crane 1983). MacGinitie attributed this extinct genus to the Betulaceae, but the discovery of tricolporate pollen sculptured like that of *Quercus* and the interpretation of cupule and fruit scars on the infructescences led to the reassignment to Fagaceae (Manchester and Crane 1983).

Juglandaceae. Along with his discussion of *Carya libbeyi* leaves and leaflets, MacGinitie (1953) figured but did not discuss fruits identified to the same species. Manchester (1987) described the isolated nuts as *C. florissantensis* and inferred that they probably represented the same species as the foliage. Staminate inflorescences containing well-preserved pollen were also recorded (Manchester 1987:66, 77, 78). Manchester (1987:108) upheld and emended *Juglans sepulta* Cockerell based on nutshell impressions. The presence of *Juglans*, as well as *Carya*, is also supported by the pollen record (Leopold and Clay-Poole 2001).

Myrtaceae. The species *Eugenia arenaceaeformis* (Cockerell) MacGinitie is of uncertain generic affinity. Similar leaves that were called *Eugenia americana* from the Eocene Green River Formation of Colorado and Utah (MacGinitie 1969) have been found on twigs with fruits and flowers that do not correspond to extant *Eugenia* (Manchester et al. 1998). A panicle of three flowers with numerous stamens has been collected from Florissant (Plate 2, Fig. 8), which resembles the flowers attached to *Syzygioides americana* (Lesquereux; Manchester et al. 1998), from the Green River Formation.

Onagraceae. A large flower with a four- or five-lobed tubular corolla about 3.3 cm long and an elongate style is represented by a single specimen (Kirchner 1898: Plate 15, Fig. 1). Previously illustrated with a diagram, it is now shown photographically (Plate 3, Fig. 4). This specimen is quite well preserved, although no stamens or pollen were observed. Kirchner's original determination that it "seems to have affinities with some of the Onagraceae" is a reasonable assessment, although the occurrence was not mentioned by subsequent workers. Kirchner described the specimen in good detail and interpreted the corolla as five-parted and noted that this is a difference from most extant Onagraceae, which have four-parted corollas. The fossil could also be interpreted as four-parted, taking into account the folding and overlapping between the two counterparts. Dispersed pollen of Onagraceae is recorded from Florissant by Leopold and Clay-Poole (2001) and Wingate and Nichols (2001).

Palmae. Although palms were unknown from the Florissant flora at the time of MacGinitie's monograph, the leaf of a fan palm was collected subsequently by Estella B. Leopold, providing the first megafossil record for palms at Florissant (Plate 3, Fig. 1). It is preserved in coarse sediment without details of venation. The unarmed petiole, short hastula, and palmate attachment of plicate leaf segments indicate that it is a fan palm conforming to the fossil genus *Palmites* Brongniart (*sensu strictu* Read and Hickey 1972). Leaves with this morphology occur among numerous extant palm genera and assignment to a particular modern genus is not possible from leaf morphology alone (Read and Hickey 1972). Fruits or flowers would be helpful in resolving more precise affinities of the Florissant palm.

Pinaceae. Howard Schorn (pers. commun., 1995) has reviewed the Florissant Pinaceae and provided the information and interpretations presented here. His

analysis confirms the presence of *Abies*, *Picea*, and *Pinus*. Species representing two sections of *Pinus* are present. Two species belong to the soft pines (*Pinus* section Strobus) and two to the hard pines (*Pinus* section Pinus).

The hard pines, characterized by fascicles with somewhat bulbous, bilaterally symmetrical bases with persistent sheaths, are represented by at least two species in the Florissant flora. The first has two- and three-needled fascicles (MacGinitie 1953, Plate 18, Fig. 1; Plate 20, Fig. 1) and has been designated *Pinus macginitiei* Axelrod (1986:621, based on MacGinitie's Plate 20, Fig. 1, as holotype). The second has five-needled fascicles (e.g., MacGinitie 1953, Plate 18, Fig. 11). Seeds with the articulate wings characteristic of the hard pines are also present in the flora (e.g., MacGinitie 1953, Plate 20, Figs. 3–4). Axelrod (1986:621) included these seeds (MacGinitie's Plate 20, Figs. 3–4) as paratypes of the new species *Pinus macginitiei*, although it is difficult to be certain to which of the two foliage species they really belong. Another representative of the hard pines is the ovulate cone (but not the leaves) that Cockerell (1908b:78, Plate 6, Fig. 5) attributed to *P. wheeleri*. Although the cone is degraded, one scale on the basal left-hand side appears to preserve the triangular apophysis with a dorsally positioned umbo (Schorn, pers. commun., 1996).

The cone of *Pinus florissantii* Lesquereux (holotype refigured in MacGinitie 1953, Plate 19, Fig. 2) represents a soft pine similar to extant *P. flexilis* James. Contrary to the opinions of Cockerell (1908b) and MacGinitie (1953), it cannot be a hard pine related to *P. ponderosa* because it has a terminally positioned umbo (Schorn, pers. commun., 1996). The cone scale figured by MacGinitie (1953, Plate 18, Fig. 2) probably also belongs to *P. florissantii* because it shows a terminal umbo. The lectotype of *Pinus wheeleri* Cockerell (1908b:78, Plate 6, Fig. 11) is a five-needled fascicle that is missing both the base and apical portion of the leaves, but it appears to represent a soft pine. (As aforementioned, the cone Cockerell attributed to the same species is, however, a hard pine.) The fascicle of four relatively short needles figured by MacGinitie (Plate 18, Fig. 3) is clearly a soft pine because of the deciduous sheath and small, cylindrical short shoot. The inarticulate winged seed figured by MacGinitie (Plate 18, Fig. 12) is that of a soft pine, but this would probably not belong with the cone of *P. florissantii* because *P. florissantii* appears to have

been a limber pine similar to *P. albicaulis*, and would be expected to have a nutlike seed with only a vestigial wing. Thus, it appears likely that there were at least two species of soft pine (Schorn, pers. commun., 1996).

Potamogetonaceae. The presence of this aquatic family at Florissant is now confirmed. Lesquereux (1883) cited but did not figure a specimen of *Potamogeton* with leaves and fruits that he assigned to *P. geniculatus* Al Br. The location of this specimen is unknown, and MacGinitie (1953) rejected the species from the flora. Another specimen has since been located that shows leaves and fruiting axes of *Potamogeton* (Plate 4, Figs. 4–5). The fruits are borne on racemes and have seeds with coiled embryos (Plate 4, Fig. 5) as in extant *Potamogeton*. Although poorly preserved, the leaves are thin and straplike, also in conformity with extant *Potamogeton*. The genus is thus hereby reinstated as a valid constituent of the Florissant megafossil flora. Lesquereux's assignment of the Florissant species to *P. geniculatus*, a species based on European fossils, is provisionally accepted, although I have not made detailed comparisons. Lesquereux (1883) also erected a new species that he called *Potamogeton* (?) *verticilatus*. MacGinitie (1953) established that "this curious aquatic plant is not a *Potamogeton*" and suggested that it might be an alga similar to *Nitella*, though in the absence of fruiting bodies, I agree with MacGinitie that the species must be treated as of uncertain affinity. Another genus from Florissant, *Palaeopotamogeton*, was established by Knowlton (1916) for an entity with opposite straplike leaves and globose fruits (Plate 4, Figs. 1–3). Although the material is well preserved, the correct familial affinities of *Palaeopotamogeton florissantii* remain to be determined.

Proteaceae (not). This Southern Hemisphere family is no longer accepted as a constituent of the Florissant flora. MacGinitie stated, "The presence of the family Proteaceae is unmistakably confirmed by both leaves and winged seeds resembling those of the living *Lomatia ferruginea* R. Brown" (1953:25). The so-called seeds of *Lomatia lineata* (Lesquereux) MacGinitie were later found attached to twigs bearing ulmaceous leaves. The "seeds" were subsequently recognized as fruits of the extinct ulmaceous genus *Cedrelospermum* (Manchester 1989a, 1989b). Accordingly, the identification of the leaves as *Lomatia* becomes highly suspect. The leaves might have affinities within Rosaceae and

are somewhat similar, for example, to those of extant *Fallugia*.

Rosaceae. As noted by MacGinitie 1953, it is likely that the leaf identified as *Panax andrewsii* Cockerell represents *Rubus*, but the preservation is too poor to confirm it. In addition, the leaf of *Acer coloradense* MacGinitie was later transferred to *Rubus coloradensis* (Wolfe and Tanai 1987:208). *Holodiscus* is a new addition to Rosaceae in the flora (Schorn 1998). MacGinitie identified both fruits and leaves as *Cercocarpus*. A recent investigation of leaf architecture of living species of *Cercocarpus* (Lis 1992) shows the systematic utility of venation and margin characters of the leaves. The fossil leaves from Florissant, *Cercocarpus myricaefolius* (Lesquereux; MacGinitie) appear most similar to extant *C. montanus* (vars. *montanus* and *argenteus*), the only deciduous species in the genus. Whether this species actually belongs to the modern genus, however, is open to question. Wolfe and Schorn (1990) present an interesting new observation and interpretation of fruits of a similar species, *C. henricksonii*, from the Oligocene Creede flora. A specimen shows that three or more, probably five, achenes were present per hypanthium tube, whereas extant species of *Cercocarpus* have only one achene per flower. "This raises the possibility that, if the leaves and reproductive structures represent the same taxon, *Cercocarpus henricksonii* (and possibly the Florissant *C. myricaefolius*) represents a genus ancestral to *Cercocarpus*" (Wolfe and Schorn 1990:29).

Rutaceae? The fruits that MacGinitie attributed to *Ptelea cassiodes* (e.g., Plate 2, Fig. 10) are now understood to represent the extinct caprifoliaceous genus *Diplodipelta* (Manchester and Donoghue 1995). In scrutinizing available collections from Florissant, I found three fruits that are especially similar to extant *Ptelea* (Plate 3, Figs. 5–6, and USNM 333175). This fruit type was described as a new genus, *Brachyruscus*, by Cockrell (1992) who considered its affinities to be within the Liliaceae. As in fruits of extant *Ptelea*, they have thin pedicel with a perianth scar at the base of the fruit; there is a slight stylar protuberance at the apex of the fruit; the fruit is indehiscent (specimens show the seeds intact within the fruit); there are two elongated, elliptical seeds, one in each carpel; and the venation of the wing is reticulate. In the fossil specimens, the wing is obovate, narrowing basally and broadest in the apical one-half, whereas the extant species has a broadly elliptical outline, widest at the midsection. These

fruits differ from extant *Ptelea*, however, in possessing only a single strong vein extending from the pedicel to the base of the locules. *Ptelea* fruits show two major veins (one on each side of the fruit axis) that diverge from the pedicel and extend to the base of the locules (Call and Dilcher 1995). Thus, it is possible that these fruits may represent another taxon convergent in fruit morphology with *Ptelea*.

Sapindaceae. This family includes the maples (*Acer*) and various other genera in the Florissant flora. Although traditionally placed in the segregate family Aceraceae, the genera *Acer* and *Dipteronia* are more logically placed in the Sapindaceae (Judd et al. 1994). The *Negundo*-like fruit called *Acer heterodentatum* by MacGinitie was renamed *Acer macginitiei* (Wolfe and Tanai 1987:100). A supplemental description of the leaves and fruits of *Acer florissantii* Kirchner was provided by Wolfe and Tanai (1987:130). The leaf initially called *Acer coloradense* by MacGinitie was transferred to the Rosaceae as *Rubus coloradensis* (MacGinitie) Wolfe and Tanai (1987:208).

Brown (1937) and subsequently MacGinitie (1953) correctly recognized fruits of *Dipteronia* from the Florissant but assigned them along with leaves to *Dipteronia insignis* (Lesquereux) Brown. The type specimen of that species is actually a leaflet (basionym *Myrica insignis* Lesquereux). Although the leaflets appear to exhibit sapindalean morphology, their relationship to *Dipteronia* is questionable. Wolfe and Wehr (1987) reassigned both the fruits and leaves to an extinct genus that they named *Bohlenia*, as *Bohlenia insignis* (Lesquereux) Wolfe and Wehr, but the genus *Bohlenia* was established based on a foliage specimen, and the relationship of the fruits to the *Bohlenia* leaflets is poorly supported. Because the fossil winged fruit from Florissant is morphologically indistinguishable from the mericarps of extant *Dipteronia sinensis*, these fossils can be placed without question in the extant genus. Despite the precise correspondence in morphology, the Florissant fossils are smaller than the extant fruits, supporting the conclusion that they represent distinct species of the genus. A new species name to accommodate *Dipteronia* fruits from the Tertiary of western North America will soon be established (McClain and Manchester 2001).

Sterculiaceae. The leaf termed *Sterculia rigida* Lesquereux was included by MacGinitie as *incertae sedis*. With the rejection of this leaf type from Sterculiaceae, the family appeared not to be represented in the megafossil record of Florissant. Reevaluation of the flower, fruit, and pollen morphology of *Florissantia speirii*, however, indicates that this extinct plant belongs to the Sterculiaceae (Manchester 1992). A newly examined specimen from the Florissant Fossil Beds National Monument collection shows the presence of small tepals inside the large perianth whorl (Plate 2, Fig. 3). These small tepals are like those demonstrated to be petals of *Florissantia quilchenensis* from Republic flora (Manchester 1992), indicating that the two species are more similar morphologically than was previously apparent. Although stamens have not been found attached to any of the *Florissantia* flowers from Florissant, they have been collected from shales of the Bridge Creek flora at Fossil, Oregon. Pollen removed from these stamens (Manchester 1992) was found to resemble the *Tilia*-like and *Fremontodendron*-like pollen that is found dispersed in the Florissant shales.

Ulmaceae. Leaves formerly attributed to *Zelkova* (Plate 1, Figs. 4–5) are the second most abundant taxon in the deposit (MacGinitie 1953). Both in the middle Eocene Green River Formation and in the late Eocene Florissant Beds, these narrow, simply toothed leaves have been found attached to twigs bearing winged fruits unlike those of *Zelkova* (Manchester 1989a). The winged fruits and, accordingly, the leaves belong to *Cedrelospermum* Saporta, an extinct genus previously recognized in the Tertiary of Europe (Manchester 1989a, Figs. 27, 30). Manchester (1989a) transferred both the leaves of "*Zelkova*" and winged fruits that MacGinitie had called *Lomatia* to *Cedrelospermum lineatus* and documented the affinities of *Cedrelospermum* as an extinct genus of Ulmaceae. In addition, the identification of *Ulmus* from Florissant has been reaffirmed and new specimens of fruits and leaves illustrated (Manchester 1989b), indicating that there were at least two genera of Ulmaceae in the Florissant flora.

The recognition of two ulmaceous silicified woods from Florissant, one extinct and possibly corresponding to *Cedrelospermum* (*Zelkovoxylon*), and the other conforming closely to extant *Zelkova* (Wheeler 2001), raises the question as to whether extant *Zelkova* (today native in southeastern Europe and eastern Asia) was actually present at Florissant. A few specimens of ulmaceous foliage from Florissant are indistinguishable from extant *Zelkova* (but they could alternatively be aberrant leaves of *Ulmus*). The wood and leaf fossils provide good circumstantial evidence for recognition of the genus,

but I consider the genus to be unconfirmed in the absence of fruits. *Zelkova* fruits are commonly preserved attached to twigs along with the leaves at lacustrine localities in Europe and Asia (Manchester 1989b), and I do not understand why we would not recover similar fossils from North American Tertiary deposits, especially at thoroughly collected sites such as at Florissant.

Verbenaceae (not). There is no longer any evidence for recognizing Verbenaceae in the Florissant flora. Although MacGinitie identified two genera to this family, *Petrea* and *Holmskioldia*, detailed investigations of fruit and floral morphology have shown these species to belong to Betulaceae (*Asterocarpinus* Manchester and Crane) and Sterculiaceae (*Florissantia* Knowlton), respectively.

Vitaceae. In a more recent publication, MacGinitie (1969) reassigned the type of *Vitis florissantella* Cockerell to *Humulus florissantellus* (Cockerell) MacGinitie (MacGinitie 1969:132). The distinctive fruits of *Humulus* have not been discovered, however. In his transfer of the species to *Humulus*, MacGinitie (1969) specifically excluded one of the specimens that he had illustrated earlier (1953, Plate 67). That specimen differs from the type in having narrower lobal sinuses and a more V-shaped notch at the base (rather than squared-off), and could perhaps be a true representative of *Vitis*. The identification of foliage to *Parthenocissus osbornii* (Lesquereux) MacGinitie has remained unchallenged.

Incertae sedis

Many of the Florissant taxa are in need of additional research in order to be identified. Some intriguing following examples are considered.

Palaeopotamogeton florissantii **Knowlton.** This species is known from two unusually complete specimens with mutually attached leaves and fruits originally figured by Knowlton (1916). Knowlton established this as a new genus based upon various differences from *Potamogeton*, and it clearly is not *Potamogeton*. The fruits are preserved only as external molds, but they show distinctive features, including globose shape, a pair of median ribs, and a persistent terminal stigma (Plate 4, Figs. 2–3). These features, together with the opposite, straplike leaves, should permit this plant to be allied to a family or genus.

Longitudinally winged fruit. A new taxon not previously published from Florissant is represented by a single, well-preserved winged fruit. The impression (Plate 4, Fig. 8) shows that there were at least two lateral wings adjoining a fusiform, longitudinally ribbed fruit body with a thick pedicel. Veins of the wing are subparallel, departing at right angles from the central body and curving to form loops or joining a vein that lies just inside the wing margin. Although somewhat similar in form to the fruit of *Dioscorea*, the latter has fruits that lack veins in the wing (Plate 2, Fig. 5). *Halesia*, a genus reported from leaves at Florissant, has similar fruits but lacks the series of subparallel veins in the wing. A handwritten label by MacGinitie identifies the specimen as *Dodonaea*, but fruits of that genus do not have a thick central body. The specimen shows a number of features that may be helpful in identification, but more specimens would be desirable to show features of the fruit apex and whether more than two wings were present.

Winged fruits with reticulate venation (MacGinitie 1953:162). These samaras (Plate 3, Figs. 8–9) are superficially similar in general outline to those of *Acer* but are nonschizocarpic, and veins of the wing form a series of loops at the margin. One specimen shows detail of the fruit body, including a basal disk (perianth scar?) and about eight longitudinal surface ribs (Plate 3, Fig. 8).

Deviacer. This extinct genus is also present at Florissant (Plate 4, Fig. 11) and was illustrated as "Unidentified fruit, *Thouinia*(?)" by MacGinitie (1953, Plate 63, Fig. 1). *Deviacer* was initially described from the middle Eocene Clarno Formation of Oregon (Manchester 1994) based on samaras that resemble those of *Acer* in shape of seed, and wing and venation, but lack the prominent proximal attachment scar of *Acer* schizocarps.

Fruits attached to twig with opposite leaves (Plate 4, Fig. 10). This exceedingly rare specimen in the Florissant collections at Waynesburg College is a twig with attached infructescences and leaves. The leaves are elongate, apparently entire-margined, and arranged oppositely on the twig. The infructescences are axillary and appear to be panicles of several to many globose fruits. If this rare and important specimen could be relocated, it is likely that additional details could be observed in order to provide a well-documented identification.

Spicate infructescence. One specimen (Plate 4, Fig. 9) is a stout woody axis with at least twelve sessile fruits attached. The fruits appear to be bicarpellate capsules with horizontal striations and are somewhat similar to those of Hamamelidaceae. Persistent recurved styles, which are easily observed in

the fruits of many extant Hamamelidaceae, do not appear to be present in this fossil specimen, however. Further comparative work is needed to ascertain its affinities.

Relative Abundances

Based upon MacGinitie's field tallies at four locations involving 5300 specimens (1953:43–45), *Fagopsis* is the most abundant megafossil in the flora (31 percent), followed by *Cedrelospermum* (leaves identified as *Zelkova* by MacGinitie 1953; 10 percent). Other genera making up more than 3 percent of the flora include *Chamaecyparis*, *Typha*, and *Populus*. These five genera together comprise 60 percent of the fossils that he recovered. The relative abundances vary among localities. For example, at two of the four localities tallied by MacGinitie (1953), *Cedrelospermum* is significantly more common than *Fagopsis* (UCMP loc. 3731, 3733; MacGinitie 1953:44). One of the localities, however, produced so many *Fagopsis* leaves that this genus scores as the most abundant even when counts from the four localities are considered collectively. How these relative abundances, based strictly on counts of fossils, relate to relative abundances of taxa within the forest is open to interpretation, and many of the biases that could affect the apparent abundance are considered in detail by MacGinitie (1953:43). Such considerations and attempts to quantify these biases have spawned the relatively new field of plant taphonomy (e.g., Gastaldo 1988), an area of endeavor that may eventually provide a better understanding of the paleoecology at Florissant.

Biogeographic Considerations

The recent identification of *Cedrelospermum* and *Eucommia* fruits in the Neogene of southern Mexico (Magallón-Puebla and Cevallos-Ferriz 1994a, 1994b) indicates that some of the taxa present in the Florissant flora had spread well into southern North America by the late Tertiary. MacGinitie (1953) cited a number of genera in the Florissant flora that he considered to indicate floristic ties with the extant flora of upland northeastern Mexico. These included *Astronium*, *Bursera*, *Oreopanax*, *Thouinia*, and *Trichilia*. In my opinion, however, each of these generic determinations is equivocal, and equally good matches may be found among genera

that occur today in other geographic regions. Although these generic determinations are plausible, they are difficult to confirm because of insufficient diagnostic characters. The hypothesis of close floristic ties between Florissant and the extant flora of Central and South America is one that requires additional testing, particularly as detailed investigations of particular systematic groups continue. There is no current evidence for the presence of Gondwana-derived taxa such as Proteaceae in the Florissant flora.

The Florissant flora thus appears to be composed entirely of Laurasian elements, a small portion of which may have subsequently spread south to Central and South America. MacGinitie (1953) pointed out the presence of some genera with affinities to the extant flora of Asia. These include *Koelreuteria*, *Ailanthus*, *Dipteronia*, and the recently added genus *Eucommia*. These four genera, confirmed by distinctive fruit remains, represent deciduous trees that are today native to Asia. They are also known from other Tertiary floras of North America, Europe, and Asia, indicating that they were once widespread around the Northern Hemisphere (Manchester 1999). Other components of this once widespread temperate forest include *Carya*, *Cedrelospermum*, *Crataegus*, *Hydrangea*, *Mahonia*, *Rosa*, and *Rubus*.

The flora also includes a number of provincial genera that extended into the Eocene and Oligocene fossil record of the Pacific Northwest: *Asterocarpinus* (Oregon, Montana); *Florissantia* (Oregon, Washington, British Columbia, Montana, Wyoming); *Diplodipelta* (Oregon, Washington, Idaho, Montana); and *Fagopsis* (Washington, Montana, British Columbia). With the exception of *Florissantia*, known from the Miocene of Sikhote-Alin, far eastern Russia (Manchester 1999), these genera apparently did not establish themselves outside of western North America and, sadly, became extinct by the end of the Oligocene.

Meyer, Kathleen Pigg, Howard Schorn, Wesley Wehr, and Scott Wing. I thank Kirk Johnson and Susan Hill for managing the final editing and publication of this issue.

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Plate Descriptions

PLATE 1.
Figures

1. *Fagopsis longifolia* (Lesquereux) Hollick. Twig with typical leaves and a globose staminate inflorescence. NYBG 15837, x1.5.
2. *Fagopsis longifolia* (Lesquereux) Hollick. Pistillate inflorescence attached to a twig with three leaves. NYBG 15834, x1.
3. *Fagopsis longifolia* (Lesquereux) Hollick. A mature infructescence axis, from which fruitlets have shed, attached to a leaf-bearing twig. UCMP 20773, x1.5.
4. *Cedrelospermum lineatum* (Lesquereux) Manchester. Vegetative branch with distichously arranged leaves. USNM 387542, x0.8.
5. Leaf of *Cedrelospermum lineatum* (Lesquereux) Manchester, showing simply toothed margin and asymmetrical base. UF 7277, x2.

PLATE 2.
Figures

1. *Apocynospermum* sp. Elongate seed with hairs spreading from the apex. UCMP 13131, x3.5.
2. Winged fruit of *Asterocarpinus perplexans* (Cockerell) Manchester and Crane showing five-lobed involucre. UCMP 3622, x3.
3. *Florissantia* flower showing prominent five-lobed calyx and inner whorl of five (one missing) petals. FLFO 111, x1.6.
4. *Chaneya tenuis* (Lesquereux) Wang and Manchester. Calyx of five sepals with impression of ellipsoidal fruit. USNM 332413, x2.
5. *Dioscorea* sp. Fruit showing about three membranous wings pulling apart (dehiscent) at the apex along the midline. UCMP 151980, x2.4.
6. *Eucommia* sp. Samaroid fruit showing apical notch (stigmatic area), asymmetrical wing venation, and seed body with venation spreading basally. USNM 333144, x4.
7. Calyx of *Hydrangea florissantia* Cockerell (holotype) and an unidentified, reproductive axis with four globose infructescences. YPM-NYBG 9811, x1.5.
8. Myrtaceous inflorescence showing three flowers with numerous stamens. DMNH 661, x2.5.
9. *"Juncus" crassulus* Cockerell. Fruit showing broadly elliptic seed with two styles and a basal tuft of hairs. USNM 40783, x6.5.

10. Winged disseminule of *Diplodipelta reniptera* (Becker) Manchester and Donoghue (orig. Lesquereux 1883: Plate 27, Fig. 8). USNM 387544, x3.

PLATE 3.
Figures

1. Leaf of *Palmites* sp., showing palmate arrangement of leaf segments radiating from the hastula. Courtesy Estella Leopold, University of Washington, Seattle, sn, x1.
2. Araliaceaous infructescence of globose heads. WC-FL-23, x1.2.
3. Another specimen showing head of longitudinally striate fruits with persistent epigynous perianth and styles. UF 18722-30277, x2.5.
4. Onagraceous flower showing inferior ovary, single style, and distinct petal lobes. USNM 33685, x1.5.
5. *Ptelea*-like fruit. UCM 38399, x3. This is the counterpart of NHM V. 18539 (Natural History Museum, London), the type of *Brachyruscus alleni* (Cockerell 1922).
6. *Ptelea*-like fruit, showing perianth scar at base, cordate wing with fine reticulate venation, two elongate seeds, and slight apical protuberance. UF 15040, x3.
7. Winged fruit similar to *Carpinus*. Waynesburg College, sn., x2.25.
8. Unidentified winged fruit, showing striated elliptical nut and reticulate venation. DMNH 16600, x 3.5.
9. Unidentified winged fruit with well-preserved venation. USNM 332599, x3.

PLATE 4.
Figures

1. *Palaeopotamogeton florissantii* Knowlton, showing opposite leaves and infructescences. USNM 34748, x1.2.
2. *Palaeopotamogeton florissantii* Knowlton. USNM 34748, x3.
3. *Palaeopotamogeton florissantii* Knowlton. USNM 34749, x3.
4. *Potamogeton geniculatus* Al Br. Faintly preserved leaves and spicate reproductive axes, WC-FL-25, x1. *(continues)*

(continued)

5. *Potamogeton geniculatus* Al Br. Detail of spike on the right. Note coiled seeds. WC-FL-25, x5.

