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PALEONTOLOGY OF THE UPPER EOCENE FLORISSANT FORMATION, COLORADO

edited by

Herbert W. Meyer and
Dena M. Smith

Paleontology of the Upper Eocene Florissant Formation, Colorado

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Cover: The Big Stump, Florissant Fossil Beds National Monument.
Back Cover: Left: *Glossina oligocena*; (tse-tse fly); University of Colorado Museum of Natural History; UCM-31594. Scale = 5 mm. Right: *Florissantia speirii*; University of California Museum of Paleontology; UCMP-3619. Scale = 2.5 cm.

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Preface

The amazing diversity of fossil organisms preserved in the Florissant fossil beds has made it the focus of more than a century of research. Not only are the organisms from Florissant interesting themselves, but Florissant has been an excellent system for testing broader questions in paleontology. The breadth of the papers in this volume not only illustrates the importance of Florissant, but shows how this site continues to contribute to our understanding of paleoecology, macroevolution, and taphonomy. New contributions to our understanding of Florissant include such topics as the history of scientific study at Florissant, mechanisms of preservation of the fossils, paleoclimate and biogeography based on fossil plants, magnetic stratigraphy of the Eocene-Oligocene floral transition, new additions to the fossil mammalian fauna, fossil evidence for plant-insect interactions, aspects of the mineralogy of the petrified trees and their conservation, and the application of information technology to the development of a paleontological database for Florissant.

This volume is an outcome of a special topical session titled “Paleontology and Stratigraphy of the Late Eocene Florissant Formation, Colorado,” which was convened by the editors during the 2004 Annual Meeting of the Geological Society of America in Denver. This session was complemented by a full day field trip to examine the paleontology and volcanic setting of the Florissant fossil beds (Meyer et al., 2004). Thirteen papers were presented during the special session, five of which are summarized in this volume. Three papers in the current volume are modifications of presentations in the symposium, and three others are new. Several of the papers presented during the symposium are not included here.

The significance of the Florissant fossil beds has been widely recognized for more than a century. The site began attracting considerable scientific attention during the Hayden Survey in the 1870s, and the fossils from Florissant were among the first to be described from the American West. They have provided the basis for ~400 published studies resulting in the description of more than 1,700 still-valid species of fossil plants, insects, spiders, fish, and mammals, making Florissant one of the world’s most diverse fossil sites. These publications have included such monumental tomes as Lesquereux’s *Contribution to the fossil flora of the Western Territories* (Lesquereux, 1883), Scudder’s *Tertiary Insects of North America* (Scudder, 1890), and MacGinitie’s *Fossil Plants of the Florissant Beds, Colorado* (MacGinitie, 1953). T.D.A. Cockerell alone published ~140 papers that dealt with Florissant’s fossils (e.g., Cockerell, 1908a, 1908b). More recently, a volume on paleobotany was published in 2001 (Evanoff et al., 2001a) following an earlier GSA symposium during the 1994 Rocky Mountain Section Meeting. That volume included contributions dealing with the stratigraphy, palynology, leaf and fruit flora, climatic implications and anatomy of fossil woods, and paleoelevation. Other paleontologists over the decades have produced numerous publications dealing with fossils from Florissant, and this long history of paleontologic research is covered by Veatch and Meyer in the first chapter of the present volume.

Florissant’s fossils were deposited in the basin of a paleodrainage in which sedimentation was strongly influenced by nearby eruptive centers in forming the Florissant Formation (Figs. 1 and 2). Volcanic lahars, pyroclastic ash, and pumice eruptions, and the effects that these had on the lake’s diatom population, all contributed to the fossilization of the organisms at Florissant. Lahars originating from the Guffey volcanic center in the Thirtynine Mile volcanic center buried the bases of large redwood trees to form Florissant’s petrified forest, and they created a natural impoundment to form a lake. Volcaniclastic lacustrine sedimentation provided the setting for the preservation of the great diversity of plants and insects, and stream and floodplain deposition aided in the preservation of fossil mammals. A model describing the

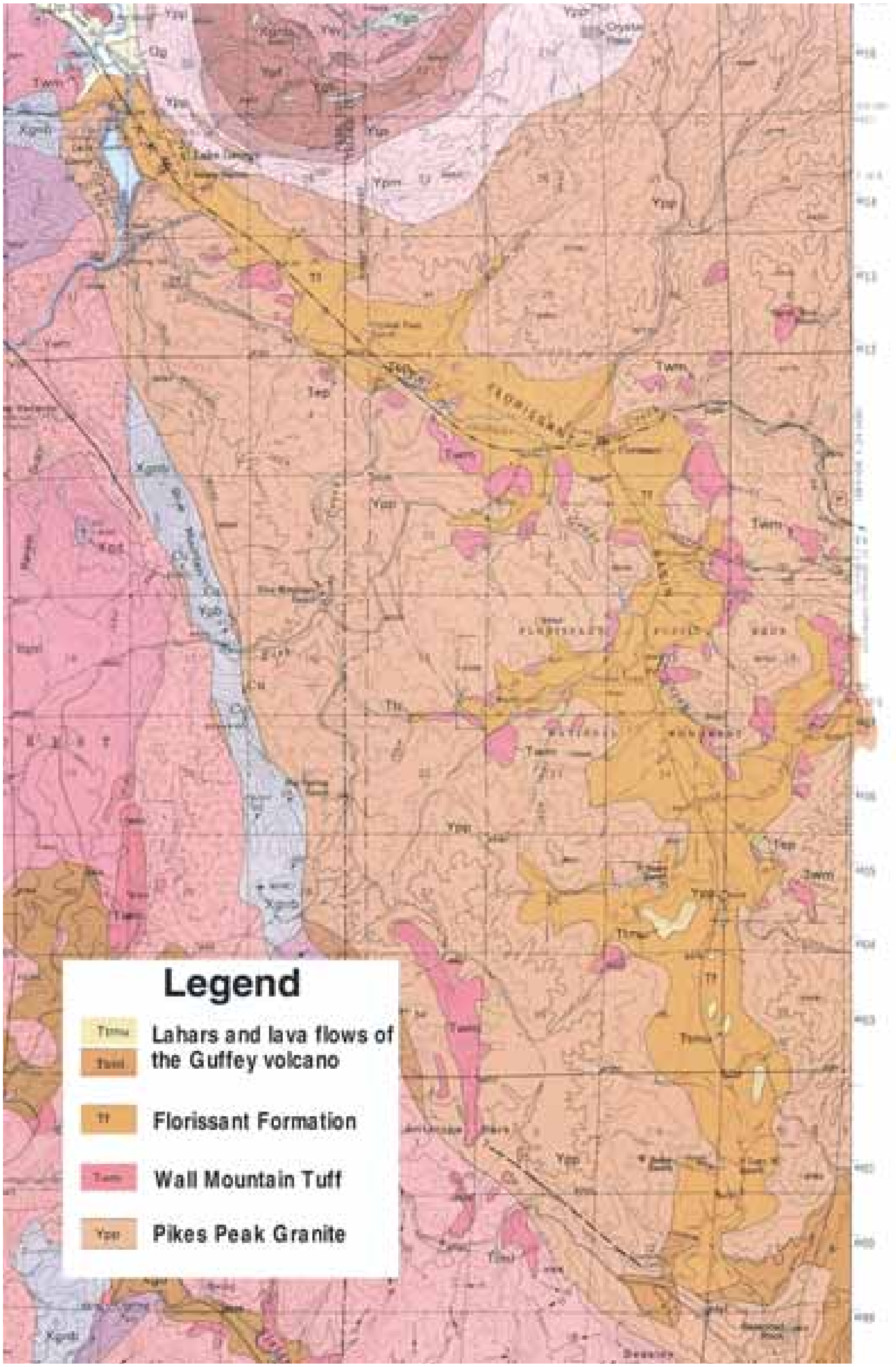

Figure 1. Geologic map of the Florissant area showing selected units, including the Florissant Formation (Tf, formerly described as Florissant "lake beds"). Lahars and lava flows of the Guffey volcano include units described as the lower member and upper member of the Thirtynine Mile Andesite (Ttml and Ttmu, respectively). Pikes Peak Granite (Ypp) forms the Precambrian basement on which the Florissant Formation was deposited. Section lines indicate scale of 1 mile. After Wobus and Epis (1978). Color reproduction funded by the Cripple Creek & Victor Gold Mining Company.

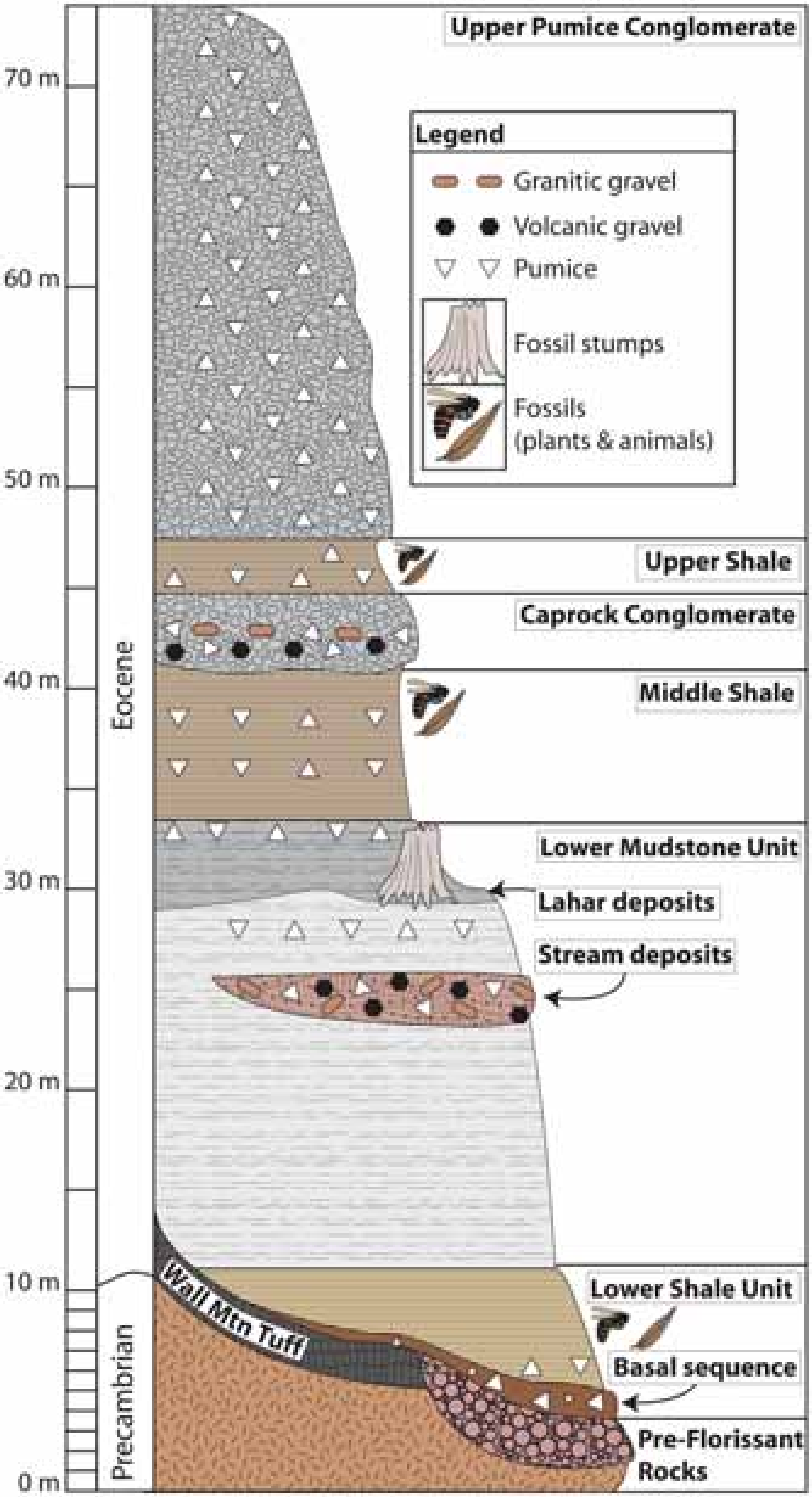

Figure 2. Stratigraphic column of the Florissant Formation and its underlying rocks. Modified from Evanoff et al. (2001b); redrafted by Joseph Hall. Color reproduction funded by the Cripple Creek & Victor Gold Mining Company.

role of microbial mats in the taphonomic processes that facilitated the remarkable preservation in the lacustrine shale is discussed in the chapter by O'Brien, Meyer, and Harding.

Examination of the fossil plants, insects, and mammals reveals a complex community that lived immediately preceding the climatic cooling of the Eocene-Oligocene transition. Studies of this paleocommunity at Florissant have stimulated important and often controversial interpretations of the paleoclimate and paleoelevation in the late Eocene Rocky Mountains. The chapter by Boyle, Meyer, Enquist, and Salas introduces and applies a new methodology for estimating climate and ecology from fossil plants based on taxonomic comparisons with genera and families in modern forest inventories. This work indicates that Florissant lacks a modern analog among forest inventories in the Americas, but shows closest similarity to temperate broad-leaved forests of eastern North America and subtropical montane forests of Mexico. The biogeographic affinities of the Florissant flora are reevaluated in the chapter by Leopold, Manchester, and Meyer, who note the strong affinity to modern warm temperate floras of eastern Asia and discuss models for changing community composition in response to climate change. The chapter by Prothero goes beyond Florissant to examine the magnetic stratigraphy of other fossil floras in western North America in an effort to relate Florissant to the broader context of major climate change during the Eocene-Oligocene transition.

Sites with excellent preservation such as Florissant provide an opportunity to study interactions between different groups of fossil organisms and how these interactions are affected by climate change. In the chapter by Smith, a comparative approach is used with two Eocene fossil sites to examine the effects of a global cooling event on the interactions between plants and their insect herbivores.

New methods for the taxonomic assessment of fossil spiders using outline morphometrics and linear leg characters are developed in the chapter by Kinchloe, Smith, Guralnick, Cushing, and Krieger. These methods provide a preliminary test for quantitative evaluation of the accuracy of family level classification for specimens that lack traditional taxonomic characters.

New collections in recent years have resulted in significant additions to the few mammalian taxa that were known previously. New occurrences of small mammals such as rodents, lagomorphs, and shrews are described in the chapter by Lloyd, Worley-Georg, and Eberle.

Florissant's petrified forest is what captures the attention of visitors to the site, and these petrified stumps are among the largest diameter fossilized trees in the world. The chapter by Mustoe examines the mineralogy and geochemistry that affected the preservation of these giants, showing that silicification occurred in several independent stages. The structural characteristics of this preservation cause the stumps to be susceptible to mechanical weathering, and the chapter by Young, Meyer, and Mustoe examines conservation measures that could be used for stabilization, particularly the use of chemical consolidants and adhesives.

Over the course of more than a century, Florissant's fossils and the publications that cite them have become widely scattered. With the advent of new information technologies during the past decade, it has become possible to synthesize much of the data about Florissant to make this information easily accessible both to researchers and the general public. The effort to inventory the entire collection of published specimens and compile this information into a database and Web site is described in the chapter by Meyer, Wasson, and Frakes.

The editors would like to thank all of their authors for their contributions to the session and to this special volume. We would also like to thank our excellent reviewers, whose thoughtful comments greatly enhanced the quality of every manuscript in this volume. We look forward to the next century of work at Florissant, as this site continues to be a focal point for innovative approaches to research in paleontology.

Herbert W. Meyer
Dena M. Smith

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History of paleontology at the Florissant fossil beds, Colorado

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ABSTRACT

Paleontological studies at Florissant have been ongoing for more than 13 decades. As the focus of these studies has shifted through this time, the site has provided important insights into the evolution of paleontology as a science from its beginnings in the nineteenth century through its subsequent development. Early studies focused on the description of new taxa from collections that were being made by the early scientific surveys of the American West, particularly the Hayden Survey during the early 1870s and an expedition from Princeton in 1877. The first studies and descriptions of these fossils were by Leo Lesquereux on the fossil plants, S.H. Scudder on the fossil insects, and E.D. Cope on the fossil vertebrates. At the beginning of the twentieth century, T.D.A. Cockerell conducted field expeditions in 1906–1908, and subsequently published ~130 papers on fossil plants, insects, and mollusks. Work by these early researchers was the first to consider the implications of the Florissant fossils for evolution, extinction, biogeography, and paleoclimate. Even greater emphasis on these broader implications began when H.D. MacGinitie made excavations during 1936–1937 and published a comprehensive monograph on the fossil flora in 1953, including numerous taxonomic revisions and detailed interpretations of stratigraphic context, paleoecology, paleoclimate, paleoelevation, biogeography, and taphonomy. Other workers during the late 1900s initiated the first studies on pollen, dicotyledonous woods, and multiple organ reconstructions of extinct plant genera, and developed more quantified methods for determining paleoelevation and paleoclimate. Current work emphasizes plant-insect interactions, the use of diatoms as fresh-water paleoenvironmental indicators and as agents in macrofossil taphonomy, and the use of insects as terrestrial environmental indicators.

Keywords: history of paleontology, Florissant, S.H. Scudder, T.D.A. Cockerell, L. Lesquereux, H.D. MacGinitie.

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INTRODUCTION

The history of paleontology and geology at Florissant reported in this paper begins with the earliest contributions that resulted from the government-sponsored geological surveys of the 1870s and concludes with current research. These contributions include ~500 publications that span an array of topics ranging from taxonomic studies of fossil plants, insects, spiders, and vertebrates, to studies of paleoecology, paleoclimatology, and paleoelevation, to studies that describe the geology and stratigraphy of the area. Some of the most recent studies that reflect the dynamic, ongoing nature of scientific investigation at Florissant are published as contributions in the current volume.

Evident within this history of 135 years is the evolution in both the concepts and methodologies of paleontology. Because Florissant was known so early and studied so intensively over such a long period, it has been a key site for providing some of the insights on the evolution of paleontology as a science. Florissant captured attention during the period of early scientific discovery in the American West. Fossils collected by early scientific parties stimulated a period of descriptive taxonomy resulting in the description of hundreds of new species. During the latter half of the twentieth century, studies of Florissant paleontology culminated with the application of multidisciplinary approaches to understanding such topics as paleoclimate, community evolution, multiple organ reconstructions of extinct genera, taphonomic processes in sedimentation, and the tectonic history of the southern Rocky Mountains.

The discovery of the Florissant fossil beds and the early paleontological work that followed occurred during a time of revolution in the earth sciences. It was during this period of the nineteenth century that geology became a major science and paleontology emerged as one of the important early disciplines of geology. Interest and research in fossils thrived as exciting fossil discoveries were made in Europe and North America, giving birth to new ideas and key scientific concepts, including the immensity of geological time, the certainty of extinction, and the recognition that organisms evolve through time.

During the late eighteenth century, geologists debated the age of the Earth. It was, however, during the early part of the nineteenth century that a sense of an older Earth emerged with the work of James Hutton (1726–1797) and Charles Lyell (1797–1875). This concept of a much older Earth was one of geology's first revolutionary contributions to science. Toward the close of the eighteenth century, Georges Cuvier (1769–1832), the brilliant French anatomist, emphasized the existence of extinctions and used fossils to understand the history of the Earth (Faul and Faul, 1983).

During the early part of the nineteenth century, fossils began to be recognized as the remains of species that no longer existed and of organisms that had changed over time. Just 14 years before the Hayden Survey brought scientific recognition to Florissant, the *Origin of Species* was published by Charles Darwin in 1859. Darwin realized that large spans of time evident in the fossil record indicated that there was sufficient time for evolution to take place, and that the fossil record provided the evidence that organisms change through time.

The science of paleontology was established during this century, captivating both scholarly and public interest by revealing prehistoric worlds. Paleontological expeditions began to explore a variety of regions in North America, and new museums were built to house the newly discovered fossils. Museums entertained and educated a public fascinated by this distant past.

In 1842, Sir Richard Owen described and named the Dinosauria. Remarkable dinosaur discoveries during the 1870s in the American West, including sites just 40 km south of Florissant, started the so-called bone wars between Edward Drinker Cope and Othniel Charles Marsh (Wallace, 1999; Jaffe, 2000). Their fossil discoveries captured the imagination of the American public.

Florissant fossils became widely recognized and made significant contributions to paleontology beginning in the second half of the nineteenth century. These fossils inspired early investigators to think about paleoclimates and paleoecosystems. Lesquereux was a pioneer who worked on Cretaceous and Tertiary floras of the western states and territories, marking the beginning of Tertiary paleobotany in North America. Florissant emerged as one of the world's most important sites for fossil insects beginning with the work of Scudder, whose monographs on Florissant helped to establish the foundation for paleoentomology in North America.

By the late 1860s, regional newspapers had mentioned Florissant's fossils. The *Daily Central City Register* (April 18, 1871) reported "about a mile from Castello's ranch in Florissant Valley, is a petrified forest near which are found, between sedimentary layers, the most beautiful imprints of leaves differing entirely from any that grow in the valley now-a-days." It was Theodore L. Mead (1852–1936), a 19-year-old college student at Cornell, who made the first collections known to be available for scientific investigation. Mead went on a butterfly collecting trip to Colorado in 1871 when he heard about fossil insects and petrified stumps near Castello's ranch (later Florissant) and decided to investigate the site (Brown, 1996). In a letter to George M. Dodge dated October 1, 1871, Mead described his Florissant excursion: "Visited some petrified stumps thirty miles from our stopping place and beside the wood secured about 20 fossil insects from the shale nearby. They were mostly Diptera and Hymenoptera" (Brown, 1996, p. 66).

The purpose of this paper is to show how the fossils of Florissant and the scientists who studied them have contributed to the science of paleontology and have changed our understanding of evolution, extinction, paleoecology, paleoclimates, paleoelevation, taphonomy, and a variety of geological processes. More recent research at Florissant is mentioned in this paper and is included in this volume.

The contributors to Florissant paleontology are too numerous to mention all of them. A complete bibliography of all works citing Florissant specimens is provided by Meyer (2003). Here we emphasize in particular the biographies of four workers whom we consider to have made the most significant historic contributions in terms of the number of species described, the number of publications produced, and/or their application of Florissant to broader perspectives in paleontology: Leo Lesquereux, Samuel H. Scudder, T.D.A. Cockerell, and Harry D. MacGinitie. Briefer biographical sketches of others whose work significantly advanced the understanding of Florissant are also included.

GEOLOGICAL SURVEY OF THE TERRITORIES: THE CORNUCOPIA OF NEW SPECIES FROM FLORISSANT

Industrialization of the United States during the Civil War made enormous demands on the country's natural resources, including an increasing need for coal. Following the war, the federal government launched an effort to explore and map the West in order to determine how much of it could be settled and farmed. Realizing that science could help support these economic objectives, on March 2, 1867, Congress authorized explorations to investigate the geology, topography, and natural resources of the West. These federally sponsored expeditions between 1867 and 1879 became known as the "Four Great Western Surveys" (Faul and Faul, 1983). They differed from the pre–Civil War state surveys by including more civilian specialists and scientists, publishing comprehensive scientific reports, and utilizing photography. The King Survey explored a 100-hundred-mile-wide area along the 40th parallel, the Hayden expedition explored Nebraska and the Rocky Mountains, the Powell Expedition explored the geology of the Grand Canyon and the canyons of the Colorado Plateau, and the Wheeler Expedition mapped and explored the area west of the 100th meridian.

Hayden's Survey of the Territories

Under the direction of Dr. Ferdinand Vandeveer Hayden, the Hayden Survey conducted the first scientific exploration of the Florissant area in 1873. Hayden's expedition was later known as the "Geological and Geographical Survey of the Territories." The Hayden Survey included paleontological work, and the fossils discovered were described in 12 volumes (published between 1873 and 1890) by some of the best American paleontologists of the time (Faul and Faul, 1983). Vertebrate fossils were studied by Joseph Leidy and Edward Drinker Cope. Leo Charles Lesquereux described fossil plants and Samuel Hubbard Scudder described fossil insects.

Albert Charles Peale (1849–1914), a geologist and medical doctor who worked as a member of the Hayden Survey, was exploring South Park in Colorado in 1873 when he rode into the Florissant valley. In his 1874 report he mentioned the fossil beds: "around the settlement of Florissant is an irregular basin filled with modern [sic] lake deposits. The entire basin is not more than 5 miles in diameter… Just below Florissant, on the north side of the road, are bluffs not over 50 ft in height, in which are good exposures of the beds… About one mile south of Florissant, at the base of a small hill of sandstone, capped with conglomerate, are 20 or 30 stumps of silicified wood. This locality has been called 'Petrified Stumps' by the people in the vicinity" (Peale, 1874, p. 210). While waiting for dinner, Peale walked around the camp area and found a fossil leaf, which led to more discoveries of fossils (Cockerell, 1927).

The Princeton Scientific Expedition of 1877

Three students from Princeton University (then the College of New Jersey)—William Berryman Scott, Henry Fairfield Osborn, and Frank Speir Jr.—organized a student expedition in 1877 to the American West to search for vertebrate fossils. These students went on to prominent careers: Scott taught geology at Princeton from 1880 to 1930, Osborn was with the American Museum of Natural History for over 45 years, including a long tenure as President during which he sponsored the Roy Chapman Andrews Expeditions, and Speir practiced law but continued his participation in later fossil-collecting trips supported by Princeton.

Known as the Princeton Scientific Expedition of 1877, the principal destinations were Colorado, Wyoming, and Utah. On June 21, 1877, the Princeton Scientific Expedition, composed of 18 students, two professors, and two Princeton employees, left New Jersey for the West. After arriving in Denver four days later, the students spent time buying equipment, wagons, mule teams, and Indian ponies (Veatch, 2003).

On Wednesday, July 11, 1877, the Princeton Expedition arrived at the fossil beds and later that day wrote in their journal: "We camped at Florissant —Judge Castello's. In the morning we set to work, all the department finding something to do … Dr. Brackett with Scott, Osborn, and Potter paid Mrs. Hill a visit and gained quite a lot of fossils, bugs, leaves, etc. Lynde and Speir worked at the fish beds discovered the day before. The fruit of the labor of the day was shared in the evening along with the mineralogists spoil. A few petrified wood pieces were found in a gully … and some pretty specimens of chalcedony were the afternoon's spoil. The old Judge was quite a character and by his kindness our stay at Florissant was rendered pleasant as well as profitable" (Princeton Scientific Expedition, 1877, box 1, folder 7).

The students spent two days acquiring some of the most impressive fossils to come from Florissant. At least 180 of the plant and insect fossils became type specimens (Veatch, 2003). Osborn, Scott, and Speir (1878) later described several fish specimens collected at Florissant, including the new species *Trichophanes copei*. The Princeton Scientific Expedition sent the fossil insects to Samuel Scudder and the fossil plants to Leo Lesquereux for description.

The students also made arrangements with Charlotte Hill, a local landowner, to send additional fossils to Princeton (Scott, 1939). Charlotte and Adam Hill lived near the "Big Stump," the petrified base of a *Sequoia* stump that had survived early exploitation. The 1870 census (U.S. Bureau of the Census, 1870, p. 1, lines 13–17) showed Adam Hill as a carpenter. Apparently the Princeton Scientific Expedition of 1877 prompted Charlotte and Adam Hill to supply many quality specimens to the early investigators of the Florissant fossil beds as a side business. The evidence for this comes from the 1880 census, which showed that Adam Hill had changed occupations to become a specimen collector (U.S. Bureau of the Census, 1880, p. 42, lines 16–21).

The Princeton Expedition collections were transferred in 1985 from Princeton University to the Smithsonian's National Museum of Natural History and the Peabody Museum of Natural History at Yale (Meyer, 2003). Several specimens are in the Natural History Museum in London.

Leo Lesquereux (1806–1889)

Lesquereux immigrated to America from Switzerland in 1847 (Faul and Faul, 1983) (Fig. 1). He was 41 years old, deaf, and could not speak English when he arrived in Boston with his wife and five children (Andrews, 1980). Lesquereux once spoke of his deafness during an interview, as noted by Lang (1994): "My associations have been almost entirely of a scientific nature. My deafness cut me off from everything that lay outside of science. I have lived with Nature, the rocks, the trees, the flowers. They know me, I know them…" After Lesquereux arrived in Boston he worked for Louis Agassiz classifying plants that Agassiz collected from Lake Superior (Orton, 1890). In 1848 he moved to Columbus, Ohio, to work on mosses at the invitation of bryologist William Sullivant (Andrews, 1980).

Figure 1. Leo Lesquereux. Courtesy of the American Philosophical Society, Philadelphia.

Lesquereux never obtained permanent scientific employment and supported himself as a watchmaker in Columbus (Lesley, 1985). He worked part-time as a paleobotanist identifying and describing specimens that were collected by state and federal government scientific surveys (Faul and Faul, 1983). His first studies were of the Carboniferous flora of Pennsylvania, and his growing reputation as a leading authority on fossil plants brought him work from other state geological surveys (Andrews, 1980).

Hayden had contracted with Lesquereux to work on fossil plants because Lesquereux was one of the few scientists who had experience with American Tertiary plants. Although there is no documentation that he ever collected at Florissant, Lesquereux did travel in 1872 under the Hayden Survey to various coal deposits, including Marshall and Golden in the Denver Basin, Colorado Springs, and Cañon City (Ewan and Ewan, 1981).

Lesquereux was the first to name Florissant's fossil plants, and he described more than 100 new species (Meyer, 2003). Lesquereux produced the first scientific paper about Florissant (Lesquereux, 1873) and also published lengthy monographs that included the fossil plants of Florissant (Lesquereux, 1878 and 1883). Lesquereux's (1883) monograph described many new plant species based on S.H. Scudder's specimens purchased from Charlotte Hill and on a rather large collection of specimens obtained by the Princeton Scientific Expedition of 1877. Lesquereux named many new species from the Princeton Expedition collection for the student members of that party.

Most of the previous paleobotanical literature available to Lesquereux dealt with European fossil plants, because little was known about American paleobotany during this time. Lesquereux assigned many of the Florissant plants to fossil species that had been described by Swiss paleobotanist Oswald Heer, French paleobotanist Louis Sapporta, and Austrian paleobotanists Franz Unger and Constantin von Ettingshausen. He also described many new fossil species based on comparisons to modern plants from various regions of the world. Most of his published collections are at the Smithsonian's National Museum of Natural History (Meyer, 2003). Lesquereux is considered one of the founders of paleobotany in North America (Andrews, 1980).

Samuel H. Scudder (1837–1911)

Samuel Scudder began his work at the Florissant fossil beds a few weeks after the Princeton Scientific Expedition had left. Scudder was a pioneering paleoentomologist and leading figure in American entomology in the mid- to late nineteenth century (Fig. 2). Born in Boston, Massachusetts, Scudder received an

Figure 2. Samuel H. Scudder. Courtesy of the Archives of the Ernst Mayr Library of the Museum of Comparative Zoology, Harvard University.

A.B. degree in 1857 and an A.M. degree in 1860 from Williams College. He received a B.S. degree in 1862 from Harvard's Lawrence Scientific School where he studied with the great naturalist Louis Agassiz (Mayor, 1924), and he remained at Harvard for an additional two years as an assistant to Agassiz. He was later awarded an honorary D.Sc. degree in 1890 from Williams College and an honorary Doctor of Laws degree in 1890 from the Western University of Pennsylvania.

From 1864 to 1870 Scudder held several positions at the Boston Society of Natural History, an organization with which he had a long-term affiliation, and in 1874 he founded the Cambridge Entomological Club and its journal *Psyche* (derived from the Greek word for butterfly). For 13 years, the regular meetings of the Cambridge Entomological Club were held in a building in the yard of Scudder's residence at 156 Brattle Street, Cambridge (Morse, 1911). This building, with a knocker in the shape of a locust on the door, housed his library, collections, a study area, and a well-equipped laboratory (Morse, 1911).

Scudder's interest in library administration earned him an appointment as the assistant librarian at Harvard University from 1879 to 1882. He was the editor of the journal *Science* from 1883 to 1886. From 1886 to 1892 Scudder was a paleontologist with the U.S. Geological Survey, where he specialized in fossil insects, particularly those from the Tertiary fossil beds of the Rocky Mountains (Kingsley, 1911). Scudder also worked on fossil insects from other North American and worldwide locations (Scudder, 1890a, 1890b) and published an important index to the known fossil insects of the world (Scudder, 1891). These works provided Scudder with a thorough understanding of fossil insects and living.

Scudder was the author of 791 papers between 1858 and 1902 on a wide range of topics such as fossil insects, spiders, and myriapods, paleobiogeography, insect behavior, insect herbivory, geology, trace fossils, and evolution (Easterday, 2002). His studies at Florissant influenced his thinking in some of these broader topics. Scudder became very interested in fossils from Florissant, and using specimens obtained by other collectors, he began publishing papers on Florissant in 1876.

Scudder arrived at the fossil beds on August 19, 1877, with F.C. Bowditch from Boston and Arthur Lakes from Golden, soon after the Princeton students had left (Kohl and McIntosh, 1997). Bowditch was interested in beetles, and Arthur Lakes taught at the mining school in Golden (which later became the Colorado School of Mines) and made many important discoveries of dinosaur fossils in the American West.

Scudder collected fossils at Florissant for five days (Scudder, 1881) and reported: "Our examination of the deposits of this lacustrine basin was principally made in a small hill, from which perhaps the largest number of fossils have been taken, lying just south of the house of Mr. Adam Hill, now owned by Mr. Thompson and upon his ranch" (Scudder, 1890b, p. 21). Arthur Lakes wrote in his expedition journal: "Prof. Scudder went over to Hill's ranch to see about some fossil insects Mrs. H. had been collecting for him. Prof Scudder came back at dinner time laden with spoils reporting that Mr. H had boxes full of fine paper like shales covered with the impressions of most perfect insects of various descriptions taken from the sedimentary Miocene tablelands or mesas near their ranch" (Kohl and McIntosh, p. 48–49).

Scudder collected near the large petrified stump (currently known as the Big Stump) near Adam and Charlotte Hill's homestead. This is also where Scudder measured the first detailed stratigraphic section of the lake deposits near Big Stump (Meyer, 2003, Fig. 7). According to Scudder, "At the opposite sloping end of this mesa a trench was dug from top to bottom to determine the character of the different layers, and the section exposed was carefully measured and studied" (Scudder, 1890b, p. 21).

The geology of the Florissant area was first mapped by Arthur Lakes, while he was at Florissant with Scudder in 1877. Lakes later produced a watercolor map in 1878 entitled "Map of sedimentary lacustrine basin at Florissant near South Park, supposed to be Upper Miocene" (illustrated by Meyer, 2003, Fig. 8; original copy in collection of Florissant Fossil Beds National Monument, FLFO-1013). This map showed the location of fossiliferous beds; informal rock units including granite, volcanic lavas, and Miocene sediment; and settlements such as the houses of Castello and Hill. The combination of Lakes's map and Scudder's stratigraphic section provided both the first descriptive study of the geology of Florissant and a paleogeographic reconstruction of the ancient lake. Scudder returned to Florissant again in 1881 or 1882 (judging from a photograph his son took near Big Stump when he was age 12) and again in 1889 (Meyer, 2003).

Scudder described fossil insects for the Hayden expedition and published many important papers on Florissant. His monograph *The Tertiary Insects of North America* (Scudder, 1890b) included a classic study of the insect fauna from Florissant in which many new species of fossil insects were described. It took him a number of years to complete the monograph, which was finally published three years after Hayden's death. Scudder noted: "the material had grown beyond all expectations, far beyond anything that could have been anticipated" (Scudder, 1890b, p. 11). Among the species he described is *Prodryas persephone* (Scudder, 1878), regarded as one of the finest fossil butterfly specimens known (Fig. 3). Butterflies are extremely rare in the fossil record, and over the years Florissant has yielded 12 species, more than any other fossil insect site (Grimaldi and Engel, 2005). Scudder's later publications focused on the description of 75 fossil beetles from Florissant (Scudder, 1893, 1900). Overall, Scudder described ~600 species from Florissant and wrote 23 papers, an overwhelming task (Meyer, 2003). Because of Scudder's descriptions Florissant emerged as one of the world's important Tertiary insect sites and one of the first major fossil insect sites to be studied in North America (Grimaldi and Engel, 2005).

In addition to his descriptions of fossil insects from the Florissant fossil beds, Scudder considered that these fossils indicated a warmer climate, "a climate which may, perhaps, best be compared to the middle zone of our Southern States, the known living species of the genera to which they belong are in general credited to regions like Georgia in this country and the two shores of the Mediterranean in Europe, or even more southern districts" (Scudder, 1890b p. 34–53). Thus, Scudder was the first to use the Florissant insect fauna to interpret Florissant's paleoclimate.

During the 1800s, systematic descriptions of fossil insects were made largely by geologists, paleontologists, and entomologists. Their studies generally focused on fossil insect assemblages from a particular site. Scudder was the first American scientist to combine these approaches into the specialized subdiscipline of paleoentomology. Scudder's contributions to paleontology were enormous. He wrote about the evolution and paleobiogeography of fossil insects, arachnids, and myriapods. His work helped transform paleoentomology from scattered observations into a branch of science, and prepared a base for its development. Most of Scudder's published specimens are at the Harvard University Museum of Comparative Zoology (Meyer, 2003). With 8000 specimens, this is the second largest Florissant collection, consisting mostly of spiders and insects.

Other Nineteenth-Century Workers at Florissant

Other early scientists worked on Florissant's fossils and made important contributions. E.D. Cope (1874, 1875, 1878, 1882, 1883) described fossil fish and a shorebird from the lake shales at Florissant. From 1871 to 1877 Cope conducted paleontological expeditions that included Kansas, Wyoming, and Colorado. Cope's intense competition with O.C. Marsh for vertebrate fossil discoveries turned into a bitter fossil feud that became known as the "Bone Wars" (Jaffe, 2000).

Walter Charles George Kirchner, a St. Louis surgeon, published a summary listing of 213 species of Florissant plants (Kirchner, 1898). He described 12 new species based on the large collection made at Florissant by Dr. Gustav Hambach, a paleontologist with the St. Louis Academy of Science (Cockerell, 1908c).

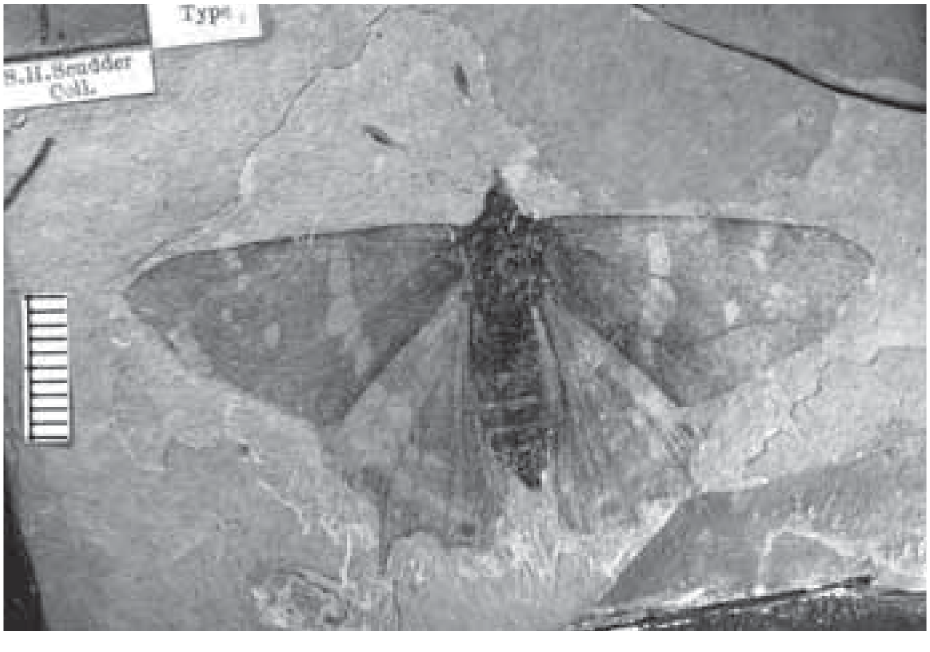

Figure 3. *Prodryas persephone*. Specimen MCZ-1, courtesy of the Museum of Comparative Zoology, Harvard University.

Lesquereux, Scudder, and members of the Princeton Scientific Expedition had made Florissant—a place unknown even to most people of Colorado at that time—famous in the paleontological literature. After this period of initial activity, interest in Florissant diminished near the close of the nineteenth century. Lesquereux had died and Scudder had retired from his work because of illness. By the time Scudder died from Parkinson's disease in 1911 (Cockerell, 1927), he had been unable to describe all the materials from Florissant that he had accumulated. Scientific collecting of the fossil beds ceased, and "it was supposed that the beds had been practically exhausted and that little of importance remained to be done" (Cockerell, 1927, p. 11). Many of the specimens already collected were left with museums and colleges or sat in cabinets, ignored.

EARLY-TWENTIETH-CENTURY SCIENTISTS STUDY FLORISSANT'S FOSSILS

Theodore Dru Allison Cockerell (1866–1948)

Twentieth-century studies of the Florissant fossil beds began in earnest with T.D.A. Cockerell (1866–1948; Fig. 4), who organized expeditions from 1906 through 1908. Cockerell was a highly regarded professor at the University of Colorado, where he taught entomology and zoology for most of his career. An expert on bees in particular, he was also regarded as an authority on fossils, other insects, roses, and sunflowers. Cockerell became one of the most influential contributors to the scientific study of Florissant (Weber, 2000).

Born in Norwood, England, a suburb of London (Surrey), Cockerell was 21 when he first came to Westcliffe, Colorado, in search of a better climate to recover from a mild case of tuberculosis (Weber, 2000). He learned of the Florissant fossil beds through Scudder's work. In a letter written in 1887 to Annie Fenn (the woman he later married, in 1891), Cockerell wrote, "I was taking notes today from Scudder's paper on fossil insects. He gives a graphic description of the place (Florissant) where they are found. It is near Pikes Peak. It is most strange and fascinating to read all about it" (Weber, 1976, p. 163).

Cockerell did not actually visit Florissant during his initial stay in Colorado. After three years in Westcliffe he returned to England in 1890. In 1903 Cockerell returned to Colorado and the following year moved to Boulder to join the faculty of the University of Colorado (Weber, 2000). According to Weber (2000, p. 1) although "he never attended college nor did he receive an earned degree … he was devoted to doing research and teaching."

Junius Henderson and Francis Ramaley of the University of Colorado initiated the university's first interest in Florissant during a field visit in 1905. During the following three summers, 1906 to 1908, Cockerell revived excavations at Florissant. The 1906 summer fieldwork included William Morton Wheeler (1865–1937), a zoologist and well-known specialist on ants from the American Museum of Natural History; Cockerell and his second wife, Wilmatte (1871–1957), a naturalist and teacher; and 20-year-old Sievert Allen Rohwer (1888–1951), who later become an important entomologist (Cockerell, 1908c).

Figure 4. T.D.A. Cockerell. Photograph courtesy of the T.D.A. Cockerell Collection, Archives, University of Colorado at Boulder.

Cockerell describes his wife's discovery of a fossil butterfly during the 1906 fieldwork: "For a long time our luck … failed [and] our most productive diggings produced no butterflies. One day the lunch was forgotten, and the party strolled toward the village [Florissant], taking a somewhat unusual path. A little of the shale was seen sticking out on a hillside north of the sawmill, and Mrs. Cockerell sat down and turned over a piece. There was the long desired butterfly, a beautiful specimen showing the spots! It proved to be a new species, and was named *Chlorippe wilmattae*, after its discoverer. Many times we returned to that place, but without any success" (Cockerell, 1927, p. 14).

In 1907 the Cockerells continued their large-scale excavation at the fossil beds. Sievert Allen Rohwer returned for another summer, along with his brother, George N. Rohwer, who was Cockerell's graduate student (Ewan and Ewan, 1981). This excavation was supported by the University of Colorado, the American Museum of Natural History, Yale University, and the

British Museum. “As a result, there has accumulated an almost embarrassing amount of material, and many remarkable things have been discovered” (Cockerell, 1908c, p. 115). One of these remarkable discoveries was when “George N. Rohwer found a very good specimen of a tsetse fly, showing the proboscis” (Cockerell, 1927, p.12). The tsetse flies were, to Cockerell, the most interesting specimens from Florissant: “They were totally unexpected at Florissant, and when the first one, unfortunately headless, fell into the hands of Scudder, he described it as a member of the Estridae, the family of bot-flies and warble-flies. In 1907 Mr. Geo. N. Rohwer found a good specimen, showing the proboscis, and there was little difficulty in determining its true identity. Such a surprising discovery was naturally met with some incredulity, but every expert who has examined the specimens has been obliged to admit the correctness of the identification. In 1909 a second pair was found, and in 1916 two more, so that we now have four species in all” (Cockerell, 1927, p. 13). Today, two of these are still recognized as valid species (Evenhuis, 1994; Grimaldi, 1992). Fossil tsetse flies from Florissant are twice the size of living species, which are confined to Africa (Fig. 5).

Figure 5. The tsetse fly *Glossina oligocenus*. Specimen AMNH-FI-45416, courtesy of the American Museum of Natural History.

Specimens from Cockerell’s expeditions of 1906 through 1908 are at the University of Colorado, the American Museum of Natural History, the Natural History Museum, London (formerly British Museum of Natural History), Yale University, the National Museum of Natural History (Smithsonian), and a few scattered elsewhere. Many of the fossils Cockerell collected from the Florissant shales consist of two corresponding halves; one of Cockerell’s common practices was to retain one of these halves for the University of Colorado and send the counterparts of these same specimens to other institutions. Most of the University of Colorado’s Florissant collection of more than 5550 specimens of plants, insects, and vertebrates came from Cockerell’s expeditions of 1906–1908.

Cockerell was the first to fully document collecting sites and localities at Florissant during his 1906 expedition (Cockerell, 1907). He listed 16 stations including the graveyard, a gully southeast of Florissant, a railroad cut, the “north end of Fossil Stump Hill,” and his most productive “station 14” southwest of Florissant. Although such information is very important for understanding the context of fossils, few of the other collectors of the late 1800s and early 1900s recorded their actual collecting sites.

Between 1906 and 1941, Cockerell published 140 papers on Florissant fossils (e.g., Cockerell, 1906, 1908a, 1908b, 1908c), more individual contributions than any other paleontologist has written about the site. Collaborating with scientists elsewhere in the United States and England, Cockerell extended his work beyond Florissant. He published his work quickly and often his publications were short, sometimes less than a page. During his career, Cockerell published ~4000 papers, including memoirs, plays, poetry, and essays on scientific, social, and educational issues (Weber, 2000).

Cockerell’s prolific publication is only part of his contribution to Florissant. He brought scientific attention to Florissant, engaged students in fieldwork, and encouraged other scientists to work there. Cockerell also revived scientific fieldwork, which had slowed for a number of years following Lesquereux and Scudder.

Other Early Contributors to the Scientific Study of Florissant

Henry Frederick Wickham (1866–1933) was an entomologist who specialized in Coleoptera (beetles). Born in Shrewton, England, Wickham arrived in Iowa in 1871 and earned an M.S. from the University of Iowa in 1894, after which he was appointed professor of zoology and entomology there (Ewan and Ewan, 1981).

Wickham was with the U.S. Bureau of Entomology for a number of summers and made many large collections in the American West, including Florissant and other sites in Colorado. Cockerell noted that “in 1912 … Wickham … dug a trench about 20 feet long and six feet deep. Out of it he got over 90 species of beetles, of which more than 40 were new to science” (Cockerell, 1927, p. 14). Between 1908 and 1920 Wickham published 15 studies on Florissant fossil beetles. He described at least 239 species of fossil beetles from Florissant, including the unworked portions of Scudder's collections and fossil beetles from Cockerell's expeditions to Florissant, but many of these identifications remain doubtful (Carpenter, 1992). Most of Wickham's beetle specimens from Florissant are at the Smithsonian's National Museum of Natural History.

The entomologist C.T. Brues (1879–1955) worked on fossil bees and wasps from Florissant from 1906 through 1910. Brues was born in Wheeling, West Virginia. He received an A.B. degree in 1901 and an M.S. in 1902 from the University of Texas. He was with the U.S. Department of Agriculture from 1904 to 1905 and was the curator of invertebrate zoology at the Milwaukee Public Museum from 1905 to 1909. Brues was later a professor of economic entomology at Harvard from 1909 until 1945. He spent considerable time in the field and conducted collecting expeditions for modern insects to Jamaica, Peru, Ecuador, Cuba, and the East Indies. Brues produced six publications on Florissant fossils—five of which dealt with Hymenoptera and one on a grass. He was particularly interested in the parasitic Hymenoptera from Florissant.

Frank Hall Knowlton (1860–1926) was a paleobotanist who made contributions to the fossil floras not only at Florissant (Knowlton, 1916) but also at John Day (Knowlton, 1902), Green River (Knowlton, 1923a), and Creede (Knowlton, 1923b). These other floras are important for understanding Florissant in the broader context of floral evolution in western North America and provided Knowlton with a broad exposure to western Tertiary floras. While Knowlton was acting as the custodian of Mesozoic plants at the U.S. National Museum (Smithsonian), he published on Florissant fossil plants in 1916. The purpose of his work was to place "on record the studies of a number of collections not previously investigated, or only partially studied … and to include practically all of the plant material from Florissant now deposited in the Untied States National Museum" (Knowlton, 1916, p. 241).

The Florissant collections that Knowlton studied included (1) the Hambach collection, which included the Florissant plants described by Kirchner; (2) the Scudder plant collection of ~150 specimens from the Hayden survey; (3) the Lacoe collection acquired by the U.S. National Museum in 1893 from Ralph Dupuy Lacoe of Pittston, Pennsylvania, including plant specimens studied and named by Leo Lesquereux (1883); (4) the old National Museum collections (Smithsonian) that had been collected during the Hayden survey and were originally examined by Lesquereux; and (5) the collection made by Knowlton and Edward W. Berry, also a paleobotanist, when they spent several days at Florissant in 1913 (Knowlton, 1916).

DECIPHERING THE BIG PICTURE: CONTRIBUTIONS TO UNDERSTANDING ECOLOGY, CLIMATE, ELEVATION, BIOGEOGRAPHY, AND EVOLUTION

The major emphasis of the earlier studies at Florissant through Cockerell's time was to describe the vast taxonomic diversity of new species of plants and insects. About 260 species of plants and more than 1300 species of insects and spiders had been described through 1930, yet the validity of many of these identifications remained questionable, as it still is today for many of the insect taxa and some of the plants.

Harry D. MacGinitie (1896–1987)

The approach to paleobotanical investigations at Florissant underwent a fundamental change beginning with the work of Harry D. MacGinitie. This change was stimulated in part by larger collections from Florissant, new studies on other localities in western North America with which Florissant could be compared, development of more rigorous methods for evaluating taxonomic assignments, and greater focus on interdisciplinary applications of geology, taxonomy, ecology, biogeography, and climatology.

MacGinitie was a paleobotanist who received his Ph.D. in 1935 from the University of California at Berkeley, where he had studied under the well-known paleobotanist Ralph W. Chaney. Beginning in 1928, and for 32 years (although interrupted), he taught natural sciences at Humboldt State College in northern California. Once retired, he moved to Napa, California, and remained active as a Research Associate at the University of California Museum of Paleontology in Berkeley; during that time he was one of the mentors to the second author of this paper. Early in his career, MacGinitie taught briefly at the University of Colorado, where he was encouraged by Cockerell and by Childs Frick of the American Museum of Natural History to undertake new excavations at Florissant and to revise some of the earlier taxonomic work on the fossil plants.

MacGinitie excavated three new sites at Florissant in 1936 and 1937 (MacGinitie, 1953). His technique involved using a horse and plow to remove the overburden and create quarries. The Florissant shales are quickly weathered in surface exposures, and the quarrying technique allowed for the removal of larger slabs that were then split with a butcher knife to obtain relatively large, complete specimens of leaves and fruits (Fig. 6). It was a labor-intensive effort, and although Florissant is often popularly regarded as a site at which fossils are very abundant, MacGinitie (1953) noted that "more labor is required to obtain a given number of specimens than at any other fossil plant locality the writer has visited." This comparison followed his extensive work at other important fossil sites, as noted below. MacGinitie's culminating work on Florissant was a monograph entitled *Fossil Plants of the Florissant Beds, Colorado*, which was published in 1953, 17 years after his work at Florissant began. This long of period of study was due in part to the interruptions of World War II, during which time MacGinitie served as an instructor of climatology and meteorology in the U.S. Army Air Corps (Wolfe, 1987).

In contrast to Cockerell's approach of publishing numerous, very short, isolated papers about specific plant and insect taxa from Florissant, MacGinitie's 1953 monograph was a single, comprehensive summary that embodied the entirety of the fossil flora and discussed its implications to understanding plant

Figure 6. Harry D. MacGinitie collecting at Florissant ca. 1936–37. The excavation was accomplished by quarrying and splitting the shales with a hammer and large butcher knife. Photo and original negative in the archival collection at Florissant Fossil Beds National Monument (FLFO-1016); also illustrated by MacGinitie (1953, Fig. 2).

geography and paleoecology. This monographic approach, although less common today, was one that MacGinitie used in most of his published contributions, which also included the Trout Creek flora of Oregon (MacGinitie, 1933), the Weaverville flora of California (MacGinitie, 1937), the Chalk Bluffs flora of California (MacGinitie, 1941), the Kilgore flora of Nebraska (MacGinitie, 1962), the Green River flora of Colorado and Utah (MacGinitie, 1969), and the Kisinger Lakes flora of Wyoming (MacGinitie, 1974). These various comprehensive treatments by MacGinitie, including the Florissant monograph, are among the highest-quality contributions to American Tertiary paleobotany during the twentieth century.

MacGinitie (1953) was the first to examine closely the basis for making valid taxonomic determinations of Florissant's fossil leaves and fruits. He paid critical attention to characters of leaf architecture and made careful comparisons of the fossil material with herbarium specimens of extant species. By reexamining the earlier collections and taxonomic descriptions of previous workers, supplemented by his new collections, he placed many of the former identifications into synonymy. One of the challenges that MacGinitie faced in this regard was that many of the species described by Lesquereux, Cockerell, Kirchner, Knowlton, and others had been based on cursory analysis and often on single fragmentary specimens that lacked unique characters necessary to define those species clearly. Even with his description of ~20 new species, MacGinitie (1953) placed so many previously described species into synonymy that by the time his monograph was completed, it had reduced the number of valid plant species at Florissant from 258 to about half that number. Additional revisions to several genera of fossil plants have been made following the completion of MacGinitie's monograph, particularly by the work of Manchester in recognizing extinct genera, as discussed later. Other identifications made by MacGinitie warrant closer scrutiny as better fossil material of multiple organs becomes available, and as methodologies for understanding classification based on leaf architecture continue to improve.

More significantly, MacGinitie was the first to thoroughly consider some of the broader implications of the Florissant fossil plants and to place them into the context of understanding ecology, climate, elevation, and the dynamic evolution of plant communities through time and space. He accomplished this by comparison with other fossil floras, both older and younger, and by examining the distribution of modern vegetation and presumed similar living species. Although some of his conclusions have been challenged by more recent studies, as discussed later, MacGinitie (1953) derived an estimate for the mean annual temperature of at least 18 °C, and an estimate of 300–900 m for the paleoelevation. Details of the geologic context of the fossils had not been examined closely by previous workers, aside from Scudder's stratigraphic section in the shale and Lakes' preliminary map, and MacGinitie measured and described the stratigraphy and structure of the shales and volcanic rocks that make up the Florissant deposits. By comparing the fossil plants and mammals with those from other sites, he made the first accurate determination for the age of Florissant prior to radiometric dating.

From his observations of the Florissant flora and his comparisons with other fossil floras, MacGinitie developed several significant concepts that pertained not just to Florissant but to the Tertiary history of the flora and vegetation of western North America more generally (Wolfe, 1987). For example, by comparing the similarities between the Florissant and Green River floras, he concluded that lineages could persist in a region by adapting to changing environmental conditions. These two floras represent different climates (Wolfe, 1994), yet some of the taxa are shared. He also noted that there was a bias favoring the preservation of lakeside plants and that this could affect reconstructions of the ancient forest and its environment. In this respect, he was among the first to consider the effects of taphonomy on the preservation of fossil floras. Furthermore, MacGinitie (1953, p. 67) was the first to note the possibility that there had been a rapid and significant floral change (and by inference climate change) during the interval that is now widely recognized as the Eocene-Oligocene transition (Wolfe 1978, 1992b; Prothero, this volume).

MacGinitie visited Florissant once again in 1979, at age 82, hosted by the National Park Service. He was informally interviewed during that visit, and tapes and transcripts of some of these interviews are in the collection at Florissant Fossil Beds National Monument (FLFO Accession 327). During that interview, MacGinitie reflected on the broader context of paleontology and its contribution to our appreciation of the continuity of time. "We get all tangled up with the present. The present is just a little flick in time between the past and the future. Things keep going on and on. We are just in this particular little time interval, and it seems so important to us. But it's part of the *whole* business. And paleontology helps us to see at least what's gone on in the past. It does help solve some problems in the present. There's just no doubt about it."

Additions, Revisions, and Compilations: Another Look at the Fossil Insect Fauna

With more than 1500 species of insects and spiders described from Florissant, it has never been practical to attempt a comprehensive revision for the entire insect fauna in a monograph comparable to MacGinitie's work on the fossil plants. Consequently, the taxonomic validity of many of the early identifications by Scudder, Cockerell, and others remains questionable, and it is uncertain whether a complete revision of the insects and spiders would produce a reduction in number of taxa proportionate to MacGinitie's synonymy of plant taxa. Studies on the fossil insects and spiders since 1930 have concentrated mostly on particular groups. These works have varied from papers specific to Florissant, to those revising the taxonomy of a certain insect group from various fossil sites, to others dealing primarily with living insects but including fossil examples. Examples include work on Diptera (James, 1937, 1939; Hull, 1945; Melander, 1949; Grimaldi, 1992), Hemiptera (Štys and Říha, 1977), Homoptera (aphids) (Heie, 1967), Neuroptera (Adams, 1967), Lepidoptera (Miller and Brown, 1989), and Hymenoptera (Zhelochovtzev and Rasnitsyn, 1972; Rasnitsyn, 1993). Noteworthy among these researchers was A.L. Melander, a well-known dipterist who compiled huge collections of modern insects and produced a treatment of the fossil Diptera from Florissant (Melander, 1949) in which he described 62 new species in a wide variety of families. Some of these papers included aspects of biogeography, evolution, and paleoclimate, incorporating Florissant into a broader perspective.

One of the most prominent paleoentomologists of the twentieth century was Frank M. Carpenter, who spent his career at Harvard University. He once remarked that he had become inspired to work on fossil insects when he saw a picture of the remarkable Florissant specimen of *Prodryas persephone* (Fig. 3), a nymphalid butterfly, when he was young (Brosius,1995). In 1920, as a senior in high school, Carpenter met entomologist W.M. Wheeler, who had collected at Florissant with Cockerell in 1906. Wheeler showed the young Carpenter his first actual specimens of fossil insects, which were fossil ants from Florissant (Brosius, 1995). Fossil ants had been largely overlooked by previous workers, and Carpenter went on to become one of Wheeler's students at Harvard, where he did his dissertation and prepared a monograph on the fossil ants of North America (Carpenter, 1930). As part of this work, Carpenter collected at Florissant in 1927, and in this monograph he described 28 new species from Florissant. Later, he reevaluated earlier descriptions of Florissant Neuroptera (Carpenter, 1935, 1936, 1943). In many of his works, Carpenter considered fossil insects in the broader context of biogeography and evolution.

Before the development of the Florissant database (Meyer et al., this volume), one of the more complete compilations of Florissant insects was in the comprehensive compendium of fossil insects that was prepared for the *Treatise on Invertebrate Paleontology* (Carpenter, 1992).

This was one of Carpenter's major legacies, published shortly before he died. Documenting most of the world's fossil insect genera, this two-volume treatise included listings for 765 genera that had been described from Florissant, making it one of the most referenced sites in this work. Carpenter also noted the need to reevaluate the taxonomic placement for some of these fossils, again emphasizing the nineteenth-century antiquity of many of these identifications.

Recognizing Florissant as a Critical Place in Time: Late-Twentieth-Century Studies in Geochronology, Paleoclimatology, and Paleoelevation

Throughout the long history of its study, Florissant was variously referred to the Pliocene, Miocene, Oligocene, and Eocene (Meyer, 2003). Using the fossil plants and mammals, MacGinitie (1953) determined the age to be early Oligocene, although new studies in the 1980s recalibrated the Eocene-Oligocene boundary (Berggren et al., 1992). This shifted the Chadronian Land Mammal Age (to which Florissant clearly belongs; see Lloyd et al., this volume) from the Oligocene into the Eocene, indicating a latest Eocene age for the site. This change did not pertain to Florissant specifically, but rather was based on the establishment of a new stratotype in Italy that more precisely defined the placement of the Eocene-Oligocene boundary at 33.7–34.0 Ma (Berggren et al., 1992) rather than ca. 38 Ma as had been widely accepted. In addition, new radiometric dates became available for Florissant, defining the age as 34.07 Ma (Evanoff et al., 2001).

Although MacGinitie (1953) had inferred the paleoclimate for Florissant from the distribution of similar living species, Jack A. Wolfe of the U.S. Geological Survey developed a method for estimating mean annual temperature initially by using leaf margin analysis (Wolfe, 1978) and later on a climate-leaf analysis multivariate program ("CLAMP") based on various physiognomic characters of fossil leaves (Wolfe 1994, 1995). From these analyses, Wolfe recognized the significance of rapid floristic, vegetational, and climatic change during the Eocene-Oligocene transition (Wolfe, 1978, 1992b). He showed that fossil floras in western North America provided evidence of rapid cooling of midlatitude mean annual temperature by ~7–8 °C within a period of perhaps less than one million years near the Eocene-Oligocene boundary (Wolfe, 1992b, 1994; see also Leopold et al., this volume; and Prothero, this volume). Applications of Wolfe's methodology to Florissant resulted in cooler temperature estimates than MacGinitie had inferred, ranging from 10.7 to 12.8 °C (Gregory, 1994a, 1994b; Wolfe 1992a, 1994). These temperature analyses, combined with the new radiometric dates from Florissant and other fossil floras, provided compelling evidence that Florissant was positioned at a critical interval in time, immediately preceding the abrupt climatic cooling of the Eocene-Oligocene transition (Wolfe, 1978, 1994; Prothero, this volume).

Another question integral to understanding Florissant's significance to the biogeographic and tectonic history of western North America was to determine paleoelevation. From his qualitative comparison of the Florissant flora with the modern distribution of similar forests, MacGinitie (1953) derived his paleoelevation estimate of 300–900 m. This estimate, which became a "paleobenchmark" in geologic studies concerning Cenozoic uplift in the southern Rocky Mountains, suggested significant late Cenozoic uplift of the region (e.g., Epis and Chapin, 1975). Development of a quantitative paleobotanical basis for determining paleoelevation was the subject of intensive study at Florissant during the 1980s and particularly during the 1990s (Meyer, 1986, 1992; Gregory and Chase, 1992; Gregory, 1994a, 1994b; Gregory and McIntosh, 1996; Wolfe, 1992a, 1994; Wolfe et al., 1998; Forest et al., 1995). Various studies used mean temperatures, lapse rates, and enthalpy to determine the paleoelevation at Florissant, resulting in estimates ranging from 1900 to 4133 m (Table 1; see also Meyer, 2001, for more detailed summary of methods). However, an analysis by Axelrod (1998) continued to argue for a lower paleoelevation of 455 m. The history of these various methodologies was developed more consistently by application to Florissant than any other fossil flora, and hence Florissant has become one of the best places to test any newly developed methodology and compare it with previous results.

The Neglected Fossils: Late-Twentieth-Century Advances

Even though most of the species of fossil leaves, fruits, seeds, and insects had been described by 1930, several important types of fossils, particularly of plant organs, remained unstudied until the 1980s and 1990s. Even among the plants that already had been described, associations of multiple organs of the same plant were still unclear. Entire groups of plant organs, such as pollen and spores and the dicotyledonous woods, had not been studied, nor had the diatoms. Several of these studies were first reported during a symposium on Florissant organized by Emmett Evanoff and Kathryn Gregory for the Rocky Mountain section meeting of the Geological Society of America in 1994, and later were published as a symposium volume by the Denver Museum of Nature & Science (Evanoff et al., 2001).