6. Unidentified fruits. MPM 2090, x1.5.

7. Unidentified fruits. Close-up of seeds with rugulate surfaces. MPM 2090, x6.

8. Longitudinally winged fruit. UCMP 151981, x2.5.

9. Unidentified spicate infructescence. UCMP 151982, x1.2.

10. Unidentified twig with attached opposite leaves and axillary fruits. WC-FL-24, photo courtesy H. Meyer, x0.8.

11. *Deviacer* samara. UF 26058, x3.5.
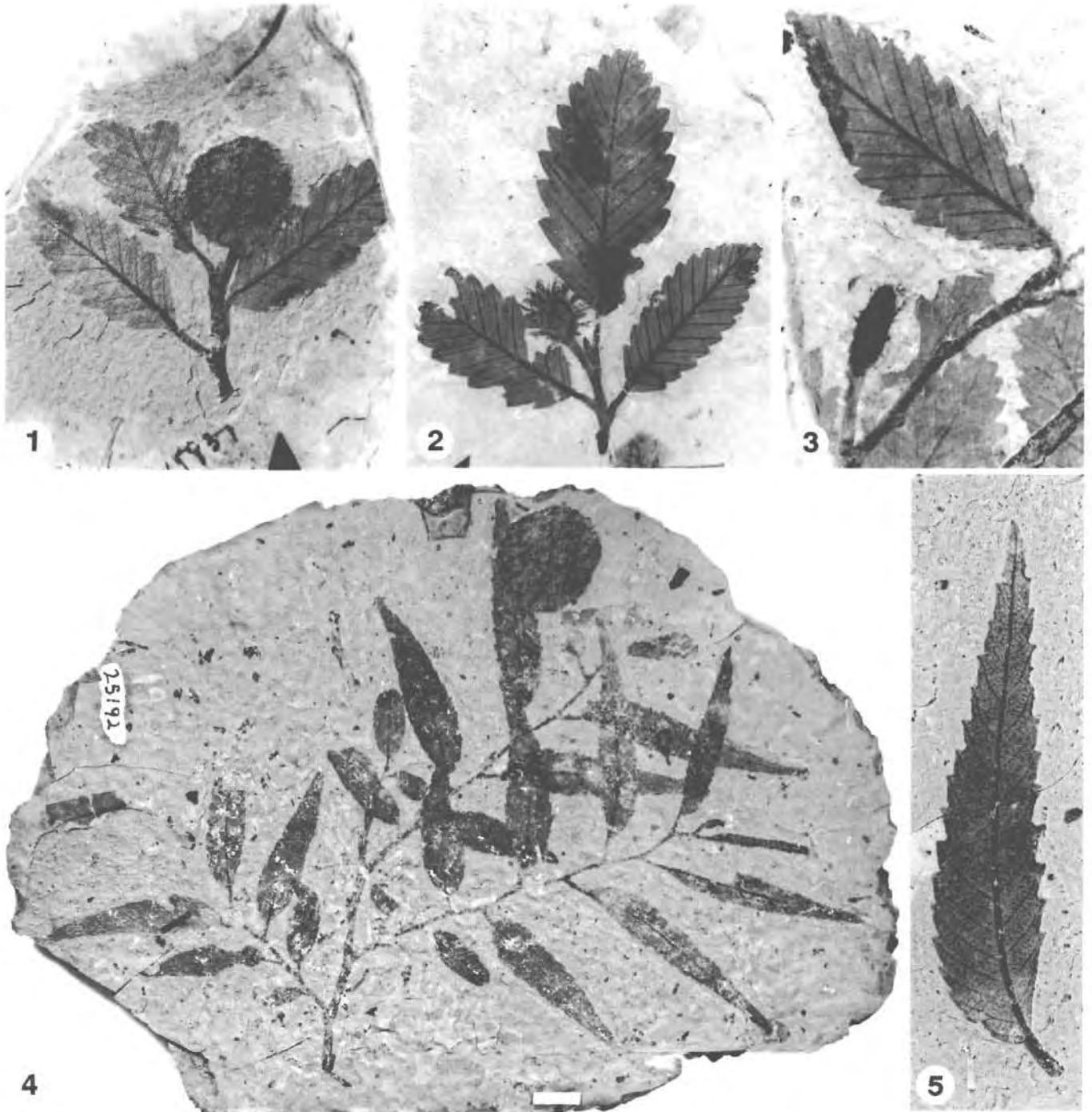
PLATE 1.
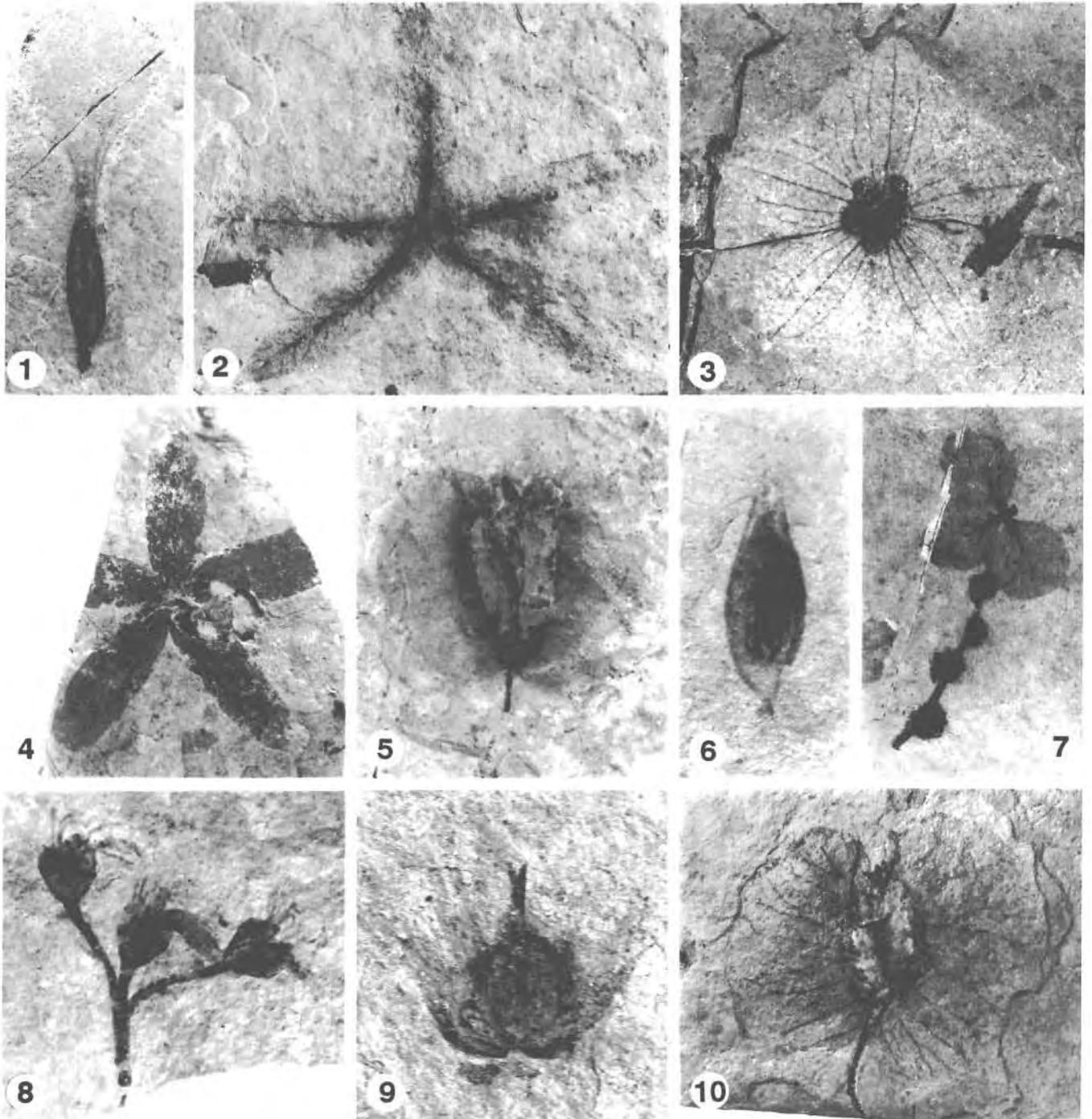
PLATE 2.
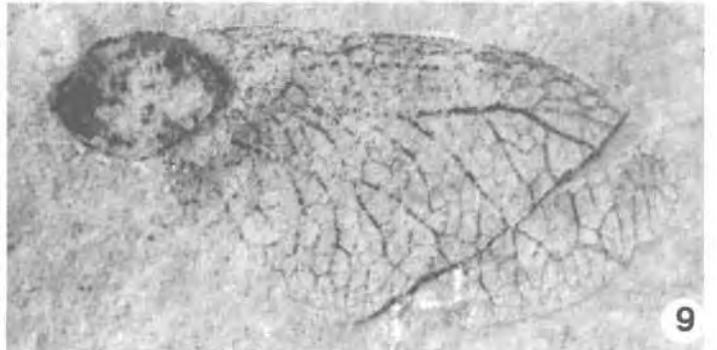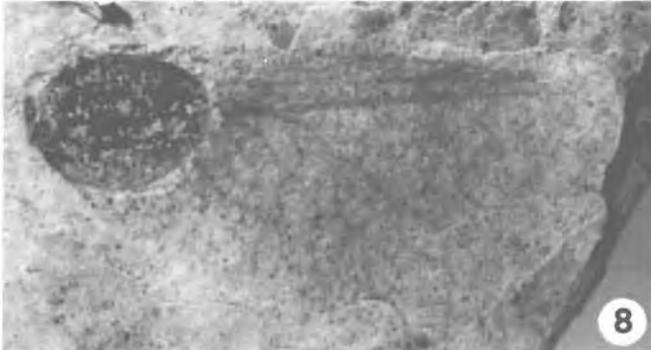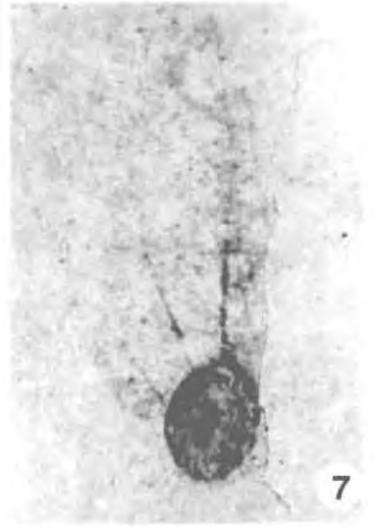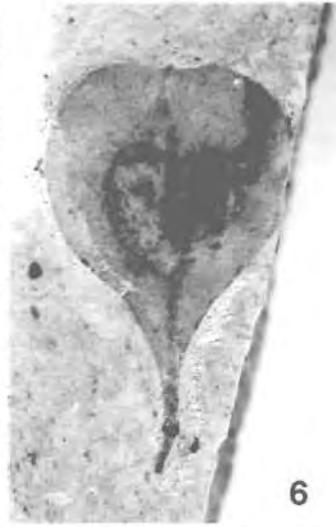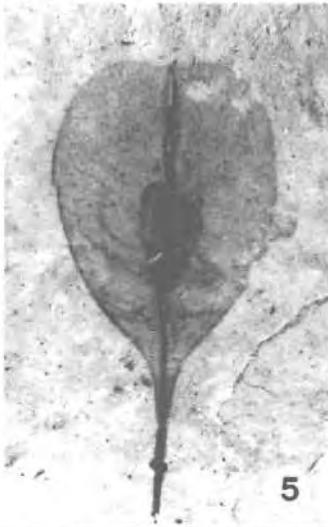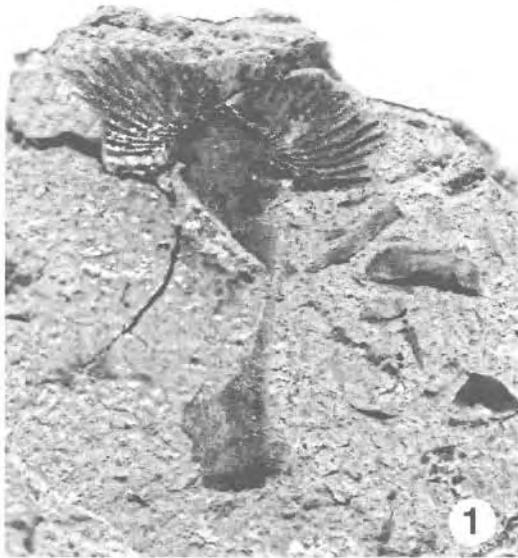
PLATE 3.
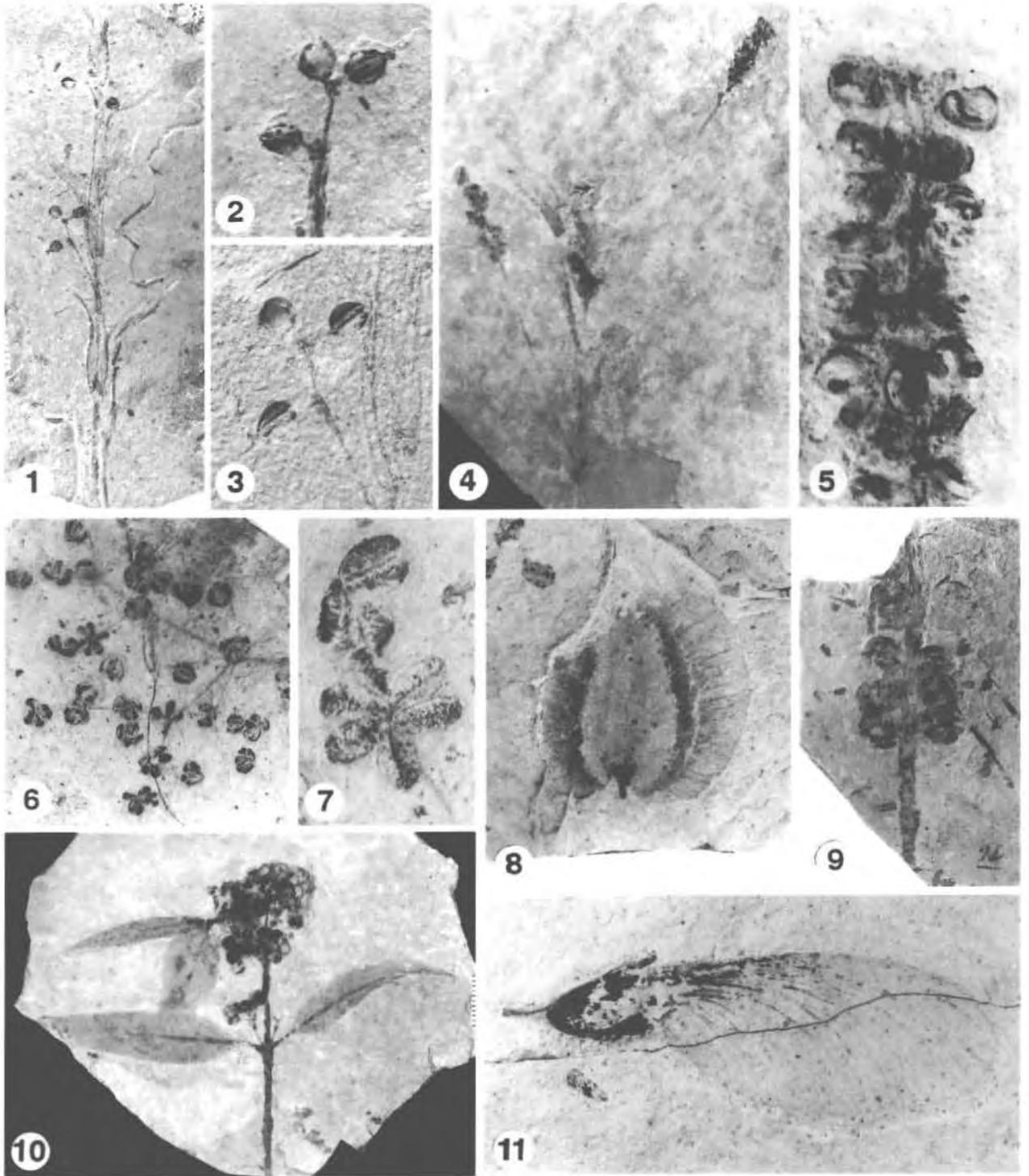
PLATE 4.

APPENDIX 1.

Systematic list of MacGinitie 1953, annotated.

Plagiopodopsis scudderi Britton and Hollick. A moss.

Plagiopodopsis cockerelliae (Britton and Hollick) Steer. A moss.

Equisetum florissantense Cockerell. Although MacGinitie stated, "The fossil is not well preserved and the identification is open to question" (1953:80), Herbert Meyer reexamined the specimen and sent me an image of the stem showing diagnostic characters of the genus, including fine longitudinal striations and regularly spaced nodes with highly reduced leaves.

Dryopteris guyotii (Lesquereux) MacGinitie. Common fern at Florissant. Although sori are preserved, investigation of spores has not been done.

Torreya geometrorum (Cockerell) MacGinitie. Isolated foliage needles.

Abies longiorostris Knowlton. A single winged seed corresponding to those of the Creede flora. Synonymized under *Abies rigida* Knowlton by Wolfe and Schorn (1990).

Picea lahontense MacGinitie. Seeds formerly considered to correspond to those of the Miocene Trout Creek flora of Oregon. The Trout Creek seed specimen to which MacGinitie (1953) referred is an atypical, abortive seed; thus there is no *P. lahontense* at Florissant. Probably all of the *Picea* winged seeds, or at least those well enough preserved to be evaluated, belong to *P. magna* (Schorn, pers. commun., 1995).

Picea magna MacGinitie. A large-seeded species. It is "doubtful whether specific differences can usually be established by means of seeds of conifers" (MacGinitie 1953:83).

Pinus florissantii Lesquereux. Cones, seeds, three-needled fascicles that MacGinitie considered to be similar to those of extant *P. ponderosa* Lawson. Schorn (pers. commun., 1995) notes that the holotype cone does not correspond to the hard pines near *P. ponderosa* because it has a terminally positioned umbo. The two- and three-needled fascicles and associated articulate winged seeds are now placed in *P. macginitiei* Axelrod (1986).

Pinus hambachii Kirchner. Rejected. A frayed axis of a reed or a twig (Wolfe and Schorn 1990:13).

Pinus wheeleri Cockerell. Five-needled bundles, seeds similar to white pine. Cockerell (1908b:78) cited two specimens in his description of this species, one a fascicle of needles, the other a degraded cone, but he did not designate a holotype. Because his description refers first to the foliage, I hereby designate the foliage specimen (Cockerell 1908b, Plate 6, Fig. 11) as the lectotype for this species.

Sequoia affinis Lesquereux. Seed cones smaller than in modern *Sequoia* and pollen cones usually terminal in contrast with their axillary position in *Sequoia* and *Sequoiadendron* (MacGinitie 1953:86).

Chamaecyparis linguaefolia (Lesquereux) MacGinitie. Branchlets and cones clearly those of *Chamaecyparis*.

Ephedra miocenica Wodehouse. A branch with poor preservation. The "preservation is not so good as could be desired, and in the absence of definite fruiting bodies there must remain some question" (MacGinitie 1953:99). Although the identification of this branch remains highly questionable, the genus *Ephedra* is confirmed by distinctive pollen from Florissant (Leopold and Clay-Poole 2001).

Typha lesquereuxi Cockerell. This species includes monocot leaves that are essentially identical to those of extant *Typha*. Other genera, however, such as *Sparganium*, have very similar foliage, and the distinctive inflorescences of *Typha* have not been recovered from Florissant.

Stipa florissantii (Knowlton) MacGinitie. "The characters clearly show that these fossils are impressions of grass fruits" (MacGinitie 1953:91). There is some uncertainty whether the precise generic assignment is correct.

Cyperacites lacustris MacGinitie. *Cyperacites* is a fossil leaf genus of Schimper. The Florissant fossils "probably represent some genus of the Cyperaceae such as *Eleocharis*" (MacGinitie 1953:92).

Smilax labidurommae Cockerell. Leaves closely similar to *Smilax*, but it may be difficult to distinguish leaves of *Smilax* from those of *Dioscorea*; the latter genus is confirmed by fruits from Florissant.

Populus crassa (Lesquereux) Cockerell. Confidently determined leaves and associated fruits.

Salix coloradica MacGinitie. Serrated leaf, accepted as representing section *Salix* by J. A. Wolfe (pers. commun., 1994).

Salix libbeyi Lesquereux. Entire-margined, poorly preserved leaves.

Salix ramaleyi Cockerell. Serrated leaves accepted as representing *Salix* section Salix by Wolfe (pers. commun., 1994).

Salix taxifolioides MacGinitie. Dentate leaves.

Carya libbeyi (Lesquereux) MacGinitie. Leaves and leaflets. This is one of the earliest well-documented occurrences for *Carya* in North America. The generic determination based on leaves is corroborated by confidently determined fruits.

"*Carpinus*" *fraterna* Lesquereux. This leaf species was transferred to *Paracarpinus fraterna* (Lesquereux) Manchester and Crane and is the probable foliage of *Asterocarpinus* Manchester and Crane (1987).

Fagopsis longifolia (Lesquereux) Hollick. An extinct genus represented by attached leaves, staminate inflorescences with *in situ* pollen, and infructescences. The isolated hairy fruits ("*Juncus*" *crassulus* Cockerell) that MacGinitie as-

(Appendix 1 continued)

signed to the genus differ from those attached to the infructescences and are no longer accepted as part of the *Fagopsis* plant (Manchester and Crane 1983).

Castanea dolichophylla Cockerell. Leaf without corresponding nuts or cupules. According to MacGinitie (1953:100), "*Castanea orientalis* Chaney, found in the Bridge Creek flora, cannot be distinguished from the Florissant species." The Bridge Creek species is now considered to represent *Quercus* (Meyer and Manchester 1997), and the generic identity of the Florissant species is in need of review.

Quercus dumosoides MacGinitie. Leaf.

Quercus knowltoniana Cockerell. Large acorn cup.

Quercus lyratiformis Cockerell. Leaf.

Quercus mohavensis Axelrod. Leaf.

Quercus orbata MacGinitie. Hollylike leaves similar to those of extant *Q. undulata* var. *pungens* (Oklahoma to northern Chihuahua).

Quercus peritula Cockerell. Leaf.

Quercus predayana MacGinitie. Leaf.

Quercus scottii (Lesquereux) MacGinitie. Leaf.

Quercus scudderi Knowlton. Leaf.

Celtis mccoshii Lesquereux. Leaf.

Ulmus tenuinervis Lesquereux. An acceptable record for the genus based on both leaves and fruits (Manchester 1989b).

"Zelkova" drymeja (Lesquereux) Brown. Leaves of *Cedrelospermum lineatum* (Lesquereux) Manchester (1989a, 1989b), an extinct genus of Ulmaceae.

Morus symmetrica Cockerell. Leaf.

"Lomatia" lineata (Lesquereux) MacGinitie. The fruits ("seeds") that were assigned to this species have been reidentified as *Cedrelospermum* (Manchester 1989a, 1989b). The generic identity of the leaves is uncertain, but affinities appear to be with the Rosaceae.

Aristolochia mortua Cockerell. Leaf.

Mahonia marginata (Lesquereux) Arnold. Leaflets.

Mahonia obliqua MacGinitie. Leaflets.

Mahonia subdenticulata (Lesquereux) MacGinitie. Leaflets.

Lindera coloradica MacGinitie. Leaf.

Persea florissantia MacGinitie. Leaf.

Sassafras hesperia Berry. "We reject the occurrence at Florissant; the specimen on which the citation is based has external veins that approach the margin more closely than do the external veins of *S. hesperia*" (Wolfe and Wehr 1987:12). Whether the Florissant leaf represents *Sassafras*, or some other genus of Lauraceae, is difficult to determine from the single unlobed specimen available.

Hydrangea fraxinifolia (Lesquereux) Brown. MacGinitie used this name both for isolated calyces of *Hydrangea florissantia* Cockerell as well as for the foliage upon which the species was originally based. The distinctive calyces provide good evidence for recognizing this genus at

Florissant. The generic identity of the leaves, on the other hand, is difficult to confirm.

Philadelphus minutus MacGinitie. Leaves.

Ribes errans MacGinitie. Leaves.

Amelanchier scudderi Cockerell. Leaves.

Cercocarpus myricaefolius (Lesquereux) MacGinitie. Distinctive leaves and fruits very similar to the modern genus. However, possibly represents a related extinct genus (Wolfe and Schorn 1990).

Crataegus copeana (Lesquereux) MacGinitie. Leaves.

Crataegus hendersonii (Cockerell) MacGinitie. Leaves.

Crataegus nupta (Cockerell) MacGinitie. According to MacGinitie (1953), this leaf type could possibly include variants of *C. copeana*.

Malus florissantensis (Cockerell) MacGinitie. Leaves.

Malus pseudocredneria (Cockerell) MacGinitie. Leaves. MacGinitie (1953) noted that *Malus* and *Pyrus* were considered synonyms by Sargent and that the fossils could represent either.

Prunus gracilis (Lesquereux) MacGinitie. Leaves.

Rosa hilliae Lesquereux. Pinnately compound leaves with fine serrations. An acceptable early record for the genus.

Vauquelinia coloradensis (Knowlton) MacGinitie. Leaves also similar to *Pyracantha* and others.

Vauquelinia liniara MacGinitie. Leaves.

Caesalpinites acuminatus (Lesquereux) MacGinitie. Genus for legume leaflets.

Caesalpinites coloradicus MacGinitie. Genus for legume leaflets.

Cercis parvifolia Lesquereux. Leaves small and heavy textured.

Conzattia coriacea MacGinitie. Leaflets.

Leguminosites lespedezoides MacGinitie. Leaflet.

Phaca wilmattae Cockerell. "The genus must be considered tentative, since there are other legumes in addition to *Phaca* (*Astragalus*) which have very similar pods" (MacGinitie 1953:125).

Phaseolites dedal MacGinitie. "Resemblances are closest to *Phaseolus*, but it appears impossible to relate the fossils definitely to any one genus" (MacGinitie 1953:126).

Prosopis linarifolia (Lesquereux) MacGinitie. Bipinnate leaves.

Robinia lesquereuxi (Ettingshausen) MacGinitie. Pinnately compound leaves also similar to *Amorpha* and *Sophora*.

Vicia sp. Knowlton. Leaf with tendril, probably Leguminosae.

Platanus florissantii MacGinitie. A platanaceous leaf similar to those of the extinct genus *Macginitiea*.

Ptelea cassiodes (Lesquereux) MacGinitie. Both fruits and leaves were placed in this species, but the fruits described and figured by MacGinitie are now considered to be Caprifoliaceae (*Diplodipelta*; Manchester and Donoghue 1995).

Ailanthus americana Cockerell. A firm record for the genus based upon distinctive fruits. MacGinitie (1953) noted that

(continues)

(Appendix 1 continued)

there is no detectable difference between these fruits and those of the Green River species *A. lesquereuxi*, but retained the two separate epithets because leaves are associated only in the Green River Formation.

Bursera serrulata (Lesquereux) MacGinitie. Trifoliate leaves.

Cedrela lancifolia (Lesquereux) Brown. Leaves and seeds. The seeds are quite similar to those of extant *Toona* as well as *Cedrela*.

Trichilia florissantii (Lesquereux) MacGinitie. Leaves.

Euphorbia minuta (Knowlton) MacGinitie. Leaves.

Astronium truncatum (Lesquereux) MacGinitie. The fruits are not *Astronium* or even anacardiaceous (Wang and Manchester 2000); the leaves are similar to *Rhus* and some other Anacardiaceae.

Cotinus fraterna (Lesquereux) MacGinitie. Leaves.

Rhus lesquereuxi Knowlton and Cockerell. Leaves.

Rhus obscura (Lesquereux) MacGinitie. Leaves.

Rhus stellariaefolia (Lesquereux) MacGinitie. Leaves.

Schmaltzia vexans (Lesquereux) Cockerell. Leaves.

Celastrus typica (Lesquereux) MacGinitie.

Staphylea acuminata Lesquereux. The absence of the bladderlike fruits, which should easily be preserved in lacustrine sediments, casts some doubt on the generic determination of these leaves.

"Acer" coloradense MacGinitie = *Rubus coloradensis* (MacGinitie) Wolfe and Tanai (1987).

Acer florissantii Kirchner. Leaves.

Acer heterodentatum (Chaney) MacGinitie. Renamed *Acer macginitiei* (Wolfe and Tanai 1987:100).

Acer oregonianum Knowlton. Leaves and fruit.

Dipteronia insignis (Lesquereux) Brown. Distinctive fruits and associated compound leaves. As *D. insignis* is based on a leaf of uncertain affinity to *Dipteronia*, a new species name, *D. brownii*, has been established for the fruits (McClain and Manchester, 2001).

Althayana haydenii (Lesquereux) MacGinitie. Pinnately compound leaves with winged rachises.

Cardiospermum terminalis (Lesquereux) MacGinitie. The assignment of these leaves to Sapindaceae appears to be valid, but the generic assignment is open to question because the distinctive membranous capsular fruits of *Cardiospermum* have not been recovered, and the leaves are thicker textured than the extant species. Fossil winged fruits also suggest the presence of some extinct genera of Sapindaceae.

Dodonaea umbrina MacGinitie. Based on leaf material without corroboration by winged fruits.

Koelreuteria allenii (Lesquereux) Edwards. This species is based on distinctive fruit valves. MacGinitie (1953) also included foliage that surely is sapindaceous and which might indeed belong to the same species as the fruits.

Sapindus coloradensis Cockerell. Beautifully complete specimens of this pinnately compound leaf are comparable to those of extant *Sapindus*, but the preservation of fine venation is not good, and as MacGinitie (1953) noted, the assignment to *Sapindus* remains equivocal.

Thouinia straciata MacGinitie. Trifoliate leaf.

Colubrina spireaefolia (Lesquereux) MacGinitie. Leaves.

Rhamnites pseudo-stenophyllus (Lesquereux) MacGinitie. Leaves, possibly Rhamnaceae.

Ziziphus florissantii (Lesquereux) MacGinitie. Leaves also similar to *Ceanothus* spp.

Parthenocissus osbornii (Lesquereux) MacGinitie. Leaves.