Steven Manchester developed a critical approach for reconstructing extinct genera from multiple organs, and many important examples of his work focused on Florissant (e.g., Manchester, 1989, 1992, 2001; Manchester and Crane, 1983, 1987). He recognized that some of the plants that previously had been assigned to extant genera were actually extinct. These reconstructions were accomplished by carefully examining the characters of different organs that were diagnostic of particular families, combined in some instances with evidence from fossils that clearly showed the attachment of different organs, such as leaves and fruits. Notable examples include the two most common plants at Florissant, *Fagopsis* and *Cedrelospermum*. Such reconstructions can be challenging in paleobotany because plant organs typically are preserved unattached and isolated in the fossil record.

Although Florissant's palynoflora (pollen and spores) is at least as diverse as the macroflora (leaves, fruits, and seeds), it remained unstudied until the 1980s, when it became the subject

TABLE 1. SUMMARY OF INTERPRETATIONS OF PALEOCLIMATE AND PALEOELEVATION

	Climate MAT (°C)	Paleoelevation (m)	References
MacGinitie	≥18	300–900	MacGinitie (1953)
Meyer	13–14	2450	Meyer (1986, 1992, 2001)
Wolfe	10.7–12.5	2255–4133	Wolfe (1992a, 1992b, 1994); Wolfe et al. (1998)
Gregory	10.7–12.8	1900–3300	Gregory and Chase (1992); Gregory (1994a, 1994b); Gregory and McIntosh (1996)
Axelrod	15.5	455	Axelrod (1998)
Boyle	14.7–15.6	n/a	Boyle et al. (this volume)

Note: MAT—mean annual temperature.

of an unpublished master's thesis (Hascall, 1988). A thorough description of the palynoflora followed in two independent studies, one by Hugh Wingate and Douglas Nichols that provided a detailed description of the palynomorphs and variations in their stratigraphic abundances at Florissant (Wingate and Nichols, 2001), and another by Estella Leopold and Scott Clay-Poole on the taxonomic relationships and ecology based on a comparison of the palynoflora and macroflora (Leopold and Clay-Poole, 2001). Both of these studies provided valuable new insights into aspects of the paleocommunity and paleoecology at Florissant that expanded on the information from MacGinitie's earlier work on the macroflora (MacGinitie, 1953), and in many cases confirmed genera identified by MacGinitie. For example, Leopold and Clay-Poole (2001) recognized 150 types of pollen and spores, corroborating the identification of 23 leaf and fruit genera and adding an additional 25 genera known exclusively from pollen and spores. Wingate and Nichols (2001) used morphotype names whereas Leopold and Clay-Poole (2001) used conventional botanical names for pollen and spores, making it difficult to compare the lists of these workers. Documenting the correspondence of palynomorph taxa with macrofossil taxa is also difficult in many cases. The multitude of taxonomic names for different fossil organs of the same biological plant species complicates estimates of total floral diversity at Florissant, but clearly true taxonomic diversity of the fossil material is substantially less than the totality of described fossil taxa.

The fossil woods from Florissant had long been known from the fossil redwood stumps, assigned to the genus *Sequoioxylon* by Andrews (1936), yet it was not until the work of Elisabeth Wheeler that the presence of hardwoods came to light. Wheeler (2001) described five dicotyledonous woods, one of which represents an extinct type, and she also recognized that the Florissant woods have distinct growth rings and are ring porous, indicating a seasonal climate. Wheeler's work doubled the number of late Eocene woods to be described from North America. Kathryn Gregory-Wodzicki was the first to analyze growth rings in *Sequoioxylon* stumps as the basis for climate reconstruction, a method that had been more widely used in Holocene studies. Gregory-Wodzicki (2001) found high mean ring widths, which were interpreted to indicate a more favorable growing environment than that of the modern coast redwood forest, and she also was able to use growth rings to cross-date the redwood stumps. These studies significantly expanded the knowledge about Florissant's petrified forest and established fossil wood as an additional source of evidence about Florissant's paleoclimate.

CATCHING THE PUBLIC'S EYE: POPULARIZATION AND INTERPRETATION OF FLORISSANT'S PALEONTOLOGICAL HISTORY

Commercial Operation of the Site

By the mid-1870s, Florissant's petrified stumps had become a noted destination for tourists, and with the coming of the Colorado Midland Railway in 1887, a special excursion train brought passengers to collect fossils. Further commercialization of the site followed, and by the 1920s, new petrified stumps had been excavated. Competing landowners developed two adjacent parcels of land as petrified forest tourist attractions. One, operated as the Colorado Petrified Forest, was near the Big Stump, and the old Colorado Midland Railroad station was moved from the town of Florissant to this site where it was used as a lodge. The other site was operated as the Pike Petrified Forest, situated near the Redwood Trio, and the building from that operation is still functioning as the visitor center for Florissant Fossil Beds National Monument in 2008.

During this period of commercial operation, visitors were allowed to collect fossils, and one of the largest of these was collected after Walt Disney visited the Pike Petrified Forest in 1956 and purchased a large stump, which was removed with a crane, shipped to California, and became an exhibit in Frontierland at Disneyland Park (Meyer, 2003). During this period of commercial operation, the site was also visited by paleontologists and by others whose visits would help inspire careers in paleontology. For example, noted paleontologist Stephen Jay Gould visited Florissant on a trip with his parents while he was a young boy during the 1950s (oral commun. to second author, 1995). While growing up in the Pikes Peak region, the first author was inspired by Florissant's fossils to follow a life-long passion in paleontology and eventually earn a degree in the geosciences.

The Florissant Fossil Quarry, opened in the 1950s by the Clare family, is a private fossil collecting site that is still operating today. Several important discoveries in recent years have come from this commercial site. For example, Nancy Clare Anderson found a new species of shorebird in 1997 (Meyer, 2003), and that specimen is now at the Denver Museum of Nature & Science. Other specimens from the site have been donated to Florissant Fossil Beds National Monument, yet as is often the case with casual collecting by the public, most of the finds end up in private collections and are never seen by paleontologists.

Conservation, Protection, and Ongoing Research: Florissant as a National Monument

Despite earlier suggestions that Florissant be preserved as a park, the fossil beds remained in private ownership until after the establishment of Florissant Fossil Beds National Monument in 1969. Conservationists had urged legislation to create the Monument, and congressional bills were under consideration during 1968 and 1969. By 1969, a bill for a 6000-acre park had passed the Senate but was locked up in the House Interior Committee. In May 1969, paleontologists Estella Leopold (Fig. 7) and Harry MacGinitie provided testimony to the U.S. Senate committee that was considering whether to establish the area as a national monument.

In 1968, real estate developers began planning a subdivision of A-frame cabins in the eastern part of the fossil beds. When they learned that a contract had been let for sale, concerned scientists such as Estella Leopold and Beatrice Willard, along with other

Figure 7. Estella Leopold was very influential in the establishment of Florissant Fossil Beds National Monument, and she also made important contributions to the study of fossil pollen from Florissant (Leopold and Clay-Poole, 2001).

citizens, including Vim Wright, formed the Defenders of Florissant in the spring of 1969 to protest these plans. This organization became a strong advocate for the protection of the valuable fossil resources and further stimulated the interest of federal legislators. Members of the group were ready to stand defiantly at the face of bulldozers to halt the development, and early in the summer of 1969 they went to court to halt the construction.

The ensuing legal battle became one of the first environmental cases to be brought before the U.S. Courts by an environmental organization (E. Leopold, Feb. 2007, personal commun.). The Defenders of Florissant hired the famous lawyers Victor Yannacone of Long Island and Richard Lamm of Denver. Lamm would later become governor of the State of Colorado, yet it was Yannacone's creativity that influenced the court's decision and made history in environmental law. Having no legal theory and no law to apply to the case, Yannacone won the injunction by his own risky presentation (Rogers, 1999, p. 3): "Your Honors, if I told you the original U.S. Constitution somehow lay buried there in the fossil beds, would you let the bulldozers roll?" asked Yannacone. The court replied, "Of course not, we'd issue an injunction." Yannacone responded, "Whatever you'd use there, I'm using here."

The trial to hear the full merits of the case was lost, but the Defenders of Florissant appealed to the Federal District Court and obtained a restraining order that temporarily halted the development. By mid-summer, Congress passed a bill to establish the national monument and purchase 6000 acres of private land. With little time to spare, the bill was flown to California to President Nixon's summer White House, where it was signed and enacted into law on August 20, 1969, establishing Florissant Fossil Beds National Monument.

The primary benefits of the national monument have been to protect one of the world's classic fossil sites and to support scientific research to advance our understanding of these fossil treasures. The national monument provides scientifically based interpretation for visitors and school groups, including fossil displays, ranger talks, and wayside exhibits along trails. The 6000-acre size of the Monument, firmly defined in the enabling legislation, remains unchanged. Annual visitation since 2000 has ranged from 60,000 to 80,000.

Beginning in 1994, the national monument recognized its role to provide for ongoing research and resource management in paleontology by adding a permanent paleontologist position, which is held by the second author. One of the first paleontology intern programs in the National Park Service was established at the monument in 1997, and this program has trained 16 students (through 2007) in fieldwork, collections management, database development, and monitoring of paleontological sites. Many of these interns came to Florissant as undergraduates and eventually went on to pursue graduate degrees related to paleontology, some even focusing their research on Florissant (e.g., Roberts et al., this volume; Worley's contribution to Lloyd et al., this volume).

One of the monument's important projects during the late 1990s consisted of a survey of the numerous collections and publications that pertained to Florissant, and a comprehensive database has been developed and made available as a Web site for scientific researchers and the general public alike (http://planning.nps.gov/flfo/; Meyer, 1998; Meyer et al., this volume). Information and photographs from this database provided some of the basis for a book about the paleontology of Florissant (Meyer, 2003).

The monument continues to support education programs and new research in paleontology. In collaboration with the Friends of the Florissant Fossil Beds and Adams State University, the Monument offers an accredited seminar series, designed primarily for teachers, with a focus on natural history, geology, and paleontology. New research permits are continually issued by the monument to support approved field-based projects. Many of these studies are reported in the present volume, including work on paleomagnetic stratigraphy (Prothero), the relation of sedimentation to taphonomy (O'Brien; see also O'Brien et al., 2002), plant-insect interactions (Smith; see also Smith, 2000), new additions to the mammalian fauna (Lloyd et al.), mineralogy of the fossil woods (Mustoe), and conservation of the petrified trees (Young et al.). Other recent studies use fossil insects as paleoenvironmental indicators (Moe and Smith, 2005). One of the best examples to bring the history of paleontology at Florissant to the doorstep of today is the fossil diatoms, an entire group of organisms that has been largely neglected even after 130 years of study at Florissant. Within this group lie answers to questions about ecology of the late Eocene lake and clues to the evolutionary history of fresh-water diatoms. In 2005, the National Park Service obtained funding through the Fee Demonstration Program (provided by visitor entrance fees) to initiate new research on fossil diatoms as a means for providing better interpretive information to the public. Mary Ellen Benson from the University of Colorado is conducting this study for her Ph.D. dissertation. New research is also being conducted to compare Florissant with the nearby and slightly younger Antero Formation.

SUMMARY

The Florissant fossil beds have been collected and studied for more than 13 decades. The major contributors to the taxonomic study of these fossils is summarized in Table 2, and the contributors to paleoclimate and paleoelevation are shown in Table 1.

From the outset of their discovery, the fossils from Florissant were important in shaping new ideas during the formative years of paleontology, particularly as it affected the understanding of North America. The paleontologists who first studied Florissant emphasized the description of new taxa from the large collections being made of these fossils. As an enormous taxonomic diversity unfolded through this work, some of the early scientists such as Scudder began to look beyond the simple classification of fossil organisms and to consider the broader perspectives of Florissant fossils in the context of evolution, extinction, biogeography, and ancient climates.

Lesquereux, Scudder, Cockerell, and the other early workers were true pioneers in developing some of the traditional approaches to paleontology and advancing the science, yet like any phase in the development of a science, they faced limitations in the resources available for completing their research. For example, Lesquereux made comparisons with primarily European fossil plants, because little was known about American paleobotany during his time and most of the previous work had been done in Europe. Cockerell recognized these limitations when he wrote, "we necessarily work with incomplete materials and more or less inadequate tools. We have to build on foundations often poorly established, and no matter how clever or industrious we may be, posterity will have to revise and correct much of what we have done" (Cockerell, 1935). MacGinitie often noted that "we work with what we have."

Many of the identifications made by the early workers were subjected to closer scrutiny and revision as approaches to the morphological basis for taxonomy improved and as larger collections of living species of plants and insects became available. Further mapping and description of the stratigraphy improved the understanding of the geologic context of Florissant. New types of fossils, such as wood and pollen, provided new insights into Florissant's diversity. Application of the fossils to broader questions revealed intriguing and often conflicting ideas about paleoclimate and paleoelevation. Some of these studies, suggesting that the Florissant fossils were deposited at high elevation, have implications for models of the uplift history of the southern Rocky Mountains.

The need to preserve Florissant as one of the world's significant fossil sites reached a flashpoint in 1969 and resulted in the establishment of the Florissant Fossil Beds National Monument. The efforts of the national monument continue to support new discoveries through excavations and research, incorporating this into interpretation for the public.

The 130 years of paleontological study at Florissant is only an instant when placing these 13 decades into the context of 34 million years, yet the amount of work and development of

TABLE 2. SUMMARY OF MAJOR CONTRIBUTORS WHO DESCRIBED FLORISSANT FOSSILS

Contributor	Life span (if deceased)	Dates of publications relating to Florissant	Number of publications	Major contributions	New species described
Lesquereux	1806–1889	1873–1883	6	First descriptions of plants	124
Cope	1840–1897	1874–1883	5	Described all of the Florissant fish and one bird	8
Scudder	1837–1911	1876–1900	23	First descriptions of insects, spiders, and geology	622
Kirchner	unknown	1898	1	Described several new plants, and compiled summary listing of plants	13
Cockerell	1866–1948	1906–1941	134	Described numerous species of insects, plants, and mollusks	453
Brues	1879–1955	1906–1908	6	Insects (parasitic wasps)	145
Wickham	1866–1933	1908–1920	15	Insects (beetles)	356
Knowlton	1860–1926	1916	1	Summary listing of plants	16
Carpenter	1902–1994	1930–1992	10	First description of the ants, and comprehensive listing of insect genera	31
Melander	unknown	1946–1949	2	Insects (flies)	64
MacGinitie	1896–1987	1953–1972	4	Comprehensive revision of plants; studies of geology, biogeography, paleoclimate	18
Manchester	–	1987–2001	10	Recognition of extinct genera of plants	1
Leopold and Clay-Poole	–	2001	1	Pollen and spores	0
Wingate and Nichols	–	2001	1	Pollen and spores	0
Wheeler	–	2001	1	Dicotyledonous woods	2

Note: Table represents research through the twentieth century and is ranked according to the sequence of the contributor's earliest Florissant publication. Number of publications as cited in bibliography of Meyer (2003).

thought that has been accomplished by paleontologists during that time is enormous. Nonetheless, advances in analytical techniques continually changes the way in which scientists approach the fossils at Florissant. These new approaches can provide more critical analysis of the validity of taxonomic identifications, and they continue to shape our understanding of paleoecology, paleoclimates, paleoelevation, taphonomy, and a variety of geological processes. New advances in the study of fossil diatoms and the nature of plant-insect interactions evident in the fossil leaves demonstrate that entire aspects of Florissant's paleontology were unrecognized until recently, leaving us to speculate about what new discoveries lie ahead.

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The role of biofilms in fossil preservation, Florissant Formation, Colorado

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ABSTRACT

Scanning electron microscopy (SEM) of insect and plant fossils in the lacustrine shales of the Eocene Florissant Formation of Florissant, Colorado, was used to investigate the mechanisms of fossil preservation. The fossiliferous Florissant "paper shales" are composed of thin laminae of diatomite that form couplets with alternating smectitic clay laminae. The millimeter-scale sedimentary couplets may preserve an episodic record of sedimentation and are interbedded with less frequent, coarser volcaniclastic layers. The insect and plant fossils are associated with biofilms of extracellular polymeric substances (EPS) secreted by diatoms. The preserved organisms are entangled in the diatom aggregates coated with the EPS biofilm. We suggest that decomposition of the organisms was arrested during sedimentation and burial by the protective nature of the mucus covering, the properties of which limited the actions of bacteria and grazers and may have enhanced fossilization. A novel contribution of the study is a demonstration that this mechanism of exceptional preservation is also common at other similar lacustrine fossil sites, as supported by a further SEM analysis of insect and plant fossils from other Cenozoic lake deposits formed in environments comparable to the Florissant Formation. The deposits include the Oligocene shale at Canyon Ferry, Montana; the Miocene Savage Canyon Formation, Stewart Valley, Nevada; and the Miocene Shanwang Beds of Shandong Province in northeast China. In addition, cultures of diatomaceous biofilms, grown in the laboratory display morphological features identical to those of the fossil diatomaceous biofilms. Our contribution indicates the significance of biofilms in fossil preservation at Florissant and other deposits.

Keywords: biofilm, diatoms, Florissant, EPS, fossil preservation.

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INTRODUCTION

The uppermost Eocene Florissant Formation of Colorado contains exceptionally preserved fossils documenting a remarkably diverse flora and insect fauna, with some 1700 described species. Through the course of 130 years of research on the Florissant fossils, questions have been raised about taphonomic mechanisms that produced such extraordinary preservation. For decades, it was thought that volcanic ashfalls had entrapped the insects and leaves in a lacustrine basin, and that rapid burial by these ashfalls provided the primary preservational mechanism for most of the fossilization at Florissant (e.g., Cockerell, 1908).

More recent works (O'Brien et al., 1998, 2002; Harding and Chant, 2000) have proposed that fossil preservation at Florissant was more complex, and in particular, that it involved the interaction of volcanic processes in the stimulation of planktonic diatom blooms, which, in turn, are thought to have produced mucilaginous biofilms into which floating organisms were incorporated, thus facilitating preservation by slowing the processes of decomposition. The purpose of this paper is to review the evidence for the biofilm mechanism associated with diatom mats at Florissant and, moreover, to examine other fossil insect and plant sites in similar lacustrine lithological settings as a comparative means for demonstrating that this mechanism for exceptional fossil preservation was widespread.

Observations of diatomaceous biofilms cultured under laboratory conditions were also made to compare the similarity of their structures (formed under controlled conditions) with biofilms in the rock record.

BACKGROUND

Fossil assemblages with soft-tissue preservation have been of major importance in paleontological investigations, because they can provide much more morphological information and community data than deposits preserving only skeletal material (Briggs, 2003a, 2003b). Such soft-tissue preservation in fossil conservation deposits (*Konservat-Lagerstätten*) is known to result from the influence of one or more physical and/or chemical factors that may include rapid burial (obrution), anoxia, early diagenetic mineralization, or preservation in sterile environments, such as permafrost or plant resin (Seilacher et al., 1985; Allison and Briggs, 1991; Martin, 1999). Another important phenomenon that has been shown to preserve soft tissues in a variety of exceptionally preserved biotas is the growth of "microbial mats" (Wilby et al., 1996; Gall, 2001; Martínez-Delclós et al., 2004).

The "microbial mats" that have been implicated in the preservation of *Konservat-Lagerstätten* can be divided into two main categories: (1) laterally persistent biofilms developed at the sediment-water interface, and (2) the more areally restricted bacterial colonization of discrete organic substrates. Both of these types of bacterial biofilms are well known in the fossil record (Briggs, 2003b) and promote preservation by both mechanical and biochemical means. The growth of laterally persistent biofilms acts to encapsulate and secure organic remains, thus providing protection from abrasion, disarticulation, scavenging, and burrowing organisms. Biofilms colonizing discrete organic substrates may also encapsulate and protect the substrate in a similar manner; however, this type of biofilm may also become autolithified and can morph soft tissues. Both types of biofilms may inhibit decay by creating a chemical microenvironment that promotes rapid mineralization (Decho, 2000; Briggs, 2003b).

An excellent example of laterally persistent biofilms is typified by the folded and torn sheetlike structures on bedding plane surfaces in the Jurassic deposits of Cerin, France (Bernier et al., 1991). These biofilms grew across the fossil remains and ponded liberated phosphate beneath the mats, thereby accelerating phosphatization of volatile tissues (Wilby et al., 1996; Wilby and Briggs, 1997). In Germany, the deposits of Paleogene lakes at Messel and Enspel provide examples of the second form of biofilm: the bacterial masses that colonized organic substrates (e.g., carcasses, coprolites) during early stages of decomposition. At Messel these bacterial masses have become autolithified by siderite, and the bacterial cells have essentially revealed the outline of soft tissues (Wuttke, 1983; Franzen, 1985; Liebig, 1998); at Enspel the bacterial biofilms appear to be less homogeneously mineralized but are also restricted to decaying organic matter, such as carcasses of putative tadpoles, and also coprolites (Toporski et al., 2002).

The fossil biofilms described to date may be classified as (sub)aquatic microbial biofilms, as defined by Krumbein et al. (2003, p. 7): a "structured community of microbial cells of different genera and species [that] modifies the chemical gradient between a solid surface(s) and the adjacent or overlying liquid." Although dominated by prokaryotic bacteria, such aquatic biofilms may also contain other microorganisms (e.g., algae, protozoans, and fungi). However, the most volumetrically important components of modern microbial biofilms are the extracellular mucilaginous secretions, variously referred to as extracellular polymeric substances (Westall et al., 2000), extracellular polymeric sections (Decho, 2000), or exopolymeric polysaccharides (Verdugo et al., 2004), all of which may be abbreviated as "EPS." EPS are hydrogels consisting of >90% biologically solidified water (Krumbein et al., 2003).

The physical characteristics of the vast majority of biofilms described from the fossil record indicate that they are likely to have been dominated by prokaryotic bacteria. However, we previously described a fossil example of a eukaryote-dominated biofilm associated with the exceptionally preserved insects and plant remains of Florissant (O'Brien et al., 1998, 2002; Harding and Chant, 2000). These eukaryotic biofilms consist of diatoms, inferred to be planktonic forms, accompanied by EPS apparently secreted by the diatom flora. Diatoms encased in an EPS matrix also have been reported in modern environments (Passow et al., 1994).

FLORISSANT GEOLOGY AND FOSSIL PRESERVATION

The Florissant Formation has been divided into six informal units: the lower shale unit, lower mudstone unit, middle shale unit, caprock conglomerate unit, upper shale unit, and upper pumice conglomerate unit. These units represent a composite thickness of 74 m and consist variously of shale, tuffaceous mudstone and siltstone, tuff, and arkosic and volcaniclastic sandstone and conglomerate (Evanoff et al., 2001). These rocks were deposited in close association with volcanic debris flows and pyroclastic eruptions from nearby volcanic centers, including the Guffey volcanic center, a stratovolcano in the nearby Thirtynine Mile volcanic field, and possibly also ash and pumice eruptions from the Mount Aetna and Grizzly Peak calderas (Evanoff et al., 2001). Detailed geochemical analysis is needed to clarify these volcaniclastic source areas further. The sediment in the Florissant formation was deposited in the basin of a south-flowing paleodrainage system and includes lacustrine, fluvial, and lahar phases of deposition. Lahars (volcanic debris flows) of the Thirtynine Mile Andesite (Wobus and Epis, 1978) impounded the lower part of this paleodrainage, forming a lake to the north of the obstruction. The stratigraphic sequence suggests that this lake may have formed at least twice, as evidenced by the separation of the lacustrine lower and middle shale units by fluvial rocks of the lower mudstone unit (Evanoff et al., 2001). ^{40}Ar/^{39}Ar dating of the upper three units of the Florissant Formation have provided a weighted mean age of 34.07 Ma (Evanoff et al., 2001), placing the formation in the latest Eocene. It has been estimated that the lake may have persisted for 2500–5000 years (McLeroy and Anderson, 1966).

Of particular interest to our study are the lacustrine “paper shales” that form much of the lower, middle, and upper shale units of the formation. These thinly laminated shales contain the extraordinarily well preserved impression and compression fossils of insect and plants for which Florissant is famous. The paper shale beds were first examined in detail by McLeroy and Anderson (1966), who reported upon the relationship between the thinly laminated couplets and the presence of fossils. Within the thick successions of the shale units of the formation, the paper shales alternate with thicker layers of tuff formed by ash and pumice, some of which was probably epiclastic in origin. Fine-grained epiclastic ash weathered to smectitic clay is also a component in the paper shales (O’Brien et al., 2002), where it forms thin laminae that alternate with the thin laminae of diatomite to form the couplets characteristic of the fossil-bearing shales. It was these fossiliferous paper shales (mainly sampled at the Clare Florissant Fossil Quarry and at the Florissant Fossil Beds National Monument) that were examined in the previous studies by O’Brien et al. (1998, 2002) and Harding and Chant (2000). These studies showed that the insect and plant fossils are associated with the diatomaceous biofilms and suggested that these biofilms were important agents in the preservation of the fossils.

To investigate if a similar pattern of exceptional fossil preservation due to the presence of mucilaginous diatom biofilms existed elsewhere in the geological record, we located other fossil sites that possess many of the same characteristics as Florissant. These characteristics include (1) thinly laminated shale, composed of couplets of diatomite and clay; (2) a lacustrine depositional system that included silicic volcaniclastic sediments; and (3) exceptional fossil preservation of refractory and volatile tissues, in terms of both morphological detail and high taxonomic diversity. Additional shale samples from three such fossil sites were collected for the present study: Canyon Ferry (Oligocene of Montana, USA), Stewart Valley (Miocene of Nevada, USA), and Shanwang (Miocene of Shandong Province, China).

MATERIALS AND METHODS

Fossils were collected from two stratigraphic levels in the Florissant Formation: the middle shale unit in the Florissant Fossil Beds National Monument and the lower shale unit at the privately owned Florissant Fossil Quarry near the town of Florissant. Detailed maps of the stratigraphy can be found in Evanoff et al. (2001) and Meyer (2003). Canyon Ferry Reservoir samples were collected from outcrops on the west side of the reservoir, southeast of Helena (Montana), in Townsend Valley at a site described by CoBabe et al. (2002). Fossils from Stewart Valley, Nevada, were collected at sites designated as Diatomite Ridge, Pacific Union, and Two Tips (Schorn et al., 1989). Additional samples from the Stewart Valley locations were provided by the Museum of Paleontology, University of California at Berkeley, and the Department of Entomology, California Academy of Science. The Shanwang samples were provided by Hong Yang from sample sites of the Shanwang Formation in Shandong Province, China (Yang and Yang, 1994).

Commercially obtained fresh-water diatoms (genera: *Navicula, Synedra,* and *Nitzchia*) were cultured in test tubes in the laboratory under fluorescent lighting in distilled water to which a dilute sodium silicate diatom nutrient solution was added. These taxa were selected mainly because they are readily available commercially, they are easily cultured in the lab, and they are common fresh-water diatoms similar to those found in our fossil sites. Fruit fly and bee remains were added to some test tubes in order to simulate conditions of fossil preservation. The remains were autoclaved to provide samples free of extraneous live bacteria, which could grow in the tubes and produce, in turn, a microbial mat. Our intent was to study a biofilm produced solely by diatoms. Diatom mucus mats formed within one week and then were extracted with the embedded insect specimens from the sealed test tubes.

The mates were air dried on aluminum stubs and samples were prepared for SEM and thin-section analysis according to the standard techniques described by O’Brien and Slatt (1990). Samples were sputter-coated with gold for 45 seconds in a vacuum and viewed in an ISI-Topcon scanning electron microscope. Care was taken during the gold sputter coating process that no gold artifacts (likely to be interpreted as fossil microbes) were produced.

OBSERVATIONS

Florissant *Konservat-Lagerstätte*

The thinly laminated shale units that contain the well-preserved fossils in the Florissant Formation display couplets (each 0.1–1.0 mm thick) composed of laminae of light-colored diatomite that alternate with dark-colored laminae of smectite clay derived from weathered volcanic ash (Figs. 1 and 2). Commonly three to

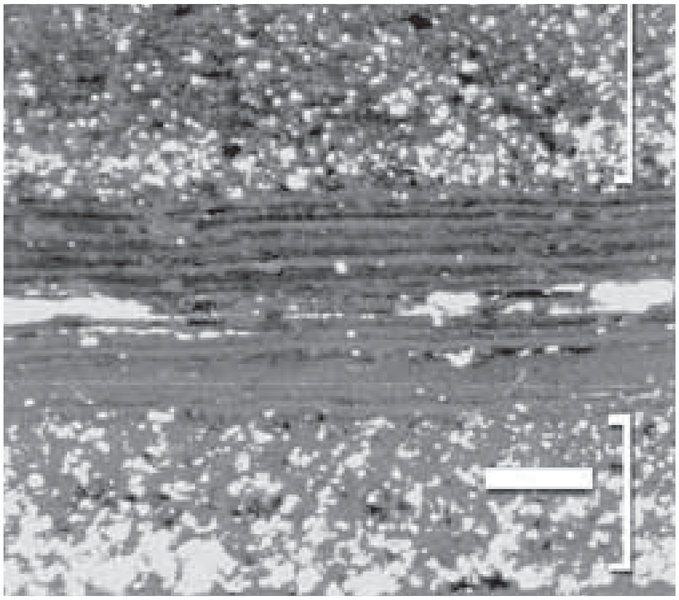


Figure 1. Example of lamination in fossil-bearing shales, Florissant Formation thin section showing alternation of couplets of light diatomite and dark smectite clay layers (middle of photo) interbedded with tuff layers (brackets). Scale = 1µm.

ten couplets occur within groups. The fossil-containing diatomite laminae (Fig. 2A shows a diatomite mat) alternate with the smectite clay (Fig. 2B) layers. Meyer (2003, p. 125) reported the presence of at least 19 genera of fresh-water diatoms at Florissant based on an unpublished analysis by E. Stoermer. Both planktic and benthic forms, which include centric and pennate taxa (Benson et. al., 2006) are found. The most abundant types are similar to the modern genera *Aulacoseira* and *Synedra*. Many of the genera represent forms living in water less than 2 m deep. The diatom-smectite couplets are interbedded with less frequently occurring tuff layers (Figs. 1 and 3).

Fossils are abundant in the diatomite laminae (Figs. 4–8). The unfossiliferous dark laminae contain abundant randomly orientated smectite clay platelets (Fig. 2B). This cardhouse fabric indicates deposition of detrital clay in the flocculated state (O'Brien and Slatt, 1990). Although some of the clay may have been of eolian origin, it seems more likely to be dominantly detrital from sediment being washed into the lake. The alteration of diatomite and volcaniclastic sedimentary layers suggests a process of episodic sedimentation.

Oligocene Canyon Ferry *Konservat-Lagerstätte*

The Canyon Ferry shale has a lithology and fossil occurrence similar to those of the Florissant Formation (compare Figs. 9 and 10 with Figs. 4–8). The fossil-bearing zones are of lacustrine origin and associated with volcaniclastic sediments and other abundant volcanic debris. CoBabe et al. (2002, p. 28) indicated that the "association between the insect *Lagerstätte* and volcaniclastic sedimentation in the Rocky Mountain region, and the strong volcaniclastic component of the Canyon Ferry deposit may have played a significant role in preservation of the *Lagerstätte*." Evidence shows the presence of a diatom mat (Fig. 9A), smectite clay (Fig. 9B), and a mucus-covered diatom mat containing fossils (Fig. 10A–D).

Miocene Stewart Valley *Konservat-Lagerstätte*

Sites at Stewart Valley, Nevada (for locations see Schorn et al., 1989), contain well-preserved insects and plants in Miocene lacustrine shales that are similar in lithology and mineralogy to

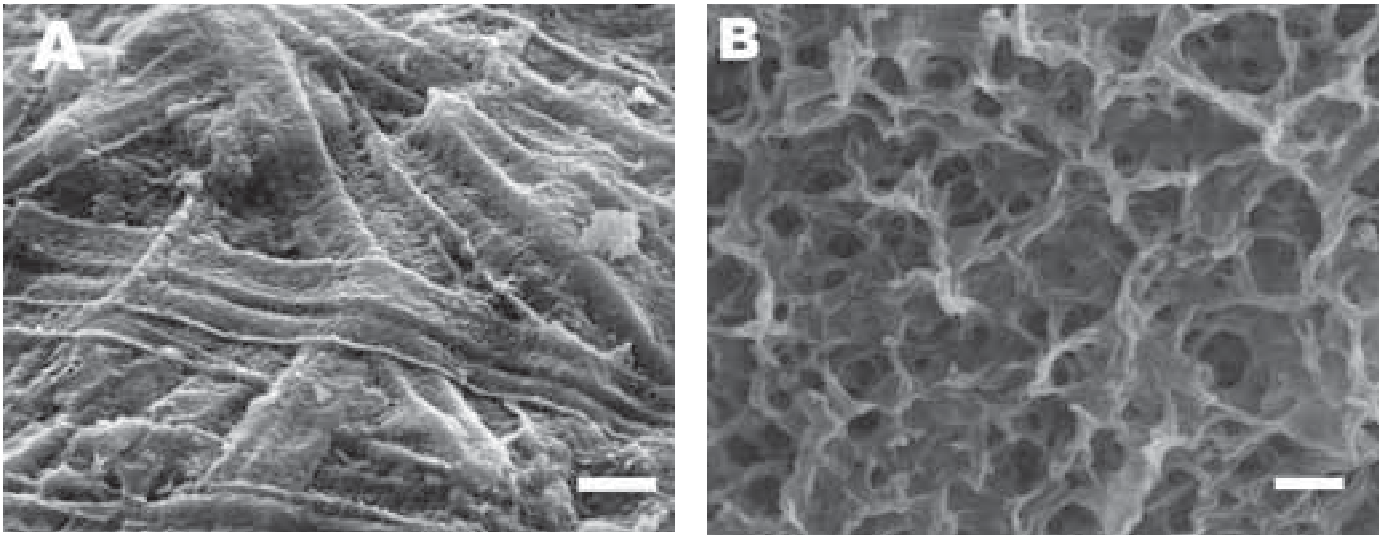


Figure 2. Scanning electron photomicrographs of details of a typical Florissant shale couplet shown in Figure 1. (A) Top surface of diatomite portion of the couplet, showing randomly oriented and densely packed frustules. Scale = 5.5 µm. (B) Flocculated fabric of smectite clay in a typical couplet. Scale = 2.27 µm.

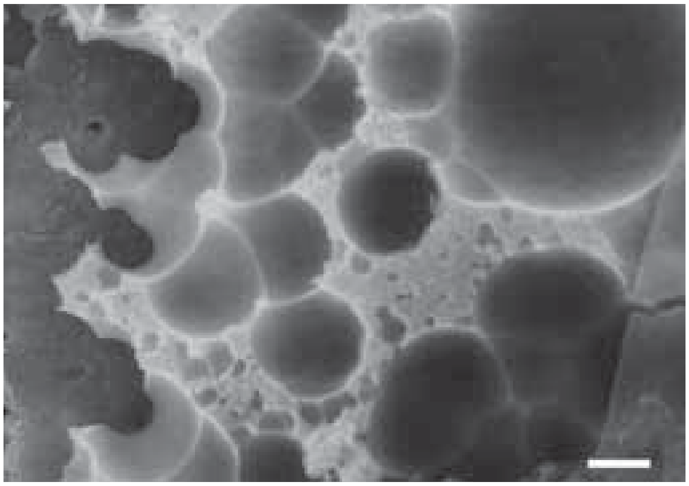
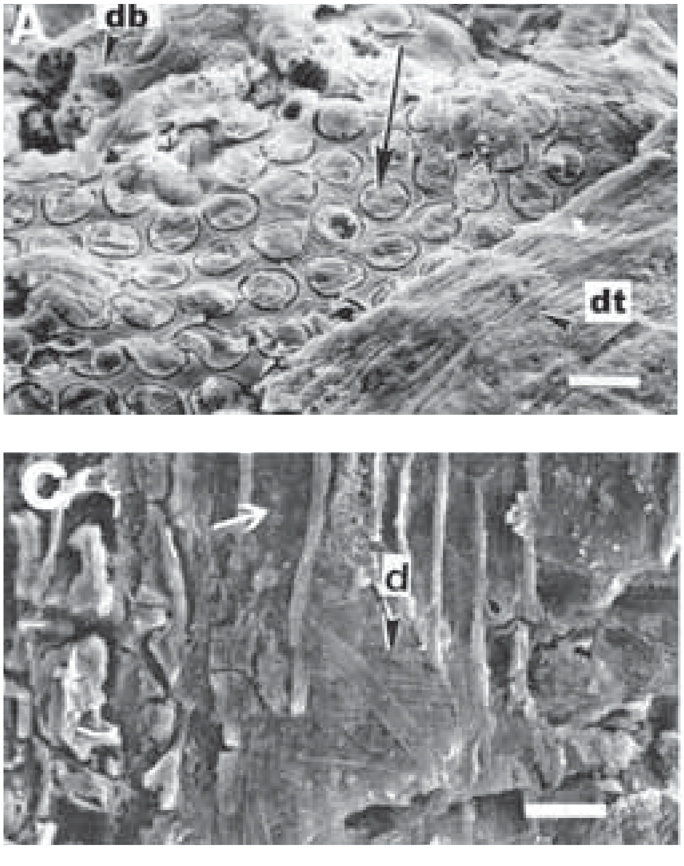


Figure 3. Scanning electron photomicrograph of ash grain typical of grains in tuff layers (shown by brackets in Fig. 1) that are interbedded between diatomite-clay couplets. Scale = 2.08 µm

those at Florissant and Canyon Ferry (compare Figs. 11–13 with Figs. 4–10). The fossils are found in the Stewart Valley laminated shales containing thin (≤1mm) alternating layers of diatomite (Fig. 11A) and smectitic clay (Fig. 11B). Significantly, these fossils are also found in the diatomite laminae (Figs. 12 and 13), with mucus strands (Fig. 12A) and mats (Fig. 12B) covering the fossils.



Miocene Shanwang *Konservat-Lagerstätte*

Yang and Yang (1994) have reported that the Miocene Shanwang biota in eastern China is one of the taxonomically most diversified and best preserved fossil deposits in the world. Over 500 fossil species have been found in sediments deposited in a Miocene lake basin. These authors report fossils showing well-preserved ultrastructure under the SEM. Figure 14 shows a biofilm associated with diatoms similar to the samples from previously mentioned sites.

Diatoms Grown in Laboratory

The living diatoms cultured in the laboratory are associated with EPS (O'Brien et al., 2002). These modern diatoms (Figs. 15 and 16) have produced mucus secretions similar to the strands and films on the insect and plant fossils. This similarity is quite striking when the modern diatom film shown in Figure 15B is compared with the ancient biofilms in Figure 10A. Strands emanating from modern diatom frustules (Fig. 16) have shapes and dimensions similar to those found on a variety of fossils (see Fig. 6A, 10B, or 12A, for example).

INTERPRETATIONS

Florissant *Konservat-Lagerstätte*

The Florissant insect and plant fossils we observed in SEM reveal very detailed morphologic features, indicating that they were little affected by decompositional processes either during or after deposition. The finely laminated couplets in which the fossils are found have been described as forming in the deeper parts of Lake Florissant (McLeroy and Anderson, 1966). However, some observations suggest that some insect and plant fossils are

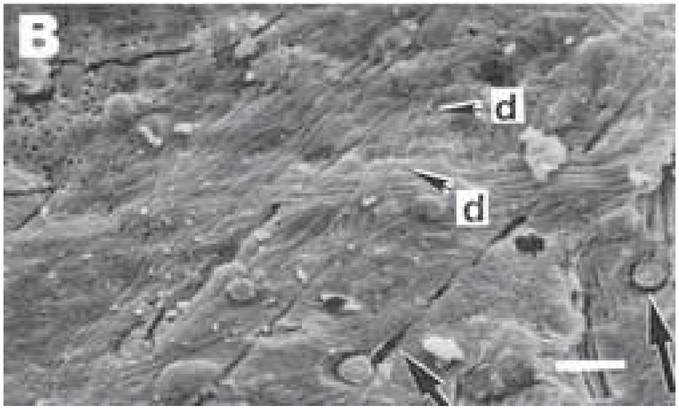


Figure 4. Scanning electron photomicrographs of typical Florissant fossils. (A) Facets of compound eye of an insect (large arrow). Fossil is between the top (dt) and bottom (db) of a diatom mat. Scale = 23.3 µm. (B) Details of impressions of setae and attachment points (large arrows) on insect leg covered by a diatom mat (d, small arrows). Scale = 14.9 µm. (C) Diatom mat (arrow d) on plant fossil. Scale 22.7 = µm.

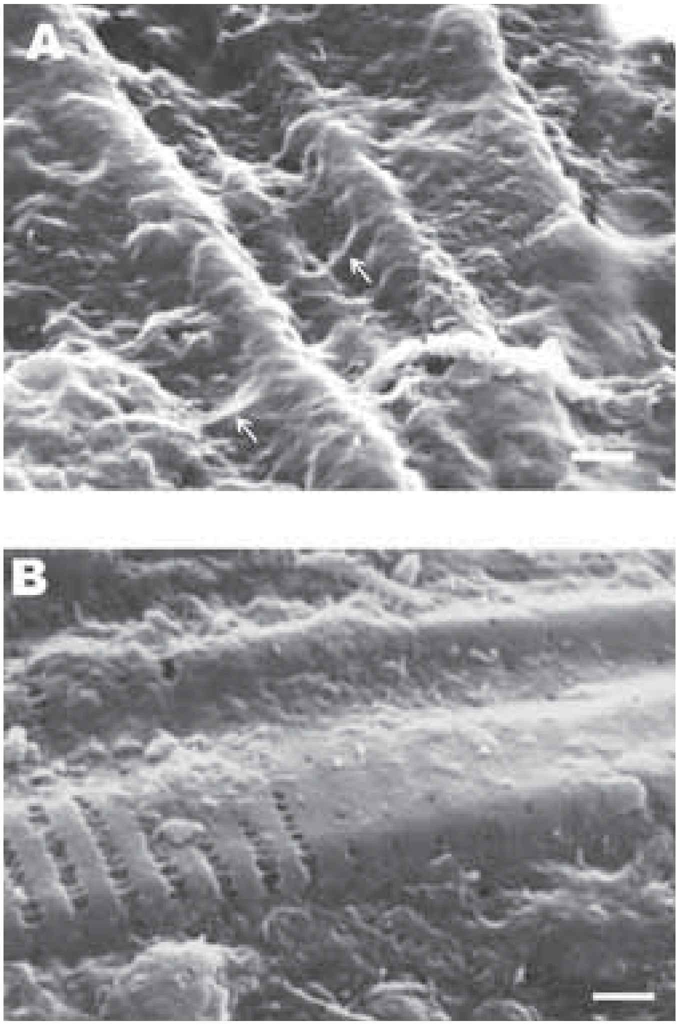


Figure 5. Scanning electron photomicrographs of biofilm mat on diatoms on Florissant leaf fossils. Note mucus strands in A (arrows). Mat covers right side of diatom in B. Scale = 1.10 µm (A); 0.76 µm (B).

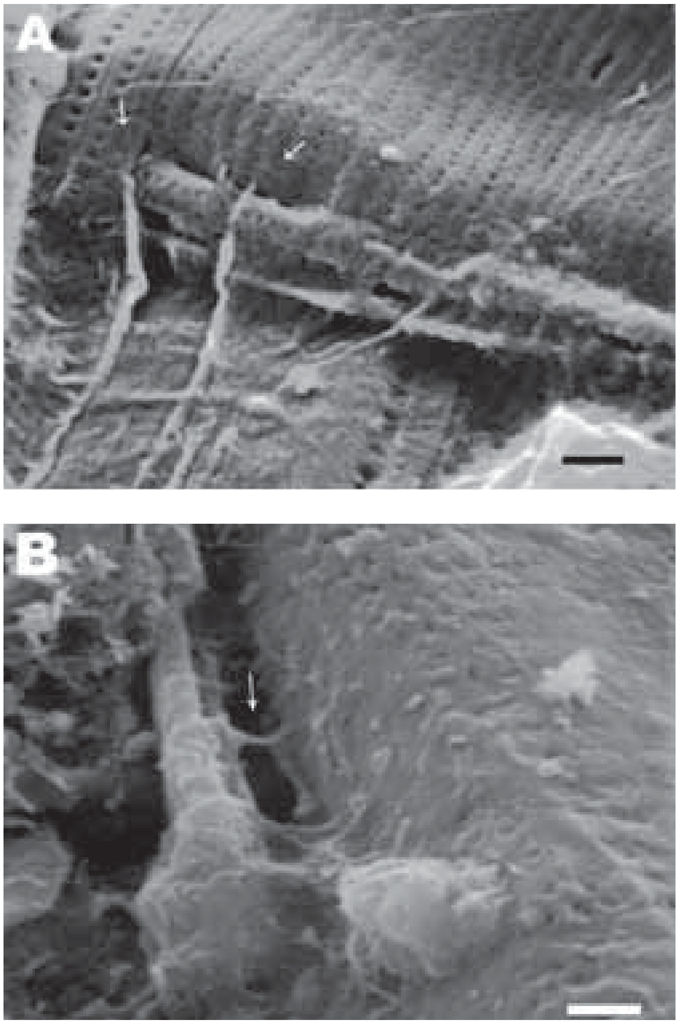


Figure 6. Scanning electron photomicrographs of strands of mucus secretions from diatoms associated with Florissant fossils. (A) Strands of mucus exuded from diatom pores (arrows). Diatom is in a mat covering an insect. Scale = 0.63 µm. (B) Mucus exuded from diatom pores (arrow). Diatom mat is on a plant fossil. Scale = 0.91 µm.

found in nearshore deposits (D. Smith, 2006, personal commun.). Regardless of the specific depositional site, the preservation of the Florissant insects and plants in the thick sequences of undisturbed laminae could be explained by rapid deposition and burial in an anoxic environment, implying that the lake was permanently stratified and that sedimentation occurred beneath the monimolimnion. However, such sedimentation may represent only part of the reason for the exceptional preservation.

The quality of the fossil preservation has also been attributed to the encapsulation of the fossil material in diatomaceous biofilms (O’Brien et al., 1998, 2002; Harding and Chant, 2000). Harding and Chant (2000) stress the added role of anoxia in the sedimentary environment. The exceptional preservation of the fossils in the Florissant Formation is illustrated in Figure 4. The diatom frustules at Florissant are usually found randomly oriented on the laminar and fossil surfaces, but are occasionally found arranged in parallel sheaves consisting of more than ten frustules. Higher magnification reveals that the diatoms and the fossils are covered with a smooth amorphous film (Fig. 5); some specimens show strands of mucus material associated with the diatom frustules (Figs. 6 and 7). This material is interpreted as EPS produced primarily by the diatoms. This interpretation is based upon the similarity of its morphology to that of the biofilm mats observed by Wetzel et al. (1997) in their study of the polysaccharides secreted by fresh-water diatoms. Other sources of biofilm, in addition to diatoms, are attributed to EPS from bacteria, algae, protozoans, and fungi (Edgar, 1983; Hoagland et al., 1993; Passow et al., 1994). We cannot completely discount the presence of a component of bacterial EPS in the mats observed. A few spherical features, interpreted as bacteria, are present but not common (Fig. 8).

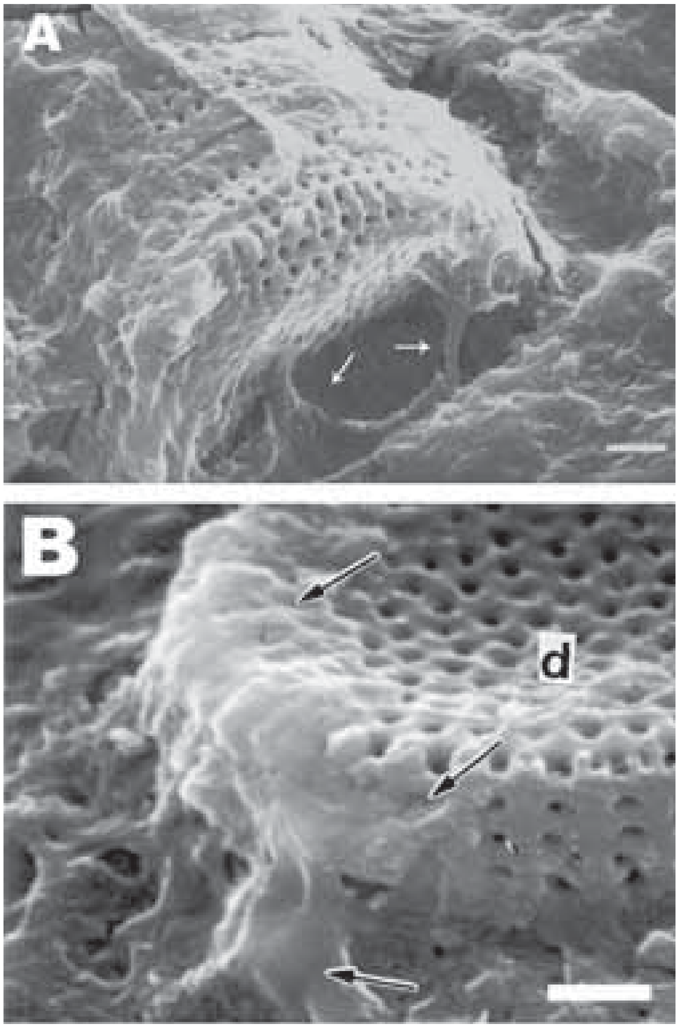


Figure 7. Scanning electron photomicrographs of strands of mucus secretions from diatoms associated with Florissant leaf fossils. Arrows show mucus strands coalescing into a biofilm mat. d—diatom. Scale = 1.79 µm (A); 1.00 µm (B).

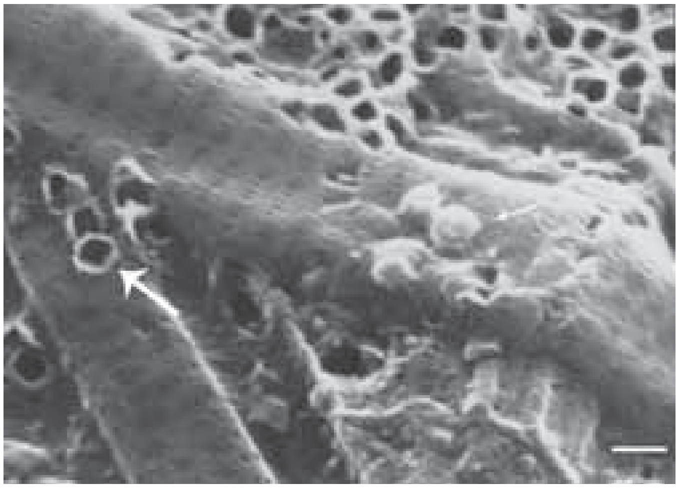


Figure 8. Scanning electron photomicrograph of features interpreted to be bacteria on a diatom mat covering a Florissant leaf. Small arrow shows bacteria spheres; large arrow shows holes left by bacteria, perhaps formed during sample preparation. Scale = 0.93 µm.

These spherical structures, found individually or in clusters, are associated with perforated or lacy EPS on the surface of diatom frustules and are found only on the diatom-covered Florissant fossil organisms. Some of these spheres are found in areas showing holes, which may indicate their former position on the mucus film (Fig. 8). The size and morphology of these structures suggest that they could be molds or mineralized remains of bacteria (Fig. 8). If they do represent the presence of fossilized bacteria, they may have been an integral part of the biofilm and contributed to the formation of the EPS matrix, although the abundance of diatoms in all of our samples would indicate that diatom EPS, and not that produced by bacteria, is likely to have dominated. However, interpretation of these structures as bacteria is controversial, and it is possible that the spheres may also represent impressions of gas bubbles or the sites of degraded pyrite crystals. One cannot discount the role played in fossilization by bacterial, or even fungal, microbial mats; however, the evidence in this study demonstrates the importance of EPS dominantly from a diatom community.

Fossil insects and plants were studied from other geologic sites to test the working hypothesis that the diatom-produced biofilm may play an important role in fossil preservation. As mentioned previously, these lacustrine shale units were selected because they share similar geological conditions with the Florissant Formation.

Oligocene and Miocene *Konservat-Lagerstätte*

Our detailed analysis of a variety of insect fossils from the Canyon Ferry site shows numerous similarities to those from the Florissant Formation. Fossils occur in paper shales and are entombed within thin diatomite laminae (Fig. 9A), which alternate with thin smectite clay layers (Fig. 9B). The level of preservation of morphological details is similar at the two sites: impressions of setae and their attachment points (Fig. 10A) and compound eye elements (Fig. 10B) of insects are very well preserved. Significantly, the fossils are preserved within a diatomaceous biofilm. A typical biofilm covering a diatom frustule is shown in Figure 10C. This SEM view is illustrative because it reveals an oblique view of the strands of mucus composing the diatom mat (small arrow, Fig. 10C) lying on top of an insect (large arrow, Fig. 10C). Mucus strands are abundant and interpreted as EPS from the diatoms (Fig. 10D).

The lacustrine shale at the Stewart Valley site also shows size and morphology features similar to Canyon Ferry and Florissant samples (compare Fig. 11 with Figs. 2 and 9). Mucus strands and film from a diatom source (Fig. 12) are associated with well-preserved insect features such as setae (Fig. 13A) and a compound

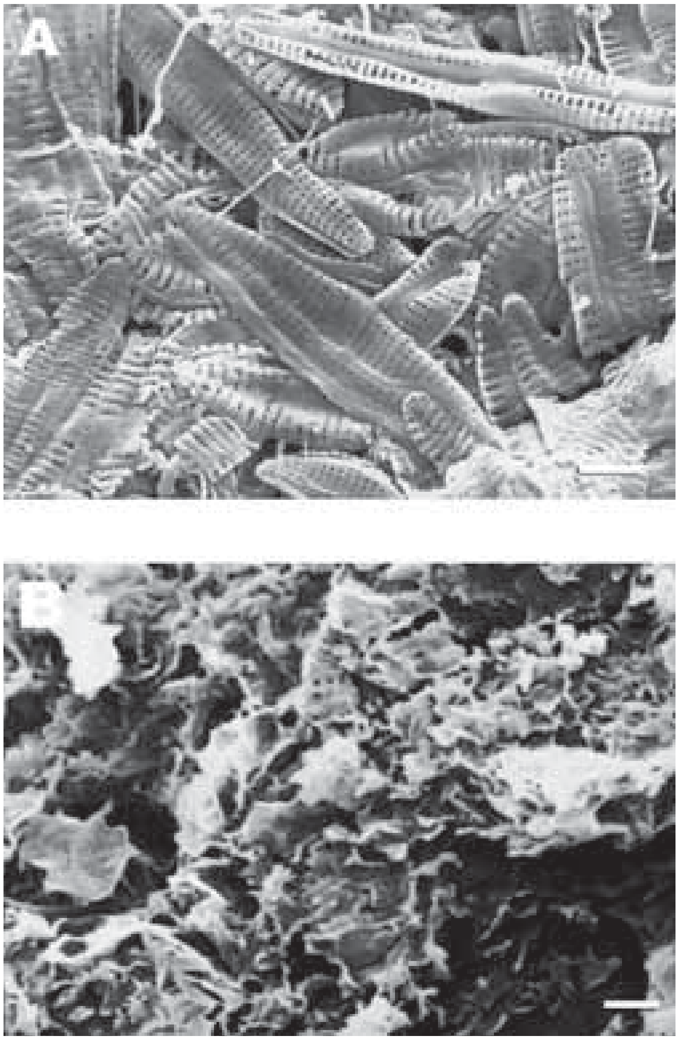


Figure 9. Scanning electron photomicrographs of fossil-bearing zone, Canyon Ferry, Montana. (A) Top view of diatom part of couplet. Scale = 2.44 µm. (B) Fabric of smectite clay layer in a couplet. Scale = 1.47 µm.

eye (Fig. 13B). Biofilms associated with diatoms and fossils are also common in the Shanwang deposit (Fig. 14).

Our investigations of samples from the fossil-bearing zones further show that well-preserved organisms are associated with diatom-rich zones. The presence of well-preserved fossil plants and insects covered with EPS-rich diatomaceous biofilms in diatom laminae is consistent with our observations of the Florissant fossil zones.

Similarity of Morphology of Fossil and Recent EPS

The similarity in morphology between the EPS from the diatoms grown in the laboratory and those preserved in the fossil record provides a useful frame of reference by which to consider the role played by diatom mucus in Florissant and other fossil deposits. This similarity is most striking when one compares the mucus strands emanating from the pores of the recent diatoms (Fig. 16B) with the strands from Florissant diatoms (Fig. 6A). In addition, the filmy nature of the covering on the Florissant fossil diatoms (e.g., Fig. 7A and 7B) is remarkably similar to EPS films produced in the laboratory (cf. Fig. 15). This resemblance supports the hypothesis that diatoms produced the material identified as EPS both at Florissant and in other deposits.

DISCUSSION

The observations presented in this study provide further support for the importance of diatom mucus in the preservation of the Florissant fossils. There is also a relationship between these biofilms of diatom origin and their occurrence in a volcaniclastically influenced lacustrine environment.

The morphological similarities between the smooth surface coatings and filamentous strands on the fossil diatomaceous biofilms and the EPS on insects covered by diatomaceous biofilms produced in laboratory cultures lead us to believe that both were produced by the same processes. In previous discussions of diatomaceous biofilms as agents of exceptional fossil preservation, O'Brien et al. (1998) and Harding and Chant (2000) described the incorporation of organic remains into diatomaceous biofilms. These fossil-encapsulating diatomaceous biofilms may be similar to the structures observed by Smetacek (1985), in which particles suspended in the water column became incorporated into diatomaceous biofilms and the resulting aggregates then settled out of the water column. Diatom-produced EPS aggregates have also been observed in the Adriatic Sea, both floating and sinking to the seafloor (Stachowitsch et al., 1990). O'Brien et al. (1998, 2002) proposed that the encapsulation of dead organisms in an EPS-rich biofilm was a key factor in preservation because the biofilm inhibited decomposition.

Our evidence indicates the importance of diatom-produced biofilm under certain geologic conditions, such as the association of lacustrine basins with nearby silicic volcanism. In summary, we suggest the following sequence of events during the deposition of the fossil-bearing paper shale units, leading to the remarkable preservation of insect and plant fossils from Lake Florissant: (1) volcanic ash from the surrounding volcanic terrain weathered into smectite clay, which was the dominant clastic component deposited in the lake; (2) the amount of sediment delivered to the lake varied episodically, and although this may have been influenced by seasonal variations, the actual periodicity is unclear from present evidence; (3) the lake water was enriched in silica during the time of greatest influx of silicic volcanically derived sediment, providing the nutrients important for the proliferation of the diatom population; (4) diatom proliferation ultimately resulted in the production of a diatomaceous biofilm in the upper lake water; (5) insects either fell onto the surface waters of the lake, or, along with the plant remains, were blown or washed into the lake, becoming encapsulated in the sticky, mucosic biofilm suspended at or near the lake surface; (6) under its own weight, the organism-containing biofilm mat sank to the lake bed, forming a thin diatom-fossil-rich layer overlying

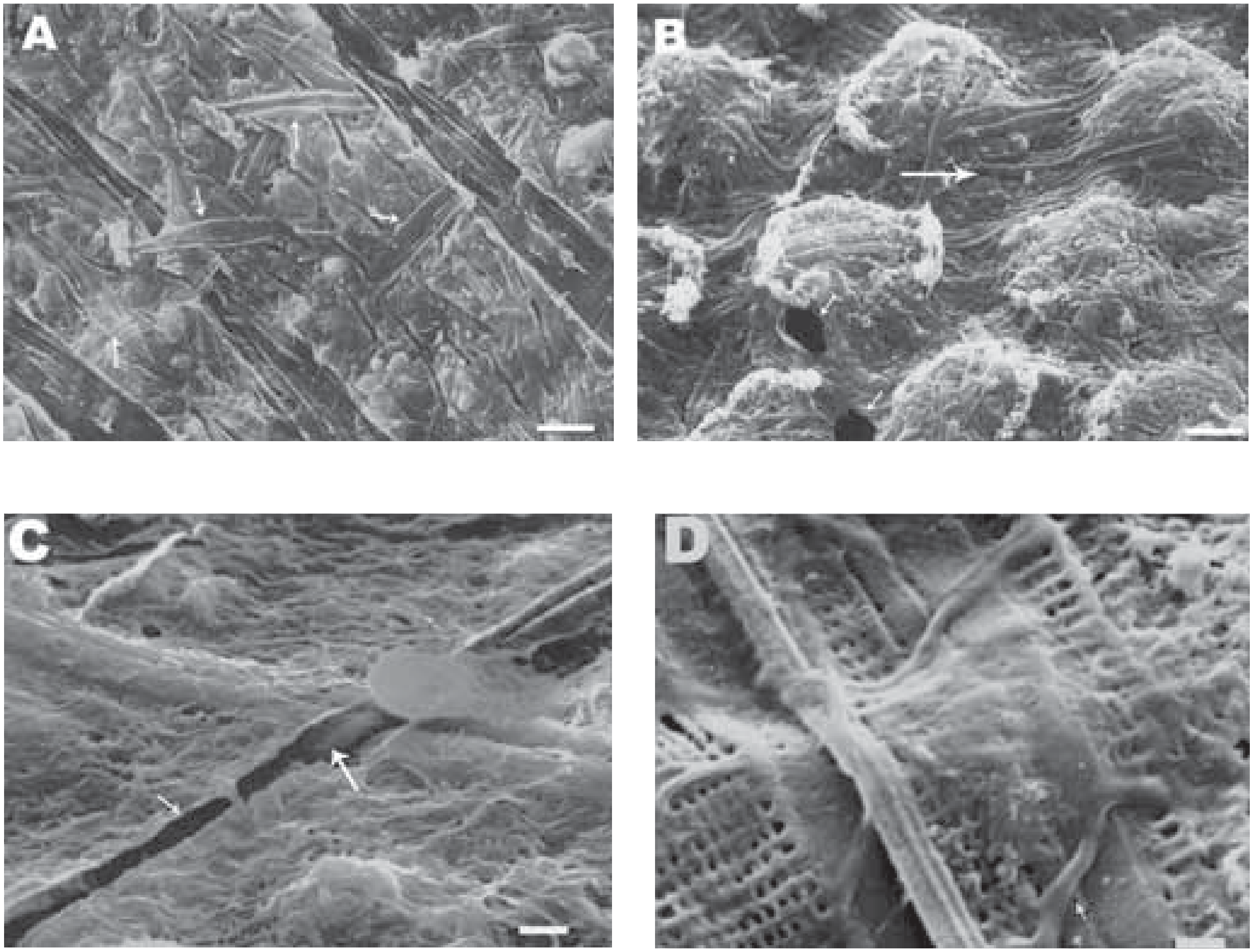


Figure 10. Scanning electron photomicrographs of fossils, Canyon Ferry site. (A) Setae and attachments of insect covered with diatom mat (arrows point to diatoms). Scale = 7.0 µm. (B) Compound eye of insect covered with diatoms (large arrow shows diatoms, small arrows point to holes in mucus mat). Scale = 7.1 µm. (C) Mucus mat (small arrow) lying on an insect hair (large arrow). Scale = 1.94 µm. (D) Mucus strands covering a diatom. Scale = 0.80 µm.

the earlier deposited clay lamina—it is also possible that anoxic conditions produced within the biofilm further retarded decomposition of the entrapped organisms; (7) more smectitic clay was deposited above the diatom mat following the bloom episode; (8) the couplet-forming events were repeated, numerous times, with irregular interruptions by influxes of coarser-grained tuffaceous sediment. The latter probably represent intervals of intense runoff (during storms) or deposition of pyroclastic ash during sporadic volcanic eruptions.

SEM observations by the first author of Eocene fossils at Republic (Washington) and the Green River Formation (Colorado-Wyoming) demonstrate neither diatoms nor biofilms, and yet fossil insects and leaves are abundant and well preserved at these localities. The absence of diatoms from the Cretaceous Yixian Formation is unsurprising because Yixian predates the occurrence of lacustrine diatoms in the fossil record; the first fresh-water diatoms were documented in the Late Cretaceous (Ambwani et al., 2003; Beraldi-Campesi et al., 2004). This however, cannot be the explanation for the absence of diatoms from the two Cenozoic localities. The lack of diatomaceous biofilms at Republic and Green River indicates that taphonomic factors besides mucilaginous diatomaceous biofilms were responsible for the exceptional fossil preservation in these deposits. What these factors were still needs to be determined by future taphonomic study.