"Vitis" florissantella Cockerell = *Humulus florissantellus* (Cockerell) MacGinitie 1969. Leaves. As this paper languished in press, Herbert Meyer pointed out to me that MacGinitie's 1969 synonymy "specifically excludes the specimen from MacGinitie 1953, Plate 67, which apparently he retains as *Vitis*, although it's not a type specimen and so can't be *Vitis florissantella*. He [doesn't] mention Cockerell's holotype specimen in the 1969 synonymy, although that one does look like MacGinitie 1953, Plate 68, f.5 (= *Humulus*). Plate 67 differs from both of those in having narrower lobal sinuses and a more 'V' shaped notch at the base (rather than squared-off), so maybe it really is something different." Hence, *Vitis* sp. may be tentatively accepted as a member of the flora, pending further study.

Tilia populifolia Lesquereux. Leaf of questionable affinity to *Tilia*.

Daphne septentrionalis (Lesquereux) MacGinitie. Leaves.

Eugenia arenaceaeformis (Cockerell) MacGinitie. Leaf without high-quality preservation; generic assignment difficult to confirm.

Araliaceous fruits. The specimen referred to by MacGinitie (refigured here as Plate 4, Figs. 6–7) does not conform to Araliaceae. Affinities remain uncertain.

Oreopanax dissectus (Lesquereux) MacGinitie. Palmately lobed leaves, "clearly those of *Oreopanax*" (MacGinitie 1953:154).

Halesia reticulata MacGinitie. The absence of the distinctive winged fruits, which should easily be preserved in lacustrine sediments, casts some doubt on the generic determination of these leaves.

Osmanthus preamissa (Lesquereux) MacGinitie. Based on a twig with leaves and fruits attached, but the preservation is too poor to make a positive generic determination unless better preserved specimens can be found.

Convolvulites orchitus MacGinitie. Leaf.

"Holmskioldia" speirii = *Florissantia speirii* (Lesquereux) Manchester. An extinct genus of Sterculiaceae (Manchester 1992).

"Petrea" perplexans = *Asterocarpinus perplexans* (Cockerell) Manchester and Crane (1987).

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(Appendix 1 continued)

Sambucus newtoni Cockerell. Confidently determined leaves and leaflets.

Incertae sedis of MacGinitie (1953).

Group 1

MacGinitie stated that none of the following generic assignments are correct, but he used the names simply for continuity with the older literature on Florissant. I have added quotes around the extant generic names to emphasize that these are incorrect assignments.

"Ficus" florissantella Cockerell. cf. Bignoniaceae. Leaves.

"Ilex" knightiaefolia Lesquereux. Leaves or leaflets.

Populites heeri (Lesquereux) MacGinitie. Leaf.

"Potamogeton" (?) *verticillatus* Lesquereux. Stem with leaves attached oppositely at nodes. "Probably an algae similar to *Nitella*" (MacGinitie 1953:161).

"Sterculia" rigida Lesquereux. Maybe Platanaceae? Leaf.

Winged fruits. Samaras of unknown affinity (Plate 3, Figs. 8, 9).

Group 2

The following species were considered by MacGinitie (1953:159) to be "of somewhat doubtful taxonomic value, kept partly in the hope that the subsequent discovery of further material will clarify their taxonomic position and partly out of respect for the original describer."

Antholithes amoenus Lesquereux. A flower of uncertain affinity.

Antholithes pediloides Cockerell. A structure of uncertain identity.

Archaeomnium brownii (Kirchner) LaMotte. "A problematic object. Possibly an aberrant twig of *Sequoia*, although it may be a moss or lycopod" (MacGinitie 1953:163).

Aster florissantia Cockerell. Leaf resembling those of *Philadelphus*, *Colubrina*, and *Abelia*.

Carpites gemmaceus Lesquereux. A panicle of three fruits.

Carpites milioides Lesquereux. A panicle of numerous ellipsoid fruits.

Crataegus sp. Knowlton. A branchlet with a thorn resembling those of *Crataegus*, but not definitely assignable to that genus" (MacGinitie 1953:163).

Croton (?) *furcatulum* Cockerell. An infructescence of uncertain affinity.

Didymosphaeria betheli Cockerell. "A supposed spot fungus on a leaf of *Typha*" (MacGinitie 1953:164).

Ficus bruesi Cockerell. An elongate fruit somewhat resembling a fig.

Ficus florissantia Knowlton. An incomplete leaf.

Hypnum haydenii Lesquereux. Uncertain affinities, probably a young twig of *Sequoia*.

Jungermanniopsis cockerellii Howe and Hollick. "A supposed fossil hepatic, but a fragmentary object of doubtful validity" (MacGinitie 1953:164).

Limnobium obliteratum Cockerell. Small orbicular aquatic leaves virtually identical to those called *Spirodela scutata* Dawson in the Paleocene of Canada (McIver and Basinger 1993) and *S. magna* MacGinitie (1974) from the middle Eocene of Wyoming. It probably should be transferred to *Limnobiophyllum scutatum* (Dawson) Krassilov.

Lomatites spinosa (Lesquereux) Cockerell. Probably the lobe of an *Oreopanax* leaf.

Najadopsis rugulosa Lesquereux. Aquatic plant of uncertain affinity.

Orontium fossile Cockerell. "Spadix?"

Paleopotamogeton florissantii Knowlton. Uncertain affinity.

Panax andrewsii Cockerell. Leaf with prickles on the petiolules.

Pellea antiquella Cockerell. Pinnately lobed leaf, poorly preserved.

Phenanthera petalifera Hollick. A well-preserved flower.

Populus pyrifolia Kirchner. "The characters of this leaf are unique in the flora. The margin, however, is not preserved" (MacGinitie 1953:166).

Quercus balaninorum Cockerell. "This is probably, although not certainly, a fossil oak leaf" (MacGinitie 1953:166).

APPENDIX 2.

Taxa now recognized in addition to those treated by MacGinitie 1953.

Araliaceous infructescence (Plate 3, Figs. 2–3).

Apocynospermum sp. seed (Plate 2, Fig. 1).

Carya florissantensis Manchester (1987:77, Figs. 33A–C), nuts probably corresponding to the foliage of *Carya libbeyi*.

Chaneya tenuis (Lesquereux) Wang and Manchester fruit (Plate 2, Fig. 4).

Devincer sp. fruit (Plate 3, Fig. 9). Specimen figured but not discussed as "Unidentified fruit, *Thouinia*(?)" in MacGinitie (1953: Plate 63, Fig. 1).

Dioscorea sp. fruit (Plate 2, Fig. 5).

Eucommia sp. fruit (Plate 2, Fig. 6).

Fruits attached to twig with opposite leaves (Plate 4, Fig. 9).

"Juncus" crassulus Cockerell (Plate 2, Fig. 9). Not *Fagopsis* as indicated by MacGinitie, but the actual systematic affinities of this distinctive wind-borne fruit remain unknown.

Longitudinally winged fruit (Plate 4, Fig. 8).

Onagraceous flower of Kirchner (Plate 3, Fig. 4).

Palmites sp. leaf of a palmate palm (Plate 3, Fig. 1).

Potamogeton geniculatus Al Br. Rejected by MacGinitie because of missing specimens, but now reinstated based on new material (Plate 4, Figs. 4, 5).

Ptelea-like fruits (Plate 3, Figs. 5–6). These are distinct from the *Diplodipelta* fruits that MacGinitie had attributed to *Ptelea*. They were described as *Brachyruscus alleni* and considered to be *Liliaceous* by Cockerell (1922).

"Rosaceous fruits." Figured but not discussed by MacGinitie (1953: Plate 40, Fig. 8).

Spiny globose fruit. Figured but not discussed by MacGinitie (1953: Plate 65, Fig. 2).

"Unidentified fruit, *Cardiopteris*?" Fruit figured but not discussed in MacGinitie (1953: Plate 57, Fig. 2).

Spicate infructescence (Plate 4, Fig. 9).

5.

PALEOCLIMATIC IMPLICATIONS OF TREE-RING GROWTH CHARACTERISTICS OF 34.1 MA *SEQUOIOXYLON PEARSALLII* FROM FLORISSANT, COLORADO

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ABSTRACT—Tree-ring width and variability are functions of the interplay among climate, site conditions, and genotype. In studies of Holocene wood, ring widths can be calibrated with year-to-year instrumental records of climate to identify the climate signal; they can then be used to retrodict past climate. A similar method can be used with pre-Holocene wood. Descriptive statistics of fossil ring-width series are compared to those from the nearest living relatives to determine the climate signal. The general paleoclimate can then be qualitatively estimated. Studies on modern trees suggest that the most useful paleoclimatic indicator is mean ring width, which is a measure of overall growth. Interannual variability, total variability, intercorrelation within and between trees, and percent missing rings are indicators of environmental stress and the genus position within its ecological range. Comparison of ring-width series from 34.1 Ma *Sequoioxylon pearsallii* from Florissant, Colorado, to series from modern coast redwood (*Sequoia sempervirens*) and giant sequoia (*Sequoiadendron giganteum*) indicates that the Florissant trees had higher mean ring widths than their modern counterparts and similar ecological statistics. Thus the Florissant redwood experienced a more favorable climate. Two of the fossil stumps cross-dated, which demonstrates that they are from a single forest. Comparison of the modern climate for coastal California and foliar physiognomic-based estimates of the Florissant paleoclimate from the literature indicates that at Florissant, mean annual precipitation was less, though a greater proportion fell during the growing season, and the mean annual temperature was similar, and the mean annual range of temperature was greater than at the modern coast. The increased growth of the Florissant trees suggests that either (1) the higher growing season precipitation at Florissant created a more favorable soil moisture balance than at the modern coast or (2) both sites had similar effective growing season precipitation because of the higher summer temperatures at Florissant. However, this comparison is limited by the fact that the valley bottom sites of the fossil trees were more favorable than any of the sites of the modern redwood and sequoia.

KEY WORDS: Colorado, dendroclimatology, fossil wood, Front Range, paleoclimatology, redwood, ring-width series, sequoia

In woody plants, xylem production is a function of climate. Cambial growth occurs only during the limited time of the year when climatic conditions are favorable in climates other than the humid tropics. Early in the growing season, temperate conifer trees form large, thin-walled earlywood cells, and late in the growing season, they form small, flatter, thick-walled latewood cells. The resulting wood, often a light/dark band, is an annual ring. Under favorable climate conditions, trees produce more and larger wood cells and thus produce a wider ring than under unfavorable conditions (Fritts 1976). Generally, ring width is narrower in alpine and arctic zones and areas with dry climates, whereas ring width is wide in subhumid temperate zones (Schweingruber 1988). Distinct growth bands may not be discernible in tropical zones.

The size and variation of ring width are a function of not only climate but also site, species differences, and other biological factors that filter the climate signal (Fritts 1976). When dealing with Holocene wood, one can identify the climatic signal in ring-width series by comparing ring widths to yearly instrumental records of climate (Fritts 1976; Fritts and Swetnam 1989). A response function is derived that defines the relationship between ring width and climate for that particular site; a tree growth versus climate regression model may then be calibrated and used to "retrodict" climatic variations for the years before instrumental records.

A direct calibration is not possible for pre-Holocene wood because there is no continuous instrumental record of climate. Rather, the strategy in pre-Holocene studies is to estimate mean or general paleoclimatic conditions by looking at ring characteristics and descriptive statistics of ring-width series as a whole. The calibration is done by comparing fossil ring-width series from more than one species (Parrish and Spicer 1988; Spicer and Parrish 1990), or by broadly comparing fossil ring-width series to ring-width series from modern trees for which climate is known (Creber 1977; Jefferson 1982; Creber and Chaloner 1984a, 1984b, 1985, 1987; Francis 1984, 1986). Characteristics that have been used for comparison in the past include presence/absence of growth rings, mean or maximum ring width, interannual variability in ring width (mean sensitivity), the presence of false rings, and the earlywood/latewood ratio.

I use such an approach in this paper to draw paleoclimatic inferences from ring-width series of 34.1 Ma *Sequoioxylon pearsallii* from Florissant, Colorado. Descriptive statistics, some never before addressed in fossil wood studies, are computed for the fossil ring-width series. In order to calibrate for genetic factors, these statistics are compared to those from the closest living relatives of *Sequoioxylon pearsallii*: coast redwood (*Sequoia sempervirens*) and giant sequoia (*Sequoiadendron giganteum*). Ring-width series from *Metasequoia* were not available. The complications of age, disturbance history, and site conditions are also addressed.

Florissant Fossil Forest

Geology

The Florissant paleovalley was part of the Eocene drainage net on the high-elevation, low-relief, Rocky Mountain erosion surface of the Front Range, Colorado (Gregory and Chase 1994; Evanoff et al. 2001; Fig. 1). As the Thirtynine Mile volcanic field and other nearby centers became active, the valley began to fill with tuffaceous lacustrine, fluvial, and mudflow deposits of the late Eocene Florissant Formation (Evanoff et al. 2001; Fig. 2). The upper 5 m of the lower mudstone unit, the lowest unit in the formation, is a tuffaceous sandy mudstone deposited by a single mudflow (Evanoff et al. 2001). It contains permineralized fossil wood stumps and logs, some up to 15 m in circumference. This unit is overlain by lacustrine shales, which contain the famous flora and insect fauna. Biotite from a pumice bed near the top of the approximately 50 m section has a $^{40}Ar/^{39}Ar$ single-crystal laser-fusion age of 34.07 ± 0.10 Ma (Evanoff et al. 2001).

When dealing with petrified trees in mudflow deposits, it is important to establish whether the trees were transported by the mudflow or were encased while in a rooted position. Evanoff (1992) mapped thirty-one fossil stumps in the "petrified forest" area of Florissant Fossil Beds National Monument using surveying techniques. He demonstrated that these stumps occur in a single plane and that 91 percent are vertical (Fig. 3). These observations, along with the cross-dating between trees discussed later, indicate that the stumps represent a single *in situ* forest. The trees were probably killed by the mudflow because burial cuts off oxygen to roots. Modern coast redwood is known to
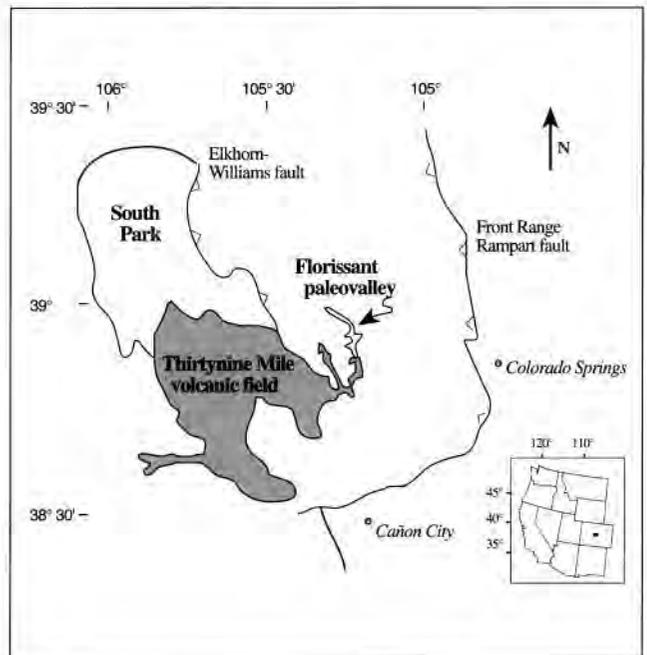
FIGURE 1. Location map of the study area in central Colorado.
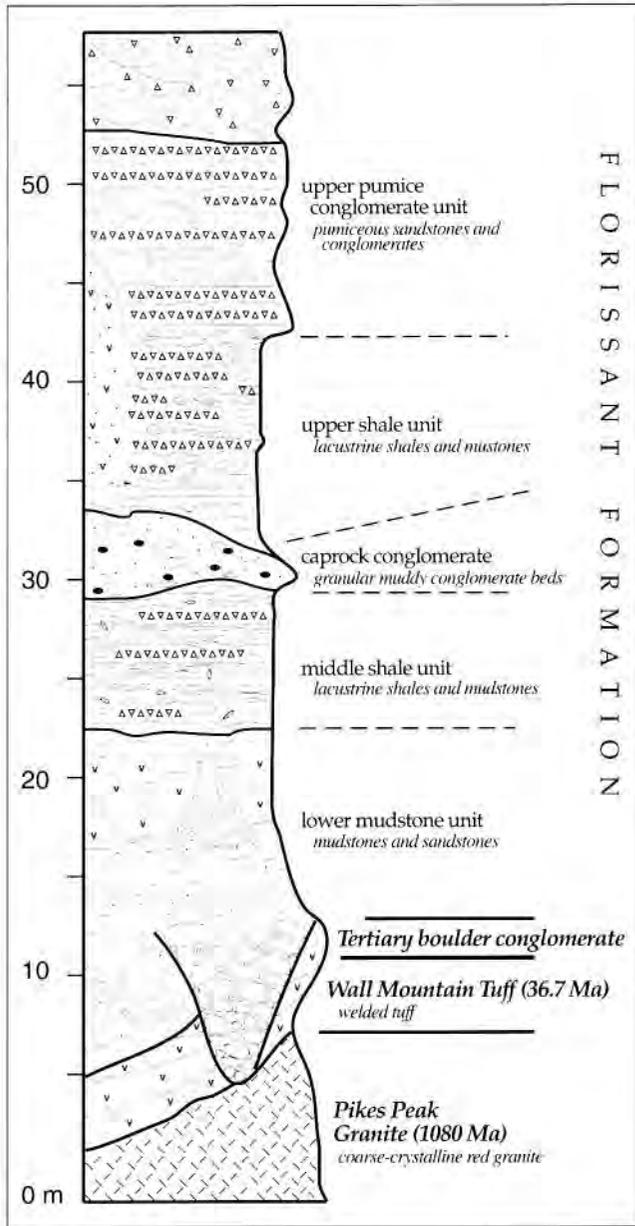
FIGURE 2. Stratigraphy of the Florissant Formation (after Evanoff and Murphy 1994).
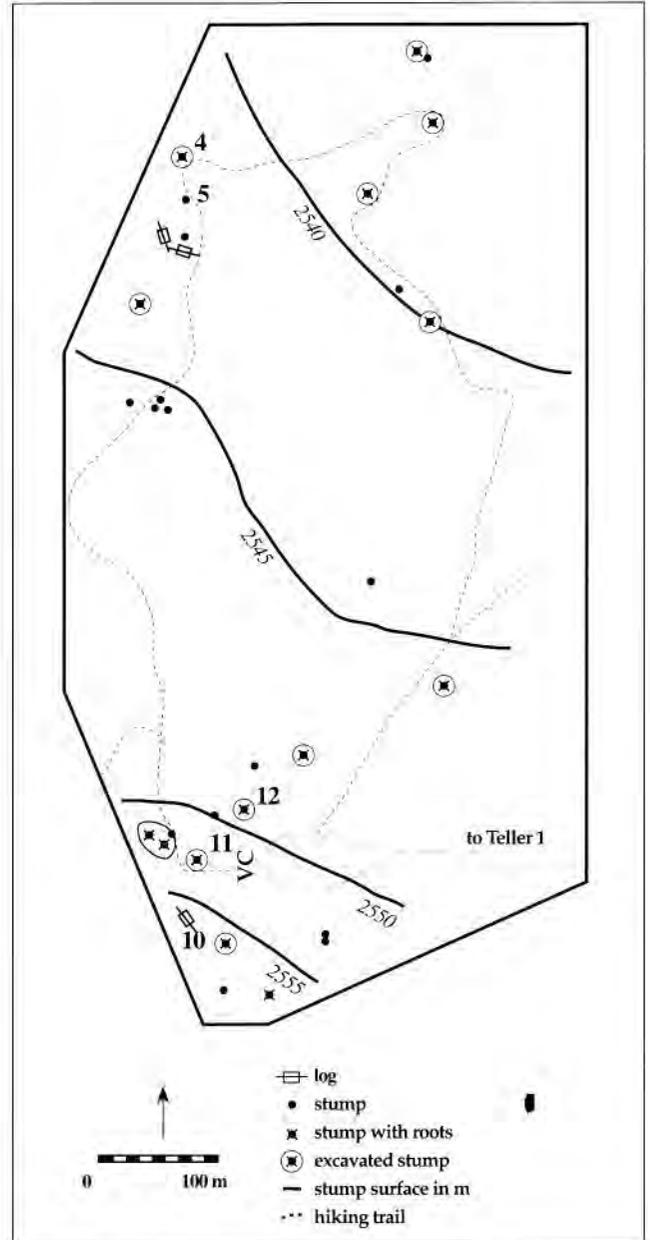
FIGURE 3. Map of the Petrified Forest area of Florissant paleovalley redrawn from Evanoff (1992). Numbers indicate stumps measured in this study, with dimensions given in Table 1. VC = Visitor Center with parking lot to the east. Stump surface contours are in meters and represent the surface Evanoff (1992) surveyed on present stump root zones. Location of the Florissant paleovalley is shown in Figure 1.

survive partial burial by sprouting new roots at a higher level (Helley and LaMarche 1968); no such features are observed in the exposed trunks at Florissant.

Unfortunately, the stump locations (Fig. 3) reveal little about late Eocene forest spacing because the area has been heavily collected. A. C. Peale of the Hayden survey described the Florissant area in 1874, mentioning twenty to thirty stumps visible above ground in the "petrified forest." In a history of the Florissant valley, Kimmet (1986) asserted that an "early photo of the forest shows such a profusion of petrified stumps, limbs, and branches that the area seemed almost impassable." By 1882, geologists were already complaining of "vandal tourists" breaking up the stumps and logs and hauling them away (Kimmet 1986). Material was removed until 1969, when the area became a national monument administered by the National Park Service (NPS). The only stumps left were those too large to be moved or those still buried. In 1984, the NPS buried an additional number of stumps to prevent vandalism.

Species Composition and Preservation

At least six genera of woods are present in the Florissant fossil forest: *Sequoioxylon pearsallii*, identified by Andrews (1936) on the basis of wood collected from stump FFB04 (Fig. 3); cf. *Robinia;* cf. *Koelreuteria;* two ring-porous Ulmaceae species most closely resembling *Zelkova;* and *Chadronoxylon* (Wheeler 2001). The *Sequoioxylon pearsallii* identification is consistent with the occurrence higher in the section of foliage and cones identified as *Sequoia affinis* by MacGinitie (1953). Based on vegetative and pollen morphology and wood anatomy, *Sequoia affinis* is most closely related to coast redwood, though it is not thought to be ancestral. Cross et al. (unpubl. data) examined wood samples from the stumps in the petrified forest area. They conclude that the conifers are probably all *Sequoioxylon*, but they caution that the wood anatomy is variable, with many stumps sharing some features with *Sequoiadendron* and *Taxodium*. It is possible that some stumps of *Chamaecyparis* are present; abundant foliage from this genera, which can attain massive growth forms, has been found in the lacustrine shales. More detailed work on wood anatomy of both the Florissant woods and extant Taxodiaceae wood is needed before the affinities can be definitively established.

The stumps range from 0.5 to 5 m in diameter and from 1 to 4 m in height (Table 1). The rings are well preserved; individual cells and details of cell structure are visible under magnification (Plate 1). Dissolution of the material in hydrofluoric acid indicates that lignin is still present.

Data Collection

In modern samples, ring widths are measured using an incremental measuring stage interfaced with a microcomputer, which is accurate to a hundredth of a millimeter (Robinson and Evans 1980). This measuring technique was used on samples FFB08A and FFB08B, which were collected, slabbed, and polished by M. Arct. Because of the hardness of the stumps and their high visibility to the public, it was not feasible to collect similar samples from each stump. However, the stumps have a prominent transverse fracture pattern, so the upper surfaces, which range from 2 to 4 m above original ground level, are often quite smooth (Plate 2). Rings were easily visible on these surfaces. I used a 10x monocle with a measuring scale accurate to a tenth of a millimeter to measure ring width on these exposed surfaces. Areas with possible microrings were examined with a 20x hand lens. Ring widths were measured only where individual cells could be discerned, and each series was measured twice. Latewood width was not recorded as a separate measurement from total ring width, because it was relatively thin and varied only slightly from ring to ring.

I tested whether the two measuring methods gave comparable results by measuring sample FFB08A using both methods and then comparing the results. The sum of the squares of twenty differences was under 0.10, and thus the accuracy was acceptable by usual dendrochronology measurement standards (Fritts 1976).

Problems encountered during measurement included deformation within rings and fracturing along ring boundaries. In some of the petrified trees, areas exist where the thin-walled earlywood cells are sheared, and the thick-walled latewood cells are unaffected or slightly flattened (Plate 1). This type of deformation is fairly common in fossil wood (Jefferson 1982; Francis 1984; Parrish and Spicer 1988) and is possibly due to waterlogging and subsequent desiccation. The deformed areas were avoided by tracing the ring to the side and measuring the undeformed width. The original width could be determined by measuring parallel to the rows of angled tracheids in the earlywood and then adding the latewood width in some slightly deformed areas. Another problem encountered was hairline fractures

TABLE 1. Stump diameter, height, and series location for Florissant trees.

Stump	Diameter (m)*	Height (m)*	Pith Sampled?
FFB01[+]	4.9	0.8	No
FFB03	2.0	0.5	No
FFB04	3.0	3.0	No
FFB05	2.0	0.3	Yes
FFB06	3.1	3.7	No
FFB08	3.2	1.7	No
FFB10	2.0	0.5	No
FFB11	4.2	2.5	No
FFB12	3.5	2.0	No
Ulmoideae[s]	0.5	0.4	Yes

*Diameter and height at widest and highest point, measured with tape measure.
[+]First three letters of name indicate site code; following two numbers indicate stump number (Fig. 3).
[s]Ulmoideae stump is from the Florissant Formation area, but otherwise has no geographic or stratigraphic context. It is housed at Sanborn's Western Education Camp, Florissant, CO.

along ring boundaries. These fractures could possibly obscure microrings and thus were noted.

In total, thirty series ranging from 63 to 434 rings were measured from nine *Sequoioxylon pearsallii* and one Ulmaceae (Table 1). Sampling was determined by preservation; these series represent all available surfaces of the exposed stumps. It was much more common for the outside of the tree to be preserved than the pith area, so most of the series were from the outer portions of the trees; only series from FFB05 and the Ulmoideae were located near the pith. Hence, the length of the ring-width series does not represent the age of the trees. Unfortunately, the bark was not present on these trees, so the xylem/phloem boundary could not be used as a datum.

As for the modern comparative data set, ring-width measurements were available for six coast redwood sites near the northern California coast: Plantation Ranch, Prairie Creek, Maillard Ranch, Wheat Field Fork, Willets, and Fort Bragg (Fig. 4; Brown and Swetnam 1994; Lamont-Doherty Earth Observatory and University of Arizona Tree-ring Lab files). The Plantation Ranch trees grow on flat benches above the Gualala River, whereas trees at the other sites were growing on slopes of various grades. These series were mostly from the outer portion of the trunks.

Descriptive statistics were available for three giant sequoia sites in the Sierra Nevada: Mountain
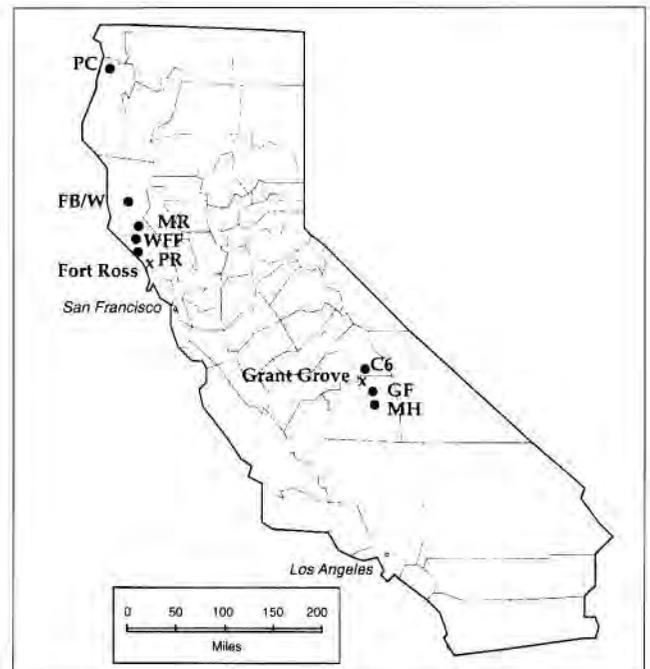
FIGURE 4. Location map for climate stations and modern giant sequoia and coast redwood sites. Coast redwood sites: PC=Prairie Creek, FB/W=Fort Bragg/Willets, MR=Maillard Ranch, WFF= Wheat Field Fork, PR= Plantation Ranch. Giant sequoia sites: C6=Camp Six, GF=Giant Forest, MH=Mountain Home, X=Climate station.