The consistent association of well-preserved insect and plant fossils encapsulated within diatomaceous biofilms at several paleontological sites with silicic volcanically derived sediment is an important observation and illustrates another mechanism that may result in extraordinary fossil preservation. It appears plausible that this association is indicative of a causal or facilitating mechanism for the exceptional fossil preservation in some

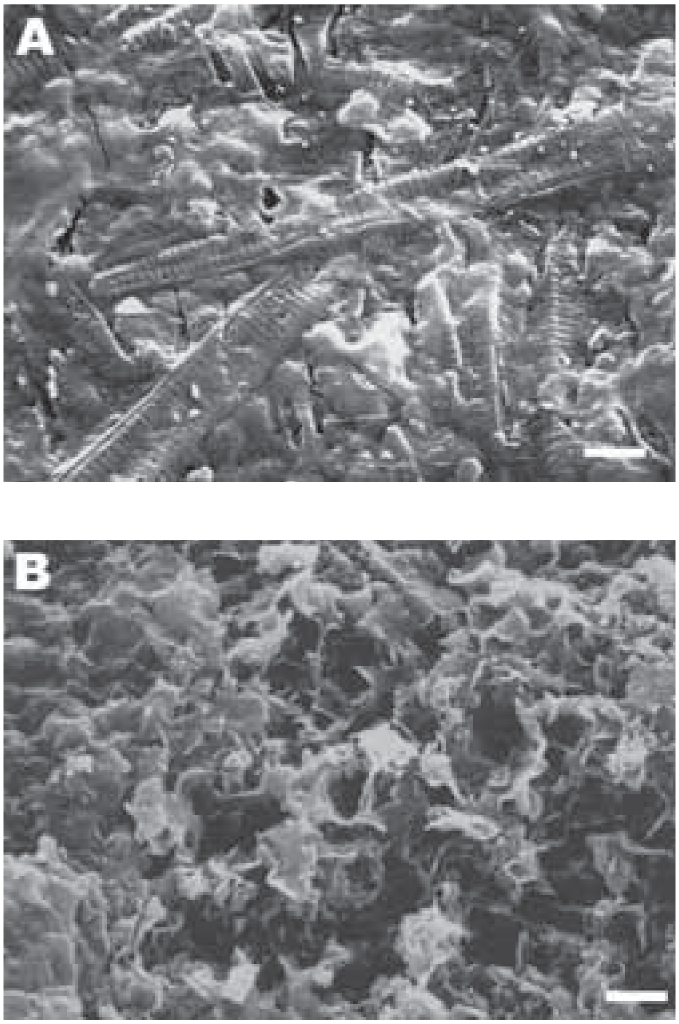


Figure 11. Scanning electron photomicrographs of lacustrine shale, Stewart Valley, Nevada. (A) Top view of insect body in diatom layer containing mucus. Scale = 2.17 µm. (B) Smectite clay portion of couple. Scale = 2.17 µm.

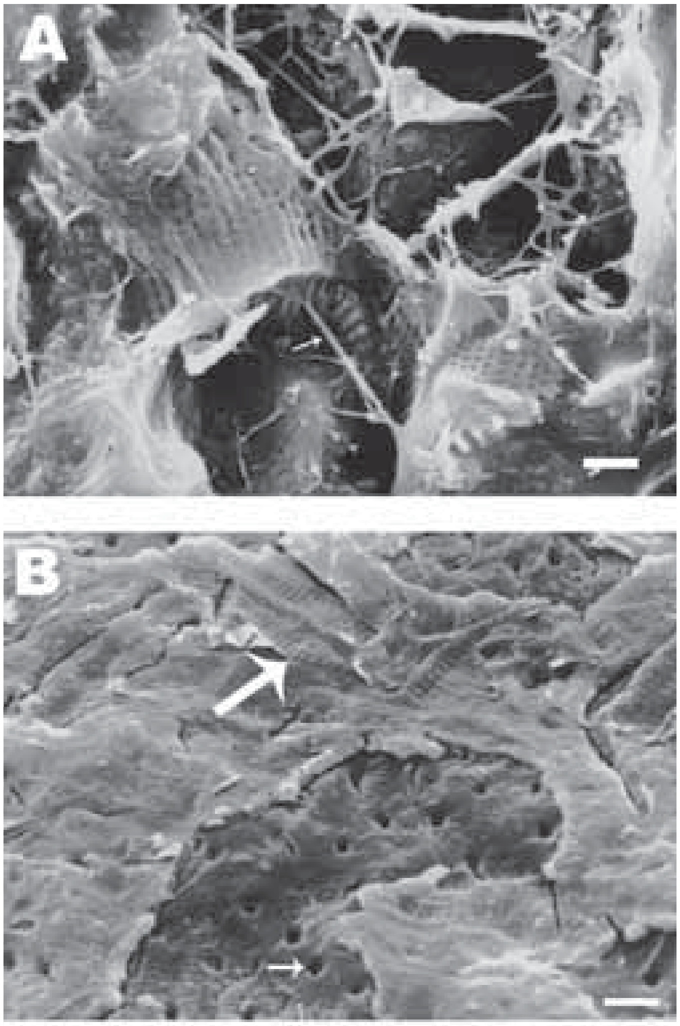


Figure 12. Scanning electron photomicrographs of diatom biofilm, Stewart Valley, Nevada. (A) Mucus strands attached to diatoms (arrow). Scale = 2.04 µm. (B) Biofilm associated with diatoms (large arrow) overlying an insect body (small arrow). Scale = 2.17 µm.

Cenozoic lacustrine settings, such as that represented by the Florissant Formation in Colorado. Future taphonomic studies of preservation in fresh-water bodies that contain diatoms may shed further light on this phenomenon.

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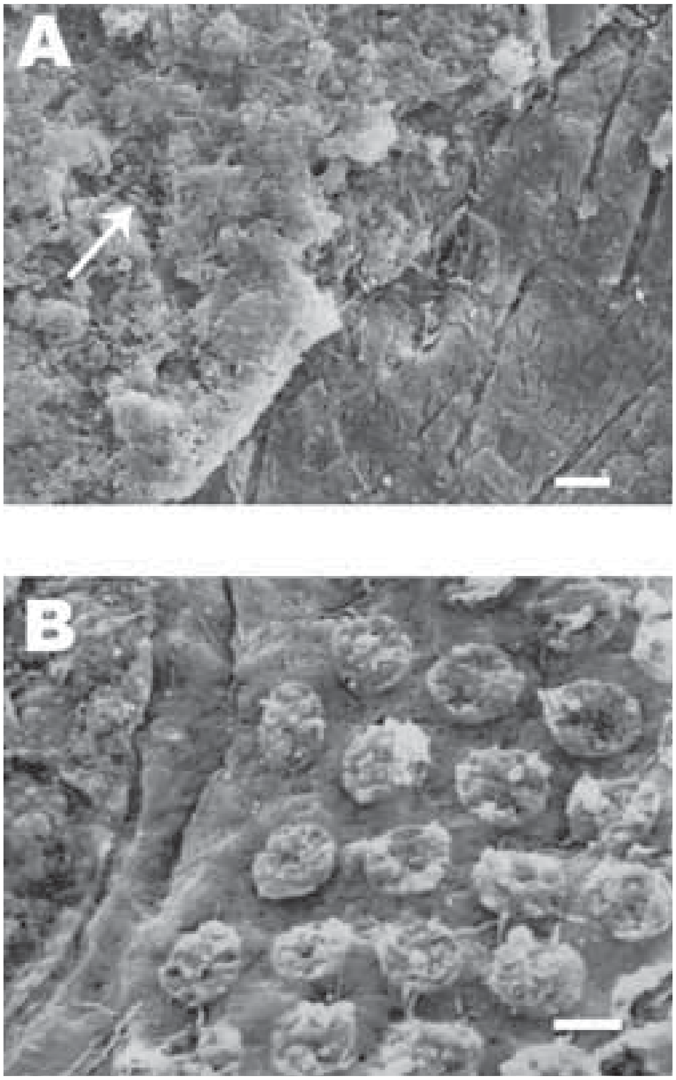

Figure 13. Scanning electron photomicrographs of fossils, Stewart Valley, Nevada. (A) Setae (small arrow) on insect leg. Large arrow points to smectite layer on top of diatom/mucus layer on leg. Scale = 6.0 µm. (B) Compound eye of insect. Scale = 1.39 µm.

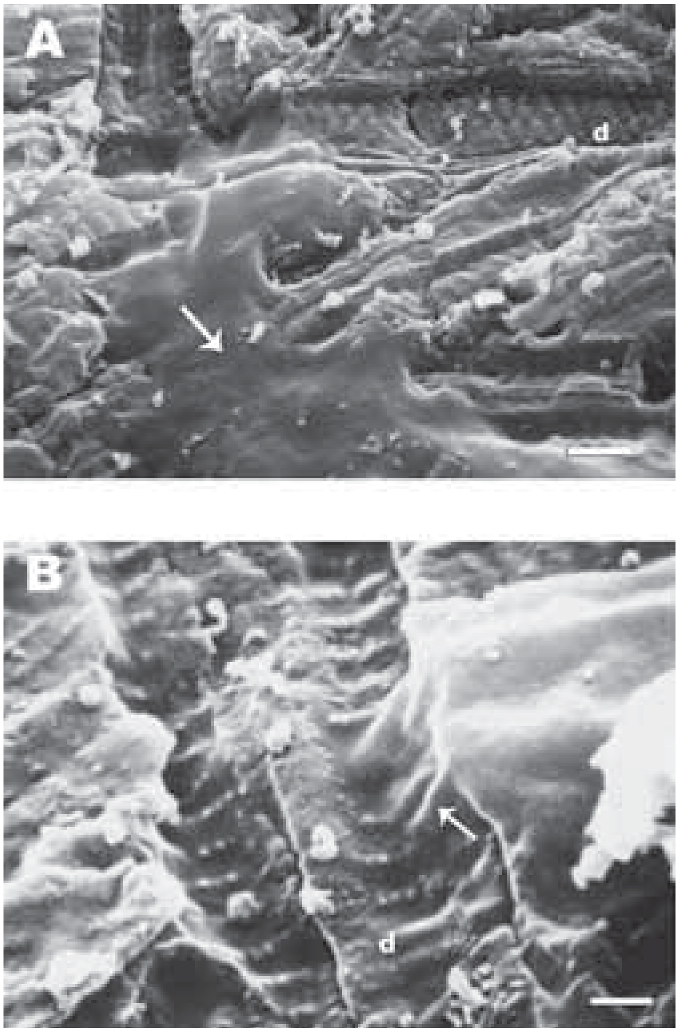

Figure 14. Scanning electron photomicrographs of biofilms on fossil diatoms, Shanwang deposit. Arrows point to biofilm on diatom (d). Scale = 1.67 µm (A); 0.77 µm (B).

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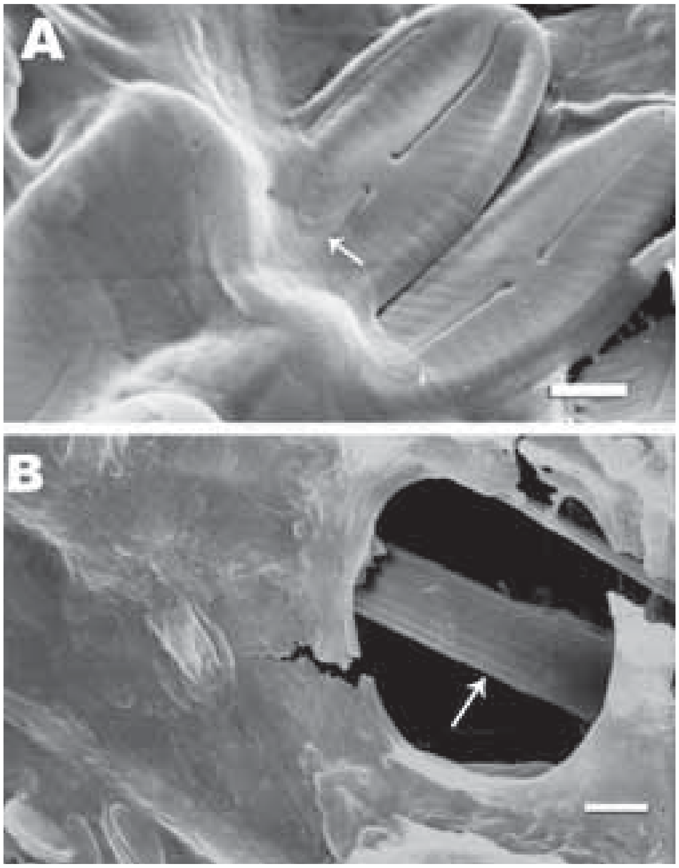

Figure 15. Scanning electron photomicrographs of biofilm mats on modern diatoms grown in the laboratory. (A) Biofilm mat (arrow) covering *Synedra.* Scale = 1 µm. (B) Hole in biofilm mat produced by *Navicula.* This mat grew on a bee, which was added to the test tube during blooming. Arrow shows setae visible below mat. Notice crack in biofilm mat at left of hole and diatoms in biofilm (lower left). Scale = 6.6 µm.

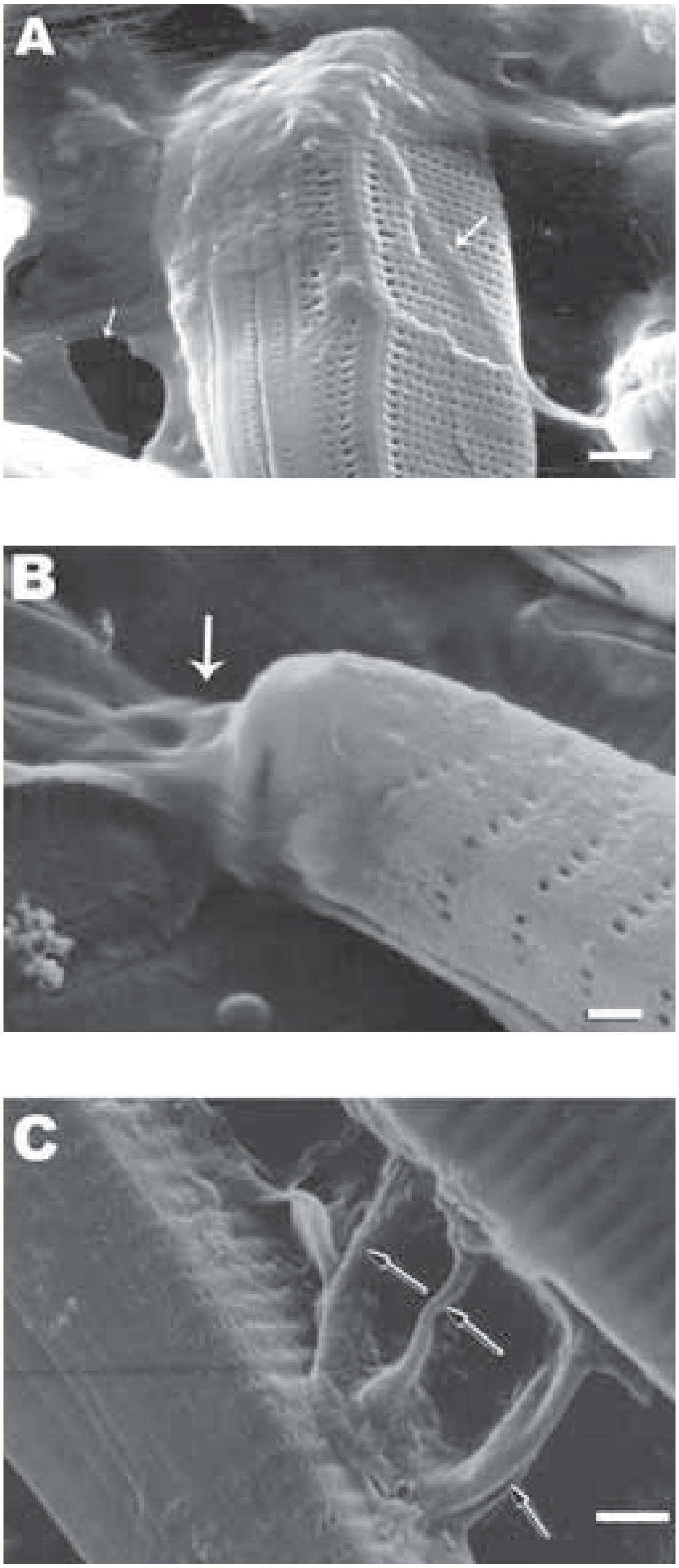

Figure 16. Scanning electron photomicrographs of mucus strands on diatoms grown in the laboratory. (A) Mucus on *Nitzschia* (strands, large arrow; hole in biofilm at small arrow). Scale = 1.12 µm. (B, C) Mucus strands emanating from *Synedra* (arrows). Scale = 0.58 µm (B); 1.85 µm (C).

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Higher taxa as paleoecological and paleoclimatic indicators: A search for the modern analog of the Florissant fossil flora

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ABSTRACT

We used higher taxonomic composition of 241 modern forest plots from across the New World to identify the closest modern analog of the Florissant fossil flora and to infer late Eocene paleotemperature for Florissant. Nonmetric multidimensional scaling (NMS) based on both genus and family presence-absence placed Florissant in a no-analog taxonomic space surrounded by North American warm temperate broad-leaved forests, Mexican humid pine-oak forests, and subtropical moist forests from Florida, Mexico, and Argentina. The site most similar to Florissant, as indicated by the mean of Euclidean distances in genus and family NMS space, was a subtropical moist forest in southern Florida, followed by the humid pine-oak forests of central and northeastern Mexico, and the broad-leaved deciduous forests of eastern North America. Weighted-averaging partial least-squares regression (WAPLS) based on genus composition predicted a mean annual temperature (MAT) for Florissant of 14.7 ± 2.2 °C. WAPLS based on family composition predicted a MAT of 15.6 ± 2.5 °C. Our estimates fall between the relatively cool temperatures predicted by leaf physiognomy and the higher temperatures predicted by the nearest living relative method. Although this study demonstrates the feasibility of using higher taxa for paleoclimate reconstruction and analog analysis, its methods are subject to many of the same biases and assumptions as other biological proxy techniques. Furthermore, interpreta-

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tion of differences between results obtained using different taxonomic levels remains unclear. Some of these limitations may be resolved by employing methods based on phylogenies rather than taxonomic ranks.

Keywords: higher taxa, modern analog, multivariate analysis, paleoclimate reconstruction, vegetation.

INTRODUCTION

Quantitative estimation of paleoclimate is fundamental to reconstruction of past environmental and biotic change and provides a baseline for predicting the effects of future regional and global climate change (Liu and Colinvaux, 1988; Wilf, 1997; Behling, 1998; Wilson et al., 2005). Some of the most widely used methods employ biological proxies such as pollen, diatoms, or plant megafossils. Recent debate has focused on the relative merits of biological proxy methodologies, in particular with regard to precision and accuracy (Wolfe, 1995; Wilf, 1997), applicability to different time periods (Liang et al., 2003; Sachs et al., 1977; Wolfe, 1995), and taphonomic artifacts (Greenwood, 1992).

Two fundamentally different biological proxy techniques are based on leaf morphology and taxonomic composition. Leaf-morphological methods, which include both univariate (LMA, or Leaf Margin Analysis; e.g., Wolfe, 1979; Wilf, 1997) and multivariate (CLAMP, or Climate-Leaf Analysis Multivariate Program; Wolfe, 1995) algorithms, use empirically observed relationships between climatic parameters and the proportions of taxa possessing particular leaf morphological traits (e.g., toothed margins and leaf sizes) in modern vegetation to estimate climate on the basis of the same characters in fossil floras. Advantages of such “taxon-free” methodologies include a lack of dependence on accuracy of identification, insensitivity to low taxonomic overlap between modern and fossil sites, and spatial and presumably temporal consistency in the correlation between climate and the convergent morphological adaptations of unrelated taxa (but see Gregory-Wodzicki, 2000; Kowalski, 2002; Greenwood et al., 2004). Thus, leaf-morphological methods can be applied to both Quaternary and pre-Quaternary fossil assemblages. Disadvantages include applicability only to dicotyledonous angiosperm macrofossils and sensitivity to taphonomic biases in leaf morphology (Greenwood, 1992; Burnham et. al, 2005). Despite uncertainty regarding the mechanistic basis of the empirical climate-leaf morphology correlation (Wilf, 1997; but see Royer and Wilf, 2006), the strong empirical correlation between climate and leaf morphology in modern analyses remains the principal argument favoring the extensive use of these techniques in paleoclimate reconstruction.

Taxonomically based methods are founded on empirical relationships between modern climate and the distributions of taxa or taxonomic assemblages. Two commonly used taxonomic techniques are nearest living relative (NLR) methods and taxonomic calibration. NLR methods (including the coexistence approach of Mosbrugger and Utescher, 1997) define the range of possible values for a given paleoclimatic parameter by determining the climatic overlap for modern living relatives of members of the fossil assemblages. As with leaf-morphological methods, NLR methods can be applied to both recent and ancient fossil assemblages (but see Meyer, 2001) and they can be applied to essentially any group of fossil organisms for which NLRs can be reliably determined (e.g., Moe and Smith, 2005). However, the dependence of NLR methods on correct specimen identifications, accuracy of the underlying classification of both fossil and living taxa, choice of nearest living relative (based solely on morphology), and the assumption that climatic tolerances of particular taxa are constant over time has led some workers to question their reliability (Meyer, 2001; Wolfe, 1995).

Taxonomic calibration uses multivariate transfer functions based on modern taxon-climate relationships (the “calibration data set”) to estimate climatic parameters by using taxonomic composition of fossil assemblages. Rather than determining the boundaries (range) of coexistence, as in NLR methods, taxonomic calibration uses a weighted averaging of unimodal response (transfer) functions for each taxon along a given climatic axis to predict the expected value and error for that climatic parameter. Unfortunately, dependence on high taxonomic overlap between modern and fossil data sets means that calibration is typically applied only to relatively recent—usually Holocene—time periods (Sachs et al., 1977; Wolfe, 1995).

Despite the extensive use of paleoecological transfer functions in paleoclimate reconstruction of Quaternary assemblages (e.g., Antoniades et al., 2004; Heiri et al., 2003; Schmidt et al., 2004), their application to deeper time is regarded as problematic for two reasons: (1) lack of overlap between modern and fossil data sets, and (2) likelihood of major shifts in environmental tolerances of calibration taxa over deep evolutionary time (Sachs et al., 1977). These limitations are exacerbated by the use of species as the taxonomic unit of choice in taxonomic calibration analyses, and the assumption that low species-level overlap (“no-analog” conditions) invalidates the method (Sachs et al., 1977). However, we are not aware of any studies that have critically examined the assumption that species are inherently preferable as units of calibration for paleoecological transfer functions.

In cases where species overlap is minimal between modern and fossil assemblages, similarity at higher taxonomic levels can still be high. For example, 100% of plant species recorded from the late Eocene Florissant fossil beds are extinct, yet ~90% of the genera and 100% of the families are currently considered to be extant (Meyer, 2003). Thus, higher taxa may permit comparison where none would be possible using species. Under some circumstances, analyses based on higher taxa may be less likely to violate assumptions of phylogenetic conservatism. Even when taxonomic overlap is sufficient to permit a species-level analysis, phylogenetic inertia of climate-associated traits (Prinzing et al., 2001; Webb et al., 2002) implies that higher taxa may provide a more conservative climatic signal in ancient fossil assemblages—albeit at the cost of decreased precision. Even in modern forests there is growing evidence that trait distributions "across forest types are closely linked with patterns of floristic composition at the genus and family level" (Chazdon et al., 2003, p. 343).

The Florissant Fossil Beds Flora: A Test of Higher Taxa as Tools for Paleoclimate Reconstruction and Modern Analog Analysis

The Florissant fossil beds of Colorado have been a focus of research concerning the climate, topography, biota, and ecological associations of the late Eocene southern Rocky Mountains (Meyer, 2003). Decades of taxonomic work on Florissant fossils have documented at least 145 species of plants and more than 1500 species of insects and spiders, as well as several fish, mammals, and birds (Meyer, 2003). Previous research has examined the biogeographic origins and affinities of the Florissant flora (Leopold and MacGinitie, 1972; MacGinitie, 1953; Manchester, 1999; Leopold et al., this volume). In addition, research has focused on reconstructing late Eocene climate at Florissant, using biological proxies such as taxonomic composition of plants and insects and leaf morphology to infer paleotemperature and precipitation (e.g., Wolfe, 1994; Leopold and Clay-Poole, 2001; Moe and Smith, 2005; see review *in* Meyer, 2001) as well as paleoelevation (Meyer, 2001, 2003). However, conflicting interpretations still exist concerning several key questions of relevance not only to Florissant, but to paleoclimatic and paleoecological research in general. In particular, the wide range of paleoclimate estimates for Florissant continues to be a focus of debate. Does fossil evidence support a temperate, subtropical, or tropical climate, and what definitions for these terms are used? Do paleotemperature estimates imply a paleoelevation similar to or substantially different from Florissant's current altitude of 2550 m (Gregory and Chase, 1992; Meyer, 1992, 2001)? Resolution of the last question in particular has profound implications for the history of tectonic uplift in the southern Rockies (Trimble, 1989; Meyer, 2001). In addition, relationships of the Florissant flora to modern-day plant communities remain controversial. Which modern plant assemblages and biogeographic regions show the strongest affinities with Florissant (Leopold and MacGinitie, 1972; MacGinitie, 1953; Manchester, 1999; Leopold and Clay-Poole, 2001; Leopold et al., this volume)? Does a contemporary equivalent to the Florissant flora exist, or was Florissant a mixture of floristic elements with no close modern analog (Meyer, 2003)? If the latter, then the rationale behind paleoclimate reconstruction for Florissant by means of NLR and other taxonomic approaches may be called into question.

In this study, we address these issues using a large, geographically extensive database of modern New World forest inventories. Although calibration data sets of diatoms and pollen have been used extensively for analog analysis and paleoclimate reconstruction (e.g., Antoniades et al., 2004; Behling, 1998; Birks, 1998; Overpeck et al., 1992; Sachs et al., 1977, Schmidt et al., 2004), to our knowledge this study is the first to use modern ecological samples of forest communities to address such questions for a macrofossil plant assemblage. Furthermore, in contrast to claims that the application of modern analog analysis (Jackson and Williams, 2004) and paleoecological transfer functions (Sachs et al., 1977; Wolfe, 1995) is limited to the Quaternary, we demonstrate the feasibility of extracting compositional information and climatic signal from a late Eocene fossil assemblage by using higher taxa as units of comparison with modern plant communities.

METHODS

Florissant Taxa

We compiled a list of families and genera known from Florissant (Table 1) based in part on Leopold et al. (this volume), Manchester's updated review of Florissant megafossil taxa (Manchester, 2001), Leopold and Clay-Poole's review of the Florissant pollen flora (Leopold and Clay-Poole, 2001), and personal observations by B.B. and H.M. of fossils documented in the Florissant fossil beds database (Meyer et al., 2002). Our list thus excludes many doubtfully determined taxa originally reported for Florissant by MacGinitie (MacGinitie, 1953). Further, it should be emphasized that some of the taxa assigned by MacGinitie to extant genera were later selectively examined in detail using multiple organ reconstructions (e.g., Manchester, 1989, 1992; Manchester and Crane, 1987), and found to represent extinct genera. It is possible, therefore, that as additional fossil material becomes available to enable further multiple organ analyses of other taxa, some of the Florissant genera that we have included as extant could be determined to be extinct. In addition, we excluded genera or families currently known to be exclusively herbaceous (e.g., Nymphaeaceae), as such growth forms are not included in the modern forest data set used in this study. We did, however, retain taxa with both herbaceous and subwoody members (e.g., Onagraceae), as many small shrubs and robust herbs potentially exceed the 2.5 cm minimum stem diameter of the 0.1 ha sampling methodology (see "Modern Forest Samples," below).

Modern Forest Samples

For comparison with the Florissant flora, we compiled a set of 241 one-tenth-hectare forest transects, the largest and most geographically extensive data set available to us at the time based on a single methodology. Despite the small area of these plots, the low size cutoff of stem diameter (which enables inclusion

TABLE 1. FAMILIES AND GENERA OF WOODY PLANTS CONFIDENTLY RECORDED FROM FLORISSANT AND USED IN THIS ANALYSIS

Family	Genus	Sources
Aceraceae	*Acer*	1, 2, 3
	Dipteronia	1, 3
Anacardiaceae	cf. *Rhus*	1, 3, 4
Apocynaceae	*Tabernaemontana**	1, 2
Araliaceae	[unidentified genus]	2, 3, 4, 6
Arecaceae	[unidentified genus]	1, 2, 3
Berberidaceae	*Berberis* (=*Mahonia*)	1, 2, 3
Betulaceae	*Alnus**	1
	Asterocarpus[†]	1, 3
	*Betula**	1
	Paracarpinus[†]	1, 3
Buxaceae*	[unidentified genus, cf. *Sarcocca or Pachysandra*]*	1, 4, 5
Cannabaceae	*Humulus*	2, 6
Caprifoliaceae	*Diplodipelta*[†]	1, 3
	Sambucus	1, 2, 3
	cf. *Viburnum**	2, 5
Chenopodiaceae*	*Sarcobatus**	1, 2
Cupressaceae	*Chamaecyparis*	1, 3
	Sequoia	1, 3
Dioscoreaceae	*Dioscorea*	1, 3
Elaeagnaceae*	*Elaeagnus**	1, 2
Ephedraceae	*Ephedra*	1, 2
Ericaceae, s.l.*	[unidentified genus]*	2, 5
Eucommiaceae	*Eucommia*	1, 3
Euphorbiaceae	*Croton**	1, 2
Fabaceae	*Caesalpinites*[†]	1, 3
	Cercis	1, 2, 3
Fagaceae	*Fagopsis*[†]	1, 2, 3
	Quercus	1, 2, 3
Grossulariaceae	*Ribes*	1, 3
Hydrangeaceae	*Hydrangea*	1, 3
	cf. *Philadelphus*	3, 6
[Incertae sedis]	*Deviacer*[†]	1
Juglandaceae	*Carya*	1, 2, 3
	*Cyclocarya**	1, 2
	[unidentified genus, Engelhardieae]*	1, 2, 5
	Juglans	1, 2
	*Platycarya**	1, 2
	Pterocarya	1, 2
Lauraceae	[unidentified genus, cf. *Lindera*]	1, 3, 6
	[unidentified genus, cf. *Persea*]	1, 3, 6
Meliaceae	[unidentified genus, *Cedrela* or *Toona*]	1, 3
Onagraceae	*Semeiandra**	1, 2
	*Xylonagra**	1, 2
	[unidentified genus]	3
Pinaceae	*Abies*	1, 3
	Picea	1, 3
	Pinus	1, 3
	*Tsuga**	1, 3
Platanaceae	*Platanus*	1
Podocarpaceae*	*Podocarpus**	1
Rhoipteleaceae*	cf. *Rhoiptelea**	1, 2
Rosaceae	*Amelanchier*	1, 3
	Cercocarpus	1, 3
	Crataegus	1, 3
	Holodiscus	1, 3
	Prunus	1, 3
	Rosa	1, 3
	(*continued*)	

TABLE 1. FAMILIES AND GENERA OF WOODY PLANTS CONFIDENTLY RECORDED FROM FLORISSANT AND USED IN THIS ANALYSIS (*CONTINUED*)

Family	Genus	Sources
Rosaceae	*Rubus*	1, 3
	Vauquelinia	3, 6
Salicaceae	*Populus*	1, 2, 3
	Salix	1, 2, 3
Sapindaceae	*Cardiospermum*	1, 2, 5
	Koelreuteria	1, 2, 3
	*Thouinia**	2, 5
Simaroubaceae	*Ailanthus*	1, 3
	Chaneya[†]	1
Smilacaceae	*Smilax*	1
Sterculiaceae	*Florissantia*[†]	1, 2, 3
	cf. *Fremontia**	4, 5
Taxaceae	*Torreya*	1, 3
Ulmaceae	*Cedrelospermum*[†]	1, 3
	*Pteroceltis**	1
	cf. *Ulmus*	1, 3
Vitaceae	*Parthenocissus*	2, 6, 7
	Vitis	2, 6, 7

Note: Taxa in square brackets excluded from genus analyses due to uncertainty at that taxonomic level. Classification follows Cronquist, 1981, after Leopold and Clay-Poole, 2001. s.l.—sensu lato. Sources: 1—Leopold et al. (this volume); 2—Leopold and Clay-Poole (2001, Table 1), 3—Manchester (2001, Table 1); 4—S. Manchester, 2007, personal commun.; 5—E. Leopold, 2007, personal commun.; 6—B. Boyle, personal observation; 7—H. Meyer, personal observation.