Home, Giant Forest, and Camp Six (Fig. 4; Brown et al. 1992; Hughes and Brown 1992; University of Arizona Tree-ring Lab files). The Mountain Home and Giant Forest trees grow on flat benches with relatively deep soils, whereas the Camp Six trees grow on a steep slope above the Kings River. The series were mostly from the outer portion of the trunks.

Methods

Cross-Dating

Cross-dating is the process by which the variation in ring characteristics—in this case ring width—is examined to determine whether matches exist between series from the same and different trees. If the patterns match, then the series are coeval. Cross-dating is the hallmark of dendrochronology; it is the fundamental principle that establishes that a common year-to-year variable signal exists in tree-ring series (Fritts and Swetnam 1989). Creber and Chaloner (1987) argued that, even for *in situ* stumps, cross-dating is not necessary in fossil wood studies because there is no reason to identify short frequency climate fluctuations; one rather desires a general indication of the climatic environment. However, I would argue that cross-dating has several advantages for studies of fossil trees.

1) The principle of "limiting factors" states that a tree cannot grow more than is allowed by the most limiting factor (Fritts and Swetnam 1989). When growth is limited, a narrow ring forms. If there are enough narrow rings, they form a pattern that allows the series to be cross-dated. Thus, if cross-dating exists, it means some climatic or environmental factor was limiting, and the amount of cross-datable variance indicates to what extent growth was limited (Fritts 1976).

2) Cross-dating allows series to be merged so that the climate signal is emphasized. The linear aggregate model of ring-width measurement of Graybill (1982) and Fritts and Swetnam (1989) is expressed as the equation:

$$R_t = G_t + C_t + D_t + E_t$$

R = ring width; G = the age-related growth trend value in year t that is shared by that species growing on that type of site; C = climate-induced growth for the stand, which includes the effects of the site, as climate is filtered through site conditions; D = the disturbance pulse, which includes endogenous factors, such as competition acting on specific trees, and exogenous factors, such as fire, insect infestation, or pollution common to the stand; and E = unexplained variance including measurement error.

Cross-dating allows the magnitude of the term E_t to be reduced, because ring widths for a given year are replicated. G and D are reduced by fitting a curve to the series and dividing the ring width at year t by the value of the curve at year t. This operation, termed "standardization," also stabilizes the mean and variance of the series, so that series can be combined with equal weight into a chronology. Because the effect of nonclimatic factors is reduced in the chronology as compared to raw ring-width series, descriptive statistics computed for the chronology are thus more characteristic of climate.

3) Cross-dating allows the identification of missing rings and false rings. If climate is severely limiting, then the tree may not produce any new xylem cells or may form new cells only along part of the circuit; this gap in the series is termed a missing ring. In the case of fossil trees, missing rings might also be caused by the hairline fractures discussed previously. If a ring wedges out along the circuit, then this type of missing ring can be identified by tracing the ring along the entire circuit of the tree. This is often not possible. Some missing rings are completely absent from the tree or specimen, and these can only be identified by cross-dating.

False rings are caused by a period of stress followed by an improvement in growing conditions within the growing season. During severe conditions, the tree starts to form latewood, but when the conditions improve, the tree switches back to forming earlywood cells (Fritts 1976). The band of latewood can be mistaken for an annual ring boundary. These can often be identified by careful examination, but some can only be identified by cross-dating (Ammons et al. 1987). The percentage of rings with missing or false rings is an important ecological indicator, and the identification of these features in a series improves the accuracy of the descriptive statistics (Fritts and Swetnam 1989).

4) If cross-identification is achieved, it proves that the fossil trees were growing at the same time.

In many fossil sites, it is unclear if vertical stumps represent one forest or many because of faulting or poor exposure. Cross-dating is very useful in such situations. If it is present, it establishes contemporaneity. For example, Arct (1979) and Ammons et al. (1987) have both used cross-dating to show that stumps in the Eocene Yellowstone petrified forest were coeval.

Descriptive Statistics of Ring-Width Series

In dendrochronology studies, descriptive statistics are computed for modern series primarily for comparative measures of the quality of chronologies (Fritts and Shatz 1975). These statistics have not been used alone to interpret climate, because more powerful analytical methods are available. With fossil wood, however, descriptive statistics can be used to compare different sets of ring-width series and in this way make interpretations about the general climate. These statistics include:

Mean ring width. Mean ring width is a measure of overall growth; it increases when conditions are more favorable. For example, Fritts et al. (1965) showed how mean ring width of Douglas-fir *(Pseudotsuga menze-*

sii), ponderosa pine *(Pinus ponderosa)*, and piñon pine *(Pinus edulis)* decreased from 1.5 mm to 0.68 mm along a gradient of decreasing elevation and precipitation in northern Arizona (Table 2, Fig. 5). LaMarche (1974) found similar results along an elevation/precipitation gradient for bristlecone pine *(Pinus longaeva)* from Nevada, with the two higher, wetter sites having larger mean ring width than the two lower, drier sites.

Ring width of trees at high elevations or high latitudes tend to be more limited by temperature than precipitation, and those at lower elevations or latitude tend to be more limited by precipitation (Kienast et al. 1987). Though these broad patterns generally seem to hold, local site conditions and topography may override them. I will argue in this study that mean ring width is the most useful and important statistic for estimating paleoclimate.

Percent missing rings/Percent false rings. The percentage of missing rings in a series is a measure of the proportion of years that were so limiting that portions of the tree did not grow; a high percentage indicates the tree was growing near the edge of its ecological range. Fritts et al. (1965) found the percent of missing rings increased as one went from the forest interior to the forest border (Table 2). In coast redwood, however, missing rings can be caused by a limiting environment,

TABLE 2. Descriptive statistics for an effective precipitation gradient in the San Francisco Mountains, Arizona.

Data from Table II (Fritts et al. 1965) for an effective precipitation gradient that decreases from right to left. The value reported for the seven stands represents the mean of five trees with four cores each. Note that two genera were collected at sites A and D. At site A, the Douglas-fir were from an east-facing slope, the ponderosa from a southeast-facing slope. At site D, the ponderosa were from a north-facing slope, the piñon from a south-facing slope. Forest interior sites for a species are the leftmost column for that species; forest border sites are the rightmost column. See Fritts et al. (1965) for additional site description. This table is graphically represented in Figure 5.

| | Douglas-fir | Ponderosa Pine | | | | Piñon Pine | |
	A	A	B	C	D	D	E
Mean RW (mm)	1.5	1.33	0.99	0.86	0.84	0.68	0.81*
Mean sensitivity	0.29	0.20	0.22	0.49	0.58	0.31	0.44
Standard dev.	0.40	0.27	0.28	0.53	0.68	0.34	0.48
% absent rings	0.0	0.1	0.0	4.0	7.8	0.7	3.5
% false rings	1.2	4.3	4.2	4.1	4.1	0.1	0.6
Intercorrelation	0.86	0.7	0.67	0.88	0.84	0.77	0.82
Intracorrelation	0.76	0.69	0.72	0.9	0.89	0.82	0.86

RW = ring width.
*Trees at this site were considerably younger than trees at the other sites, thus the higher mean ring width despite the drier and warmer conditions.
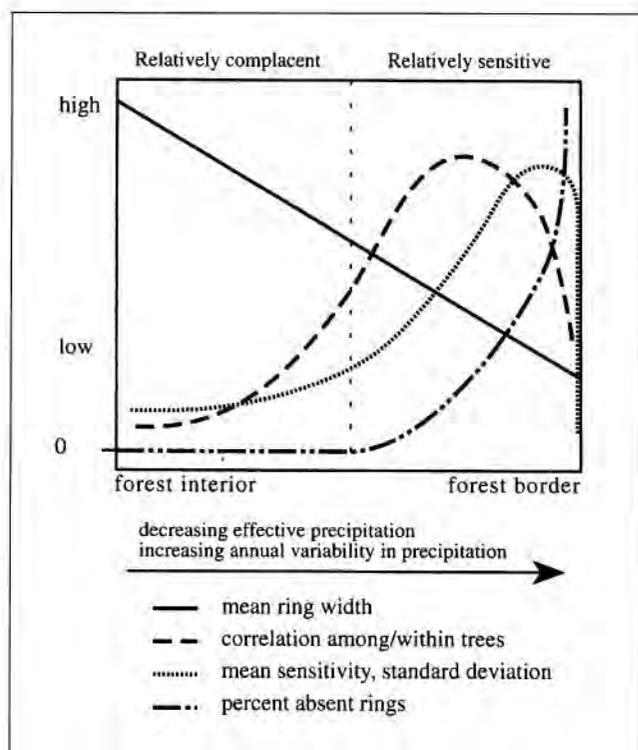
FIGURE 5. Trends in descriptive statistics as one moves from the forest interior to the forest border generalized from data in Table 2. After Fritts et al. (1965).

and they are also caused by sprouting (Brown and Swetnam 1994). This statistic has not been calculated in previous fossil wood studies.

The percentage of false rings indicates climatic variability within the growing season. False rings in nontropical conifers are more characteristic of arid climates than of moist climates. Genetic potential helps determine which species of arid-site conifers form false rings. Fritts et al. (1965) found that along a gradient experiencing the same regional climate, only one species out of three formed abundant false rings; absent rings were more likely to form in ponderosa pine than Douglas-fir (Table 2, Fig. 5).

Mean sensitivity. Mean sensitivity is a special dendrochronological statistic and is a measure of the year-to-year variability of a series. It is calculated by the following equation:

$$ms_x = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - X_t)}{x_{t+1} + X_t} \right|$$

Essentially, this statistic expresses the mean proportional change in year-to-year ring values. Mean sensitivities of conifer species in the western United States usually vary between about 0.1 and 0.5 (Fritts and Shatz 1975). Chronologies with values above 0.3 are considered relatively "sensitive" and those below about 0.2 relatively complacent.

Mean sensitivity for a given species tends to increase from forest interior to forest border, as the tree nears its ecological limit (Fig. 5). For example, Fritts et al. (1965) and LaMarche (1974) found that mean sensitivities for interior versus border sites (where precipitation was more variable) were 0.20 and 0.58 in ponderosa pine, 0.31 and 0.44 in piñon pine (Table 2), and 0.15 and 0.26 in bristlecone pine.

Francis (1986) considered mean sensitivity to be the most useful statistic for making paleoclimate inferences, interpreting that high mean sensitivity indicates a variable climate. The aforementioned data suggest that mean sensitivity may be more a measure of where a tree is located within its ecological range than a measure of climate conditions. More work comparing mean sensitivity of ring-width series from various climates is needed to determine if there is any climatic significance in this variable.

Standard deviation. The standard deviation of a ring-width series is a measure of the total variation of ring widths around the mean. One standard deviation expresses the distance from the mean within which 65 percent of the values fall. It is calculated for standardized series so that the effects of growth trends and disturbances are minimized. Like mean sensitivity, high standard deviation may suggest the tree is near the edge of its ecological range. It generally increases as one moves from the forest interior to the forest border (Fritts et al. 1965; LaMarche 1974; Table 2, Fig. 5). This statistic is not as reliable an indicator of year-to-year climatic variance because ring series with intermittent or a few persistent excursions in values may have inflated standard deviations. This statistic has not been included in previous fossil wood studies.

First-order autocorrelation. First-order autocorrelation is a measure of the correlation between the ring width for year t and the ring width for the subsequent year, t + 1. Autocorrelation is ubiquitous in tree-ring series and is thought to derive from physiological processes, such as storage or depletion of food resources or disturbance (Fritts 1976; Biondi and Swetnam 1987). The ecological or climatic significance of autocorrelation in tree-ring series is essentially unknown, though it tends to decrease as trees become more limited (Fritts

1969). Usually dendrochronologists are concerned with removing autocorrelation from tree-ring series because it violates statistical assumptions of parametric time series tests and regression models (Monserud 1986).

Comparing Statistics Between Fossil and Modern Wood

There are four primary factors to consider when comparing descriptive statistics for modern sites with those from fossil forests:

Age-related trends. As discussed previously, the linear aggregate model of ring-width measurement indicates ring width is a function of not only climate but also the age of the tree and disturbance history. Young trees have relatively large rings. As the tree gets older, ring width decreases because the circumference of the trunk increases while the rate of xylem production declines (Fritts 1976). This decrease is often similar to a negative exponential curve, with ring width decreasing rapidly in young trees and then decreasing less and less as the tree ages. Growth trends in relatively old trees often become essentially flat.

Mean sensitivity also varies with the age of the tree. The juvenile portion of ring series tends to be less sensitive than the mature portion. This pattern, however, is much less pronounced than that of mean ring width with age. Standard deviation and first-order autocorrelation are calculated for standardized series and generally do not show trends with age. Thus, when interpreting mean ring width in the context of climate, one needs to compare samples with similar age structure or account for the age differences among samples.

Disturbance history. Disturbances, such as a fire or the death of a neighbor, often cause growth releases in coast redwood and giant sequoia in which ring widths increase by an order of magnitude or more for several decades (Brown et al. 1992; Brown and Swetnam 1994). Thus the maximum ring-width statistic used by Creber and Chaloner (1984a, 1984b, 1987) is not useful for these genera. Maximum ring width could reflect a onetime growth surge after a disturbance event rather than growth averaged over a long period of time. Note that growth surges are not necessarily an indication of a disturbance event; they can also arise because of climatic conditions.

Disturbance-related growth surges bias values of the various descriptive statistics, especially mean ring width. In practice, however, if the percentage of the series consisting of growth release is small, these effects are probably minor and can be ignored. When compar-

ing mean ring width between sites, one should exclude series in which more than 50 percent of the length consists of sudden, steplike increases in ring width. If series contain only a few growth releases, one could either delete the disturbed portions or log transform the series. Taking the log of ring width has the effect of reducing the influence of high outliers and is a typical transformation for this type of data.

Site conditions. Slope, slope exposure, soil conditions, and forest spacing act as filters of regional climate. Given a drainage basin in the Northern Hemisphere, one would expect the highest values of soil moisture on the valley floor and the lowest values of soil moisture on steep, south-facing slopes. Even though trees from the slope and valley sites are growing in the same regional climate zone, the water balance for each tree would be quite different. In dendroclimatic studies of Holocene wood, trees growing on well-drained slope sites with an exposed aspect are usually sampled as opposed to trees growing in a valley bottom. Climate conditions are more likely to be limiting for the slope trees. Hence they are more sensitive, and patterns of wide and narrow rings are more closely related to climate than in trees growing in the valley (Douglass 1928; Fritts 1976; Fritts and Swetnam 1989).

In the geologic record, *in situ* petrified stumps are often preserved in mudflows. Because mudflows travel down valley bottoms, they usually preserve floodplain vegetation rather than the hillside vegetation. Thus, the type of sites fossil wood workers are likely to encounter differs from those sampled in most modern dendroclimatic studies.

It is difficult to quantify the difference in descriptive statistics likely between trees growing in a valley bottom versus a slope. Fritts (1969) conducted the most intensive quantitative study of these patterns. He looked at bristlecone pine, limber pine, and piñon pine growing on a variety of sites in the White Mountains of California and found that the greatest differences in ring-width characteristics were related to site characteristics and genotype. In comparison to bristlecones growing on slopes, bristlecones in valleys had higher mean ring width and first-order autocorrelation, fewer missing rings, and lower mean sensitivity, standard deviation, and correlation within trees (Fig. 6). The valley site in his study had a mean ring width 23 percent larger than the slope sites (Fig. 6).

Douglass (1928) noted a difference in ring-width characteristics in giant sequoia depending on distance from the valley bottom. He suggested mean ring width can be up to four times higher in the basins
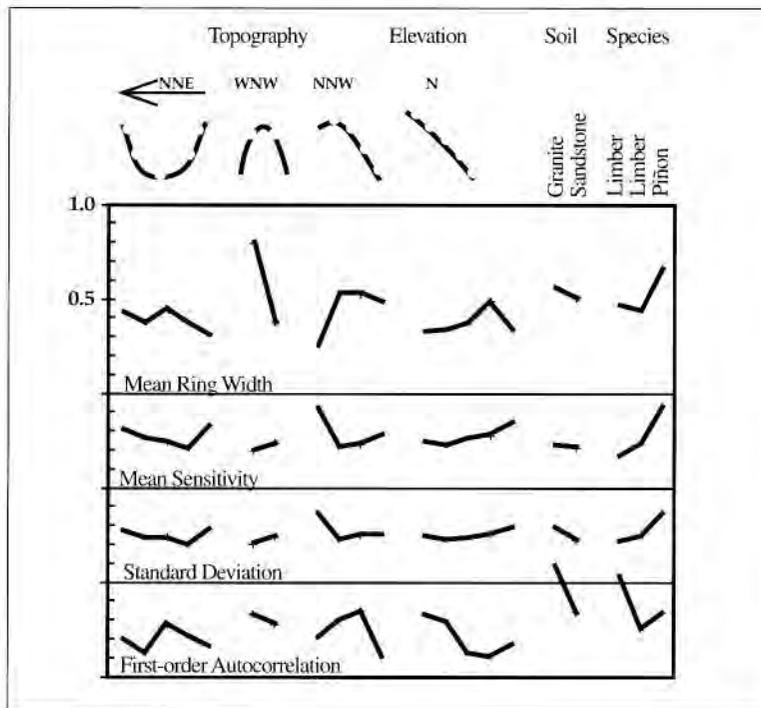
FIGURE 6. Comparison of values of descriptive statistics for different slope, slope exposure, and soils for stands of bristlecone pine, along with two stands of limber pine, and one stand of piñon pine (right side of diagram) in the White Mountains, California, modified from Fritts (1969). Ticks on y axis in 0.1 increments, with values increasing upward, but restarting at 0 for each descriptive statistic. Explanation of sites along x axis given at top of graph. The valley site mentioned in the text is the lowest in the NNE facing set; the slope sites are the other sites in the NNE set, along with the WNW and NNW sites. For more detailed description of sites, see Fritts (1969).

(Douglass 1936). This large difference has not been observed between slope and valley bottom samples in coast redwood sites (G. Jacoby, Lamont-Doherty Earth Observatory, pers. commun., 1994).

Thus, when choosing sites for comparison of tree-ring growth characteristics, one should try to minimize differences in site conditions between the sites, including percent slope, slope exposure, soil conditions, and forest spacing.

Genotype. Relatively little work has been done comparing chronologies between different species from a single site. Fritts (1969) found differences in mean ring width, mean sensitivity, standard deviation, first-order autocorrelation, and percent missing rings between species, though he states these differences are less than those related to site conditions.

Mean ring width appears to be the least taxon-dependent statistic. Schweingruber (1988) found little difference between mean ring width between silver fir

and spruce at the same sites. Fritts et al. (1965) found that Douglas-fir and ponderosa pine at the same site had mean ring widths of 1.5 mm and 1.33 mm, respectively, and that further down the effective precipitation gradient, ponderosa pine and piñon pine at the same site had mean ring widths of 0.84 mm and 0.64 mm, respectively (Table 2). These values are comparable, especially considering that within the sites the two stands had different slope exposures, and thus some of the difference in mean ring width is due to differing site conditions (Table 2). Fritts (1969) found that limber pine had similar descriptive statistics to bristlecone pine, whereas piñon pine had higher mean ring width, mean sensitivity, and standard deviation (Fig. 6). Again, some of this difference is due to site conditions, as the piñon site was the lowest elevation site in the study.

Year-to-year growth differs from species to species because of factors such as needle phenology and persistence (Fritts 1976; Schweingruber 1988). Mean

sensitivity and standard deviation will differ for trees at the same site because species have different environmental tolerances. In the aforementioned gradient study, Douglas-fir and ponderosa pine at the same site had mean sensitivity of 0.29 and 0.20 and standard deviation of 0.40 and 0.27, respectively (Table 2). Ponderosa pine and piñon pine at the same site had mean sensitivity of 0.58 and 0.31 and standard deviation of 0.68 and 0.34, respectively (Table 2; Fritts et al. 1965). Thus, fossil wood should be compared to wood from the closest living relatives because of the importance of genotype. Also, if possible, more than one fossil species should be sampled as in Parrish and Spicer (1988) and Spicer and Parrish (1990).

Treatment of Florissant Sample

I examined the twenty-eight *Sequoioxylon pearsallii* ring-width series for cross-dating. First, ring-width series from the same tree were checked for internal cross-dating. The skeleton plot method, which plots only narrow rings, was not entirely successful. Similar difficulties have been encountered in cross-dating modern coast redwood because the ring-width series tend to have little interannual variation in ring width, and ring "wedge-outs," in which several rings pinch out along the circuit of the tree, often occur (Swetnam 1987; Brown and Swetnam 1994). These two factors make coast redwood difficult to cross-date. Swetnam (1987) and Brown and Swetnam (1994) both found that using a light table to check for matches between ring-width plots was more successful than the usual skeleton plot method, which emphasizes the importance of patterns of narrow rings. Thus, ring-width plots of the Florissant series were examined on a light table in order to check visually for matches.

Series that were tentatively cross-dated in this fashion were then statistically analyzed using the computer program COFECHA (Holmes 1983). COFECHA removes autocorrelation and long frequency trends from each series, and then slides fifty-year segments of one series against another and computes Pearson correlation coefficients for the initial dated position and at lagged positions forward and backward. Missing rings were identified by comparing graphical plots and COFECHA output and then checking field notes and the actual wood for indications of irregularities to aid placement. No missing ring was added if the overlap between series was less than fifty rings.

The Florissant ring-width series were standardized using a forty-year cubic spline, which is a series of piecewise third-order polynomials (Cook and Peters 1981). Descriptive statistics for raw and detrended series were computed using the computer program ARSTAN (Cook 1985). To calculate the descriptive statistics for the Florissant samples, series along the same radius, but separated by a small break such as FFB01SW1 and FFB01SW2, were combined so that trees with several short sequences were not unduly weighted. Only one tree at Florissant, FFB05, had the pith preserved, and these series were deleted from the data set used for comparison. Growth releases did occur in the Florissant ring-width series, but where present constituted only a minor portion of the series; thus none of the fossil series was deleted from the data set for this reason. The Florissant ring-width series were log transformed using ARSTAN, and mean log ring width was also computed to further reduce the effect of high outlying ring widths.

Treatment of Modern Data

In the modern coast redwood data set, the Prairie Creek trees were cross-dated by Swetnam (1987) and the Wheat Field Fork, Willets, and Fort Bragg trees were cross-dated by Buckley and by Schulman (Schulman 1940; Buckley, pers. commun., 1992). Maillard Ranch and Plantation trees were not cross-dated because of problems with ring wedging in the period 1450 to 1880 (Buckley, pers. commun., 1992). All series were detrended with a forty-year cubic spline, as were the Florissant series.

Disturbance was especially a problem at the Plantation site, for which there were several short series dominated by growth surges beginning around 1890. If growth release constituted more than 50 percent of a series, then the series was deleted from the data set, because it was inferred that the mean ring widths for these series were responding more to disturbance history than general climate. Using this criterion, seven trees were removed from the Plantation data set, three from Wheat Field Fork, and one from Maillard Ranch.

The giant sequoia series were cross-dated and then standardized with a forty-year cubic spline (Brown et al. 1992). These data could not be examined for growth surges because only descriptive statistics were available for the series, as opposed to raw ring-width data. Relatively short series with extreme outliers in the mean ring-width histogram were deleted, because these were probably either young trees or series with a high proportion of growth surges. This included one tree from Mountain Home and two trees from Camp Six.

The descriptive statistics calculated for the Florissant series were compared to descriptive statistics from ring-width sequences from the closest living relatives to *Sequoioxylon pearsallii* using ANOVA. In Gregory (1992), the two data sets from coast redwood and giant sequoia were divided into five smaller subsamples: level sites and slope sites for coast redwood and two level sites and one slope site for giant sequoia. In the present study, the two combined data sets are used for comparison with the Florissant data set for simplicity because of the lack of significant differences between subsets of these combined samples.

Age-related trends are not considered a problem in this comparison, because the fossil and modern ring-width series were long and were predominantly from the outside portion of the trees where age trends are not pronounced. Series in which the pith was sampled were deleted from the data sets. Disturbance is also not considered to be a problem, as short sequences with growth surges were deleted. The complications of site conditions and genotype will be discussed later.

Results

Cross-Dating

I interpreted the clearly visible rings in the Florissant *Sequoioxylon pearsallii* to have been formed annually because they were clearly defined. Nonannual rings are usually less clearly defined with diffuse boundaries (Fritts 1976; Jefferson 1982). The earlywood/latewood transition was sharp. The latewood band was narrow, typically ranging from three to twelve xylem cells, with an average of seven cells. Latewood represented less than 10 percent of ring width. In the ring-porous species, latewood width was variable, ranging from 29 to 88 percent of ring width and averaging 63 percent of ring width. Raw ring-width values for the Florissant trees are given in Gregory (1992).

Within-tree cross-dating was achieved in stumps FFB01 (Fig. 7), FFB03, FFB05, FFB06, FFB08, and FFB12. FFB11 did not internally cross-date, probably because of problems with ring wedging. This characteristic was also observed in stumps FFB01, FFB02, FFB05, and most notably FFB12, in which ten rings could be seen wedging out over approximately 5 cm of circuit length. FFB04 did not internally cross-date, but it appeared in the field that the radii measured from this stump were from portions of the upper surface that did not overlap in time; thus the lack of cross-dating is not surprising. Within-tree Pearson correlations for the cross-dated series ranged from 0.48 to 0.74 as calculated by COFECHA, which are typical values for coast redwood (Table 3).

Missing rings were identified in series from stump FFB01 by cross-dating the individual radii. The percent missing rings ranged from 0 percent in stumps FFB03, FFB05, FFB06, and FFB08, to 0.8 to 2.6 percent in FFB01, to 12 percent in stump FFB12 (Table 3). No false rings were found.
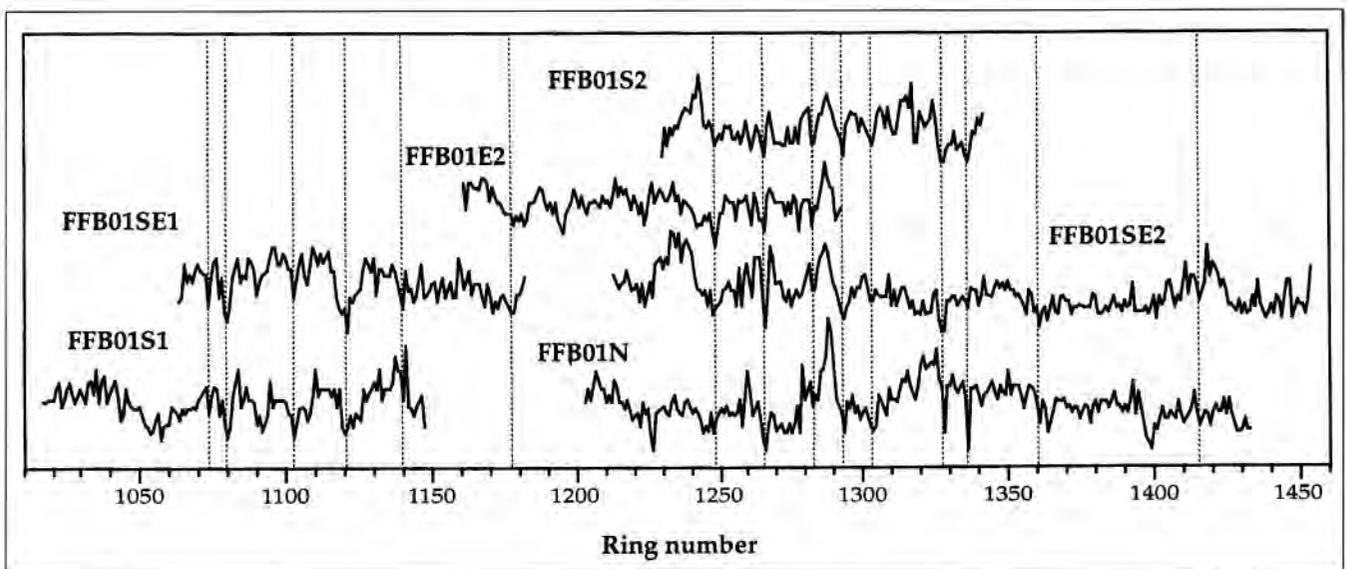

FIGURE 7. Cross-dating between series from stump FFB01. Ring numbers given are arbitrary.

TABLE 3. Intercorrelation of *Sequoioxylon pearsallii* ring-width series and percent missing ring values.