*Known from pollen only; all other taxa documented from macrofossils, or macrofossils and pollen combined.

[†] Extinct.

not only of trees, but also of shrubs, lianas, hemiepiphytic climbers, and even robust herbs such as Heliconiaceae) provides a more complete sample of whole-community plant diversity than many other widely used sampling methodologies (see Phillips et al., 2003, for a quantitative evaluation of the merits of 0.1 ha transects).

Our largest source of 0.1 ha transect data was "The Alwyn H. Gentry Forest Transect Data Set," a compilation of 228 one-tenth-hectare transects of plants ≥2.5 cm dbh (diameter at breast height) collected in temperate and tropical forests by the late Al Gentry and colleagues (Phillips and Miller, 2002; raw data available from http://www.mobot.org/MOBOT/research/gentry/transect.shtml). Four of these samples were collected in part or in their entirety by the first author (KITLOPE1, KITLOPE2, GUANUP, MAQUIPUC; Appendix 1). We used the version of the Gentry data set available from the SALVIAS Web site (www.salvias.net; Enquist et al., 2002), as this version has undergone extensive error correction and taxonomic standardization (see http://www.salvias.net/pages/database_info.php#Plant_inventories). Taxonomic standardization is currently complete only for New World samples; thus we restricted our analysis to the subset of 181 plots from North, Central, and South America (source 1 in Appendix 1).

We included an additional 60 plots collected at New World localities using the same 0.1 ha transect methodology. Of the 56 plots collected by the first author (Boyle, 1996; sources 2–4 in Appendix 1), seven were collected specifically for this study (CEILO750, ELCUJETE, LAGLORIA, LAMARCEL, LAPENA, MIQUIHUA, SANJOSE, all from Tamaulipas state in northeastern Mexico; Appendix 1) with the assistance of the second and third authors. Three plots were collected by the fourth author (ELCHORR, LABAMBA, LACOTOR; source 5 in Appendix 1; unpublished data). An additional plot was provided by S. DeWalt (BVGENTRY; source 6 in Appendix 1; DeWalt et al., 1999). All plot data used in this study can be downloaded from the SALVIAS Project Web site (www.salvias.net).

Eighty-four plots (35%) had existing climatic data from long-term observations at weather stations located close by at the same elevation. For the remaining sites, we estimated MAT using the WORLDCLIM 2.5 min gridded climate database (see Hijmans et al., 2005 for details of this high resolution global climate model). WORLDCLIM data (version 1.4) were obtained from the WORLDCLIM Web site (Hijmans et al., 2004).

We classified plots into Holdridge life zones (Holdridge, 1967), a widely used climate-based vegetation classification system (Lugo et al., 1999; Ray et al., 2006; Roy et al., 2006). Holdridge life zones are categories of actual and potential evaporation based on three climatic parameters: (1) mean annual biotemperature, (2) annual precipitation, and (3) potential evapotranspiration ratio (PET). Mean annual biotemperature (MAB) is equivalent to mean annual mean temperature, with the exception that all temperatures below zero are set to zero (for most tropical and subtropical localities, biotemperature and mean annual temperature are identical). In practice, the life zone of a given site is summarized by the combination of a latitudinal belt (based on the mean annual biotemperature at sea level for the latitude of the site), an altitudinal belt (based on mean annual biotemperature at the site), and a humidity province (based on total annual precipitation). Latitudinal belts span the following ranges of MAB at sea level: >24 ºC (tropical), 18–24 ºC (subtropical), 12–18 ºC (warm temperate), 6–12 ºC (cool temperate), and 3–6 ºC (boreal). Altitudinal belts span the following ranges of MAB: >24 ºC (lowland, not included in life zone name), 18–24 ºC (premontane), 12–18 ºC (lower montane), and 6–12 ºC (montane). The altitudinal belt immediately above lowland becomes the lowland belt at the next higher latitude; hence, the altitudinal belt immediately above lowland in Subtropical life zones is Lower Montane, whereas in Warm and Cool Temperate life zones it is Montane. Transitions between adjacent humidity provinces are equivalent to a doubling of total annual precipitation. For Tropical (lowland) life zones, the humidity provinces Arid, Very Dry, Dry, Moist, Wet, and Pluvial correspond to categories of >250–500, >500–1000, >1000–2000, >2000–4000, >4000–8000, and >8000 mm total annual precipitation, respectively (see Holdridge, 1967).

The final data set contained 241 forest plots ranging from 40°S in temperate Chile to boreal forest at 54°N in Canada (Fig. 1; Appendix 1). Represented were 36 different life zones (Appendix 2), with best coverage of tropical moist and wet forest ("tropical rainforest"), tropical lower montane and montane wet to pluvial forest ("cloud forest"), tropical dry forest, and warm temperate and cool temperate moist forest ("temperate broad-leaved forest"). By latitudinal belt, the majority of sites were tropical (182 plots), followed by subtropical (27 plots), warm temperate (25 plots), and cool temperate (6 plots), with only one boreal sample. Plots were divided roughly equally between lowland (131 plots) and upland sites (110 plots; premontane, lower montane, and montane forests combined).

Several major vegetation types were absent from or underrepresented in this data set. These included Boreal forest, Temperate Dry forest, and Arid to Very Dry vegetation (deserts and "thorn forest") at all latitudes. Important New World floristic regions absent or underrepresented included semi-arid eastern Brazil (Caatinga and Cerrado vegetation), subtropical South America, and California Floristic Province. Despite these shortcomings, these data represent the most geographically and ecologically extensive set of vegetation samples currently available based on a single methodology.

Modern Analog Analyses

We used nonmetric multidimensional scaling (NMS) to assess similarity between Florissant and modern forest plots. We did this in two steps. First, we performed a nonmetric multidimensional scaling (NMS) ordination of the site-by-taxon matrix of 241 modern plots, excluding Florissant. Second, we used the NMS Scores method (see McCune et al., 1997) to predict Florissant's scores, based on extant taxa, on ordination axes from step one, thus providing an independent projection of the Florissant taxonomic assemblage in modern taxonomic space.

We performed separate NMS analyses using genera and families. We did so to examine the differences between the information transmitted at different taxonomic levels. In particular, if families and genera produce similar results, then families may be preferable as biological proxies, given their reduced sensitivity to identification error and the potentially greater overlap between modern and ancient fossil assemblages.

To assess overall taxonomic similarity, we standardized NMS scores to vary from 0 to 1, where 0 is the minimum and 1 is maximum score along a given axis. We then calculated pairwise standardized distances between all 241 modern forest plots in each analysis. Overall taxonomic distance between any two sites was calculated as the mean of the standardized Euclidean distances in genus and family space. We then ranked overall taxonomic similarity of all sites to Florissant, based on ascending overall taxonomic distance.

Finally, we addressed the question, "Is Florissant a no-analog assemblage with respect to the higher taxonomic composition of modern vegetation?" by comparing taxonomic distances between Florissant and its ten nearest modern samples with ten-nearest-neighbor distances for each of the 241 modern forest plots.

To permit comparison between modern and fossil floras, we used taxon presence-absence in all analyses, and the Sorensen Index as the distance measure (Magurran, 1988). NMS ordinations

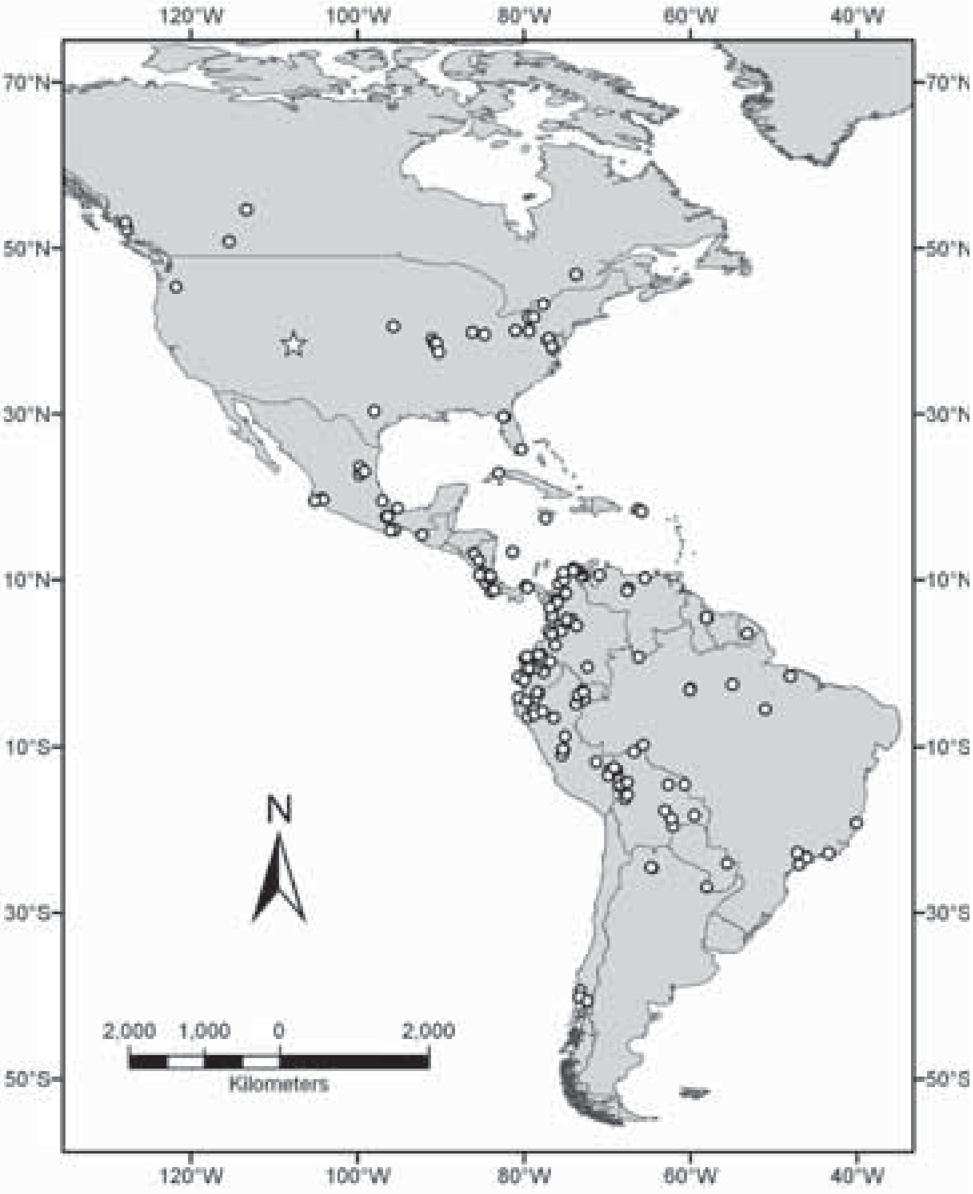

Figure 1. Locations of the 241 modern forest plots used in this analysis. For comparison, location of the Florissant fossil beds indicated by star. See Appendix 1 for details of plot localities, vegetation, climate, and sources.

were performed using PC-ORD, version 4.14 (McCune and Mefford, 1999).

Paleotemperature

Validation Analysis: Higher Taxa and Ecological Transfer Functions

To assess differences in precision and accuracy of predictions of calibration models based on different taxonomic levels, we performed a validation test using families, genera, and species to construct separate weighted-averaging partial least-squares regression (WAPLS) estimates of MAT for modern forest plots. We randomly divided the original 241 modern forest plots into independent training (n = 120) and test (n = 121) data sets. We then used the program WAPLS, version 1.5 (Juggins and Ter Braak, 2002) to model the relationship between MAT and taxonomic composition of the training data set, and used the resultant transfer functions to obtain independent MAT estimates for the test data set. We performed this analysis using family, genus, and species presence-absence, and compared differences in error and bias of actual versus predicted MAT of the test data set, as well as sample-specific error and bias estimates for calibration models, as based on leave-one-out jackknife estimates with 9999 randomizations (Birks, 1995).

Paleotemperature Estimation

We constructed WAPLS calibration models based on composition and MAT of the 241 modern forest plots, and applied the resulting transfer functions in estimating MAT for Florissant. We performed two sets of predictions, one based on genera and the other based on families. Because taxa known only from pollen may not reflect local environmental conditions, and consequently may generate climatic signals different from those of taxa documented by macrofossils (Mosbrugger and Utescher, 1997), we also repeated the above analyses using a reduced Florissant taxonomic list restricted to taxa documented by macrofossils (or macrofossils plus pollen), excluding taxa documented by pollen alone. Sample-specific root mean squared error of prediction (RMSEP), average bias, and maximum bias were calculated by the leave-one-out jackknife method with 9999 permutations. Model selection followed Birks (1998). WAPLS modeling and predictions were performed using WAPLS, version 1.51 (Juggins and Ter Braak, 2002).

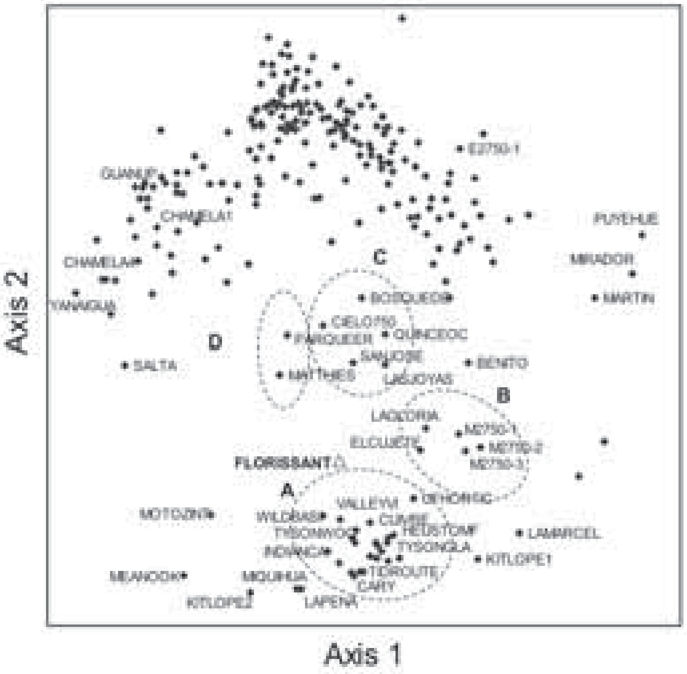

Figure 2. Nonmetric multidimensional scaling (NMS) of genus presence-absence of 241 one-tenth ha modern forest inventories, with the predicted NMS scores of the Florissant fossil flora in modern taxonomic space. Axis 2 corresponds to a temperature gradient of increasing mean and decreasing variance (seasonality) from bottom to top; Axis 1 to a precipitation gradient of increasing total and decreasing variance (seasonality) from left to right. Thus, tropical humid forests fall toward the upper right, tropical dry (seasonally deciduous) forests toward the upper left quadrant, cloud forests at middle-right, and temperate forests along the bottom. Dashed lines group plots of similar forest types closest to Florissant: (A) Temperate broad-leaved forests of eastern North America. (B) Humid montane pine forests of northern and central Mexico. (C) Humid montane broad-leaved forests (cloud forests) of northern and central Mexico. (D) Subtropical semi-deciduous forests of Florida, northeastern Mexico, and Argentina. For clarity, only labels of selected plots closest to Florissant (open triangle) are shown.

RESULTS

Modern and Fossil Data Sets

Excluding undetermined genera and one incertae sedis family, the final list of Florissant woody taxa (Table 1) consisted of 67 identified genera, 58 of which (86.6%) are extant, and 39 families, all of which are extant. The database of 241 modern forest plots contained a total of 159 families, 1199 genera, and 1771 species (the latter total excluding morphospecies not referable to known taxa). Of the families and genera included in our list of Florissant woody taxa, 30 families (76.9%) and 35 genera (51.5%) also were present in the modern data set. Excluding taxa known only from pollen reduced this overlap to 27 families (69.2%) and 27 genera (39.7%).

Modern Analog Analysis

NMS analyses of modern forest plots resulted in significant two-axis solutions with final stresses of 17.74 (genera) and 14.14 (families; both $p < .05$, Figs. 2 and 3, respectively). Both analyses grouped plots into clusters corresponding to similar climate and vegetation categories, with one axis (Axis 2 in Figs. 2 and 3) corresponding to parallel gradients of increasing mean and decreasing variance (seasonality) of temperature, and a second axis (Axis 1 in Figs. 2 and 3) corresponding to parallel gradients of increasing total and decreasing seasonality of precipitation. Thus, plots tended to separate into temperate, subtropical, and tropical groupings along the temperature axis, and to spread

Figure 3. Nonmetric multidimensional scaling (NMS) of family presence-absence of 241 one-tenth-hectare modern forest inventories, with the predicted NMS scores of the Florissant fossil flora in modern taxonomic space. Details as in Figure 2.

out along aseasonal-dry to a seasonal-wet precipitation gradient along the precipitation axis.

In both analyses, Florissant's predicted NMS scores placed it in an unoccupied space surrounded by the subtropical semi-deciduous forests (Subtropical Moist life zone) of Florida, northern Mexico, and Argentina, the humid pine-oak forests (Subtropical Montane Moist and Wet life zones) of central and northern Mexico, and the temperate broad-leaved forests (Warm Temperate Moist life zone) of eastern North America (Figs. 2 and 3). Florissant's position varied only along Axis 2 between the two analyses, placing it closer to temperate forests in the genus-level analysis, and closer to subtropical forests in the family-level analysis. Although positions of some low-diversity plots (three or fewer species) varied dramatically owing to shared families but nonoverlapping genera (e.g., sites BURSTALL, TIMBERLI and LAMARCEL in Figures 2 and 3 all have only a single family, Pinaceae, but one to three species each in different genera), the placement of modern sites differed little between the two analyses.

The single most similar plot to Florissant, as measured by the mean of standardized Euclidean taxonomic distances in family and genus NMS space, was a Subtropical Moist forest from southern Florida (MATTHIES, also the single most similar plot at genus level; Table 2). Of the next 19 most similar plots, three were from pine-oak and humid pine-oak forest (subtropical montane moist, subtropical montane, and lower montane wet life zones) of central and northeastern Mexico (SANJOSE, LAGLORIA, LASJOYAS), and three from subtropical semi-deciduous forest (subtropical lower montane moist life zone) in Mexico (CIELO750, BOSQUEDE) and northern Argentina (PARQUEER). Three of the five Mexican plots (CIELO750, SANJOSE, LAGLORIA) were from different elevations along a single elevational gradient in the El Cielo Biosphere Reserve in the northeastern state of Tamaulipas (Appendix 1). All of the remaining 12 most similar forests were from temperate broad-leaved forests of the eastern and south-central United States (warm temperate moist and warm temperate montane moist life zones). Two of these (CUIVRE and WILDBASI, from Missouri and Texas, respectively) were the most similar plots at the family level.

Despite these similarities, Florissant was significantly more dissimilar from its ten nearest neighbors than the majority of modern forests (mean Florissant nearest-neighbor distance = 0.166; median modern plot nearest-neighbor distance = 0.064; t = 5.85, $p < .0001$). However, Florissant was not the only taxonomically distinctive site: comparing ten-nearest-neighbor distances for Florissant with those of all 241 modern forest plots, Florissant ranked 13th in mean Euclidean taxonomic distance, 12th in family distance, and 18th in genus distance (Table 3).

Paleotemperature

Validation Analysis

For the modern test data set, WAPLS based on the higher taxonomic levels of family and genus provided similar (but not identical) predictions of MAT to the species-level WAPLS (Fig. 4). Slopes of the regression lines of observed versus predicted

TABLE 2. MODERN FOREST PLOTS MOST SIMILAR TAXONOMICALLY TO THE FLORISSANT FOSSIL FLORA

Plot code	Location	Forest type	Genus distance	Family distance	Mean taxonomic distance
MATTHIES	USA, Florida	Subtropical moist	0.09	0.18	0.14
SANJOSE	Mexico, Tamaulipas	Subtropical lower montane wet	0.14	0.17	0.16
CUIVRE	USA, Missouri	Warm temperate moist	0.20	0.12	0.16
WILDBASI	USA, Texas	Warm temperate montane moist	0.22	0.10	0.16
VALLEYVI	USA, Missouri	Warm temperate moist	0.23	0.10	0.17
CEDARBLU	USA, Indiana	Warm temperate moist	0.20	0.14	0.17
TYSONWOO	USA, Missouri	Warm temperate moist	0.23	0.12	0.18
BABLERSP	USA, Missouri	Warm temperate moist	0.18	0.17	0.18
INDIANCA	USA, Nebraska	Warm temperate moist	0.20	0.16	0.18
LAGLORIA	Mexico, Tamaulipas	Subtropical montane wet	0.20	0.16	0.18
POTOMAC	USA, Virginia	Warm temperate moist	0.18	0.20	0.19
HEUSTOBM	USA, Ohio	Warm temperate moist	0.25	0.15	0.20
LASJOYAS	Mexico, Jalisco	Subtropical montane wet	0.21	0.19	0.20
TYSONGLA	USA, Missouri	Warm temperate moist	0.25	0.16	0.20
PARQUEER	Argentina	Subtropical lower montane moist	0.17	0.24	0.20
CIELO750	Mexico, Tamaulipas	Subtropical lower montane moist	0.18	0.24	0.21
UFHORTIC	USA, Florida	Warm temperate moist	0.28	0.15	0.21
BOSQUEDE	Mexico, Veracruz	Subtropical lower montane moist	0.14	0.28	0.21
HEUSTOMF	USA, Ohio	Warm temperate moist	0.27	0.16	0.21
SANFELAS	USA, Florida	Warm temperate moist	0.26	0.17	0.22

Note: Distance is Euclidean distance in NMS (nonmetric multidimensional scaling) analyses of family and genus presence-absence. Taxonomic distance is mean of genus and family distance. All distances scale from 0 to 1, where 0 is minimum distance and 1 is maximum distance observed among all pairwise contrasts of 241 modern forest plots. Double underlining indicates most similar and single underlining second most similar values in each column.

TABLE 3. TWENTY MOST DISTINCTIVE FORESTS

Site	Family	Genus	Mean Taxonomic Distance
BURSTALL	0.30	0.25	0.37
TIMBERLI	0.30	0.22	0.34
LAMARCEL	0.30	0.19	0.30
PUYEHUE	0.24	0.24	0.27
MEANOOK	0.20	0.23	0.26
MIRADOR	0.21	0.23	0.24
MOTOZINT	0.21	0.21	0.23
MARTIN	0.14	0.20	0.19
KITLOPE1	0.14	0.15	0.18
KITLOPE2	0.13	0.15	0.18
M2750-2	0.18	0.13	0.18
MATTHIES	0.15	0.18	0.17
FLORISS	0.17	0.13	0.17
M2750-3	0.17	0.13	0.16
M2750-1	0.17	0.13	0.16
LAGLORIA	0.16	0.12	0.16
ALTERDOC	0.13	0.10	0.16
MIQUIHUA	0.18	0.10	0.16
LAPENA	0.15	0.09	0.16

Note: Table represents the 20 most distinctive forests (among 241 modern plots, plus the Florissant fossil flora) as determined by mean Euclidean distance to the ten nearest neighbors in NMS taxonomic space (see Figs. 2 and 3). Sites are ranked in descending order by mean taxonomic distance (the mean of family and genus distance). Florissant ranked 13th in mean taxonomic distance, 12th in family distance, and 18th in genus distance. See Appendix 1 for details of modern plot locations and vegetation types.

MAT did not differ (combined ANCOVA with interaction term, interaction $F_{2,2} = 0.982$, $p = .376$). Family-level and genus-level intercepts were 0.34 and 0.74 degrees lower, respectively, than species-based estimates. However, only the genus-level estimate was significantly different ($F_{1,359} = 1.27$, $p = .261$, and $F_{1,359} = 4.676$, $p = .032$; LS means contrasts of family versus species, and genus versus species, respectively).

Coefficients of determination increased with increasing taxonomic resolution, with R^2 increasing from 0.73 to 0.77 to 0.82 at the family, genus, and species levels, respectively (an increase of 12% overall from family to species level). This increase in precision toward lower taxonomic levels was accompanied by a large increase in the number of taxa used to build the calibration model: 159 families versus 1199 genera and 1771 species. All three taxonomic levels shared the similar and well-known bias of "the pull to the mean" (Birks, 1998): the tendency to overestimate low values and underestimate high values.

Florissant Paleoclimate

WAPLS calibration based on genera produced an estimated MAT for Florissant of 14.7 ± 2.2 ºC; family-level calibration produced an estimate of 15.6 ± 2.5 ºC (Table 4). Exclusion of

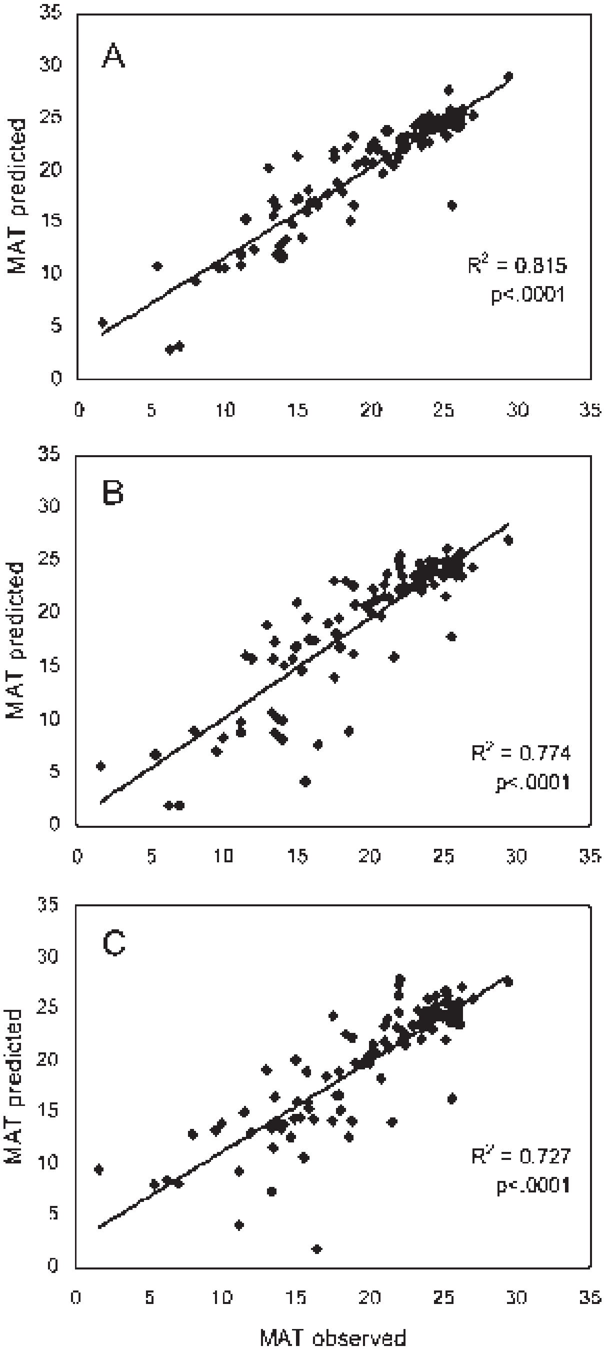

Figure 4. Observed versus predicted mean annual temperature (MAT) for test data set of 121 modern forest plots. Predictions were derived from weighted-averaging partial least-squares regression (WAPLS) models of taxonomic composition and MAT for a training data set of 120 plots. Training and test data sets are independent and were selected randomly from the full data set of 241 plots (see Appendix 1). Panels show the single best model at each of three taxonomic levels. Taxonomic level, number of model components, and prediction errors from leave-one-out jackknife validation as follows: (A) Species (1 component, RMSEP = 3.639, avg. bias = 1.096, max. bias = 17.813, jackknife $R^2 = 0.64$) (B) Genera (1 component, model, RMSEP = 2.930, avg. bias = 0.802, max. bias = 10.226, jackknife $R^2 = 0.74$). (C) Families (2 components, RMSEP = 2.462, avg. bias = 0.851, max. bias = 5.069, jackknife $R^2 = 0.85$).

TABLE 4. ESTIMATES OF MEAN ANNUAL PALEOTEMPERATURE (MAT, °C) FOR THE LATE EOCENE FLORISSANT FLORA, BASED ON WEIGHTED-AVERAGING PARTIAL LEAST-SQUARES REGRESSION OF FAMILY AND GENUS PRESENCE-ABSENCE

Climate variable	Model components	RMSEP	R^2	AVG. BIAS	MAX. BIAS	Estimate ± 1 SSE
Genus-level analysis						
MAT	2	2.1379	0.87	0.3136	8.4219	14.7 ± 2.2
Family-level analysis						
MAT	2	2.4247	0.81	0.2385	8.9794	15.6 ± 2.5

Note: Data based on 241 modern forest plots. RMSEP—(root mean squared error of prediction. AVG. BIAS, MAX. BIAS, and SSE (sample-specific standard error) are from leave-one-out jackknife simulation with 9999 randomizations.

Florissant taxa documented only from pollen had little effect on the genus-level temperature estimate (14.8 ± 2.3 ºC) and increased the family-level estimate slightly (to 16.8 ± 2.5 ºC).

DISCUSSION

What is the Closest Modern Analog of Florissant?

NMS at both genus and family level confirmed the intermediacy of the Florissant flora between modern deciduous forests of the eastern United States and the humid subtropical montane forests of central and northeastern Mexico. These results agree with previous qualitative comparisons that have aligned Florissant with one or the other, or both, of these major vegetation types (Leopold and Clay-Poole, 2001; Leopold and MacGinitie, 1972; MacGinitie, 1953). More surprising was Florissant's great similarity to subtropical semi-deciduous forests, as represented by the three samples MATTHIES (from near sea level in southern Florida), CIELO750 (from 750 m in Tamaulipas, Mexico) and PARQUEER (from 1000 m in northern Argentina). All three of these sites share moderately high annual temperatures and seasonality of precipitation. Taxonomically, all three sites share with Florissant characteristic proportions of taxa in the families Lauraceae, Sapindaceae, Vitaceae, and Rosaceae.

Although Florissant was indeed isolated taxonomically from its nearest neighbors relative to the majority of modern forest plots (Figs. 2 and 3, Table 3), the even greater "distinctiveness" of several modern plots, particularly from cool temperate and boreal North America, suggest that such dissimilarity could result in part from gaps in the modern data set. Thus, a more definitive answer to the question, "Is Florissant 'no analog' with respect to modern vegetation?" must await comparison with a more representative sampling of modern vegetation, in particular from regions such as California and temperate and subtropical Asia, where many nearest relatives of Florissant taxa survive to this day (e.g., Leopold et al., this volume).

The Florissant Climate

The range of temperatures spanned by our WAPLS-based temperature estimates (12.5–18.1 ºC) are consistent with a Warm Temperate lowland or Subtropical to Tropical highland climate (Fig. 5), and agree with results of other taxonomically based estimates (e.g., Leopold and Clay-Poole, 2001) in predicting higher temperatures than leaf-morphology methods (Table 5; Meyer, 2001; see also Liang et al., 2003). However, the values of 17.5–18 ºC estimated by MacGinitie (1953) and Leopold and

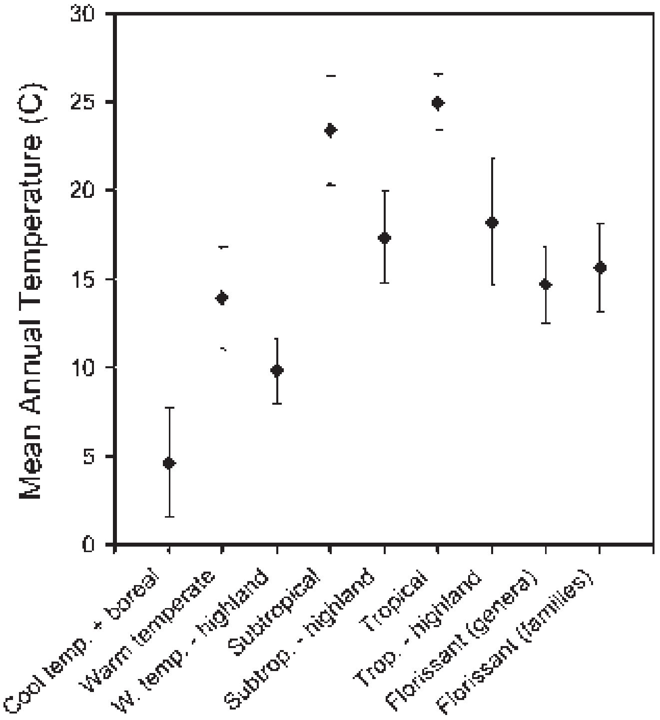

Figure 5. Estimated mean annual temperature (MAT) for late Eocene Florissant, as based on weighted-averaging partial least-squares regression (WAPLS) of genus and family composition of the Florissant flora, with 241 modern forest plots as the calibration data set. Separate estimates (mean ± 1 sample-specific standard error) were derived from genus and family presence-absence. Shown for comparison are mean values of MAT (±1 SE) for modern forest plots, grouped by the latitudinal and elevation components of their Holdridge life zones classifications (see Appendices 1 and 2). For tropical, subtropical, and warm temperate sites, elevational categories above lowland are combined as "highland." Cool temperate and boreal sites, both lowland and highland, are combined into the single category "Cool temperate + boreal."