Stump[*]	Intercorrelation[†]	Series[§]	% Missing Rings	Relative Dates of Missing Rings[**]
FFB01	0.59	FFB01SW1	0.8	1121
		FFB01SW2	0.8	1327, 1328
		FFB01N	1.7	1227, 1266, 1336, 1399
		FFB01S1	0	
		FFB01S2	2.6	1327, 1328, 1336
		FFB01E1	0	
		FFB01E2	0.8	1249
		FFB01E3	0	
FFB03	0.74	FFB03S1	0	
		FFB03S2	0	
		FFB03S3	0	
		FFB03SW	0	
FFB05	0.62	FFB05NW1	0	
		FFB05NW2	0	
		FFB05NW3	0	
		FFB05N1	0	
		FFB05N2	0	
FFB06	0.74	FFB06N1	0	
		FFB06N2	0	
		FFB06W	0	
FFB12	0.48	FFB12SW	0	
		FFB12SSW	12.1	1041, 1043, 1046, 1054, 1055, 1056, 1057, 1058, 1059, 1060, 1061, 1085

[*] See Table 1 for explanation of stump names.

[†] The overlap between series FFB08A and FFB08B was postulated by M. J. Arct from the location of the samples within the tree (Loma Linda University, pers. commun., 1991) but was too short for intercorrelation to be calculated.

[§] The letters following the stump name indicate compass direction of series, and the following number, if any, indicates the series identification for that direction.

[**] Cross-dated stumps were given a relative starting date of 1000. This column gives the relative years that had missing rings. These missing rings were identified by cross-dating, except for FFB12SSW in which missing rings were identified by observation of ring wedging in the field.
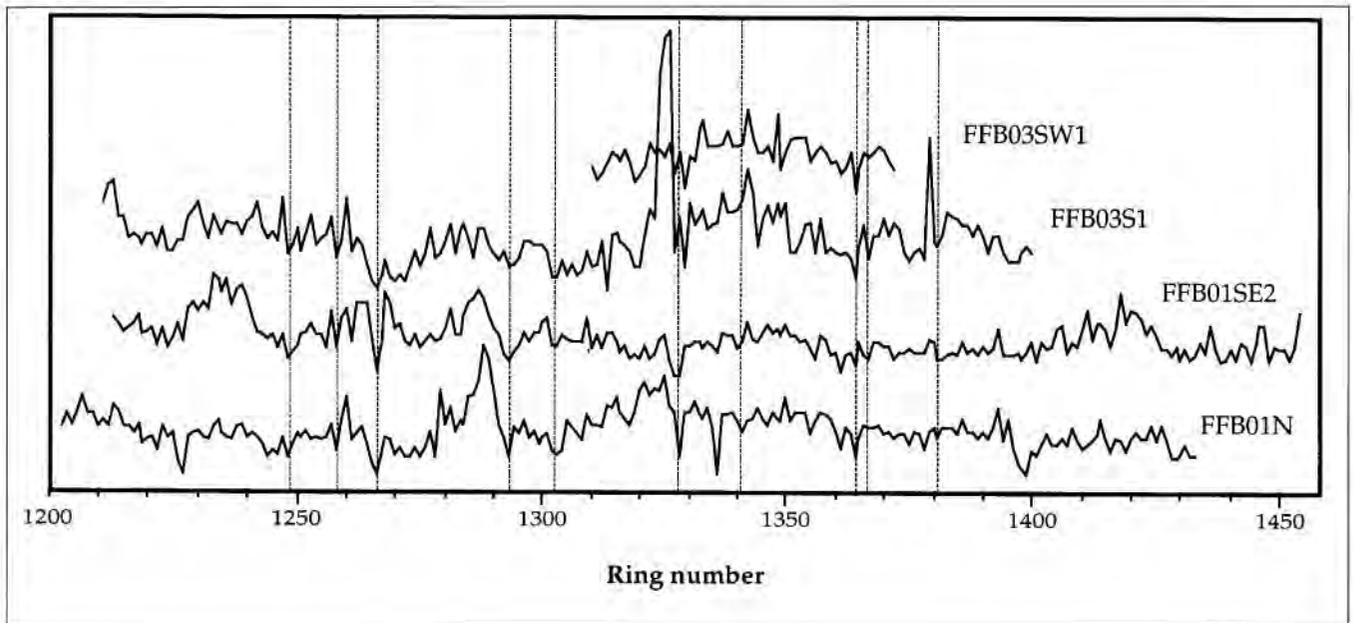
FIGURE 8. Cross-dating between stumps FFB01 and FFB03. Ring numbers given are arbitrary.

Between-tree cross-dating was achieved for FFB01 and FFB03 (Fig. 8), which were growing 160 m apart from each other (Fig. 3). The two trees have an overlap of 180 years and a correlation of 0.57. This correlation is fairly typical for coast redwood and is the best cross-dating relationship based on ring widths yet found in fossil wood. This finding clearly establishes that at least these two trees grew contemporaneously.

Descriptive Statistics

Although it is desirable to calculate the descriptive statistics for a summed chronology rather than individual ring-width series, there were not enough series in the Florissant sample to be combined into a single chronology for the site. Only two of the trees cross-dated. Instead, statistics for individual ring-width series were computed (Table 4). Note that each radius is treated as a separate data series rather than being combined with other series from the same stump. Simply averaging statistics for each tree does not maximize the variance due to climate. Descriptive statistics from each site were normally distributed except where noted (Table 5).

There are some similarities among the descriptive statistics for the three samples (Table 5). The Florissant *Sequoioxylon pearsallii* series has an average mean sensitivity of 0.31, which is on the borderline between sensitive and complacent. This value is similar to the

value for modern coast redwood. Standard deviation for Florissant, again on the sensitive side, is also indistinguishable from the average standard deviation for coast redwood. The moderate value of first-order autocorrelation, 0.34, is similar to that for giant sequoia.

The statistics for percent missing rings and mean intercorrelation could not be compared using ANOVA, but they appeared to be similar for both the fossil and modern redwood. Comparing the percentage of missing rings in the two samples may not be valid, however, because only a small percentage of the coast redwood trees had series that cross-dated. Many of the missing rings in the samples that were not cross-dated probably went undetected.

In the other comparisons, the Florissant sample differs significantly from the modern trees (Table 5). Note that the 1.4 mm mean ring width for the Florissant trees is significantly higher than both coast redwood and giant sequoia, which have mean ring widths of 1.01 mm and 0.87 mm, respectively. Mean sensitivity and standard deviation for Florissant were significantly higher than the value for the fairly complacent giant sequoia, while first-order autocorrelation was highest in coast redwood.

Interestingly, the values for each modern genus are closer to the values for the fossil redwood than to those for their modern relative. Coast redwood and giant sequoia have significantly different values for

TABLE 4. Descriptive statistics for the Florissant ring-width series.

RW (ring width) and Log mean RW were calculated for raw ring-width series, rather than detrended series, because detrended series are normalized so that they have a mean ring width of one. The other statistics were calculated on standardized series.

Series	Years	Mean RW	Log Mean RW	Mean Sensitivity	Standard Deviation	FOAC*
FFB01SW	362	1.26	2.51	0.33	0.34	0.34
FFB01N	231	1.32	2.55	0.34	0.34	0.40
FFB01S	248	1.24	2.49	0.35	0.37	0.40
FFB01E1	123	1.38	2.65	0.24	0.25	0.31
FFB01E2	132	1.28	2.57	0.28	0.28	0.41
FFB03S1	180	2.01	2.96	0.28	0.36	0.35
FFB03S2	136	1.87	2.90	0.30	0.33	0.30
FFB03SW	63	1.48	2.71	0.30	0.27	0.16
FFB04W	230	1.37	2.52	0.27	0.36	0.61
FFB04SE	220	2.02	2.99	0.22	0.26	0.40
FFB04S	95	1.90	2.93	0.26	0.29	0.37
FFB05NW	82	1.92	2.72	0.46	0.47	0.38
FFB05N	121	2.24	2.92	0.41	0.53	0.47
FFB06N	201	2.31	3.02	0.24	0.26	0.32
FFB06W	67	0.82	2.07	0.29	0.38	0.37
FFB08	599	0.52	1.73	0.38	0.37	0.27
FFB10	71	1.15	2.46	0.25	0.26	0.19
FFB11S	355	1.13	2.28	0.40	0.42	0.36
FFB11E	436	1.45	2.66	0.30	0.31	0.31
FFB12SW	81	1.17	2.42	0.32	0.36	0.31
FFB12SSW	99	0.84	2.03	0.50	0.53	0.26

* FOAC = first-order autocorrelation.

TABLE 5. Mean values for descriptive statistics.

If different letters follow two values in a row, then these values are statistically different at the 95 percent confidence interval. The same letter indicates the values are statistically indistinguishable. Some statistics missing for giant sequoia because raw ring-width series were not available. Values for the individual series in the modern data sets are listed in Gregory (1992).

	Sequoioxylon pearsallii	Coast Redwood	Giant Sequoia
Number of series	19	49	93
Mean ring width (mm)	1.40a*	1.01b*	0.87c*
Mean log ring width	2.55a	2.22b	
Mean sensitivity	0.31a	0.29a	0.18b*
Standard deviation	0.033a	0.33a	0.19b[†]
First-order autocorrelation	0.34a*	0.40b*	0.30a[†]
% missing rings (average)	0.55	0.44	
Mean intercorrelation	0.63	0.53	

*Values log transformed to obtain a normal distribution.
+Distribution differed from normal.

every statistic compared, with coast redwood having higher mean ring width, mean sensitivity, standard deviation, and autocorrelation (Table 5).

Discussion

Variation in Descriptive Statistics Due to Genotype

A crucial question for this study is how much of the difference in the statistics for the Florissant redwood, coast redwood, and giant sequoia ring-width series is due to climatic factors and how much is due to genotype. This question can be addressed by comparing the aforementioned statistics for coast redwood and giant sequoia to instrumental climate data.

Hughes and Brown (1992) found that low-growth years in giant sequoia correlate most highly with extreme drought events as measured by the Palmer Drought Severity Index (PDSI) for August. PDSI is a measure of soil water balance and therefore represents a combination of temperature and precipitation factors. Swetnam (1987) found that coast redwood ring growth correlated best with July precipitation and temperature, with increased growth occurring during warm/wet

summers. Therefore, it appears that both giant sequoia and coast redwood respond most strongly to July/August temperature and precipitation. Even though giant sequoia grows under a lower mean annual temperature (MAT) and higher mean annual precipitation (MAP) climate regime than coast redwood, drought stress is greater for giant sequoia because of the higher temperatures in the summer due to a higher mean annual range in temperature (Fig. 9). Also, coast redwood grows in the coastal fog belt, and daily summer fogs in this habitat reduce the loss of water due to evaporation and transpiration (Azevedo and Morgan 1974).

For two meteorological stations in the giant sequoia and coast redwood regions, mean July/August temperature is 16.8 °C and 14.0 °C and mean July/August precipitation is 0.25 cm and 0.6 cm, respectively (Table 6). In terms of variability, PDSI values have a higher mean sensitivity in the San Joaquin drainage, where giant sequoia grows, as opposed to the north coast, where coast redwood grows (Table 7). Mean sensitivity of July/August precipitation is similar for both sites, while standard deviation is much higher at the coast.

If there were no species differences in growth potential, one would expect to see larger mean ring widths for coast redwood because of the more favorable
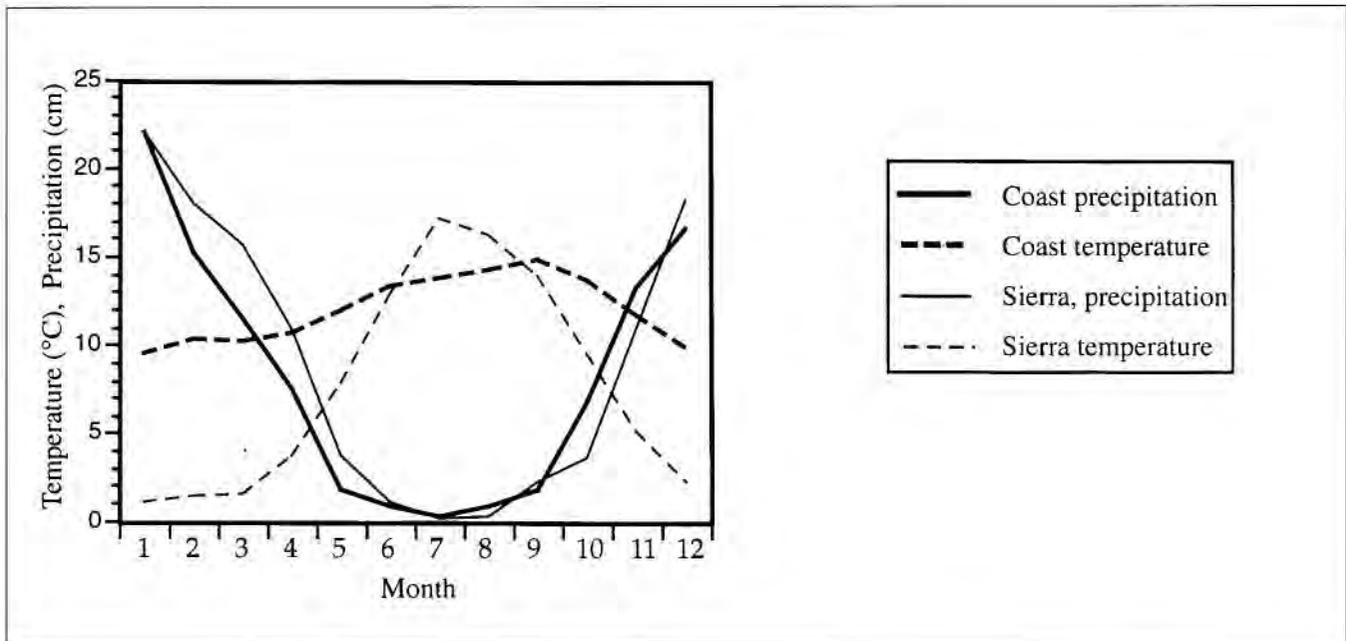
FIGURE 9. Monthly temperature and precipitation for the northern coast of California, from the Fort Ross climate station (coast redwood) and for the Sierra Nevada, from the Grant Grove climate station (giant sequoia). The locations of these climate stations relative to the sample sites are shown in Figure 4.

TABLE 6. Climate data for modern California and Florissant in the late Eocene.

	Giant Sequoia[*]	Coast Redwood[†]	Florissant[§]
MAT (°C)	7.8	11.8	12.8 ± 1.5
MART (°C)	17	8	~20+
MAP (cm)	107	99	72 ± 31
GSP (cm)[**]	3.8	3.8	57 ± 16
Mean July temp. (°C)	17.2	13.9	~22?
Mean Aug. temp. (°C)	16.3	14.3	~22?
Mean July precip. (cm)	0.2	0.3	~10?
Mean Aug. precip. (cm)	0.3	0.8	~10?

MAT = mean annual temperature.
MAP = mean annual precipitation.
GSP = growing season precipitation.
MART = mean annual range of temperature.
temp. = temperature.
precip. = precipitation.
[*]Climate data from Grant Grove climate station, with 48 years of temperature record and 54 years of precipitation record.
[†]Data from Fort Ross climate station, with 40 years of temperature record and 115 years of precipitation record.
[§]Climate estimated from leaf physiognomy of the 34.9 Ma Florissant flora (Gregory and McIntosh 1996); MART from Schorn (1998).
[**]Growing season for California defined as June through September. For Florissant, GSP estimated from multiple regression model of a modern data set in which GSP is defined as months with mean monthly temperature > 10 °C. This would be a poor definition of the growing season for coast redwood, but is probably acceptable for Florissant because of the higher mean annual range of temperature.

soil moisture regime. This trend is observed (Table 5). However, one might also expect to see higher mean sensitivity and similar standard deviation for giant sequoia, because the mean sensitivity of PDSI is higher than, and standard deviation of PDSI is similar to, that for coast redwood (Table 7). These trends are not observed (Table 5). Low mean sensitivity and standard deviation in giant sequoia may be due to the fact that genetically, giant sequoia is more drought tolerant than coast redwood. Another possibility is that coast redwood might have a higher capacity for growth in favorable years than giant sequoia.

Thus genotype is important, because mean sensitivity is significantly lower for giant sequoia even though the climate is more xeric and variable, suggesting this genus is more drought-tolerant than coast redwood. This observation agrees with the observations in Fritts et al. (1965) of large differences between mean sensitivity and standard deviation between species at the same site (Table 2).

However, if genetic potential was the overriding factor in determining growth, one would expect to see greater growth in giant sequoia, which appears to be

less limited by climate. In fact, one sees larger mean ring widths in coast redwood that suggests climate plays a more important role than species in determining growth potential and thus mean ring width. This conclusion is consistent with data discussed previously, especially the decrease in ring width across three species observed for a decreasing precipitation gradient (Table 2). Of course, these conclusions must be considered preliminary because of the small data set; more work needs to be done to quantify the genetic contribution to wood growth.

Mean sensitivity and standard deviation appear to be highly taxon-dependent, and should be used to make inferences about paleoecology, that is, where a species is in its ecological range, rather than paleoclimate. First-order autocorrelation should also be considered an ecological indicator, but lack of data makes the interpretation of this statistic less clear. If compared to a close-enough relative that has similar "ecological" statistics, mean ring width is a useful paleoclimate indicator. Specifically, mean ring width appears to be a function of effective precipitation, both for coast redwood and giant sequoia, along with Douglas-fir, ponderosa pine, and piñon pine (Table 2).

TABLE 7. Comparison of climate and ring-width series statistics for coast redwood and giant sequoia.

Mean, mean sensitivity, and standard deviation compared for climate and ring-width data. Statistics for climate calculated by ARSTAN. Climate station information given in Table 6.

	CR	GS	Comments
MEAN:			
July/Aug T	↓	↑	Generally less drought stress and
July/Aug Ppt	↑	↓	larger rings in coast redwood than giant
Ring width	↑	↓	sequoia
MEAN SENSITIVITY:			
July/Aug T	—	—	Less year-to-year variability in coast redwood
July/Aug Ppt	—	—	climate, yet higher mean sensitivity than
PDSI	↓	↑	giant sequoia
Ring-width series	↑	↓	
STANDARD DEV.:			
July/Aug T	↓	↑	Similar PDSI values, yet greater total
July/Aug Ppt	↑	↓	variability for coast redwood
PDSI	—	—	
Ring-width series	↑	↓	

CR = coast redwood.
GS = giant sequoia.
T = temperature.
Ppt = precipitation.
PDSI = Palmer Drought Severity Index.
— = similar values.
↑ = significantly higher values.
↓ = significantly lower values.

Paleoclimatic Inferences from the Florissant Wood

The sharp earlywood/latewood transition seen in the Florissant wood is similar to that of coast redwood and indicates a rapid end to the growing season; this could be due to either lack of rainfall, lower temperatures, or shorter day length. The lack of false rings at Florissant is an indication that conditions were fairly moist; that is, apparently there was no climatically induced stress interrupting the growing season. Although there are differing genetic potentials for formation of false rings in nontropical conifers, they are usually characteristic of arid regions.

Because the Florissant trees were growing in a valley bottom, they should be compared to modern relatives growing in similar environments. The modern coast redwood and giant sequoia trees were not all growing in valley bottoms; some grew on flat benches, an environment somewhat analogous to valley bottoms, with others growing on slopes of various grades.

Thus, some variation due to site conditions should be expected.

The similar mean sensitivity and standard deviation and lower first-order autocorrelation for the Florissant trees as compared to coast redwood indicate that the fossil redwood was as close or closer to the limits of its ecological range than coast redwood. The Florissant redwood was closer to its ecological limit than the modern giant sequoia given the low values for mean sensitivity and standard deviation for giant sequoia.

High cross-dating quality often indicates that the trees were limited by the ecological conditions, but this conclusion is not necessarily true for coast redwood. The fact that two of the Florissant trees cross-dated and five of the trees had internal cross-dating probably indicates ring wedging at Florissant was less prevalent than in the coast redwoods either due to a less limiting microenvironment or less sprouting. Taken together, these factors indicate that the Florissant redwood is in the same, or slightly more marginal, portion of its ecological

range than the modern coast redwood sites. It is impossible to make any paleoclimate inferences from this conclusion, as coast redwood and the Florissant redwood most likely have differing ecological sensitivities.

Assuming that modern coast redwood and giant sequoia provide partial analogs for the Florissant trees, the significantly higher mean ring width in *Sequoioxylon pearsallii* suggests more favorable conditions during the growing season for the Florissant trees. This increased growth as compared to coast redwood associated with similar values for mean sensitivity and standard deviation raises the possibility that the fossil redwood was less drought resistant than its modern counterpart. Because growth is greater for *Sequoioxylon pearsallii*, one may also expect to see statistics indicating a less limiting environment; yet the fossil redwood was just as limited as coast redwood growing in a harsher climate.

More favorable conditions for the Florissant trees, rather than the modern trees, can be explained in several ways. The first possibility is that the greater growth of the Florissant trees is from higher rainfall during the growing season. Using the foliar physiognomic method of Wolfe (1993), Gregory and McIntosh (1996) estimate that the mean annual temperature (MAT) at Florissant 34.1 Ma was 12.8 ± 1.5 °C with a mean annual precipitation (MAP) of 72 ± 31 cm, with 57 ± 16 cm during the growing season; the growing season was defined as months with mean monthly temperatures greater than 10 °C.

The Florissant paleoMAT of 12.8 ± 1.5 °C falls within the observed 11 to 14 °C MAT thermal field of coast redwood (Axelrod 1986), and is comparable to the MAT at the Fort Ross climate station of 11.8 °C during the last century (Table 6). The MAP of 72 ± 31 cm estimated for Florissant is somewhat less than the 99 cm recorded at the modern coast, but the percentage of that precipitation that falls during the growing season is much greater (Table 6). At least today, only 3.8 cm of precipitation occurs during the growing season for the sequoia and redwood sample sites in California, while 57 ± 16 cm of growing season precipitation (GSP) is estimated for Florissant (Table 6). Greater amounts of rain falling during the growing season at Florissant are a likely explanation of the higher ring widths, though this interpretation is complicated by different definitions of GSP for the modern and fossil sites (Table 6).

Florissant at 34.1 Ma could have been receiving more precipitation from the Pacific than it does today; in the late Eocene, the present Sierra Nevada had not yet uplifted, so these moist air masses could have carried precipitation further into the continental interior (Axel-

rod 1986). MAP in this scenario does not seem to be as important as GSP in determining ring width; even though the Florissant trees received less MAP than the modern sites, especially considering that more would have evaporated during the warmer summers, they experienced greater growth.

The second explanation for the higher growth rates for the Florissant trees is higher levels of CO_2 in the atmosphere. Using geochemical carbon cycle models, Berner (1991) estimates early Oligocene levels of CO_2 were up to two times the levels of today. Cerling (1991) estimates similar values for the Eocene and Miocene by using stable carbon isotopes in paleosols. It has been suggested that CO_2 in the atmosphere would enhance growth efficiency if levels were increased. However, evidence for this fertilizing effect in natural vegetation is sparse.

In one of the longest growth chamber experiments, Idso and Kimball (1993) found increased stem diameter in sour orange trees (*Citrus aurantium* L.) growing under increased CO_2. In contrast, D'Arrigo and Jacoby (1993) examined 300-year-long ring-width series for white spruce (*Picea glauca* [Moen.] V.) at three North American tree-line sites and found no increased growth due to increasing CO_2. Graumlich (1991) found a similar lack of response to CO_2 in foxtail pine (*Pinus balfouriana*), lodgepole pine (*Pinus murrayana*), and western juniper (*Juniperus occidentalis*). Graybill and Idso (1993) found that in strip-bark forms of bristlecone pine (*Pinus aristata, P. longaeva*), in which almost all stored carbon is allocated to the cambium along a single radius, ring width increased with increasing CO_2. However, this result is not applicable to sequoia and redwood. Thus it seems unlikely that increased CO_2 levels are responsible for the large Florissant ring widths.

The third possible explanation for increased growth for the Florissant trees is that general climate was similar, but the river valley location had soil/topographic conditions that were much more favorable than conditions at any of the modern sites. The Florissant sample has a mean ring width 40 percent greater than modern coast redwood. It is difficult to evaluate whether this amount of variation is possible just due to site conditions, given the lack of modern studies. However, given that valley bristlecones only had a mean ring width 23 percent higher than slope bristlecones in the study of Fritts (1969), some climate effects are probably represented. A conclusion of similar climate given the greater summer rainfall at Florissant could be explained by the high mean annual range of temperature (MART) at Florissant of 20+ °C compared to 8 °C for coast redwood

(Table 6). Higher MART means high summer temperature and evaporation, which could render the water balance similar to the modern coast. Ring-width series from coast redwood growing in valley bottom sites are needed to evaluate this hypothesis.

The fourth possibility is that narrow ring sequences in the Florissant fossil stumps are preferentially weathered because of the larger number of ring boundaries per volume; these ring boundaries are zones of weakness. This hypothesis is unlikely because the standard deviations for mean ring widths are similar for the three data sets. If smaller rings were not represented at Florissant, one would expect lower standard deviation for the mean ring-width sample as compared to standard deviations for the modern trees.

Acknowledgments

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PLATE 1. *Sequoioxylon pearsallii*. Top, transverse section. Middle, radial section. Bottom, transverse section showing deformation of tracheids. Photos are 2 mm across.

PLATE 2. Top, stump FFB11, illustrating how the upper surface tends to be horizontal. Bottom, natural surface on stump FFB01 showing tree rings. Scale in centimeters.

6.

FOSSIL DICOTYLEDONOUS WOODS FROM FLORISSANT FOSSIL BEDS NATIONAL MONUMENT, COLORADO

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ABSTRACT—Five types of fossil dicotyledonous woods from Florissant are described. The characteristics of these Florissant dicotyledonous woods, and the few other known late Eocene woods (Chadronian) from Nebraska and Wyoming, contrast markedly with middle Eocene dicotyledonous woods from Wyoming; whereas middle Eocene woods often lack distinct growth rings (suggesting equable climates) and are rarely ring porous, the Chadronian woods have distinct growth rings and are often ring porous or semi-ring porous (indicating markedly seasonal climates). The most abundant dicotyledonous wood at Florissant occurs intermixed with the *Sequoia*-like stumps in the main fossil forest area of the monument. This wood is diffuse-porous, and is of uncertain affinities, with a combination of characters that occurs today in more than one family, and is described as a new genus, *Chadronoxylon*. The other four woods are distinctly ring porous. Ring porosity is a feature that today is characteristic of middle latitudes of the Northern Hemisphere and seasonal climates. Two of these ring-porous woods have characteristics of the Ulmoideae (Ulmaceae, elm family), and most closely resemble *Zelkova* (Chinese elm). One resembles *Koelreuteria* (Sapindaceae); one resembles *Robinia zirkelii* (black locust, Leguminosae). Three of the ring-porous woods occur in the lower tuff, but not in main fossil forest areas. The *Robinia*-like wood occurs in the upper tuff. These five Florissant woods double the number of late Eocene woods from North America that have been described anatomically.

KEY WORDS: Paleobotany, fossil wood, Eocene, Chadronian, Florissant, wood anatomy, Ulmaceae, Sapindaceae, Leguminosae, *Zelkova*, *Robinia*

The spectacular petrified stumps of *Sequoia*-like wood are a main attraction of the Florissant Fossil Beds National Monument, Colorado. Dendrochronological work has shown some of these stumps within the main fossil forest to be contemporaneous (Gregory 1992, 1994a; Gregory-Wodzicki 2001). Andrews (1936) described the anatomy of the large *Sequoia*-like stumps. Silicified dicotyledonous woods (hardwoods) also occur at Florissant, but to date none have been described anatomically. The purpose of this paper is to describe dicotyledonous woods collected from the Florissant Formation, document their characteristics and probable affinities, and compare them to Chadronian woods known from other localities as well as to early and mid-

dle Eocene dicotyledonous woods known from the Rocky Mountains. Little is known of late Eocene dicotyledonous woods (Wheeler and Baas 1991; Wheeler and Landon 1992). The five wood types described and discussed herein double the number of dicotyledonous woods described from the late Eocene of North America.

Various characteristics of dicotyledonous woods are correlated with climate (Baas 1986; Baas and Schweingruber 1987; Wheeler and Baas 1991, 1993; Carlquist 1975, 1988; Woodcock 1994a, b). Accordingly, fossil woods provide useful supplementary data for climate reconstruction for the Florissant region during the late Eocene. Comparison of the Florissant woods and other late Eocene woods to middle Eocene woods provides

data for developing methodologies for using dicotyle-donous woods for Tertiary climate reconstruction.

In conifers a single cell type functions for both water conduction and support; in dicotyledons there are at least two cell types for these functions—vessel elements for water conduction, and fibers for support. Variations in vessel diameter, density, grouping, and arrangement represent differences in hydraulic conductivity and safety. Conductivity is proportional to the fourth power of the radius of the conduit; thus a few large vessels conduct more water than many narrow vessels (Zimmermann 1983).

The strategy of a few large (>200 μm diameter) vessels evenly distributed throughout a wood is consid-

ered risky because the loss of conductance in any one vessel due to an air embolism represents the loss of a relatively large proportion of the conducting system (Carlquist 1988). Trees and shrubs of temperate regions of North America, Europe, and Asia do not have this type of wood (diffuse porous with large-diameter vessels) however, tropical trees commonly have this wood type (Fig. 1).

Ring-porous woods have a distinct ring of relatively large-diameter vessels that are produced early in a growing season. In the eastern United States, the earlywood ring of large-diameter vessels is produced before the leaves expand. The earlywood is of near-constant width each year, followed by a variable amount
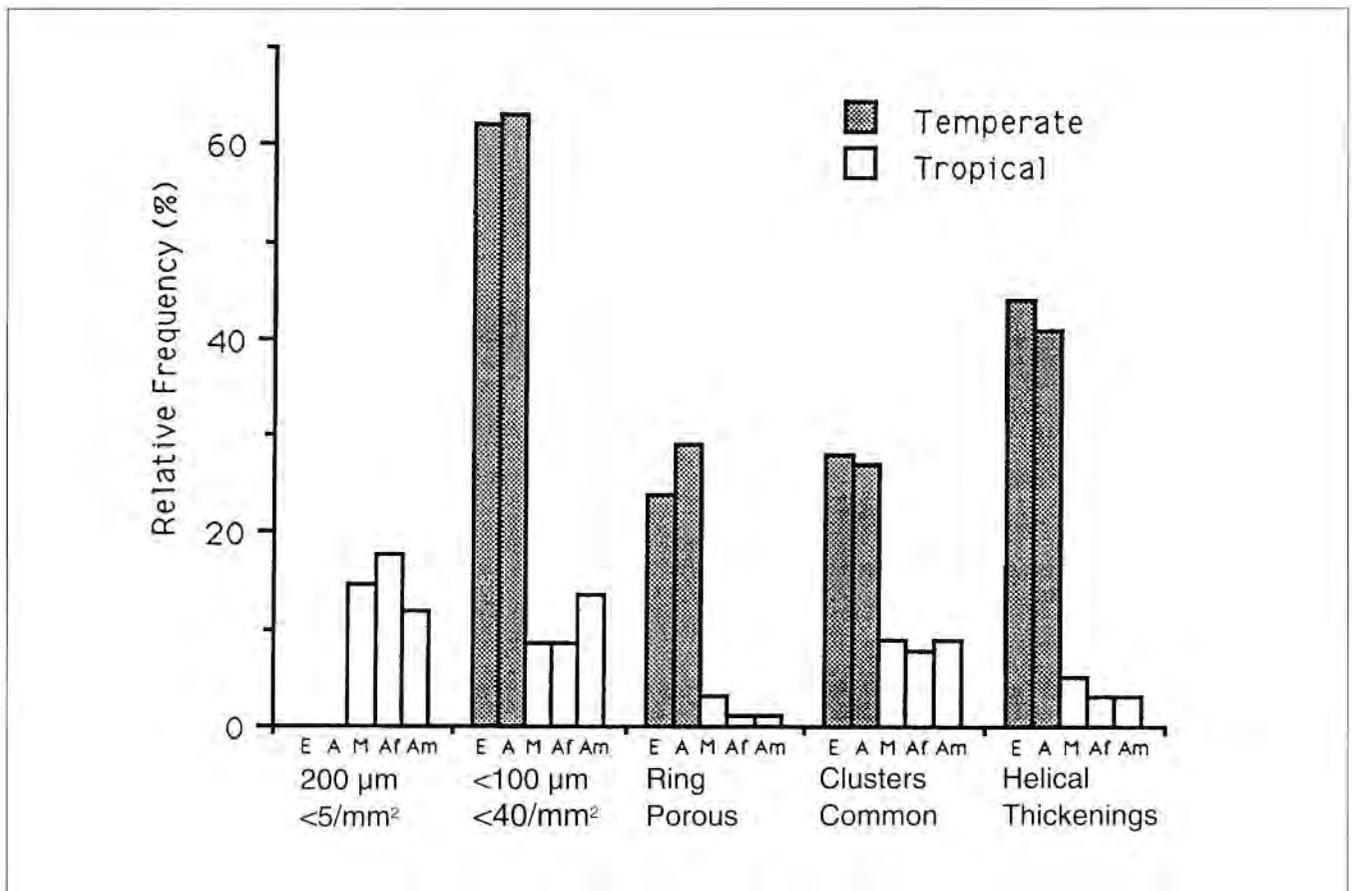

FIGURE 1. Incidence of selected anatomical features in the recent flora. 200 μm, < 5/mm² = mean tangential diameters of the vessels is more than 200 μm, and there are fewer than 5 vessels per square mm. <100μm, >40/mm² = mean tangential diameter of the vessels is less than 100 μm and there are more than 40 vessels per square mm. E = Europe and temperate Asia; A = North America; M = Malaysia and Southeast Asia; Af = Africa; Am = tropical Central and South America; regions correspond to those used in the IAWA feature list (IAWA Committee 1989); data shown here were presented in tabular form by Wheeler and Baas (1993).

of latewood with relatively narrow vessels. Earlywood vessels in extant ring-porous woods function for only one season, and the amount of latewood is affected by the current year's growing conditions (Zimmermann 1983). The strategy of ring porosity is common in north temperate forests, and extremely rare in the tropics, occurring only in some trees of monsoonal climates (Gilbert 1940; Wheeler and Baas 1993; Woodcock 1994a, b, Fig. 1). Wood anatomical characteristics of trees and shrubs of tropical Asia, Africa, and the Americas are similar, as are wood anatomical characteristics of trees and shrubs of temperate Asia, Europe, and North America (Fig. 1). However, wood anatomical characteristics of trees and shrubs of temperate and tropical regions differ (Fig. 1). Thus, wood anatomical features have potential for inferring paleoclimate (Wiemann et al. 1998, 1999).

The Eocene is an important time in the modernization and diversification of many dicotyledonous families; woods add to our understanding of the differences between Eocene plants and extant plants, as well as the past distribution and diversity of dicotyledonous genera and families. Of the woods described in this paper, two resemble *Zelkova* (Chinese elm) and are referable to the elm family (Ulmaceae), one is referable to *Robinia* (black locust, Leguminosae), one to *Koelreuteria* (golden rain tree, Sapindaceae), and one is of uncertain affinities.

Materials and Methods

Samples from the monument area all are from the lower mudstone unit of Evanoff et al. (2001) and were collected by park personnel, A. Cross, K. Gregory-Wodzicki, and Wheeler. This is the level in which the *Sequoia*-like stumps occur. Samples collected by M. Arct were from north of the monument, and are also from the lower mudstone unit (Evanoff, pers. commun., 1995). Chadronian woods from Wyoming were collected by E. Evanoff. Details on the Florissant Formation are provided elsewhere in this volume. The age is calculated to be 34.07 ± 0.10 Ma (see Evanoff et al. 2001).

One sample (DMNH 12981/FLFO 2385) was collected from section 24, a few km south of the petrified forest area, and in the caprock conglomerate unit of Evanoff and Murphey (1994) and Evanoff et al. (2001), a volcaniclastic-rich conglomerate. It is the only fossil wood known to have come from the upper tuff (Gregory, pers. commun., 1995).

All samples are silicified, and were thin-sectioned for examination. Sections and samples were deposited at the Denver Museum of Nature and Science (formerly known as the Denver Museum of Natural

History), and assigned both DMNH numbers and National Park Service Numbers. FLFO is the standard abbreviation for the Florissant Fossil Beds National Monument (NPS-FLFO).

Descriptions of the woods follow the format of the IAWA List of Features suitable for hardwood identification (IAWA Committee 1989).

Affinities of the fossil woods initially were determined by consulting descriptions in *Anatomy of the Dicotyledons* (Metcalfe and Chalk 1950), and through searches of the computerized OPCN (Oxford/Princes Risborough/CTFT/NCSU) wood database, which contains more than 5000 coded descriptions of dicotyledonous wood (Wheeler et al. 1986; LaPasha and Wheeler 1987). The Florissant woods were compared to other fossil woods of known provenance using a database prepared for a survey of changes in dicotyledonous wood structure through time (Wheeler and Baas 1991, 1993), and to extant woods in the NCSU wood collection, and also in standard references (as listed in Gregory 1980, 1994). When extant generic names are used for the Florissant wood, this indicates that the fossil wood has a suite of anatomical features that today are characteristic of that one genus. This does not preclude the possibility that the whole plant the wood represents is an extinct genus with leaves and/or reproductive structures that differ from any present-day genus.

Systematic Descriptions

Incertae sedis
Chadronoxylon florissantensis
Wheeler gen. & sp. nov.

PLATE 1, FIGURES A–K

Description: Growth rings present, marked by radially flattened fibers and at times some smaller diameter vessels in the latewood. Wood diffuse porous, vessels solitary (9 to 33 percent) and commonly in radial multiples of 2 to 6. Mean tangential diameter between 64 (sd = 14) and 88 (sd = 18) μm; mean number of vessels per square mm 40 to 92. Perforations exclusively simple. Intervessel pitting crowded alternate, 8 to 10 μm, polygonal in outline with included apertures, not extending to the border. Vessel-ray parenchyma pits with reduced borders and restricted to the upright marginal ray cells, typically somewhat horizontally elongated. Tyloses common, but not filling the vessels.

Multiseriate rays two to seven cells wide, heterocellular, with a variable number (one to ten) of upright

TABLE 1. Quantitative features of *Chadronoxylon florissantensis*.

Sample	TD Mean (SD) Range	VPMM	% Sol	VEL	MRH Cell No. μm	MRW Cell No. μm	RPMM
DMNH 12982 (FLFO 2374)	69(15) 37–108	66	11		4-24-53 166-541-1399	2–6 35-57-85	3–9
DMNH 12984 (FLFO 2376) 022*	79(17) 44–121	49	23	499(57) 410–622	8-19-31 181-421-932	2–5 42-70-127	3–7
DMNH 12983 (FLFO 2375) 018*	81(13) 58–105	61	17	490(88) 333–699	4-17-37 123-361-937	2–5 43-63-89	4–10
DMNH 12985 (FLFO 2377) 024*	64(14) 39–102	66	33		4-15-26 111-372-804	2–7 37-68-106	4–10
DMNH 12987 (FLFO 2377) 5/7/94-2	87(13) 64–115	58					4–6
DMNH 12989 (FLFO 2381) 5/7/94-5B	79(18) 42–113	69			191-503-1195		5

TD = tangential diameter of vessel.

SD = standard deviation.

VPMM = mean number of vessels per square millimeter.

% SOL = percentage of the vessels that are solitary.

VEL = vessel element length.

MRH = height of the multiseriate portion of the multiseriate rays, in cell number and in μm.

MRW = ray width in cell number, and in μm.

RPMM = number of rays per millimeter, linear distance.

[In some samples it was not possible to measure vessel element lengths with certainty because vessel element end walls could not be easily distinguished from tyloses.]

marginal ray cells. Upright cells distinctly taller than the procumbent cells. Marginal cells often with heavily pitted end walls as viewed in radial section. Uniseriate rays present and composed exclusively of upright cells. Nonstoried. Mean height of multiseriate portion of the rays 270 to 541 μm; maximum heights 793 to 1400 μm; three to ten per mm.

Axial parenchyma rare, occasionally some scanty paratracheal. Non-storied. Fibers all septate, pits without distinct borders, thin-medium-thick-walled. Crystals occasional in some samples, solitary crystals in the upright ray parenchyma cells of the uniseriate margins of the rays (sometimes with two chambers), and in upright cells of the uniseriate rays, occasionally in chambers in septate fibers, especially common near the growth ring boundaries.

Holotype: DMNH 12982/NPS FLFO 2374.

Material: DMNH 12983/NPS FLFO 2375 (Cross 018), DMNH 12984/NPS FLFO 2376 (Cross 0122); DMNH 12985/FLFO 2377 (Cross 024). These samples collected by Cross from stumps north of the main fossil forest area and subsequently buried to protect them from vandalism. DMNH 12986/NPS FLFO 2378 (FFB 02, a stump 1.1 m in diameter, collected by Gregory in the main fossil forest area; see Gregory 1994a); DMNH 12987/NPS FLFO 2379 (FFB 5/7/94-2, stump 1.7 m in diameter in

main forest area, collected by Wheeler); DMNH 12988/ NPS FLFO 2380 (FFB 5/7/94-3, stump from the Hornbeck Ranch, collected by Wheeler); DMNH 129989/ NPS FLFO 1281 (FFB 5/7/94-5, stump north side of Twin Rock Road, collected by Wheeler).

Remarks: This wood is the most abundant dicotyledonous wood at Florissant and occurs in the main petrified forest area and at the Hornbek Ranch. *Chadronoxylon* grew to be a large tree; one *in situ* stump was 1.7 m in diameter. The stumps do not have bark, so this tree's original diameter would have been greater. Data for the relationship between diameter and height suggest the height of this tree would have been more than 30 m (Rich et al. 1986).

Some of the samples were very well preserved. Usually fungal hyphae are visible in well-preserved fossil woods (Wheeler, pers. commun., 2001), but no hyphae were observed in the *Chadronoxylon* samples. However, in some samples the fiber walls' appearance suggests the activity of tunneling bacteria (Plate 1, Figure J). Possible bacterial activity and the apparent absence of fungal hyphae are consistent with these woods being preserved in anaerobic conditions, as would occur when the trees were covered by flooding from rising lake levels.

The affinities of *Chadronoxylon* are uncertain; it is easier to say what it is not, rather than what it is. It does not have characteristics of the families abundant as compression or pollen at Florissant; it does not resemble woods of extant Aceraceae, Betulacae, Fagaceae (*sensu strictu*), Leguminosae, Rosaceae, Salicaceae, Sapindaceae, or Ulmaceae. The combination of features found in this wood (radial multiples common, Plate 1, Figs. A, B; simple perforation plates and alternate pitting; Plate 1, Fig. C; vessel-ray parenchyma pits with reduced borders, Plate 1, Figs. D, E; septate fibers, Plate 1, Figs. I, J, K; markedly heterocellular multiseriate rays, Plate 1, Figs. E, F, H, I; rare, absent axial parenchyma, Plate 1, Figs. A, B; crystals in upright ray cells) occurs most commonly in the Flacourtiaceae and Euphorbiaceae (Metcalfe and Chalk 1950; Wheeler et al. 1986), but neither family is represented in the Florissant compression flora.

It is tempting to think that this abundant wood is *Fagopsis*, which is an extinct genus now assigned to the Fagaceae (Manchester 1983) and the most abundantly occurring leaf at Florissant in the middle shale unit (MacGinitie 1953; Manchester 1983, 2001; Gregory 1994a). However, the characteristics of this wood do not agree with those of extant Fagaceae; axial parenchyma is rare scanty paratracheal (Plate 1, Figs. A, B, H), while in

extant Fagaceae there is abundant apotracheal diffuse-in-aggregates parenchyma; rays in *Chadronoxylon* are markedly heterocellular and three to six cells wide (Plate 1, Figs. E, F, H, I), while in extant Fagaceae, rays usually are homocellular, and either exclusively uniseriate or of two distinct size classes, uniseriate plus very wide and tall.

There is some resemblance to the wood of *Nothofagus*, a Southern Hemisphere genus commonly placed close to, or within, the Fagaceae. The wood of *Nothofagus* is distinct from woods of the Fagaceae *sensu strictu*, but is similar to *Chadronoxylon*. Both have numerous relatively narrow vessels that are commonly in radial multiples, rare axial parenchyma, septate fibers (some species of *Nothofagus*), alternate to subopposite intervessel pitting, vessel-ray parenchyma pits that have reduced borders and are horizontally elongated.

However, *Chadronoxylon* has different ray structure than *Nothofagus*, whose rays are usually not wider than two cells, and has fewer rows of marginal cells (Metcalfe and Chalk 1950). Cladistic analysis of chloroplast DNA supports the recognition of a separate family, Nothofagaceae, and some cladistic analyses using morphological characters suggest *Nothofagus* may be more closely related to the Betulaceae than to the Fagaceae (Manos et al. 1993; Nixon 1989). Given that *Fagopsis* represents an extinct genus, it is difficult to predict what its wood would be like. It is possible that it could have wood that resembles wood of *Nothofagus*, given the suggested relationships of *Nothofagus* to the Fagaceae and Betulaceae. *Fagopsis* was at one time assigned to the Betulaceae (MacGinitie 1953). There are no reliable records of *Nothofagus* in the fossil record of the Northern Hemisphere (Manchester 1983).

Resolving the affinities of this wood and whether it has any relationship to *Fagopsis* awaits discovery of anatomically preserved woody twigs attached to *Fagopsis* leaves or reproductive structures. If this wood were found in attachment to *Fagopsis* leaves or reproductive structure, it would indicate that *Fagopsis* was a large tree, not a shrub.

Family Ulmaceae
cf. *Zelkova* sp.

PLATE 2, FIGURES A–H

Description: Growth rings present and distinct. Wood ring porous. Earlywood vessels predominantly solitary and rounded in outline; latewood vessels in clusters. Mean tangential diameter of earlywood vessels 168 µm (SD = 40), mean radial diameter 147 µm (SD = 33).

Perforations exclusively simple. Intervessel pitting crowded alternate with included apertures, non-vestured, 7 to 9 µm. Vessel-ray parenchyma pits similar in size to intervessel pits. Helical thickening present throughout the body of the narrow vessel elements. Axial parenchyma apparently paratracheal, intermixed with the vessels. Strands usually of four cells.

Multiseriate rays typically six to eight seriate, homocellular composed exclusively of procumbent cells, or more commonly with a single marginal row of square cells. Marginal ray cells rarely enlarged. Rays tending to be of two sizes; multiseriate rays typically six to eight seriate, with one to two seriate rays extremely rare, and less than ten cells high. No sheath cells observed. Mean multiseriate ray height 264 (112) µm, seventeen cells, range 70 to 517 µm, nine to thirty-eight cells, three to seven rays per mm.

Fibers without obvious bordered pits, nonseptate, medium-thick- to thick-walled. No inclusions observed, but possibly the rare enlarged ray cells were crystalliferous.

Material: DMNH 12978/FLFO 2382 (FFB 84-2).

Remarks: The combination of ring porosity (Plate 2, Figs. A, B), latewood vessels commonly in clusters (Plate 2, Figs. A, B), helical thickenings distinct in narrow vessel elements (Plate 2, Figs. C, F), and homocellular to heterocellular multiseriate rays (Plate 2, Figs. G, H) occurs today in woods of the Ulmaceae (Sweitzer 1971). Because of the importance of Ulmaceae as timber trees and ornamentals, the wood anatomy of this family has been well studied and there are characteristics to distinguish the genera. The occurrence of both homocellular and heterocellular rays in the same sample is a characteristic of *Zelkova*, which has five species, one native to Crete, and four species native to western and eastern Asia, and *Hemiptelea*, which has one species native to China and Korea (Mabberley 1997). Both *Hemiptelea* and *Zelkova* are members of the Ulmoideae. *Zelkova* has crystals in enlarged ray parenchyma cells; *Hemiptelea* does not (Zhong et al. 1992). The vast majority of the rays in this fossil wood do not have enlarged crystalliferous cells (Plate 2, Fig. H). However, in radial section, inflated cells that likely were crystalliferous were rarely seen. Because of the presence of these cells the wood is tentatively assigned to *Zelkova*.

Cedrelospermum, an extinct genus known from twigs with attached leaves and fruits (Manchester 1989a), is the second most abundant dicotyledonous angiosperm in the Florissant compression flora (MacGinitie 1953; Manchester 1989a; Gregory 1994a). This wood may have some relationship to *Cedrelospermum* (see discussion following for *Zelkovoxylon chadronensis*). Leaves of *Cedrelospermum* formerly were referred to *Zelkova*. *Ulmus* leaves and fruits also occur in the Florissant compression flora (Manchester 1989b). This wood is more likely to represent *Cedrelospermum* than *Ulmus* because *Ulmus* has exclusively homocellular rays and the fossil does not. However, without attachment of wood to leaves it is not possible to determine the relationships of the wood to leaves.

Genus *Zelkovoxylon* Greguss 1969

Zelkovoxylon chadronensis Wheeler sp. nov.

PLATE 2, FIGURES I–P

Description: Growth rings present and distinct. Wood ring porous. Earlywood vessels circular to oval in outline, mostly solitary. Earlywood zone with multiple rows of large vessels. Latewood vessels in clusters, arranged in tangential bands. Mean tangential diameter of earlywood vessels 180 µm (SD = 45), mean radial diameter 204 µm (SD = 39). Perforations exclusively simple. Mean vessel element length of 252 (SD = 33), range 207 to 336. Intervascular pits crowded alternate, polygonal in outline. Vessel-ray parenchyma pits similar in size to intervascular pits but with reduced borders. Spiral thickenings not observed, tyloses not common.

Multiseriate rays heterocellular with a single marginal row of square to slightly upright cells; enlarged marginal cells with a large solitary crystal common, occasionally sheath cells near the margin of the rays enlarged and crystalliferous. Multiseriate rays typically four to six seriate; uniseriate rays rare. Mean height of multiseriate ray 466 (SD = 188) µm, 31 (12) cells; range 116 to 843 µm high, five to fifty cells high, four to ten rays per mm.

Axial parenchyma paratracheal, associated with vessel clusters in latewood, usually four cells per strand. Fibers without obvious bordered pits, nonseptate, medium-thick- to thick-walled. Solitary crystals in enlarged marginal ray cells, rarely in strands of two adjacent to rays.

Holotype: DMNH 12979/FLFO 2383 (S-1). From a stump 0.5 m in diameter, found in the road south of the monument. Samples collected by Gregory from the very outside of the stump, along one radius more than ninety growth rings counted.

TABLE 2. Comparison of *Zelkova*-type woods.

Species	Porosity	H Th	MTD	RW	RH
Zelkovoxylon chadronensis	RP, multiple rows	–	180	4–6	116–843
Z. occidentale 1	SRP	+	112	to 4	170–860
Zelkova microporosum 2	RP, 1 few	+	119	4–10	245–564
cf. *Zelkova* (84–2)	RP, 1 row	+	168	6–8	70–517

RP = ring porous, number indicates the number of earlywood vessels.
SRP = semi–ring porous.
H Th = helical thickenings in narrow vessel elements.
+ = present.
– = absent.
MTD = mean tangential diameter of earlywood vessels, in μm.
RW = multiseriate ray width in cell number.

Remarks: The combination of ring porosity, latewood vessels commonly in clusters and in tangential bands, and homocellular to heterocellular rays indicates affinities with the Ulmaceae. The occurrence of enlarged marginal ray cells with crystals (Plate 3, Figs. C, G, I, J) is characteristic of *Zelkova* (Sweitzer 1971; Zhong et al. 1992).

All extant *Zelkova* woods that were examined (samples of the four Asian species) had earlywood pore rings only one to two vessels deep. Depth of the earlywood pore ring is a feature used to distinguish groups of species in *Ulmus* (Zhong et al. 1992; Wheeler et al. 1989). Although the wood was reasonably well preserved, no helical thickenings were observed in the narrow vessel elements. This is unusual, as helical thickenings occur in latewood vessels of *Zelkova*, and are present in other fossil woods with the characteristics of *Zelkova*. It is often difficult when dealing with Eocene plants to determine what degree of difference constitutes grounds for assigning them to extinct rather than extant genera. Because of the differences in the earlywood pore ring and the occurrence of helical thickenings between this fossil and extant *Zelkova*, this wood is assigned to *Zelkovoxylon* rather than *Zelkova*.

Although MacGinitie (1953) identified *Zelkova* leaves at Florissant, these leaves typically are narrower than those of extant species in this genus. The attachment of these leaves to twigs bearing winged fruits, quite distinct from the wingless nuts of *Zelkova*, shows that the leaves are *Cedrelospermum* and not *Zelkova* (Manchester 2001). Foliage, fruit, and pollen characters indicate that *Cedrelospermum*, like *Zelkova*, belongs to the

Ulmoideae. Because it is an extinct genus based on fruits, the wood anatomy of *Cedrelospermum* is open to speculation. However it would not be surprising if the wood were similar to *Zelkova*, as were the leaves. The presence of *Zelkova* species and *Zelkovoxylon* wood at Florissant may be interpreted as (1) good evidence for reinstating *Zelkova* as a component of the Florissant flora, and/or (2) evidence that the wood of *Cedrelospermum* was virtually indistinguishable from that of *Zelkova*. Only one species of *Cedrelospermum* is recognized at Florissant (Manchester 1989a), so the occurrence of two types of *Zelkova*-like wood and their relationships to the compression flora need resolution.

In addition to the two Florissant taxa, two other *Zelkova*-type woods are known from the Eocene of North America: *Zelkovoxylon occidentale* from the middle Eocene Yellowstone Fossil Forests (Wheeler et al. 1978) and *Zelkova microporosum* from the Chadronian of Nebraska (Wheeler and Landon 1992). *Zelkovoxylon chadronensis* differs from the older *Zelkovoxylon occidentale* in porosity and tangential diameter of the earlywood vessels, and from the Nebraskan Chadronian wood in depth of the earlywood zone, tangential diameter of the earlywood vessels, and ray size (Table 2).

Family Sapindaceae
cf. *Koelreuteria* sp.
PLATE 3, FIGURES A–F

Description: Growth rings present and distinct. Wood ring porous. Earlywood vessels solitary and in radial multiples of two to three; latewood vessels in radial

multiples and in small clusters. Earlywood zone broad, more than five vessels deep. Mean tangential diameter of earlywood vessels 123 (SD = 24); mean radial diameter 177 (SD = 30). Perforations exclusively simple. Intervessel pits crowded alternate, with linear apertures extending to the edges of the borders, appearing vestured, 5 to 6 µm. Vessel-ray parenchyma pits similar in size and shape to intervessel pits, half-bordered. Helical thickenings present throughout the body of the narrow vessel elements.

Rays homocellular, composed exclusively of procumbent ray cells, one to two (three) seriate. Mean height of multiseriate rays 122 (65) µm, seven (three) cells; range 17 to 313 µm, three to sixteen cells high. Non-storied. Strands of two to eight (ten) cells.

Axial parenchyma predominantly paratracheal and marginal. Non-storied. Strands of two to eight (ten) cells). Fibers without distinctly bordered pits, septate. Solitary crystals occasional in procumbent ray cells.

Material: DMNH 12980/FLFO 2384 (FFB 84-3).

Remarks: The combination of ring porosity, latewood vessel elements in clusters, and with helical thickenings present is a common syndrome in temperate-zone woods and occurs in at least eighteen extant families of dicotyledons. However, these three features in combination with septate fibers, vessel-ray parenchyma pits of similar size as the intervessel pits, and narrow rays occur only in the extant genus *Koelreuteria*, a genus of three species native to China and Taiwan (Mabberley 1997). According to Baizhong et al. (1995), biseriate rays are rare in *Koelreuteria;* however, biseriate rays are typical of this Florissant wood. To my knowledge, no fossil woods of *Koelreuteria* have previously been described.

MacGinitie (1953) reported that the Sapindaceae were relatively numerous at Florissant (six species). *Koelreuteria alleni* (Lesquereux) Edwards, based upon distinctive fruit capsule valves, was one of the species.

Family Leguminosae
cf. *Robinia zirkelii* (Platen)
Matten, Gastaldo, & Lee 1977
PLATE 3, FIGURES G–M

Description: Growth rings present, distinct. Wood ring porous, with a pronounced difference between the earlywood vessel diameters and latewood vessel diameters. Earlywood vessels mostly solitary, with some oblique pairs, latewood vessels in clusters and

arranged in branched tangential pattern. Width of earlywood zone variable, one to two vessels deep in narrow rings, typically three to four vessels deep in wider rings. Mean tangential diameter of earlywood vessels 129 µm (SD = 24), mean radial diameter 133 µm (SD = 27). Vessel elements 185 to 224 µm long. Perforation plates exclusively simple. Intervascular pitting alternate, possibly vestured. Vessel-ray parenchyma pits of similar size and shape to intervascular pits, half-bordered. Distinct helical thickenings in narrow latewood vessel elements. Thin-walled tyloses common.

Rays tending to be of two sizes, multiseriate rays typically four to five cells wide, and short one to two seriate rays. Mean multiseriate ray height is 241 (109) µm, sixteen (eight) cells, range 38 to 575 µm, five to thirty cells high. Non-storied. Four to eleven rays per mm.

Parenchyma predominantly paratracheal; strands mostly of four cells. Fibers thick-walled, non-septate, without obvious bordered pits. Solitary crystals rare in axial parenchyma strands.

Material: DMNH 12981/FLFO 2385.