TABLE 5. PREVIOUS PREDICTIONS OF MEAN ANNUAL TEMPERATURE (MAT) FOR THE LATE EOCENE FLORISSANT FLORA

Source	Method	MAT (°C)
MacGinitie (1953)	Nearest living relative	$\geq$18.0
Meyer (1986, 1992)	Physiognomic and floristic criteria	14 ± 1
Wolfe (1992)	Leaf morphology	12.0
Gregory and Chase (1992)	Leaf morphology	11.2 ± 2.0
Wolfe (1994)	Leaf morphology	10.8
Gregory (1994a)	Leaf morphology	10.7 ± 1.5
Gregory (1994b)	Leaf morphology	12.8 ± 1.5
Gregory and McIntosh (1996)	Leaf morphology	12.8
Leopold and Clay-Poole (2001)	Nearest living relative	~17.5

Clay-Poole (2001; Tables 4 and 5) lie within the upper end of our confidence limits, which also encompass at their low end the highest estimates based on leaf morphology.

The genus-level estimate of 14.7 ± 2.2 ºC may mark the lower bounds of plausibility for paleotemperature. The coldest end of the range of temperatures predicted (MAT = 14.5 °C; Table 4) implies a mean coldest month temperature of ~5 °C, with the possibility of infrequent but biologically significant freezing events. Such a climate approaches the modern temperature limits of several genera recorded from Florissant (e.g., *Tabernaemontana,* Arecaceae, *Cardiospermum, Cedrela/ Toona).* These taxa are widely scattered across the angiosperm phylogeny (e.g., Judd et al., 2002); their presence within the Florissant flora suggests either the independent loss of freezing resistance across multiple unrelated lineages or a late Eocene temperature regime for Florissant no colder than the montane subtropical and warm temperate climates where these taxa currently reach their northernmost distributional limits.

Although predictions at the two taxonomic levels were broadly overlapping, the family-level estimates were higher by roughly 1–2 ºC, with somewhat higher sample-specific errors. The reason for this difference is not clear, although it is notable that genera also tended to predict lower temperatures in the validation analysis as well (Fig. 4). One possible explanation is suggested by two aspects of the distribution of genera within families at Florissant: (1) the relatively large number of families with wide tropical distributions but represented at Florissant by one or two genera with mostly temperate distributions (e.g., Anacardiaceae–*Rhus*; Fabaceae–*Cercis*) or no currently identified genera (e.g., Lauraceae, Araliaceae, Arecaceae, Meliaceae), and (2) the presence of families with numerous temperate genera (e.g., Juglandaceae–*Carya, Cyclocarya, Juglans, Platycarya, Pterocarya*; Pinaceae–*Abies, Picea, Pinus, Tsuga*; Rosaceae–*Amelanchier, Cercocarpus, Crataegus, Holodiscus, Prunus, Rosa, Rubus, Vauquelinia*; see Table 1). Thus, in addition to overall higher error terms, higher taxa may introduce biases by obscuring patterns evident at lower taxonomic levels.

In the case of Florissant, it appears that taxa documented by pollen introduce little or no bias into the taxonomic temperature signal. Removal of the three pollen-only families increased the family-based temperate estimate by slightly more than 1 °C (well within the standard error of the estimate based on the full sample), and removal of eight genera resulted in an insignificant increase of only 0.1 °C in the genus-based estimate. The constancy of the genus-level results is especially surprising given the relatively large proportion (22%) of genera removed for the second analysis.

The WAPLS temperature estimates may imply a lower paleoelevation for Florissant than the previous lapse-rate, leaf-morphology-based paleoelevation estimates, which range from 1900 to more than 4100 m (see summary in Meyer, 2001). Application of WAPLS to lapse-rate-based paleoelevation modeling would require that it be used to analyze late Eocene sea-level floras for comparison, yet the taxonomy of these floras would need to be critically revised before this would be possible. If the lower, genus-based WAPLS estimate of 14.7 ºC is used to evaluate paleoelevation in combination with the previous leaf morphology estimates of late Eocene sea-level temperature (see summary in Meyer, 2001), then Florissant's estimated elevation would fall within the range of ~1600–2800 m, depending on which previous methodology and lapse rate are used. If application of taxonomic calibration to these sea-level floras produces results that are warmer than leaf morphology estimates, as they do for Florissant, then paleoelevation estimates for Florissant may be close to those reported by previous workers who have used leaf morphology. Furthermore, the difference between these two methods essentially disappears if the 2–5 °C "cool bias" demonstrated by Burnham et al. (2001) and Kowalski and Dilcher (2003) for leaf morphology techniques is factored in.

Sensitivity of Calibration Models to Taxonomic Level

As highlighted by our validation analysis using independent training and test data sets of modern assemblages, the use of higher taxa in climatic calibration models has both advantages and disadvantages. Each taxonomic level predicted similar values of MAT, with quite similar levels of overall bias. At the same time, accuracy declined from species to genus to family, as shown by increasing coefficients of determination. However, test and training data sets were drawn randomly from the same pool, and we cannot evaluate whether the accuracy of species-level predictions would remain higher than genus- or family-level estimates as overlap between calibration and prediction data sets decreases. As calibration and prediction data sets become progressively less analogous, errors of estimates based on lower taxa might be expected to increase proportionally faster simply because of the greater loss of sample size for lower taxa. Furthermore, any decay in precision due to decreasing sample size is independent of effects due to changing climatic tolerances over evolutionary time. Detailed empirical sensitivity analyses as well as simulations are needed to help disentangle the relative importance of such sources of error and bias for analyses using different taxonomic levels across different temporal and spatial scales.

The Use of Higher Taxa in Paleoclimatic Calibration

Depending on the degree of taxonomic overlap between fossil and modern assemblages, the use of higher taxa in analog analysis and paleoclimate calibration can have several distinct advantages over species-level analysis: (1) applicability to deeper time periods, (2) less sensitivity to identification errors in fossil and modern data sets, (3) greater ease of data collection (both modern and fossil) owing to less stringent identification requirements, and (4) possibly decreased sensitivity to evolutionary change in taxon-climate associations. Against these advantages must be weighed the major disadvantage of using higher taxa—a decrease in precision (e.g., Fig. 4).

Despite the advantages of this method, potential biases in the underlying data set suggest that results of this study should be interpreted with caution. Particularly important are gaps and biases in the coverage of major vegetation types and biogeographic regions. In this study, coverage of many temperate vegetation types was sparse, particularly for western North America. Indeed, in the absence of samples from coastal and montane-interior California and the humid broad-leaved forests of temperate and subtropical China—both regions where several Florissant genera are now endemic—conclusions regarding the closest modern analog of the Florissant flora should be regarded as tentative. Some of the "non-analog" space comparable to our plot for the Florissant flora (Figs. 4 and 5) might occur within these other regions.

A second source of bias less easily resolved is the assumption that modern taxonomic assemblages and their associations with climate are constant through time. Indeed, the very existence of no-analog fossil communities suggests that this assumption may be untenable. Such decay in the reliability of taxonomic signals might be expected not only due to evolutionary change, but also to the effect of changing environmental conditions. For example, the demonstration that plants freeze at warmer temperatures at higher CO_2 concentrations (Royer et al., 2002) has profound implications for the reconstruction of climate by means of biological proxy techniques.

A third potentially important artifact is the mismatch between the temporally and spatially extensive assemblage of taxa represented by our Florissant list (Table 1) and the spatially restricted "snapshots" of modern forest used in this study. At least part of the apparently no-analog composition of the Florissant flora may due to the mixing of potentially different plant communities across multiple shale units representing at least 2–5 k.y. each (McLeroy and Anderson, 1966). One means of controlling for this potential artifact would be to analyze each shale unit separately; unfortunately, data on the distribution of taxa at Florissant with respect to specific shale units are insufficient to permit such a fine level of analysis.

A fourth source of bias could result from the taphonomic mixing of plant remains from different environments along the steep topographic and ecotonal gradient that may have existed between the Eocene lakeshore and the drier surrounding habitats (MacGinitie, 1953; Meyer 2003). Although it is possible that taxa as ecologically different as *Cedrela*, *Acer*, and *Abies* existed side by side in the same forest, a more parsimonious explanation for their co-occurrence within the Florissant flora is that they grew at different elevations or different exposures (e.g., north-facing, south-facing, shaded ravines) but in close geographic proximity, much as they do today along the steep slopes of the Sierra de Guatemala in the El Cielo Biosphere Reserve of northeastern Mexico (Leopold and Clay-Poole, 2001; B. Boyle, personal observation). Deliberately combining inventories from local regions into larger pseudosamples might reveal a closer match to the Florissant flora. A perhaps even better approach would be to use local florulas rather than forest plots as the unit of comparison (McLaughlin, 1995). Florulas typically contain an exhaustive compilation list of all taxa within a defined area, without bias toward particular growth forms. Large, continent-wide compilations of local florulas have recently become available (McLaughlin, 2007), and we will explore their application for taxonomic calibration and modern analog analysis in a future publication.

Perhaps the most important methodological improvement would be to eliminate altogether the use of taxonomic ranks in favor of an explicitly phylogenetic approach. Among other disadvantages, the use of ranks can lead to loss of information when taxa from a given site are determined to different levels of taxonomic precision: for example, the exclusion from our genus-level analysis of samples determined as "*Toona/Cedrela*." By contrast, mapping both modern and fossil taxa onto the same phylogenetic backbone would in theory permit all taxa to be included in the same analysis, without having to interpolate between separate analyses at arbitrarily different taxonomic levels. Technically, the incorporation of community phylogenies into multivariate methods such as NMS presents little difficulty. The first step in such analyses is typically the preparation of a site-by-site similarity matrix, and such matrices can be constructed by using phylogenetic distances between community samples instead of matching taxa (e.g., Weiblen et al., 2006). Although the limiting factor in such analyses will more likely be the availability of large "supertrees" spanning large samples of organismic diversity, these are now becoming increasingly available, as are the informatics tools for mapping phylogenies onto communities and testing ecological and evolutionary hypotheses within a community phylogenetic context (Webb, 2000; Webb et al., 2002). The application of such methods to similarity analysis and taxonomic calibration of fossil assemblages may provide insights unavailable via techniques based on traditional taxonomic ranks.

APPENDIX 1. LOCATION, CLIMATE, AND VEGETATION OF THE 241 MODERN NEW WORLD FOREST PLOTS USED IN THIS ANALYSIS

Plot	Country	Forest Type	Latitude	Longitude	Elevation	MAT	Test/train	Source
PARQUEER	Argentina	Subtropical lower montane moist	24°34'59"S	64°41'59"W	1000	18.0	Train	1
RIACHUEL	Argentina	Warm temperate moist	27°00'00"S	58°00'00"W	60	21.9	Test	1
SALTA	Argentina	Subtropical lower montane dry	24°40'00"S	64°30'00"W	1300	17.5	Test	1
BVGENTRY	Bolivia	Tropical moist	14°22'00"S	67°33'00"W	180	25.9	Test	6
CALABATE	Bolivia	Tropical lower montane wet	14°55'00"S	68°19'59"W	1540	18.8	Test	1
CHAQUIMA	Bolivia	Tropical lower montane moist	14°34'00"S	68°28'00"W	1000	21.0	Train	1
CURUYUQR	Bolivia	Tropical arid (thorn woodland)	18°46'00"S	62°17'59"W	350	22.0	Test	1
CURUYUQU	Bolivia	Tropical arid (thorn woodland)	18°45'56"S	62°13'59"W	350	22.0	Test	1
ENCANTO	Bolivia	Tropical moist	14°37'59"S	60°42'00"W	280	23.0	Train	1
INCAHUAR	Bolivia	Tropical lower montane wet	15°55'00"S	67°34'59"W	1540	20.0	Test	1
MADIDI	Bolivia	Tropical wet	13°34'59"S	68°46'00"W	280	24.1	Test	1
MADIDIRI	Bolivia	Tropical wet	13°34'59"S	68°46'00"W	370	23.7	Test	1
NUEVOMUN	Bolivia	Tropical dry	10°38'59"S	66°46'00"W	160	24.8	Train	1
PERSEVER	Bolivia	Tropical moist	14°37'59"S	62°37'00"W	100	23.9	Train	1
QUIAPACA	Bolivia	Tropical dry	18°19'59"S	59°30'00"W	300	22.0	Test	1
RIONEGRO	Bolivia	Tropical dry	9°49'59"S	65°40'00"W	100	25.0	Train	1
SACRAM	Bolivia	Tropical montane pluvial	16°17'59"S	67°48'00"W	2450	18.0	Test	1
SANTACRU	Bolivia	Tropical moist	17°46'00"S	63°4'00"W	375	22.2	Test	1
SANTIAGO	Bolivia	Tropical dry	18°19'59"S	59°30'00"W	750	20.2	Train	1
YANAIGUA	Bolivia	Subtropical arid (Thorn woodland)	19°42'00"S	62°5'59"W	250	22.1	Test	1
ALTERDOC	Brazil	Tropical moist	2°30'00"S	54°58'00"W	50	24.5	Train	1
BELEM	Brazil	Tropical moist	1°30'00"S	47°58'59"W	20	25.9	Test	1
BORACEIA	Brazil	Subtropical lower montane pluvial	23°22'59"S	46°00'00"W	800	17.2	Train	1
CAMORIN	Brazil	Subtropical moist	22°55'59"S	43°22'00"W	200	19.4	Train	1
CAMPINAS	Brazil	Tropical lower montane moist	22°49'59"S	47°7'59"W	575	18.3	Test	1
CARAJAS	Brazil	Tropical premontane moist	5°30'00"S	51°00'00"W	620	21.8	Train	1
CARLOSBO	Brazil	Subtropical lower montane wet	24°15'00"S	46°55'59"W	575	17.8	Train	1
DUCKE	Brazil	Tropical moist	3°00'00"S	59°58'00"W	75	27.0	Train	1
LINHARES	Brazil	Tropical moist	19°17'59"S	40°4'00"W	50	24.0	Test	1
MANAUS	Brazil	Tropical moist	3°7'59"S	60°1'00"W	75	24.9	Train	1
BURSTALL	Canada	Cool temperate montane moist (subalpine coniferous forest)	50°46'1"N	115°22'4"W	2135	-0.6	Train	4
KITLOPE1	Canada	Cool temperate pluvial	53°4'19"N	127°49'29"W	10	6.2	Test	1
KITLOPE2	Canada	Cool temperate pluvial	53°12'20"N	127°47'31"W	20	7.0	Test	1
MEANOOK	Canada	Boreal moist	54°37'1"N	113°19'58"W	705	1.6	Test	4
MARTIN	Chile	Warm temperate wet	39°30'00"S	73°10'00"W	30	11.5	Train	1
MIRADOR	Chile	Warm temperate montane pluvial	40°13'59"S	73°18'00"W	800	8.0	Test	1
PUYEHUE	Chile	Warm temperate montane pluvial	40°43'00"S	72°18'00"W	500	9.5	Train	1
ALTODEMI	Colombia	Tropical premontane wet	10°55'00"N	73°49'59"W	1180	20.4	Test	1
ALTOSAPA	Colombia	Tropical montane pluvial	7°10'00"N	75°54'00"W	2660	15.6	Train	1
ANCHICAY	Colombia	Tropical moist	3°45'00"N	76°49'59"W	300	25.4	Train	1
ANTADO	Colombia	Tropical lower montane pluvial	7°15'00"N	75°55'00"W	1560	19.9	Test	1
ARARACUA	Colombia	Tropical moist	0°25'00"S	72°19'59"W	200	25.6	Train	1
ARCATING	Colombia	Tropical moist	0°25'00"S	72°19'00"W	250	25.4	Test	1
CALIMA	Colombia	Tropical wet	3°55'00"N	77°00'00"W	100	26.2	Test	1
CAMPANO	Colombia	Tropical lower montane moist	11°7'59"N	74°1'00"W	1690	18.4	Train	1
CARPANTA	Colombia	Tropical montane pluvial	4°34'59"N	73°40'00"W	2900	14.8	Train	1
CEDRAL	Colombia	Tropical lower montane wet	4°45'00"N	75°33'00"W	2140	18.0	Train	1
CERROESP	Colombia	Tropical montane wet	10°28'00"N	72°49'59"W	2560	15.0	Test	1
COLORADO	Colombia	Tropical dry	9°58'00"N	75°10'00"W	225	24.5	Test	1
COLOSOI	Colombia	Tropical dry	9°30'00"N	75°48'00"W	300	24.4	Test	1
CUEVA	Colombia	Tropical premontane moist	11°4'59"N	73°28'00"W	360	23.6	Test	1
CUEVAS	Colombia	Tropical lower montane pluvial	6°40'00"N	76°30'00"W	1670	19.6	Test	1
FARALL	Colombia	Tropical lower montane moist	3°30'00"N	76°34'59"W	1930	19.0	Test	1
FINCAM	Colombia	Tropical lower montane wet	2°16'00"N	76°11'59"W	2290	17.7	Test	1
FINCAZ	Colombia	Tropical lower montane moist	3°31'59"N	76°34'59"W	1960	18.9	Train	1
GALERAZ	Colombia	Tropical very dry	10°48'00"N	75°15'00"W	10	25.2	Test	1
HACHIMAL	Colombia	Tropical lower montane moist	3°37'59"N	76°33'00"W	1860	19.3	Train	1
KENNEDY	Colombia	Tropical montane wet	11°4'59"N	74°1'00"W	2600	14.9	Test	1
LAPLANAD	Colombia	Tropical lower montane pluvial	1°7'59"N	77°58'00"W	1800	19.9	Train	1
LARAYA	Colombia	Tropical moist	8°19'59"N	74°55'00"W	65	25.5	Train	1
MANAURE	Colombia	Tropical premontane moist	10°22'00"N	73°7'59"W	540	23.0	Train	1
MARIQUIT	Colombia	Tropical dry	5°15'00"N	74°49'59"W	560	24.0	Train	1
MURRI	Colombia	Tropical premontane pluvial	6°34'59"N	76°49'59"W	910	22.6	Train	1
NEUSA	Colombia	Tropical montane moist	5°10'00"N	74°7'59"W	3050	14.2	Test	1
PROVIDEN	Colombia	Tropical wet	13°21'00"N	81°22'00"W	230	24.3	Test	1

(*continued*)

APPENDIX 1. LOCATION, CLIMATE, AND VEGETATION OF THE 241 MODERN NEW WORLD FOREST PLOTS USED IN THIS ANALYSIS (*CONTINUED*)

Plot	Country	Forest Type	Latitude	Longitude	Elevation	MAT	Test/train	Source
RIOMANSO	Colombia	Tropical wet	7°30'00"N	76°4'59"W	200	25.2	Test	1
SABANARU	Colombia	Tropical montane wet	10°30'00"N	70°55'00"W	2940	13.4	Test	1
SANTOTOM	Colombia	Tropical dry	4°55'00"N	74°49'59"W	320	25.0	Test	1
SIETECUE	Colombia	Tropical lower montane wet	4°34'59"N	73°40'00"W	2350	17.0	Train	1
TAYRONA	Colombia	Tropical dry	11°19'59"N	74°1'59"W	50	24.8	Train	1
TUTUNEND	Colombia	Tropical pluvial	5°46'00"N	76°34'59"W	90	25.9	Test	1
UCUMARI	Colombia	Tropical lower montane wet	4°00'00"N	75°30'00"W	2620	16.2	Train	1
C1000-1	Costa Rica	Tropical premontane pluvial	10°16'37"N	84°4'56"W	1000	21.0	Test	2
C1250-1	Costa Rica	Tropical lower montane pluvial	10°11'59"N	84°5'59"W	1250	19.7	Train	2
C1750-1	Costa Rica	Tropical lower montane pluvial	10°12'38"N	84°6'45"W	1750	17.2	Train	2
C1750-2	Costa Rica	Tropical lower montane pluvial	10°3'42"N	84°1'1"W	1750	17.1	Test	2
C1750-3	Costa Rica	Tropical lower montane pluvial	10°12'47"N	84°6'5"W	1750	17.1	Train	2
C2000-1	Costa Rica	Tropical lower montane pluvial	10°10'56"N	84°6'24"W	2000	15.8	Test	2
C2000-2	Costa Rica	Tropical lower montane pluvial	10°11'00"N	84°6'25"W	2000	15.9	Test	2
C2250-1	Costa Rica	Tropical lower montane pluvial	10°10'6"N	84°6'47"W	2250	14.7	Test	2
C2750-1	Costa Rica	Tropical montane pluvial	10°8'13"N	84°6'20"W	2750	11.8	Train	2
C2750-2	Costa Rica	Tropical montane pluvial	10°8'17"N	84°6'26"W	2750	12.0	Test	2
C2750-3	Costa Rica	Tropical montane pluvial	10°8'17"N	84°7'23"W	2750	12.0	Train	2
C500-1	Costa Rica	Tropical wet	10°19'58"N	84°4'44"W	500	23.5	Train	2
C750-1	Costa Rica	Tropical premontane pluvial	10°17'49"N	84°4'24"W	750	22.3	Test	2
C750-2	Costa Rica	Tropical premontane pluvial	10°17'44"N	84°4'36"W	750	22.2	Test	2
C750-3	Costa Rica	Tropical premontane pluvial	10°17'26"N	84°3'38"W	750	22.2	Test	2
CARARA	Costa Rica	Tropical moist	9°34'59"N	84°34'59"W	130	25.9	Test	1
GUANGF	Costa Rica	Tropical dry	10°30'00"N	85°10'00"W	50	24.0	Test	1
GUANUP	Costa Rica	Tropical dry	10°31'59"N	85°18'00"W	100	24.0	Train	1
LASELVA	Costa Rica	Tropical wet	10°25'59"N	84°1'00"W	40	26.1	Test	1
LS-00-9	Costa Rica	Tropical wet	10°23'59"N	84°00'00"W	50	26.0	Test	3
LS-1	Costa Rica	Tropical wet	10°23'59"N	84°00'00"W	50	26.0	Test	3
LS-2	Costa Rica	Tropical wet	10°23'59"N	84°00'00"W	50	26.0	Train	3
MAGSASAY	Costa Rica	Tropical wet	10°23'59"N	84°3'00"W	150	25.6	Train	1
MT	Costa Rica	Tropical lower montane wet	10°48'00"N	84°48'00"W	1550	20.1	Train	3
OSASIREN	Costa Rica	Tropical moist	8°30'00"N	83°55'00"W	30	26.5	Train	1
PV-1	Costa Rica	Tropical dry	10°30'00"N	85°18'00"W	40	26.2	Test	3
PV-1-00	Costa Rica	Tropical dry	10°30'00"N	85°18'00"W	130	25.8	Test	3
PV-2	Costa Rica	Tropical dry	10°30'00"N	85°18'00"W	10	26.3	Test	3
PV-2B	Costa Rica	Tropical dry	10°30'00"N	85°18'00"W	40	26.2	Train	3
PV-2S	Costa Rica	Tropical dry	10°30'00"N	85°18'00"W	40	26.2	Train	3
PVRIVERI	Costa Rica	Tropical dry	10°30'00"N	85°18'00"W	10	26.3	Train	3
RANCHOQU	Costa Rica	Tropical moist	8°41'59"N	83°33'00"W	300	25.3	Test	1
SIERRARO	Cuba	Subtropical wet	22°49'59"N	83°00'00"W	380	20.6	Train	1
ACHUPALL	Ecuador	Tropical lower montane wet	3°27'00"S	78°22'00"W	2100	18.9	Test	1
BILSA	Ecuador	Tropical moist	0°37'00"S	79°52'00"W	280	26.0	Train	1
CAPEIRA	Ecuador	Tropical very dry	2°00'00"S	79°58'00"W	50	25.5	Test	1
CENTINEL	Ecuador	Tropical wet	0°34'59"S	79°19'59"W	725	22.5	Test	1
CUANGOS	Ecuador	Tropical premontane wet	3°28'59"S	78°13'59"W	1550	21.0	Train	1
DURENO	Ecuador	Tropical moist	0°15'00"S	76°45'00"W	300	25.7	Test	1
E1250-1	Ecuador	Tropical lower montane pluvial	1°1'59"N	78°15'00"W	1250	18.0	Train	2
E1750-1	Ecuador	Tropical lower montane pluvial	0°52'00"S	78°10'59"W	1750	15.7	Test	2
E1750-2	Ecuador	Tropical lower montane pluvial	0°52'00"S	78°10'00"W	1750	17.9	Train	2
E1750-3	Ecuador	Tropical lower montane pluvial	0°52'59"S	78°10'00"W	1750	17.9	Test	2
E2250-1	Ecuador	Tropical lower montane wet	0°52'59"S	78°5'59"W	2250	13.6	Train	2
E2250-2	Ecuador	Tropical lower montane wet	0°49'59"S	78°13'00"W	2250	15.7	Train	2
E2750-1	Ecuador	Tropical montane wet	0°15'38"S	78°8'13"W	2750	25.6	Test	2
E2750-2	Ecuador	Tropical montane wet	0°15'51"S	78°8'9"W	2750	13.5	Test	2
E750-1	Ecuador	Tropical premontane wet	0°52'59"S	78°26'59"W	750	20.2	Test	2
E750-2	Ecuador	Tropical premontane wet	0°52'59"S	78°26'59"W	750	22.4	Train	2
E750-3	Ecuador	Tropical premontane wet	0°52'00"S	78°25'59"W	750	22.4	Test	2
ELCORAZO	Ecuador	Tropical montane wet	0°34'59"S	77°41'59"W	3150	14.6	Train	1
ESMERALD	Ecuador	Tropical dry	0°53'59"S	79°37'00"W	1503	21.2	Test	1
HUAMANI	Ecuador	Tropical premontane moist	0°40'00"S	77°40'00"W	1150	22.5	Train	1
JATUNSAC	Ecuador	Tropical wet	1°4'00"S	77°35'59"W	400	23.0	Test	1
JAUNECHE	Ecuador	Tropical dry	1°6'00"S	79°37'59"W	60	25.0	Test	1
MAQUIPUC	Ecuador	Tropical lower montane wet	0°7'00"S	78°37'00"W	1600	20.8	Test	1

(*continued*)

APPENDIX 1. LOCATION, CLIMATE, AND VEGETATION OF THE 241 MODERN NEW WORLD FOREST PLOTS USED IN THIS ANALYSIS (*CONTINUED*)

Plot	Country	Forest Type	Latitude	Longitude	Elevation	MAT	Test/train	Source
MIAZI	Ecuador	Tropical moist	4°18'00"S	78°40'00"W	850	23.8	Train	1
NANGARIT	Ecuador	Tropical wet	4°18'00"S	78°40'00"W	930	23.5	Train	1
PASOCHOA	Ecuador	Tropical montane wet	0°28'00"S	78°25'00"W	3010	11.5	Test	1
PERROMUE	Ecuador	Tropical dry	1°36'00"S	80°41'59"W	440	25.6	Train	1
RIOPAL1	Ecuador	Tropical moist	0°34'00"S	79°19'59"W	200	23.0	Test	1
RIOPAL2	Ecuador	Tropical moist	0°34'00"S	79°19'59"W	200	23.0	Train	1
SANSEBAS	Ecuador	Tropical moist	1°36'00"S	80°41'59"W	550	25.2	Test	1
SAUL	Fr. Guyana	Tropical moist	3°37'59"N	53°12'00"W	220	23.3	Test	1
BERBICER	Guyana	Tropical moist	5°30'00"N	58°4'59"W	160	23.8	Train	1
ROUNDSLO	Jamaica	Subtropical moist	17°19'59"N	77°25'00"W	40	23.5	Test	1
ROUNDTOP	Jamaica	Subtropical moist	17°19'59"N	77°25'00"W	40	23.5	Test	1
BENITO	Mexico	Tropical lower montane moist	15°19'59"N	92°15'00"W	2100	17.6	Test	1
BOSQUEDE	Mexico	Subtropical lower montane moist	19°30'00"N	96°56'59"W	1200	20.2	Train	1
CHAMELA1	Mexico	Subtropical dry	19°30'00"N	105°3'00"W	50	27.5	Train	1
CHAMELA2	Mexico	Subtropical dry	19°30'00"N	105°3'00"W	50	27.5	Train	1
CHAMELA3	Mexico	Subtropical dry	19°30'00"N	105°3'00"W	50	27.5	Train	1
CHAMELA4	Mexico	Subtropical dry	19°30'00"N	105°3'00"W	100	27.5	Test	1
CIELO750	Mexico	Subtropical lower montane moist	23°3'27"N	99°10'43"W	835	21.6	Test	4
ELCHORRO	Mexico	Tropical very dry	15°52'31"N	96°00'16"W	140	29.4	Train	5
ELCUJETE	Mexico	Subtropical montane wet	23°2'28"N	99°18'28"W	2060	16.4	Test	4
LABAMBA	Mexico	Tropical very dry	16°1'15"N	95°25'14"W	140	29.4	Test	5
LACOTORR	Mexico	Tropical very dry	15°59'3"N	95°31'24"W	90	29.4	Train	5
LAGLORIA	Mexico	Subtropical montane wet	23°2'42"N	99°14'9"W	1755	17.7	Train	4
LAMARCEL	Mexico	Subtropical montane moist	22°39'47"N	99°43'10"W	3200	11.6	Train	4
LAPENA	Mexico	Subtropical montane moist	23°37'39"N	99°42'47"W	2800	13.3	Test	4
LASJOYAS	Mexico	Subtropical montane wet	19°34'59"N	104°7'58"W	1950	17.9	Test	1
M1250-1	Mexico	Tropical lower montane pluvial	17°34'59"N	96°20'59"W	1250	18.8	Train	2
M1250-2	Mexico	Tropical lower montane pluvial	17°34'40"N	96°19'59"W	1250	18.8	Train	2
M1750-1	Mexico	Tropical lower montane pluvial	17°37'14"N	96°22'00"W	1750	16.2	Train	2
M1750-2	Mexico	Tropical lower montane pluvial	17°29'14"N	96°24'5"W	1750	16.2	Test	2
M1750-3	Mexico	Tropical lower montane pluvial	17°34'15"N	96°21'32"W	1750	16.2	Train	2
M2250-1	Mexico	Tropical lower montane pluvial	17°35'35"N	96°28'35"W	2250	13.7	Train	2
M2750-1	Mexico	Tropical montane pluvial	17°35'14"N	96°31'30"W	2750	11.2	Test	2
M2750-2	Mexico	Tropical montane pluvial	17°33'29"N	96°27'29"W	2750	11.2	Test	2
M2750-3	Mexico	Tropical montane pluvial	17°23'6"N	96°26'12"W	2750	11.2	Train	2
M750-1	Mexico	Tropical premontane pluvial	17°37'00"N	96°16'59"W	750	21.3	Test	2
M750-2	Mexico	Tropical premontane pluvial	17°39'50"N	96°18'5"W	750	21.3	Train	2
MIQUIHUA	Mexico	Subtropical lower montane dry	23°34'42"N	99°42'52"W	2260	15.6	Test	4
MOTOZINT	Mexico	Tropical lower montane dry	15°19'59"N	92°11'59"W	1600	21.5	Train	1
QUINCEOC	Mexico	Subtropical montane moist	19°43'59"N	104°15'00"W	1800	18.5	Train	1
SANJOSE	Mexico	Subtropical lower montane wet	23°2'4"N	99°12'50"W	1205	20.0	Train	4
TUXTLAS	Mexico	Tropical wet	18°34'59"N	95°7'59"W	200	23.5	Train	1
CERROELP	Nicaragua	Tropical lower montane wet	13°00'00"N	85°55'00"W	1420	13.0	Test	1
CERROOLU	Nicaragua	Tropical premontane moist	12°18'00"N	85°24'00"W	840	23.5	Test	1
CURUNDU	Panama	Tropical dry	8°58'59"N	79°33'00"W	20	26.9	Train	1
MADDEN	Panama	Tropical moist	9°6'00"N	79°35'59"W	50	27.0	Test	1
PIPELINE	Panama	Tropical wet	9°10'00"N	79°45'00"W	300	26.0	Test	1
JEJUIMI	Paraguay	Subtropical moist	24°7'59"S	55°31'59"W	150	22.2	Train	1
ALLPAHUA	Peru	Tropical moist	3°57'00"S	73°25'00"W	155	26.0	Test	1
AMOTAPE	Peru	Tropical premontane moist	4°9'00"S	80°37'00"W	830	22.1	Train	1
CABEZADE	Peru	Tropical wet	10°19'59"S	75°18'00"W	320	23.5	Test	1
CANDAMO	Peru	Tropical premontane pluvial	13°30'00"S	69°49'59"W	790	22.2	Train	1
CERROAYP	Peru	Tropical montane wet	4°34'59"S	79°31'59"W	2770	16.3	Train	1
CHIRINOS	Peru	Tropical lower montane moist	5°25'00"S	78°52'59"W	1780	20.1	Test	1
CHORROBL	Peru	Tropical lower montane moist	6°10'00"S	78°45'00"W	2380	17.7	Train	1
COCHACAS	Peru	Tropical premontane moist	11°51'00"S	71°19'00"W	380	24.2	Train	1
CONSTANC	Peru	Tropical moist	4°15'00"S	72°45'00"W	160	25.9	Test	1
CUTERVO	Peru	Tropical lower montane moist	6°10'00"S	78°40'00"W	2230	18.3	Train	1
CUYAS	Peru	Tropical lower montane dry	4°31'59"S	79°43'59"W	2410	17.8	Train	1
CUZCOAMA	Peru	Tropical premontane wet	12°34'59"S	69°9'00"W	200	24.6	Train	1
ELPARGO	Peru	Tropical montane wet	6°30'00"S	79°31'00"W	3000	15.4	Test	1
HUMBOLDT	Peru	Tropical moist	8°49'59"S	75°00'00"W	270	25.4	Test	1
INDIANA	Peru	Tropical moist	3°31'00"S	73°4'00"W	130	26.0	Test	1