Remarks: This sample is the only one from the upper tuff. It is markedly ring porous with an abrupt transition from earlywood to latewood. In extant *Robinia*, there is variation in the abruptness of this transition and in the occurrence of transition wood. Page (1993) suggested that the presence and amount of transition wood are related to equable conditions and adequate moisture during the late spring and (early) summer. This Florissant wood does not have transition wood. Some rings (Plate 3) have no latewood at all. The lack of latewood could reflect very limited rainfall, with little precipitation during the late spring and summer, or, alternatively, this sample was from the outside of a mature tree. In extant trees, ring widths of older trees typically are narrow and in ring-porous wood often have only earlywood.

The two crushed rings of all earlywood apparently mark some event after which the earlywood width was consistently and significantly narrower because of a decrease in the number of vessels deep the earlywood ring was, not a decrease in earlywood vessel diameter. Three of the six inner rings were all earlywood; four of the five measurable outer rings had more latewood than earlywood, although total ring widths of the inner and outer portions of the sample did not differ significantly. Usually the characteristics of the earlywood zone are relatively stable from year to year, no matter the ring width. It is not known what type of phenomenon would alter the earlywood characteristics.

The mean tangential diameter of the earlywood vessels (129 μm) is smaller than that reported for Miocene *Robinia* from California (nine samples, mean tangential diameters of 158 to 243 μm; Page 1993), Montana (one sample, 184 μm), Washington (one sample, 200 μm), and Oklahoma (ten samples, 172 μm; Matten et al. 1977), but nearly identical to that of another Chadronian *Robinia* from Nebraska (132 μm; Wheeler and Landon 1992). The Miocene *Robinia* woods had relatively wide growth rings (typically more than 9 mm), while the Florissant wood has ring widths less than 2 mm (<1 mm in seven of the eleven measurable rings). The narrower rings and narrower earlywood vessels suggest the Chadronian *Robinia*-like woods from Nebraska and Florissant experienced less favorable growing conditions, with shorter growing seasons and/or less growing season precipitation than the Miocene *Robinia*-like woods of Montana, Oklahoma, Oregon, and California. MacGinitie (1953) reported leaves of *Robinia lesquereuxi* at Florissant and noted their similarity to extant *R. pseudoacacia* and *R. neomexicana*, as well as to *Amorpha* and *Sophora*.

Discussion

The characteristics of the Florissant dicotyledonous woods parallel those from the Chadronian of Nebraska (Wheeler and Landon 1992). There is a combination of markedly ring-porous woods (e.g., members of the Ulmaceae and Leguminosae) and diffuse-porous woods with numerous small-diameter vessels. The ring-porous woods were recovered outside of the main fossil forest and not adjacent to the *Sequoia*-like stumps. Although it seems likely because they were recovered from the lower mudstone unit, it is not possible to state with certainty they were contemporaneous with the *Sequoia*-like stumps. The presence of distinctly ring-porous woods with latewood vessels with helical thickenings and a diffuse-porous wood with narrow vessels mainly in groups is consistent with the suggestion that Chadronian plants grew under a highly seasonal climate, consistent with Wing's (1988) suggestions for Chadronian climate.

Prothero (1994) describes the late Eocene climate as not that different from the middle Eocene, yet the characteristics of the Florissant woods contrast markedly with woods from the middle Eocene of Wyoming, probably because of the effects of altitude. The paleoaltitude of Florissant has been variously estimated as more than 2450 m (Meyer 1986; Gregory 1992, 1994b) or approximately 2900 m (Wolfe 1992a). None of the middle Eocene woods are markedly ring porous

(Wheeler et al. 1977, 1978). Some middle Eocene woods lack distinct growth rings, and some have few large vessels with abundant paratracheal parenchyma (the last features occurring only in tropical woods). Ring-porous and semi-ring-porous woods are common in the few late Eocene woods known, while ring-porous woods are extremely rare in the middle Eocene of the Rocky Mountain region.

Characteristics of a wood that affect whether or not it is petrified are not established, but may include composition of the cell wall (particularly the ratio of cellulose to lignin), permeability (the ease with which liquid penetrates a wood), and inherent durability (resistance to decay). Permeability apparently was not a factor for the preservation of the Florissant woods, as they have tyloses that fill vessels and reduce wood permeability. *Robinia* has many tyloses and is highly impermeable, but it is relatively common in the fossil record, as is *Quercus* (oak), which also has tyloses. These woods may be commonly reported because they are easy to recognize, but they are also both resistant to decay. Heartwood typically is more resistant to decay than sapwood because of the higher extractive content of heartwood. *Robinia*, in particular, and *Quercus* are both noted for their durable heartwood. Ring-porous woods typically have little sapwood, generally fewer than ten growth rings (Panshin and DeZeeuw 1980), and so the higher proportion of heartwood in such trees is likely to make them enter the fossil record more often, on average, than diffuse-porous wood, which would have a higher proportion of sapwood (which would not be resistant to decay) or be entirely sapwood. Thus, the absence of ring-porous woods from the middle Eocene likely indicates original absence of such woods.

Data for the living flora of the eastern United States indicate that the incidence of species of ring-porous woods has value for climatic prediction, as does Wiemann et al.'s (1998, 1999) examination of wood characteristics of floras from a variety of sites. Woodcock (1989) concluded that ring-porous woods in North America occur where there is (1) precipitation adequate for tree growth, and (2) a cold season requiring dormancy, with the coldest month averaging 10 °C or below 3 °C, and winter temperatures not below –40 °C. At middle latitudes, ring-porous tree species are common where moisture is limiting for growth; in the eastern deciduous forests they comprise 70 to 80 percent of the upland tree flora where precipitation is 100 cm or below. Ring-porous trees dominate in environments that are xeric by virtue of topography or soil, and in associations of early forest succession. However, ring-porous

species also occur in wetlands (e.g., species of *Fraxinus* and some species of *Quercus*). Gregory (1992, 1994b) used leaf physiognomy to calculate a growing season precipitation of 57 ± 16 cm and a mean annual temperature of 12.8 ± 15 °C for the Florissant region of ca. 35 million years ago. Characteristics of these five Florissant dicot woods do not contradict those climatic inferences. There are not enough dicot wood types present at Florissant to use in models for inferring paleoclimate (Wiemann et al. 1998, 1999).

The aforementioned conclusions about the incidence of ring-porous woods and their climatic significance are based primarily on examination of the eastern North American flora. It would be helpful to investigate the incidence of ring-porous woods in extant eastern Asia forests and European floras. Many of the Eocene plants of North American have Asiatic affinities, so the distribution and incidence of ring-porous woods in Asia would be of equal, if not greater, value in interpreting the paleoclimatic significance of ring-porous woods from Florissant and other localities. In addition, it would be important to refine our knowledge of the relationships of wood structure to climate and whether the incidence of particular anatomies can reliably indicate growing season length, amount of precipitation and its seasonal distribution, and temperature ranges and averages.

While not many fossil wood assemblages with dicotyledons have been studied in detail, all the middle Eocene assemblages of the United States examined to date contain *Plataninium*, a sycamore-like wood, and most have evergreen oak woods that are diffuse-porous to semi-ring porous. These wood types have not yet been found at Florissant or at the Chadronian localities in Wyoming and Nebraska. MacGinitie (1953) commented on the extreme rarity of sycamore (*Platanus*) leaves at Florissant, which was considered noteworthy because leaves of *Platanus* are "among the most abundant plant fossils from the Cretaceous on." Similarly, the absence of *Platanus*-like woods at Florissant seems noteworthy.

The five dicotyledonous woods described herein are only a small sampling of the total flora, and do not reflect the diversity of leaves and pollen known. Manchester (2001) recognizes ca. eighty-two genera and ninety-five species of dicotyledons. The low diversity of wood types relative to the compression and pollen flora is most likely a result of taphonomic factors and, perhaps, human factors. Leaves could have been blown or readily rafted into the lake, while the woods must have been in the ash flow or somehow transported into the depositional environment. In part, because it is neces-

sary to prepare at least three thin sections per sample for the microscopic examination of silicified woods, the study of fossil wood has always lagged behind that of other plant parts. The compression flora at Florissant has been studied for more than a century (see Manchester 2001), while investigations of dicotyledonous woods have just begun (this is the first report on the anatomy of dicotyledonous woods from Florissant). MacGinitie (1953) referred only to the *Sequoia*-like stumps in his monograph. Apparently in the early part of the 20th century fossil wood was extremely abundant at Florissant; large silicified logs and stumps were so common that it was difficult to drive wagons through the area (see Gregory 1994a; Gregory-Wodzicki 2001). However, silicified wood is an attractive souvenir, and so before the establishment of the monument, much of the wood was removed. Whether additional dicotyledonous woods will be found with additional investigation remains to be seen.

Acknowledgments

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Plate Descriptions

PLATE 1. *Chadronoxylon florissantensis* gen. & sp. nov.
Figures

A. Cross-section showing diffuse-porous wood with numerous vessels, which are commonly in radial multiples.

B. Growth-ring boundary marked by a radial narrowing of the fibers, and narrower latewood vessels.

C. Intervessel pitting, alternate to somewhat subopposite.

D. Vessel-ray parenchyma pits with reduced borders and enlarged relative to the intervessel pits.

E. Radial section showing vessel-ray parenchyma in marginal upright cells and in procumbent cells.

F. Radial section showing normal and chambered ray cells with solitary prismatic crystals.

G. Ray cell with nodular thickenings.

H. Tangential section showing numerous uniseriate rays composed of upright cells and multiseriate rays 3 to 4 cells wide.

I. Tangential section showing heterocellular rays, with variable number of upright ray cells, and septate fibers.

J. S2 microfibril angle apparent in fiber wall, possibly evidence of tunneling bacteria.

K. Detail of septate fibers with thick septae. Scale bars = 500 μm in A; = 200 μm in H; = 100 μm in E; = 50 μm in B, C, F; = 25 μm in D, G, K; = 12 μm in J.

PLATE 2. Ulmaceae woods. cf. *Zelkova*.
Figures

A. Cross-section showing narrow growth rings, earlywood vessels solitary, relatively widely spaced, and rounded, and latewood vessels in clusters.

B. Detail showing earlywood vessels and latewood clusters.

C. Crowded alternate intervessel pitting and helical thickenings.

D. Tangential section, homocellular multiseriate rays, up to 8 cells wide.

E. Helical thickenings in latewood vessels.

F. Vessel-ray parenchyma pitting.

G. Radial section showing marginal row of ray cells with some cells enlarged.

H. Thick-walled fibers (top), cluster of latewood vessels.

Zelkovoxylon chadronensis.

I. Cross-section showing earlywood zone more than 2 vessels deep, and tangential bands of latewood vessels.

J. Growth-ring boundary.

K. Latewood, clusters of narrow vessels, and medium-thick-walled fibers.

L. Vessel-ray parenchyma pitting.

M. Crowded alternate intervessel pitting.

N. Tangential section showing rays typically 4 to 5 cells wide, tendency toward storied axial elements, and to right vessel elements with horizontal to barely inclined end walls.

O. Radial section showing enlarged marginal ray cells with solitary crystals.

P. Tangential section; note enlarged marginal cells with crystals. Scale bars = 1 mm in I; = 500 μm in A; = 200 μm in B, D, J, N, P; = 100 μm in P; = 50 μm in G, K; = 25 μm in C, E, F, H, M, O; = 12 μm in L.

PLATE 3. Ring-porous woods of Florissant. cf. *Koelreuteria*.
Figures

A. Cross-section showing wide earlywood zones.

B. Growth-ring boundary, latewood with very narrow clustered vessels.

C. Crowded alternate intervessel pitting.

D. Latewood vessel elements with helical thickenings and simple perforations.

E. Tangential section, rays 1 to 2 cells wide, and septate fibers.

F. Radial section, homocellular ray with the top row of cells tending to be square.

cf. *Robinia zirkelii.*

G. Cross-section, rings at bottom with relatively wide earlywood zone, rings at top with narrow latewood zone.

H. Detail showing abrupt transition from earlywood to latewood, and latewood vessels in clusters.

I. Crowded alternate intervessel pitting, outline of apertures suggesting vesturing.

J. Latewood vessel element with coarse helical thickenings.

K. Thick-walled fibers, cross-section.

(continues)

(continued)

L. Tangential section.
M. Storied elements with helical thickenings. Scale
bars = 1 mm in G; = 500 µm in A; = 250 µm in

H; = 200 µm in B; = 100 µm in E, L; = 50 µm in
D, F, M; = 25 µm in J, K; = 12 µm in C, I.
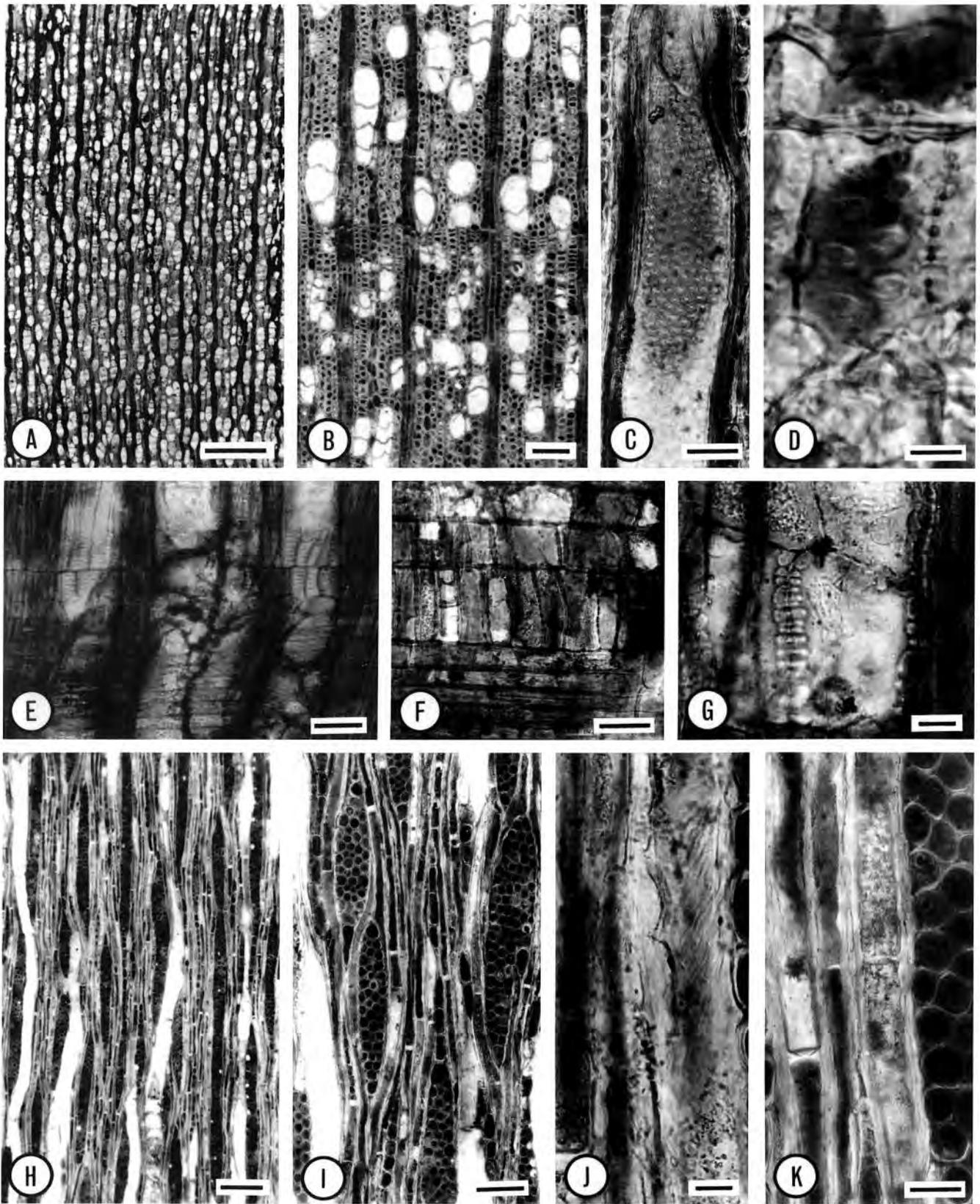
PLATE 1. *Chadronoxylon florissantensis* gen. & sp. nov.
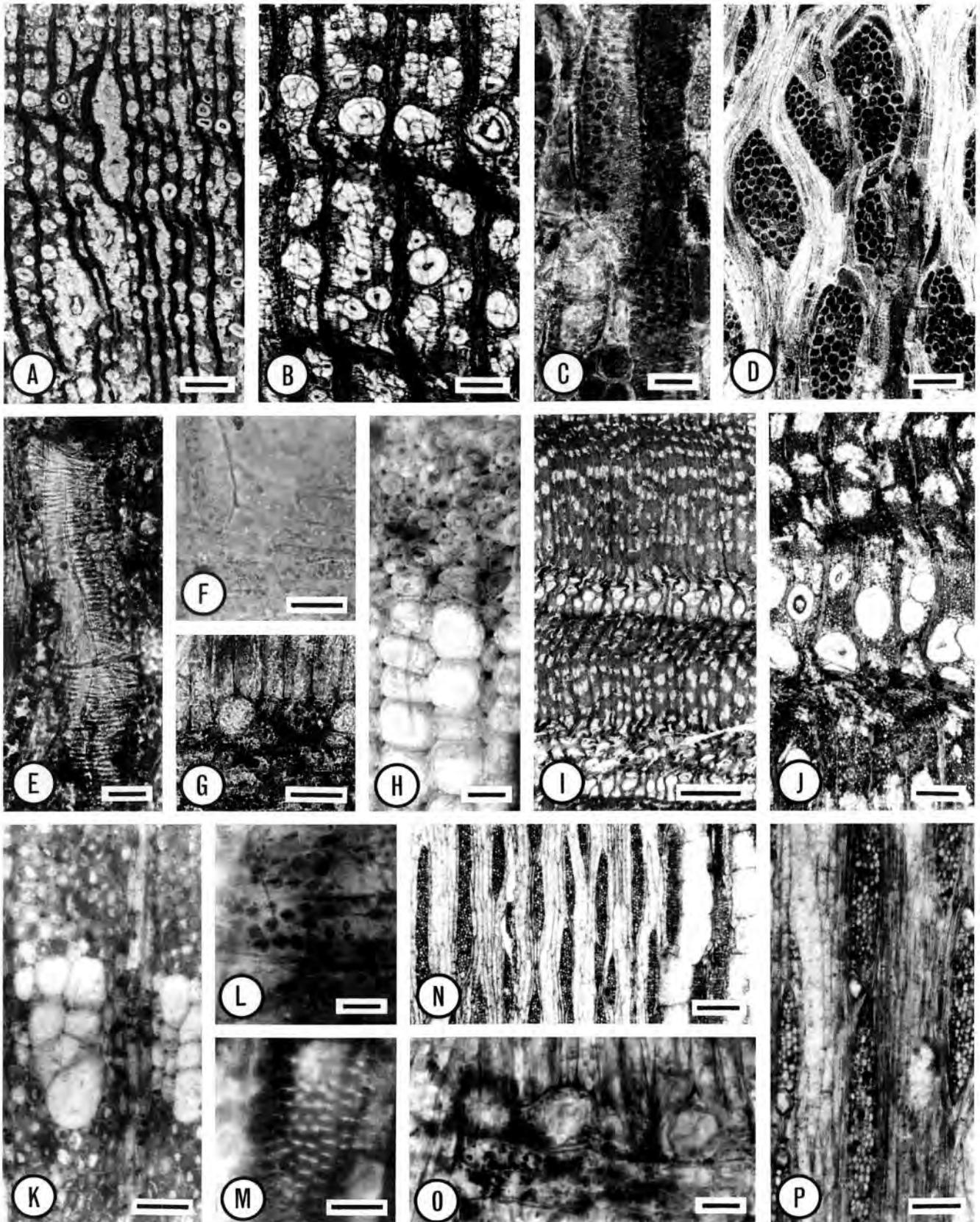
PLATE 2. Ulmaceae woods. cf. *Zelkova*.
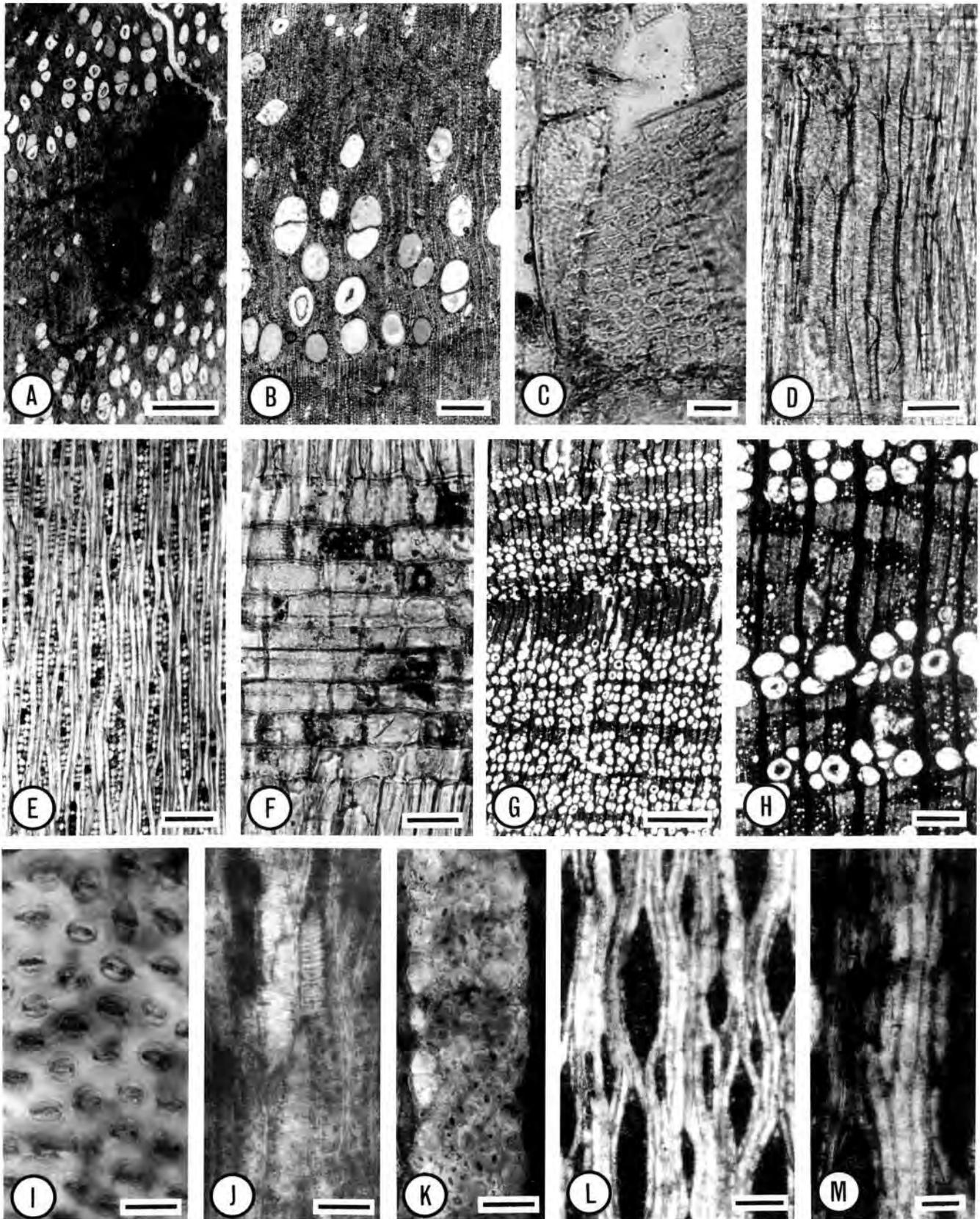
PLATE 3. Ring-porous woods of Florissant.

7.

A REVIEW OF THE PALEOELEVATION ESTIMATES FOR THE FLORISSANT FLORA, COLORADO

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ABSTRACT—One of the significant aspects of the Florissant flora of Colorado has been its application in estimating paleoelevation. The paleoelevation at Florissant is important because of its significance in interpreting the tectonic uplift history of this region during the Tertiary. When the flora was first comprehensively studied by MacGinitie in 1953, the paleoelevation was estimated as 300 to 900 m based upon qualitative comparisons with the distribution of modern vegetation. During the 1990s, various workers applied different quantitative methodologies based upon lapse rates and paleotemperature estimates, or paleoenthalpy using moist static energy in the atmosphere, to derive paleoelevation estimates. Most of these more recent estimates have indicated a higher paleoelevation ranging from 1900 m to more than 4100 m, although an estimate by Axelrod gave results of 455 m. The variations in results by different workers are due to differences in estimated paleotemperatures, the manner in which lapse rates are calculated, and the nature of corrections that are made for paleolatitude, sea level changes, and geographic patterns of temperature variations. This chapter reviews the similarities and differences between these methodologies and estimated paleoelevations in order to better facilitate and evaluate comparisons between them.

Fossil plants from Florissant, Colorado, have been collected and studied since the 1870s. In a comprehensive monographic revision of the flora by MacGinitie (1953), the first attempt was made to derive an estimate of the paleoelevation based upon the fossil flora. Since that time, various other workers, particularly during the 1990s, have applied quantitative methods for estimating Florissant's paleoelevation. Indeed, few topics in the history of scientific research at Florissant have attracted as much published attention as has paleoelevation. The results are important because of their application to interpreting the tectonic history and timing of uplift in the southern Rocky Mountains.

The Florissant flora is known from leaves, fruits, and pollen that were preserved in lacustrine diatomaceous-tuffaceous sediments. These sediments were deposited in a lake that developed when a volcanic debris-flow impounded the paleovalley. Associated mudflows contain large *in situ* stumps of *Sequoia*. The Florissant Formation was deposited on the late Eocene erosion surface of the southern Rocky Mountains (Epis and Chapin 1975). $^{40}Ar/^{39}Ar$ dates indicate an age of 34.07 ± 0.10 Ma for the Florissant Formation (Evanoff et al. 2001), that is, late Eocene (Berggren et al. 1992). The megafloral assemblage is composed of well over 100 species, primarily woody dicotyledons but also including several conifers (see Manchester 2001). In a monographic revision, MacGinitie (1953) recognized eighty-four genera in forty-four families, with a large representation of Fagaceae, Rosaceae, Leguminosae, Anacardiaceae, and Sapindaceae, many of which are still recognized by Manchester (2001).

MacGinitie (1953) concluded that the flora was deposited at an elevation of 300 to 900 m. His estimate was based upon qualitative comparisons with the ecological distribution of living relatives of the fossil plant association, using primarily floristic rather than physiognomic criteria. This estimate has since

served as a widely accepted benchmark on the late Eocene erosion surface. In the decades following MacGinitie's work, it was cited as evidence for significant uplift of the region during the late Tertiary (e.g., Epis and Chapin 1975).

Methods for quantitatively estimating paleoelevations were first developed by Axelrod (1965), and these methods were reevaluated and revised by Meyer (1986, 1992). Application of this quantitative methodology produced the first evidence that the Florissant flora was deposited at an elevation much higher than that suggested by MacGinitie (Meyer 1986, 1992). Subsequent work has made other modifications to the application or methodology (Wolfe 1992a, 1994; Gregory and Chase 1992; Gregory 1994a, 1994b; Gregory and McIntosh 1996), with results consistently indicating a high to very high paleoelevation. These high elevation estimates are supported by a new methodology that uses enthalpy instead of temperatures and lapse rates (Forest et al. 1995; Wolfe et al. 1998).

Although these various quantitative estimates share some significant tenets, there are also important differences in the specific methodological applications and paleotemperatures that are used, and hence in the results. This has resulted in a recent body of literature that reports numerous estimates, and comparisons between them may appear confusing. The purpose of this chapter is to briefly review the methodologies for estimating the late Eocene elevation at Florissant, and to summarize and compare results from different studies into a more easily comparable tabular format (Table 1).

Comparison of Methodologies

The most commonly used method for determining paleoelevation from fossil floras uses estimates of mean annual temperature (MAT) from isochronous sea level and upland paleofloras in conjunction with terrestrial lapse rates (Axelrod 1965; Axelrod and Bailey 1976). In the simplest calculation, paleoelevation is estimated using the following equation: $(MAT^{sl} - MAT^{u})$ $(1000 \text{ m}/5.5 \text{ °C})$, where MAT^{sl} = mean annual temperature of a sea level flora, MAT^{u} = mean annual temperature of the upland flora, and 1000/5.5 derives the reciprocal (182 m/1 °C) of the reputed mean terrestrial lapse rate (usually taken as 5.5 °C/km).

Axelrod's methodology for estimating paleotemperature was based upon the nearest living relative (NLR) method, wherein environmental tolerances for living relatives of the various floristic components in a fossil flora are used to infer paleoclimate. Such an approach has been criticized (e.g., Wolfe 1971, 1993, 1995) because it is based upon evolutionarily sensitive tolerances of nearest living relatives that can evolve and change through time. The method is dependent upon reliable identification of the fossil plants, and upon valid comparisons to the climatic distribution of putative "nearest living species." However, careful research (Manchester 2001) continues to show that many of the Florissant plants originally assigned to extant genera actually represent not only extinct species but also extinct genera, having no close relatives with which meaningful comparisons of climatic distribution can be made. The method is still employed by some workers (e.g., Leopold and Clay-Poole 2001), although it is most reliable for very young floras and decreasingly so for older floras, and may have greater validity for some taxa than for others. The NLR method can be useful as a means to supplement the leaf physiognomy method, although additional work (e.g., Mosbrugger 1993) is needed to develop the method more quantitatively.

An alternative method that has been widely used over the past three decades, and has its origins in the work of Bailey and Sinnot (1916), relies on the physiognomy of vegetation. The method is based on the premise that certain morphological characters (e.g., leaf size, shape, and margin) represent evolutionary adaptations to the physical environment, including climate. The physiognomy of vegetation is spatially repeated under the same climatic regimes in different regions of the world, even when floristic components are dissimilar because of geographic separation. Thus, physiognomy is adapted to particular climatic parameters and is stable through space and, presumably, time.

One of the most widely used aspects of physiognomy has been with leaf-margin analysis, wherein increases in percentages of entire-margined (i.e., smooth-margined) species are directly correlated with increasing MAT (e.g., Bailey and Sinnot 1916; Chaney and Sanborn 1933; Wolfe 1971, 1978, 1979). The physiognomic approach is well quantified and avoids some of the pitfalls of the nearest living relative method, such as invalid taxonomic identification of fossil material and the potential for evolutionary change in the tolerances of taxa. Statistical analysis of multiple characters of leaf physiognomy (e.g., margin characters, size, apical and basal characters, shape, length to width ratios, etc.) has produced the climate-leaf analysis multivariate program (CLAMP) of Wolfe (1993), which provides estimates of MAT. Because it has been developed into a well-quantified methodology and avoids the theoretical

TABLE 1. Comparisons of different methods for estimating paleoelevation of the Florissant flora.

Source	Florissant MAT (°C)	Sea Level Flora	Sea Level MAT (°C)	Lapse Rate (°C/km)	Correction Factors	Paleoelevation (m)
MacGinitie (1953)	≥ 18	—	—	—	—	305–915
Meyer (1986, 1992)	14 ± 1	Comstock, Type Kummerian	26 ± 1*	6.7 ± 1.0	Paleolatitude*; +3 °C projected sea level temp.[†]; sea level +200 m[§]	2450 (1900–3200 range)
Wolfe (1992a)	12	LaPorte	20	3.0	sea level +200 m for higher estimate[§]	2700–2900
Gregory and Chase (1992), Method 1	10.7 ± 1.5 to 11.6 ± 1.5	LaPorte	22.8 ± 1.5*	5.89 ± 0.5	Paleolatitude*; sea level +200 m[§]	2300 (±400 @ 68% confidence)
Gregory and Chase (1992), Method 2	10.7 ± 1.5 to 11.6 ± 1.5	Goshen	20.3 ± 1.5	3.0 ± 0.5	sea level +200 m[§]	3200 (±800 @ 68% confidence)
Wolfe (1994)	10.8	Not specified	23.2	3.0 and 5.5	—	4133 and 2255
Gregory (1994a), Method 1	10.7 ± 1.5	LaPorte	22.9 ± 1.5	5.89	sea level +200 m[§]	2300 (±370 @ 68% confidence)
Gregory (1994a), Method 2	10.7 ± 1.5	Goshen	20.0 ± 1.5	3.0	sea level +200 m[§]	3300 (±750 @ 68% confidence)
Gregory (1994b)	12.8 ± 1.5	Goshen Sweet Home Bilyeu Creek	19.5 ± 1.5	3.0	sea level +200 m[§]	2400 (±720 @ 68% confidence)
Forest et al. (1995)	na[‡]	Goshen, LaPorte	na[‡]	na[‡]	sea level +200 m[§]	2900 ± 670

(Table 1 continues)

(Table 1 continued)

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Source	Florissant MAT (°C)	Sea Level Flora	Sea Level MAT (°C)	Lapse Rate (°C/km)	Correction Factors	Paleoelevation (m)
Gregory and McIntosh (1996) "Wolfe Method"	12.8	Goshen	21.6*	3.0	Paleolatitude* sea level +200 m[§]	3100 (± 800 @ 68% confidence)
Gregory and McIntosh (1996) "Meyer Method"	12.8	LaPorte	22.7*	5.9	Paleolatitude* sea level +200 m[§]	1900 (± 500 @ 68% confidence)
Gregory and McIntosh (1996) "Forest et al. Method"	na[‡]	Goshen, LaPorte	na[‡]	na[‡]	sea level +200 m[§]	2900 (± 700 @ 95% confidence)
Axelrod (1997)	15.5	Goshen	18	5.5	—	455
Wolfe et al. (1998)	na[‡]	Goshen, Comstock, LaPorte	na[‡]	na[‡]	?	3800 ± 800

* = MAT estimate as corrected to Florissant paleolatitude (41°) using inferred paleolatitudinal temperature gradient.
[†] = °C (in addition to indicated sea level MAT) used as a correction for thermal effects due to continentality and elevated base level.
[§] = Correction (meters) used to calibrate paleoelevation results to modern sea level.
na[‡] = Not applicable because the methodology uses paleoenthalpy instead of MAT and lapse rates.

problems inherent in the NLR methodology due to changing evolutionary tolerances within taxa, the physiognomic approach utilizing CLAMP is reported to provide estimates for paleoclimate that are more repeatable and valid than the NLR approach (Wolfe 1993, 1995). Compared to Axelrod's approach, Wolfe, Meyer, and Gregory have relied primarily upon physiognomy, with Wolfe and Gregory using specifically the CLAMP methodology. My analysis has secondarily considered floristic tolerances for particular taxa.

The reliability and precision of the CLAMP methodology have been challenged based upon evidence suggesting the method's poor ability to predict mean annual temperature, as well as biases due to the process of fossilization, the allocation of specimens to taxa, and other factors besides temperature that affect physiognomy (Jordan 1997). Although CLAMP considers a complexity of parameters, leaf-margin characters still emerge as the strongest climatic signal of leaf physiognomy, and the primary contribution of CLAMP may be to simply substantiate the reliability of univariate leaf-margin analysis as a means for estimating paleotemperature (Wilf 1997). Foliar physiognomic interpretations of paleoclimate can also be constrained by taphonomic factors (Greenwood 1992), although this limitation also would apply to the NLR approach. Any imprecision in the estimate of paleotemperature will, of course, be propagated into the estimation of paleoelevation.

Revision of Axelrod's methodology for estimating paleoelevation (Meyer 1986, 1992) recognizes other variables that need to be considered in its application, including the effects of continental climates, elevated regional lowlands (i.e., the lowest land surfaces within a region are at moderate to high elevation), extensive mountain massifs, geographical and seasonal variability in lapse rates, climatic changes, sea level fluctuations, and paleogeography. This revised methodology is based upon analyses of modern local terrestrial lapse rates calculated by linear regression using altitudes and long-term mean temperatures from climatic records within narrowly confined geographical regions. These results demonstrate that, within the western United States, modern variability exists both in local terrestrial lapse rates (ranging from about 5.0 to 8.1 °C/km) and in projected sea level MAT (i.e., the mathematical projection of the MAT lapse rate to 0 m in regions where the lowest elevations are actually above sea level; these range from 10.9 to 26.5 °C, as determined from local lapse rates). Such variability is due largely to the effects of continentality, elevated regional lowlands, and the location of the subtropical high-pressure zone.

The method proposes corrective factors that can be used to compensate for this variability when Pacific Coast (sea level) and interior (e.g., Florissant) paleofloras are used to estimate paleoelevation. For example, modern MAT projected to sea level (using local lapse rates) increases 2 to 10 °C between coastal and interior locations, while mean annual range of temperature (MART) increases 18 to 21 °C (Meyer 1992, Fig. 8). It is probable that the magnitude of such change would have been less pronounced during the early and middle Tertiary resulting from (1) less intense pre-middle Miocene cold water upwelling along the Pacific Coast (White et al. 1992; Barron and Keller 1983); (2) a more weakly developed subtropical high-pressure zone due to a lower latitudinal temperature gradient (inferred from temperature data of Savin et al. 1975; Wolfe 1994); and (3) the lower nature or absence of modern mountain barriers parallel to the coast (e.g., the Cascade Mountains and Sierra Nevada). Although upwelling is believed to have been present along the west coast of North America since the Mesozoic (Parrish and Curtis 1982), it intensified during the middle Miocene. The upwelling is presently concentrated into a narrow coastal zone where it is much more intense and offshore temperatures are cooler than during the Miocene (John Barron, pers. commun., 1996).

In another approach, Wolfe (1992a) calculates modern regional lapse rates from two-point data compared over long distances; that is, they are derived from the difference between Pacific Coast MAT and interior (usually upland) MAT divided by the elevation difference between these climatic stations. This methodology derives regional lapse rates that are lower than the local lapse rates calculated by Meyer (1986, 1992), with values of about 3 °C/km for intramontane basins of the Rocky Mountains. To some extent, this method for calculating lapse rates incorporates the effects due to continentality, the sharp temperature gradient inland from the Pacific Coast, and the effects of elevated regional lowlands. Wolfe (1992a, 1994) applies this lower lapse rate to the calculation of paleoelevation for this region during the Tertiary. However, the value of these lapse rates in part may be reflective of the modern magnitude of cold water upwelling along the Pacific Coast and the presence of near-coastal mountain barriers, and hence early to middle Tertiary regional lapse rates may have been higher. Wolfe (1992a) argues that upwelling has probably occurred along the Pacific Coast since the Cretaceous, but it must also be considered that the magnitude of this upwelling intensified during the Miocene (and even more so at present) due to significant changes

in oceanic circulation caused by shifting continents and increasing Antarctic glaciation (White et al. 1992; Frakes et al. 1992; Barron and Keller 1983; Keller and Barron 1983; Barrera et al. 1985). Because it uses lower lapse rates, Wolfe's methodology usually produces very high estimates of paleoelevation relative to Meyer's method.

An alternate approach, developed by Forest et al. (1995, 1999) and Wolfe et al. (1998), uses fossil leaf assemblages to infer enthalpy, rather than temperature, in order to estimate paleoelevation. Enthalpy is related to moist static energy in the atmosphere, which is nearly conserved by air parcels. This method is claimed (Forest et al. 1995, 1999; Wolfe et al. 1998) to avoid some of the assumptions of the lapse rate method, particularly the implicit assumption that variations in atmospheric water vapor through time had no effects on variations in surface temperatures. In the enthalpy method, the foliar physiognomic characters for modern North American sites (using the data from Wolfe 1993) are analyzed to determine their relation to mean annual enthalpy. Paleoenthalpy is then estimated from upland and sea level fossil floras to determine the difference in mean enthalpy. This difference is divided by gravitational acceleration to derive paleoelevation. The enthalpy approach is considered to be relatively insensitive to paleoclimate, and therefore provides an alternative paleobotanical means for testing the results of the methodologies that are based on paleotemperature analyses and lapse rates.

Comparison of Paleotemperature Estimates

Only megafloral remains are considered in paleoelevation estimates because they best represent the vegetation proximal to the depositional basin (Spicer and Wolfe 1987). Pollen is more widely dispersed and is more likely to include taxa from different elevations. Megafloral remains of conifers and angiosperms are diverse at Florissant, and preserve the foliar physiognomic characters of the dicotyledonous angiosperms that are useful in deriving estimates of climate independent of taxonomy. Physiognomically, the Florissant megaflora consists of many broad-leaved deciduous and broad-leaved evergreen taxa as well as several conifers (e.g., *Sequoia*, *Chamaecyparis*, *Torreya*, *Pinus* [probably three species], *Abies*, and *Picea*). Based upon physiognomic characteristics of modern vegetation (Wolfe 1979), Meyer (1986, 1992) suggested a setting analogous to the

transition between Microphyllous (or possibly Notophyllous) Broad-leaved Evergreen forest and Mixed Coniferous forest, demarcated by MAT 13 °C.

More recently, statistical analysis of leaf physiognomy (including the CLAMP, of Wolfe 1993) has provided the following MAT estimates for the Florissant flora:

1) 12.0–12.5 °C (Wolfe 1992a, b).
2) 10.8 °C (Wolfe 1994, 1995; using a larger CLAMP database than previously).
3) 10.7 ± 1.5 °C (Gregory and Chase 1992; Gregory 1994a; based upon a single-site sample with twenty-nine species).
4) 11.6 ± 1.5 °C (Gregory and Chase 1992; Gregory 1994a; based upon analysis of ninety-seven species from MacGinitie's large collection from multiple sites).
5) 12.8 ± 1.5 °C (Gregory 1994b; Gregory and McIntosh 1996; based upon analysis of a single-site sample with twenty-nine species).
6) 13.9 ± 1.5 °C (Gregory 1994b; Gregory and McIntosh 1996; based upon analysis of ninety-seven species from MacGinitie's large collection from multiple sites). This value was not applied in the estimates for paleoelevation; hence, it is not repeated in Table 1.

With the exception of the last estimate, these results place the flora within the thermal parameters of Mixed Coniferous forest (as defined by Wolfe 1979). Although the forest canopy locally may have formed from such conifers as *Sequoia*, *Chamaecyparis*, *Torreya*, and *Pinus*, these genera include species that also can occur under conditions of MAT warmer than the maximum 13 °C that demarcates Mixed Coniferous forest. The lack of high coniferous diversity also suggests a setting transitional to rather than entirely within Mixed Coniferous forest. The two genera of cooler adapted conifers, *Picea* and *Abies*, are more typical of Mixed Coniferous forest, although they are very rare in the fossil flora (only one megafloral specimen of *Abies* is known), and their seeds could have reached the depositional basin from nearby, slightly higher elevations occupied by Mixed Coniferous forest.

Floristically, the presence of a palm implies a MAT >10 °C and a cold month mean temperature of >5 °C (Greenwood and Wing 1995); this is contrary to Wolfe's (1995, Fig. 12) CLAMP estimate placing the flora near 1 °C for the cold month mean, transitional between analogues of Mixed Broad-leaved Evergreen and Coniferous forest and Mixed Coniferous forest. Axelrod (1997)

gave an estimate of 15.5 °C MAT, although his reason for this estimate (apparently based on floristic criteria) was not given.

The statistical methodologies analyzing foliar physiognomy (e.g., CLAMP) provide MAT estimates ranging from 10.7 to 13.9 °C, although for the reasons discussed above, I believe that the MAT was slightly warmer than that indicated by the cooler CLAMP estimates, probably closer to the 13 °C MAT that marks the transition between dominantly coniferous and dominantly Broad-leaved Evergreen vegetation (as defined by Wolfe 1979). CLAMP estimates typically show errors of ±1.5 °C (see Table 1).

Sea Level Floras and Temperatures

Because Tertiary terrestrial climates have involved significant temperature fluctuations over short intervals of time (Wolfe 1978, 1992b, 1994), it is important that an upland flora such as Florissant be compared with an isochronous sea level flora when estimating paleoelevation. Florissant's radiometric age of 34.07 Ma corresponds with the Kummerian megafloral stage defined by Wolfe (1968, 1981) from the Puget Group in Washington; Wolfe also assigns the Comstock flora (Sanborn 1935) of Oregon to this stage. Both floras are associated with intertonguing marine formations, demonstrating their presence at sea level. Although neither flora is radiometrically dated, the Puget Group assemblage represents the type area for the Kummerian stage, and the Comstock is associated with beds containing Refugian stage foraminifera (Wolfe 1981; Armentrout 1981). The Goshen flora (Chaney and Sanborn 1933) of Oregon is assigned by Wolfe (1981) to the informal Goshen stage; it also represents a near–sea level depositional setting, and although undated, is correlated by Wolfe with the LaPorte flora (Potbury 1935) of California, K-Ar dated as 33.2 Ma (Evernden and James 1964; corrected to new constant). The LaPorte flora is not associated with marine deposits and may have grown somewhat above sea level. Current geochronologic evidence for all of these floras is weak, and additional dating is needed before an age equivalence with Florissant can be demonstrated clearly. Taphonomic differences between these floras may also complicate their comparison, as the depositional environments were not the same. The various estimates of MAT for these sea level floras, as determined by different workers, are summarized in Table 1.

Comparison of Paleoelevation Results

The first estimate of paleoelevation for Florissant was that of MacGinitie (1953:53), who concluded that "the plant association indicates a region of moderate elevation, probably not more than 3000 nor less than 1000 feet. No flora of similar age is known from the region to the southeast with which a useful comparison can be made, with a view to gaining a more definite idea of elevation." This estimate (about 300 to 900 m), which was not based on a quantitative methodology, has served as the elevation benchmark for tectonic and geomorphic studies dealing with the timing of the region's uplift (e.g., Epis and Chapin 1975). MacGinitie also considered that the geologic evidence of river cutting indicated a Pliocene to Pleistocene paleoelevation of 1830 m (6000 feet), but he noted (MacGinitie 1953:53) that it was impossible to "arrive at even an approximate estimate of the combined effects of erosion and uplift from the middle Pliocene back to the Oligocene [sic]."

The first use of a quantitative method to estimate high paleoelevation at Florissant was by Meyer (1986, 1992), with results of 2450 m or within a probable range of 1900 to 3200 m (Table 1). According to this methodology, in order for the sea level temperature estimate to be applied in estimating paleoelevation for Florissant, it is first necessary to make adjustments for differential paleolatitudes. During the late Eocene, the Florissant flora was about 2° north of its present 39° latitude, while the Comstock and Goshen floras were about 5° north of their present 44° latitude (Smith et al. 1981); hence, they were separated by about 8° paleolatitude. A paleolatitudinal temperature gradient of 0.35 °C/1° lat was used for the late Eocene of western North America (Meyer 1992), which is generally consistent with Wolfe's (1994) estimate (based upon CLAMP data) of 0.3 °C/1° lat during the Eocene and 0.4 °C/1° lat for the post-Eocene, and with Greenwood and Wing's (1995) middle latitude estimate of 0.4 °C/1° lat during the Eocene. It is therefore necessary to add about 3.0 °C to the MAT (23 °C) for the Comstock and Goshen floras to estimate West Coast sea level MAT (26 °C) at Florissant's paleolatitude of 41°.

A further adjustment is needed to compensate for the probable effects of continentality and elevated regional lowlands (Meyer 1992). Such an adjustment assumes that the late Eocene erosion surface did in fact occur at moderate to high elevation, and that marine upwelling (though less pronounced than today) had some effect on lowering terrestrial MAT and MART

nearer the Pacific Coast. This presumption of at least moderate elevation, while unavoidably circular in its reasoning, is indicated by a simplistic calculation of paleoelevation in which such an assumption is not made, with paleoelevation instead estimated simply from the difference between sea level MAT (using 23 °C, based on CLAMP estimates of about 20 to 21 °C for Goshen from Gregory [1994a] and Gregory and McIntosh [1996], latitude-adjusted 3 °C per Meyer [1992]) and Florissant MAT (13 °C, as discussed previously), multiplied by the average of world lapse rates (5.9 °C/km as per Meyer 1992), to obtain a value of 1700 m (1900 m calibrated to modern sea level). An analysis of modern temperatures (Meyer 1992, Fig. 8) indicates that projected sea level MAT increases at least 2 °C to as much as 10 °C from coastal to interior areas, with about 8 °C at lat 40°. Mean annual range of temperature increases about 20 °C. It is assumed that this pattern was less pronounced during the late Eocene due to less intense coastal upwelling and the absence of mountain barriers, an assumption that is supported by the low mean annual range of temperature (MART) inferred for the Florissant flora relative to modern temperatures in central Colorado. This suggests a value of 29 °C projected sea level MAT during the late Eocene in the Florissant vicinity (Meyer 1992, Fig. 14). A local lapse rate of 6.7 °C/km (150 m/−1 °C) is applied to the equation based upon modern local lapse rates within the continental interior (derived from modern lapse rates in the Florissant region calculated by linear regression analysis by Meyer 1992, Fig. 9), giving a paleoelevation of 2250 m. In order that paleoelevation can be calibrated to modern sea level, 200 m must be added to the estimate for Florissant because latest Eocene sea level was higher (Haq et al. 1987).

By contrast, if Wolfe's method is applied, no correction for the effects of continentality and elevated regional lowlands is used to derive a projected sea level MAT, assuming that these effects have already been incorporated by his method for calculating modern lapse rates regionally, over long distances, rather than locally as in the Meyer method. Instead, the difference between actual sea level MAT and Florissant MAT is multiplied by 333 m (reciprocal of lapse rate 3.0 °C/km), and 200 m is added for sea level calibration. Wolfe has applied this methodology (using a lapse rate of 3.0 °C) for estimating paleoelevation of the Florissant flora and obtained estimates of 2700 to 2900 m (Wolfe 1992a) and 2255 to 4133 m (Wolfe 1994). The differences between his estimates are due to differing CLAMP estimates for MAT, resulting from additions to the modern CLAMP database. Wolfe calculates elevation relative to the LaPorte flora of

California, although LaPorte is about 1 million years younger than Florissant and was probably deposited at some elevation. Note that when Wolfe's (1992a) lapse rate of 3.0 °C/km is used, small errors in estimated paleotemperatures translate into greater elevation differences than they would if a lower lapse rate was used in conjunction with corrective factors for continentality and elevated regional lowlands (as per Meyer 1992). However, when these corrective factors are used, they are hypothetical values modified from modern temperature patterns, thus introducing a degree of uncertainty in the equation. Wolfe's estimates are higher than Meyer's primarily because of the lower lapse rate and the lower estimated MAT for Florissant.

Gregory and Chase (1992), Gregory (1994a, b), and Gregory and McIntosh (1996) have derived other estimates based upon modified applications of both the Meyer and Wolfe methodologies. They apply paleotemperature estimates, derived from multivariate physiognomic analyses, ranging from 10.7 ± 1.5 °C to 12.8 °C for the Florissant flora (Table 1). The comparison at sea level is with the Goshen and LaPorte floras. They derive paleoelevation estimates using variations in lapse rates and sea level temperatures (Table 1) based on the two methodologies. Method 1, or the "Meyer methodology," uses LaPorte as the sea level flora and 5.89 °C/1000 m as the lapse rate, giving results ranging from 1900 ± 500 m to 2300 ± 400 m (at the 68 percent confidence interval). Method 2, or the "Wolfe methodology," uses Goshen as the sea level flora and 3.0 °C/1000 m as the lapse rate, giving results ranging from 2400 ± 720 m to 3300 ± 750 m (at the 68 percent confidence interval). The Meyer methodology is actually somewhat modified from my original application (Meyer 1986, 1992), in that the procedure for estimating projected sea level temperature is different. Instead, Gregory et al. use the LaPorte flora as a proxy for the projected sea level temperature in Colorado (e.g., see Gregory 1994a:49); however, it is not clear that the LaPorte flora actually grew at sea level. In the application by Gregory and Chase (1992), the range in the estimate of 10.7 ± 1.5 ° to 11.6 ± 1.5 °C for the Florissant flora is because the lower estimate is derived from the analysis of a single-site sample collected by Gregory, and the higher estimate is derived from analysis of MacGinitie's (1953) sample of the entire flora combined from several sites.

Applying his early methodology to Florissant for the first time, Axelrod (1997) estimated a paleoelevation of 455 m. As previously discussed, this early methodology, while pioneering for its time, was simplistic and failed to recognize many complications that

significantly influence paleoelevation estimates, as previously discussed. For that reason, even though this estimate was published in 1997, it is the least accurate because it does not consider the entire complexity of lapse rates nor does it provide documentation for the MAT and MART temperature estimates. Because he had the warmest MAT estimate for Florissant and the coolest for the sea level Goshen flora, his method gives the lowest results for paleoelevation.

Forest et al. (1995) were the first to apply the approach that uses fossil leaf assemblages to infer enthalpy, rather than temperature, in order to estimate paleoelevation. Paleoenthalpy is estimated from the fossil floras at Florissant, Goshen, and LaPorte to determine the difference in mean enthalpy between sea level (Goshen and LaPorte) and Florissant. This difference is divided by gravitational acceleration to derive a paleoelevation for Florissant of 2700 ± 670 m; when calibrated to modern sea level, this estimate is 2900 ± 670 m. In a later application of the paleoenthalpy model, Wolfe et al. (1998) obtained an estimate of 3800 ± 800 m. The difference in the estimates of moist enthalpy between Forest et al. (1995) and Wolfe et al. (1998) results from the use of linear statistics in one case and nonlinear in the other, and from differences in the samples used for the modern database.

Problems

All of these methods are problematical and assume the validity and precision of the variables that are the basis for their estimates, including paleotemperature, lapse rate, paleoenthalpy, paleolatitude corrections, sea level fluctuations, selection of sea level flora and temperature, corrections for the effects of continentality and elevated regional lowlands, and geochronology. Most of the variation between the results of different workers using the paleotemperature and lapse rate method (Table 1) is due to differences in these various estimates. Certain aspects of the models are based upon known patterns of modern variability in these factors, yet these are always uncertain when applied to the late Eocene.

Better chronology using $^{40}Ar/^{39}Ar$ dating is needed to substantiate the age of the Goshen, LaPorte, and Comstock floras and their relevance to the major climatic deterioration near the Eocene-Oligocene boundary. If the Goshen and LaPorte floras are 33.2 Ma as indicated by the K-Ar date from LaPorte, they may be too young for comparison with the 34.07 Ma Florissant flora. However, a further complication is that assemblages of the Bridge Creek flora are now dated by

$^{40}Ar/^{39}Ar$ from 32.24 to 33.62 Ma (Meyer and Manchester 1997). The Bridge Creek assemblages represent a significantly cooler post-deterioration flora (Wolfe 1978, 1992b, 1994; Meyer and Manchester 1997). This suggests that the climatic deterioration may have occurred earlier than 33.62 Ma, raising a conflict with the interpretation of the presumed pre-deterioration Goshen and LaPorte floras as discussed in the above models. The Comstock flora is stratigraphically lower than Goshen (Wolfe 1981), and although it has not been dated radiometrically, Comstock in Oregon and the type Kummerian assemblage from the Puget Group in Washington may be more applicable for comparison with Florissant.

Conclusions

The most important point to emerge from the numerous recent studies using new techniques to estimate Florissant's paleoelevation is that they suggest a much higher paleoelevation than that originally estimated by MacGinitie (1953). These new estimates range from 1900 m to more than 4100 m. My interpretations using paleotemperatures and local lapse rates (Meyer 1986, 1992), as well as results by Gregory and Chase (1992, Method 1) and Gregory (1994a, Method 1; 1994b), all suggest values at the lower end of this range, while estimates that are derived using a lower regional lapse rate of 3.0 °C/km (Wolfe 1992a, 1994; Gregory and Chase 1992, Method 2; Gregory 1994a, Method 2) produce estimates at the higher end of this range. The methodologies using a low lapse rate may not be applicable to the late Eocene because of intensified post-early Miocene marine upwelling and the development of mountain barriers near coastal regions. Methodologies based upon enthalpy provide another approach to modeling paleoelevation, providing results within a range of 2900 to 3800 m. The fact that the enthalpy method, which is independent of lapse rate, provides similar results as the lapse rate–based estimates strengthens the argument in support of high paleoelevation.

While an unequivocal and precise estimate is not possible, the high paleoelevations estimated by these different applications based upon paleobotany should provide a stimulus for studies reconstructing the tectonic history of this region. The various methods for estimating paleoelevation are problematical and assume the validity and precision of paleotemperature estimates, lapse rate estimates, paleoenthalpy estimates, paleolatitude corrections, sea level fluctuations, and geochronology. Certain aspects of the models are based upon known patterns of modern lapse rate and temperature

variability, yet inferences must be made when applying these to the late Eocene. Although estimated paleoelevations are consequently speculative, they nevertheless provide a useful framework for comparison with other interpretations regarding late Eocene elevation in the southern Rocky Mountain region.

These various studies serve to provide a good applied illustration of the scientific process, wherein hypotheses and results are retested in view of alternative methodologies. Much of this effort thus far has been confined to the paleobotanical community. The results are controversial not only among the paleobotanists who have estimated Florissant's paleoelevation (see Table 1), many of whom nevertheless agree that the paleoelevation was high, but also among geologists who have been reluctant to accept *any* generally high paleoelevations for this region during the late Eocene (Steven et al. 1997). The paleobotanical results still remain to be tested, either challenged or supported, by other lines of evidence such as physical geology and paleoentomology.

Acknowledgments

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