(*continued*)

APPENDIX 1. LOCATION, CLIMATE, AND VEGETATION OF THE 241 MODERN NEW WORLD FOREST PLOTS USED IN THIS ANALYSIS (*CONTINUED*)

Plot	Country	Forest Type	Latitude	Longitude	Elevation	MAT	Test/train	Source
JENAROHE	Peru	Tropical moist	4°55'00"S	73°45'00"W	130	26.1	Test	1
LAGENOA	Peru	Tropical premontane moist	11°4'59"S	75°25'00"W	1140	21.8	Train	1
MISHNFL	Peru	Tropical moist	3°46'59"S	73°30'00"W	130	26.1	Train	1
MISHWS	Peru	Tropical moist	3°46'59"S	73°30'00"W	140	26.0	Test	1
RIOHEATH	Peru	Tropical premontane wet	12°49'59"S	68°49'59"W	250	24.3	Train	1
RIOTAVAR	Peru	Tropical wet	13°21'00"S	69°40'00"W	400	23.7	Test	1
SHIRINGA	Peru	Tropical premontane pluvial	10°19'59"S	75°10'00"W	300	24.0	Test	1
SUCUSARI	Peru	Tropical moist	3°15'00"S	72°55'00"W	140	26.0	Test	1
TAHUAMPA	Peru	Tropical moist	3°46'59"S	73°30'00"W	130	26.1	Train	1
TAMBLAT2	Peru	Tropical moist	12°46'59"S	69°16'59"W	260	24.3	Train	1
TAMBO	Peru	Tropical moist	12°46'59"S	69°16'59"W	260	24.3	Train	1
TAMBOALL	Peru	Tropical moist	12°49'59"S	69°16'59"W	260	24.3	Train	1
TAMBUPL	Peru	Tropical moist	12°49'00"S	69°43'00"W	260	24.4	Test	1
TARAPOTO	Peru	Tropical dry	6°34'59"S	76°25'00"W	500	24.8	Test	1
VENCER	Peru	Tropical lower montane moist	5°45'00"S	77°40'00"W	1850	15.0	Test	1
YANAM1	Peru	Tropical moist	3°25'59"S	72°50'59"W	140	26.0	Train	1
YANAM2	Peru	Tropical moist	3°25'59"S	72°50'59"W	140	26.0	Test	1
YANAMTAH	Peru	Tropical moist	3°28'00"S	72°49'59"W	130	26.0	Test	1
LUQUILLO	Puerto Rico	Subtropical wet	18°10'59"N	65°49'59"W	300	21.0	Test	1
MOGOTE	Puerto Rico	Subtropical moist	18°25'00"N	66°15'00"W	50	21.9	Train	1
BABLERSP	USA	Warm temperate moist	38°31'59"N	90°40'00"W	150	14.0	Test	1
BANKAMP	USA	Warm temperate moist	40°2'59"N	81°1'00"W	250	11.2	Train	1
BURLING	USA	Warm temperate moist	38°57'00"N	77°10'00"W	60	13.5	Train	1
CARY	USA	Cool temperate moist	46°49'59"N	73°45'00"W	210	5.4	Test	1
CEDARBLU	USA	Warm temperate moist	39°46'00"N	86°9'00"W	215	12.0	Train	1
CUIVRE	USA	Warm temperate moist	39°1'00"N	91°00'00"W	140	13.3	Train	1
HEUSTOBM	USA	Warm temperate moist	39°32'59"N	84°43'00"W	200	12.1	Train	1
HEUSTOMF	USA	Warm temperate moist	39°32'59"N	84°43'00"W	200	12.1	Train	1
INDIANCA	USA	Warm temperate moist	40°30'00"N	95°43'00"W	320	10.5	Train	1
JONESMIL	USA	Warm temperate montane wet	40°4'59"N	79°20'59"W	500	10.0	Test	1
KANEALLE	USA	Warm temperate montane wet	41°40'00"N	78°48'00"W	500	8.8	Train	1
LAURELRI	USA	Warm temperate montane wet	39°57'00"N	79°22'00"W	670	9.4	Train	1
MATTHIES	USA	Subtropical moist	25°43'00"N	80°16'00"W	15	20.5	Train	1
MONTGOME	USA	Cool temperate moist	43°10'00"N	77°37'00"W	210	8.7	Train	1
NWBRANCH	USA	Warm temperate moist	39°1'59"N	77°1'59"W	20	13.5	Test	1
POTOMAC	USA	Warm temperate moist	38°4'59"N	76°34'00"W	33	12.9	Train	1
ROCKCREE	USA	Warm temperate moist	37°30'00"N	90°15'00"W	285	13.7	Test	1
SANFELAS	USA	Warm temperate moist	29°40'59"N	82°25'59"W	30	18.6	Train	1
TIDROUTE	USA	Warm temperate montane wet	41°42'00"N	79°24'00"W	310	9.6	Test	1
TIMBERLI	USA	Cool temperate montane wet (Subalpine coniferous)	45°16'59"N	121°45'00"W	2000	4.5	Train	1
TYSONGLA	USA	Warm temperate moist	38°30'00"N	90°31'00"W	150	14.0	Train	1
TYSONWOO	USA	Warm temperate moist	38°30'00"N	90°31'00"W	150	14.0	Test	1
UFHORTIC	USA	Warm temperate moist	29°40'00"N	82°19'59"W	50	18.6	Test	1
VALLEYVI	USA	Warm temperate moist	38°15'00"N	90°37'00"W	225	13.5	Train	1
WILDBASI	USA	Warm temperate montane moist	30°19'59"N	97°55'00"W	1600	13.7	Test	1
BLOHMR	Venezuela	Tropical dry	8°34'00"N	67°34'59"W	100	24.5	Test	1
CERONEB1	Venezuela	Tropical moist	0°49'59"S	66°10'59"W	140	25.2	Train	1
CERONEB2	Venezuela	Tropical moist	0°49'59"S	66°10'59"W	140	25.2	Train	1
LLANO	Venezuela	Tropical dry	8°55'59"N	67°25'00"W	100	27.5	Train	1
UCHIRE	Venezuela	Tropical dry	10°8'48"N	65°25'40"W	150	23.8	Train	1

Note: All plots are 0.1 ha samples of woody plants ≥2.5 cm dbh. Forest types are Holdridge life zones (Holdridge, 1967). MAT—mean annual temperature. Test/train indicates use in test or training data set for WAPLS validation. Sources: 1—Gentry transects (see Phillips and Miller, 2002); 2—Boyle transects (Boyle, 1996); 3—OTS transects (B. Boyle, personal observ.); 4—Enquist lab transects (B.J. Enquist, personal observ.); 5—Serbo Oaxaca forest plots (S. Salas, personal observ.); 6—DeWalt 0.1 ha data set (DeWalt et al., 1999). All plot data obtained via the SALVIAS Project database (Enquist et al., 2002).

APPENDIX 2. DISTRIBUTION AMONG VEGETATION TYPES (HOLDRIDGE LIFE ZONES; HOLDRIDGE, 1967) OF THE 241 MODERN NEW WORLD FOREST PLOTS USED IN THIS ANALYSIS

Latitudinal + Altitudinal Belt	Humidity Province					
	Arid	Very Dry	Dry	Moist	Wet	Pluvial
Tropical	2	5	25	43	18	1
Tropical Premontane				8	7	9
Tropical Lower Montane			2	11	12	20
Tropical Montane				1	9	9
Subtropical	1		4	6	2	
Subtropical Lower Montane			2	3	2	1
Subtropical Montane				3	3	
Warm Temperate			8	9	1	
Warm Temperate Montane				1	4	2
Cool Temperate				2		2
Cool Temperate Montane					2	
Boreal				1		

Note: Latitudinal belts lacking altitudinal designations are "lowland" altitudinal belts. See "Methods" for details of determination of life zone categories.

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Phytogeography of the late Eocene Florissant flora reconsidered

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ABSTRACT

The biogeographic affinities of the Florissant flora are in need of reevaluation. We give a critical review, based on megafossil and pollen records representing genera whose affinities we accept as well founded. The Florissant assemblage includes taxa of diverse modern geographic distribution. The flora is composed mainly of Laurasian elements, some of which are now confined to Asia (*Ailanthus, Dipteronia, Eucommia, Platycarya, Pteroceltis*) and a wide number co-occurring in the eastern United States and Asia. Others are now confined to western North America (*Sequoia, Cercocarpus, Sarcobatus*) and many occur in Mexico. The major geographic affinities of the Florissant genera discussed here are broad and include the present-day warm temperate and subtropical floras of Mexico, central and southern China, and the southeastern United States. Many taxa appear to have been shared between North America and Asia by Eocene time. The Rocky Mountain flora was distinct from that of the southeastern United States, probably because of the barrier represented by the Cannonball epeiric sea that traversed the Midcontinent in the Paleocene. Similarity of Florissant taxa to the South American flora is low.

The deterioration of climate after the time of Florissant deposition represents one of the most significant decreases in temperature of the entire Tertiary. Following the warm interval of the latest Eocene, a few Florissant genera were locally extirpated, a few became extinct, some were already at or dispersed to lower-elevation regions, and others persisted in the southern Rocky Mountains. Over longer geologic time spans, some taxa seem to have persisted on the West Coast of North America through the Miocene, and in a few cases even up to the present. Many deciduous taxa have persisted in the summer-wet climate area of the eastern United States.

Keywords: woody Eocene genera, late Eocene climate, biogeography, megafossils, pollen.

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INTRODUCTION

The fossil flora at Florissant, Colorado, provides important insights into the late Eocene vegetation and flora of the southern Rocky Mountain region, and contributes valuable data for understanding changing patterns of plant distribution in the Northern Hemisphere. By analyzing past and present distribution patterns of the genera known from the Florissant flora, it is possible to glean information on the geographic relationships of the flora. The Florissant fossil beds are especially important because they may represent the last diverse warm temperate and mainly deciduous flora to occur in the Rocky Mountain region before the great deterioration of climate in the early Oligocene.

The rich leaf flora of the Florissant lake beds has been studied since the 1870s by paleobotanists including Leo Lesquereux (1883), F.H. Knowlton (1916), and T.D.A Cockerell (1908), among others. The first comprehensive account of the flora was the monograph by Harry D. MacGinitie (1953) who reported 114 species of plants in 44 families, including 84 genera of higher plants. He reevaluated the taxa reported by earlier workers. In addition, he placed 27 species into two categories of incertae sedis, having uncertain generic identity. In his monograph on the Florissant megafossil flora, MacGinitie identified most of the taxa to extant genera and examined the modern geographic distribution on the basis of presumed nearest living relatives in those genera to gain an understanding of ecological habits and phytogeographic relationships. Since that work, many of the taxonomic determinations for megafossils have been reevaluated, and eight Florissant genera have been determined to be extinct (reviewed in Manchester, 2001; Meyer, 2003). New data from studies on pollen (Leopold and Clay-Poole, 2001; Wingate and Nichols 2001) have significantly expanded our knowledge of the flora. These studies provide a broader basis for determining some of the phytogeographic affinities of the flora. Our analysis refers to a wide number of Eocene floras in the western United States, as well as records of taxa in other floras of the Northern Hemisphere. By comparison with these we can investigate where the Florissant genera seem to have originated and into what areas they have dispersed.

MacGinitie's (1953) phytogeographic comparisons focused on what he judged to be the nearest living relatives or analogs at the species level. His hypotheses of closest living species are, in most cases, still in need of testing with phylogenetic analyses that include more species from throughout the range of the indicated genus as well as related genera with similar morphology. In the present analysis we focus mainly on generic-level comparisons, although we acknowledge that a careful comparison at the species level, where possible, would be more informative. Some of the Florissant genera are widely distributed in the Northern Hemisphere today, such as *Alnus*, *Abies*, *Acer*, *Cercis*, and *Pinus*. Other than indicating broad Northern Hemisphere affinities, these taxa are uninformative phytogeographically unless relationships can be confirmed at the species level.

MacGinitie (1953) chose eight areas or regions of modern vegetation for his comparison with the species of the Florissant flora; in order of similarity these are:

1. southern Rockies from southern Colorado to Chihuahua;
2. Edwards Plateau of central Texas, south to San Luis Potosí;
3. central and southern China from Sichuan to Kiangsi;
4. Ozark Plateau, east to the southern Appalachians;
5. western Mexico from Sinaloa north into southern Arizona;
6. central and northern California;
7. southern Mexico, from Jalisco to Veracruz; and
8. midlatitude South America.

Three of these Mexican geographic categories represent north-south transects beginning near the Mexico-U.S. border through northern and central Mexico parallel with the Sierra Madre mountain ranges, and the southernmost category runs east and west across southern Mexico between 16° N and 22° N. The Ozark Plateau eastward to the southern Appalachians embraces the rich deciduous forest area of the southeastern United States, including the American mixed mesophytic forest. In south-central China and Japan is the rich warm temperate mixed mesophytic forest and subtropical areas of eastern Asia.

In this paper our purpose is severalfold: (1) to compile a list of taxonomic determinations that we consider to be based on strong morphologic evidence; (2) to compare the Florissant genera with modern distributions in order to illuminate the history of a lineage and to estimate the present-day affinities of the Florissant genera; (3) to compare occurrences of Florissant taxa with some other Paleogene floras of western United States (Fig. 1) in order to discern paleo-distribution patterns; and (4) to discuss responses of Florissant genera to climate cooling and possible drying during the Eocene-Oligocene transition.

METHODS

The Florissant flora is one of the best-sampled paleobotanical sites in North America, with collections representing investigations of more than 130 years. Because many of the specimens from Florissant have been available to us through our own collections, through firsthand examination of the vast published material, or on the new database Web site documenting all previously published Florissant specimens (Meyer et al., this volume), we have had a great advantage in viewing diverse materials from the flora. We have carried out a critical review of collections reported and figured in recent literature for Florissant taxa, and we studied a breadth of evidence for identifications based on modern plants.

Much of our method involved the examination of previous publications to obtain floral data. We reviewed MacGinitie (1953), Leopold and Clay-Poole (2001), Wingate and Nichols (2001), Manchester (2001), Meyer (2003), and other authors. Our list of 37 families includes the 62 genera for which we have the strongest morphological evidence. Our criteria for accepting identifications are conservative and include the following: (1) the morphology of multiple, co-occurring fossil plant organs (e.g., leaves, fruits, wood, and pollen) corroborate an identification; (2) organ attachment of leaves with fruit and flowers provides a strong basis for generic identification; (3) unique character combinations of leaf, fruit, or pollen morphology common to only one modern genus are considered diagnostic.

Rather than presenting a comprehensive analysis of the flora as attempted earlier (Cockerell, 1908; Knowlton, 1916; MacGinitie, 1953; reviewed and revised by Manchester, 2001, and Meyer, 2003), we focus here on those genera and subgenera for which taxonomic relationships are most confidently determined,

Figure 1. Location of some well-known Eocene (squares) and Oligocene (triangles) floras (after Wolfe and Wehr, 1987).

based on characters that are diagnostic of, and unique to, the specified taxa. In many instances a leaf, pollen, or fruit type may closely resemble more than one extant and/or fossil genus because of convergent and parallel evolution. Higher certainty of identification comes when there are unique characters, and when multiple organs are known from the same species. Some of the genera previously recognized in the Florissant flora that played a role in earlier phytogeographic interpretations have now been recognized as extinct genera and can no longer be used as direct analogs to extant genera for phytogeographic inference (Manchester, 2001). These include *Zelkova* (transferred to *Cedrelospermum*), *Lomatia* (fruits transferred to *Cedrelospermum*), *Holmskioldia* (transferred to *Florissantia*), *Petrea* (transferred to *Asterocarpinus*), *Carpinus* (transferred to *Paracarpinus*), *Ptelea* (transferred to *Diplodipelta*), *Astronium* (transferred to *Chaneya*), and *Limnobium* (*Limnobiophyllum*). Fossils previously assigned to these eight living genera are now all considered to represent extinct genera. Table 1 lists the living genera and families of Florissant accepted and used in our investigation, and in Table 2 we list these taxa according to their present distribution. Families for which genera are not yet identified and extinct genera are omitted from Table 2.

Many of the Florissant genera have very widespread ranges today. The data we used to document modern distributions are based on sources such as Mabberley (1997), various regional floral guides, and Thompson et al. (2000). We also consulted the Web site for the Global Biodiversity Information Facility (GBIF), which contains worldwide distributions of genera. (http://www.cbif.gc.ca/mapdata/cbif/gbifwmsmc.php). We also consulted with B. Boyle (2007, personal commun.) on the use of the SALVIAS Project Database (http://www.salvias.net/pages/index.html), a geographically extensive database of modern New World forest inventories.

To MacGinitie's (1953) biogeographic categories we have added two other categories in our Tables 2 and 3 that were needed for our generic analysis: (1) Northeastern U.S., New England and the northern Appalachians, and (2) the Pacific Northwest, Oregon north to southern Alaska. To the California group we have added southern California and Baja California. We have broadened the category "midlatitude South America," by expanding beyond the "midlatitude." In our summary of Paleogene occurrences of Florissant genera (Table 4), we included groups that did not appear in the fossil record of North America prior to the late Eocene; in that analysis, we were attempting to determine the geographic origin/source of the Florissant flora to answer such questions as, How many genera seemed to have arisen in situ in the western interior? and How many appeared first in Asia or Europe and crossed the land bridges of the Northern Hemisphere to populate the western states? For that we relied on a recent survey of world literature on the general biogeography of floras by Manchester (1999) to recount and summarize the dispersal patterns shown by the Florissant genera.

TABLE 1. FAMILIES AND GENERA OF WOODY PLANTS RECORDED FROM FLORISSANT AND USED IN THIS ANALYSIS

Families	Genera
Aceraceae	*Acer**, *Dipteronia*
Anacardiaceae	*Rhus*
Apocynaceae	*Tabernaemontana*[†]
Arecaceae	[undetermined genus]
Berberidaceae	*Mahonia* [= *Berberis*]*
Betulaceae	*Asterocarpinus/Paracarpinus*[§], *Alnus*[†], *Betula*[†], cf. *Ostrya**
Rhoipteleaceae[†]	[undetermined genus]
Buxaceae	*Pachysandra/Sarcococca*[†]
Caprifoliaceae	*Diplodipelta*[§], *Sambucus**
Chenopodiaceae	*Sarcobatus*[†]
Cupressaceae	*Chamaecyparis, Sequoia*
Dioscoreaceae	*Dioscorea*
Elaeagnaceae	*Elaeagnus*[†]
Ephedraceae	*Ephedra* cf. *E. nevadensis**
Eucommiaceae	*Eucommia**
Euphorbiaceae	*Croton*[†]
Fabaceae	*Cercis, Arcoa, Caesalpinites*
Fagaceae	*Fagopsis*[§], *Quercus**
Grossulariaceae	*Ribes*
Hydrangeaceae	*Hydrangea*, cf. *Philadelphus*
[Incertae sedis]	*Deviacer*[§]
Juglandaceae	*Carya* cf. *C. cordiformis**, *Pterocarya*[†], *Cyclocarya*[†], *Engelhardieae*[†], *Juglans*[†], *Platycarya*[†]
Lauraceae	[undetermined genera]
Meliaceae	*Cedrela/Toona**
Onagraceae	*Semeiandra*[†], cf. *Xylonagra*[†]
Pinaceae	*Abies* cf. *A. bracteata**, *Picea**, *Pinus**, *Tsuga* cf. *T. canadensis*[†]
Platanaceae	*Platanus*
Podocarpaceae	*Podocarpus*[†]
Rosaceae	*Amelanchier, Cercocarpus, Crataegus, Holodiscus, Prunus, Rosa, Rubus, Vauquelinia*
Salicaceae	*Populus**, *Salix**
Sapindaceae	*Cardiospermum**, *Koelreuteria**, *Athyana*
Simaroubaceae	*Ailanthus*
Smilacaceae	*Smilax*
Sterculiaceae	*Florissantia*[§], cf. *Fremontodendron*[†]
Taxaceae	*Torreya*
Ulmaceae	*Cedrelospermum*[§], *Pteroceltis*[†], cf. *Ulmus**
Vitaceae	*Vitis, Parthenocissus*

Note: Classification follows Cronquist (1981). Sources: After Leopold et al. (this volume); Leopold and Clay-Poole (2001, Table 2); Manchester (2001, Table 1); B. Boyle, 2007, personal observ.; H. Meyer, 2007, personal observ.; includes Leopold's identification of pollen in Wingate and Nichols (2001).

*Known from pollen.

[†] Known only from pollen.

[§] Extinct.

In our section on biogeographic responses to climate change (Tables 5 and 6) we examine the extirpation, extinction, and dispersal of Florissant genera following the late Eocene. To do this, we surveyed representative western American Tertiary floras, chiefly those west of the Mississippi River that are well dated, to assess changes in floral composition through time. In addition, we sought floras for which paleotemperature and precipitation had been estimated. Some of the paleoclimate estimates

TABLE 2. MODERN DISTRIBUTION OF FLORISSANT GENERA

		1 Southern Rocky Mountains from southern Colorado to Chihuahua	2 Edwards Plateau of central Texas south to San Luis Potosí	3 Western Mexico from Sinaloa north into southern Arizona	4 Southern Mexico, from Jalisco to Veracruz	5 Central and southern China from Sichuan to Kiangsi	6 Ozark Plateau, east to the southern Appalachians	7 Northeastern U.S., New England and northern Appalachians	8 California and Baja California	9 Pacific Northwest, Oregon to southern Alaska	10 South America	11 Pantropical
	Total affinities	27	23	23	24	36	31	27	29	21	20	10
Families	Genera											
Aceraceae	*Acer**	X	X			X	X	X	X	X		
	Dipteronia					X						
Anacardiaceae	*Rhus*	X	X	X	X	X	X	X	X	X		
Apocynaceae	*Tabernaemontana*[†]	X		X	X						X	X
Arecaceae	[undetermined genus]											X
Berberidaceae	*Mahonia**	X	X	X	X	X	X	X	X	X	X	
Betulaceae	*Alnus*[†]	X	X	X	X	X	X	X	X	X	X	
	Betula[†]					X	X	X	X	X		
Buxaceae	*Pachysandra*[†]					X	X					
Cannabaceae	*Humulus*	X					X	X				
Caprifoliaceae	*Sambucus**	X	X	X	X	X	X	X	X	X	X	
Chenopodiaceae	*Sarcobatus*[†]	X										
Cupressaceae	*Chamaecyparis*					X		X	X	X		
	Sequoia								X			
Dioscoreaceae	*Dioscorea*	X	?	X	X						X	X
Elaeagnaceae	*Elaeagnus*[†]					X	X	X		X		
Ephedraceae	*Ephedra* cf. *E. nevadensis**								X			
Eucommiaceae	*Eucommia**					X						
Euphorbiaceae	*Croton*[†]	X	X	X	X	X	X		X		X	X
Fabaceae	*Cercis*	X	X			X	X		X	X		
Fagaceae	*Quercus**	X	X	X	X	X	X	X	X			
Grossulariaceae	*Ribes*	X	X	X	X	X	X	X	X	X	X	
Hydrangeaceae	*Hydrangea*				X	X		X			X	X
	cf. *Philadelphus*	X				X		X				
Juglandaceae	*Carya* cf. *C. cordiformis**						X					
	Cyclocarya[†]					X						
	Engelhardieae[†]				X	X					X	
	Juglans[†]				X	X	X		X		X	
	Platycarya[†]					X						
	Pterocarya[†]					X						
Meliaceae	*Cedrela/Toona**				X	X					X	X
Onagraceae	*Semeiandra*[†]			X	X							
	cf. *Xylonagra*[†]								X			
Pinaceae	*Abies* cf. *A. bracteata**								X			
	*Picea**	X		X		X		X	X	X		
	*Pinus**	X	X	X	X	X	X	X	X	X		X
	Tsuga cf. *canadensis*[†]						X	X				
Platanaceae	*Platanus*	X	X	X	X	X	X	X	X			
Podocarpaceae	*Podocarpus*[†]		X	X	X	X					X	X
Rosaceae	*Amelanchier*						X	X		X		
	Cercocarpus	X	X						X	X		
	Crataegus		X				X	X	X	X		
	Holodiscus			X	X				X	X	X	
	Prunus	X	X	X	X	X	X	X	X	X	X	
	Rosa	X	X	X		X	X	X		X		
	Rubus	X	X	X	X		X	X	X	X	X	
	Vauquelinia	X	X	X								
Salicaceae	*Populus**	X	X				X	X	X	X		

(*continued*)

TABLE 2. MODERN DISTRIBUTION OF FLORISSANT GENERA (*CONTINUED*)

Families	Genera	1 Southern Rocky Mountains from southern Colorado to Chihuahua	2 Edwards Plateau of central Texas south to San Luis Potosí	3 Western Mexico from Sinaloa north into southern Arizona	4 Southern Mexico, from Jalisco to Veracruz	5 Central and southern China from Sichuan to Kiangsi	6 Ozark Plateau, east to the southern Appalachians	7 Northeastern U.S., New England and northern Appalachians	8 California and Baja California	9 Pacific Northwest, Oregon to southern Alaska	10 South America	11 Pantropical
	*Salix**	X	X	X	X		X	X	X	X	X	
Sapindaceae	*Athyana*										X	
	*Cardiospermum**	X	X	X	X		X		X		X	X
	*Koelreuteria**					X						
Simaroubaceae	*Ailanthus*					X						
Smilacaceae	*Smilax*		?		X	X	X				X	X
Sterculiaceae	cf. *Fremontodendron*[†]								X			
Taxaceae	*Torreya*					X	X		X			
Ulmaceae	*Pteroceltis*[†]					X						
	*Ulmus**	X	X	X	X	X	X	X				
Vitaceae	Parthenocissus	?	?	X			X	X				
	Vitis	X	X		?	X	X	X			X	

Notes: Families with unidentified genera are omitted except for Arecaceae. ?—not counted in tally.
*Known from fossil pollen.
[†] Known only from fossil pollen evidence.

TABLE 3. OCCURRENCES (SUMMED) OF FLORISSANT GENERA AND SUBGENERA BY GEOGRAPHIC CATEGORY

Geographic area	Number of taxa: MacGinitie (1953)	Number of taxa: Leopold and Clay-Poole (2001)*	Number of taxa: This study
(1) Southern Rocky Mountains from southern Colorado to Chihuahua (temperate, humid)	30	28	27
(2) Edwards Plateau, Texas to Potosi (temperate)	32	28	23
(3) Western Mexico from Sinaloa north into southern Arizona (subhumid scrub flora and tropical)	10	13	23
(4) Southern Mexico, from Jalisco to Veracruz (subtropical)	8	5	24
(5) Central and south China; Szechuan and Kiangsi (warm temperate to subtropical, humid)	24	28	36
(6) Ozark Plateau east to southern Appalachians (warm temperate)	22	15	31
(7) Northeastern U.S., New England to northern Appalachians* (cool temperate)	–	–	27
(8) California and Baja California[†] (temperate, seasonally dry)	9	12	29
(9) Pacific Northwest, Oregon to southern Alaska* (temperate)	–	–	21
(10) South America[§]	2	1	20
(11) Pantropical*	–	–	10
Totals	137	130	272

Note: Rows 1–6 are those categories used by MacGinitie (1953).
*Rows are added geographical categories needed for the generic analysis.
[†] Row is altered from usage of MacGinitie to include Baja and southern California.
[§] Row is altered from usage of MacGinitie to eliminate "midlatitude." In the records here, note that MacGinitie counted megafossil species, Leopold and Clay-Poole (2001) counted pollen genera, and this study combines megafossil and pollen genera.

TABLE 4. PALEOGENE OCCURRENCES OF FLORISSANT FAMILIES AND GENERA

Amer-Asian*	Euro-American†	Widespread§	Endemic#
Acer	*Cedrelospermum*	*Ailanthus*	*Carya*
Betula	Engelhardieae	Fagaceae	*Cercocarpus*
Dipteronia	*Hydrangea*	Platanaceae	*Cyclocarya*
Eucommia	*Platycarya*	*Pinus*	*Florissantia*
		Podocarpus	*Juglans*
		Sequoia	*Koelreuteria*
			Mahonia
			Pachysandra
			Sarcobatus

Note: Data from Manchester, 1999.

*Groups crossing the Beringian corridor before the late Eocene.

†Groups crossing North Atlantic before the late Eocene.

§Europe-North, America-Asia by the Late Eocene.

#Known only in North America in the Eocene.

have been based on the character of the plant genera and where they grow today (the nearest living relatives method). Other estimates utilized the CLAMP method of Wolfe (e.g., 1992) based on the architecture of leaves (size, venation, teeth) and its statistical relation to local climate data.

After the Florissant deposition ceased, one of the most significant changes in Tertiary climate (the earliest Oligocene deterioration) occurred (Zanazzi et al., 2007; Retallack et al., 2004), and the dispersal of plants in the West were deeply affected by the environmental cooling and perhaps drying characteristic of this event.

REEVALUATING PRESENT-DAY AFFINITIES OF THE FLORISSANT FLORA

In the assessment of MacGinitie (1953, p. 40–41), "the majority of the species are found…in the southwestern interior of North America. A circle of radius 400 miles (645 km), centered in southwestern Coahuila, Mexico, would encompass the habitat of the first three groups, 52 of the most similar species, or approximately 57 percent." It is difficult to be sure of these conclusions, however, because a number of the taxa included in his study are based on identifications that have since been rejected (e.g., *Petrea*) or are of uncertain reliability (e.g., *Cotinus*, *Ptelea*, *Prosopis*). Many of the modern analog species (MacGinitie, 1953, p. 38–39), belong to genera that are more broadly distributed geographically (e.g., *Acer, Bursera, Carya, Celastrus, Celtis, Ephedra, Morus, Quercus, Rhus*, *Salix*, and *Ulmus*), and MacGinitie's suggested affinities with particular species are still in need of testing.

Western North America

Sequoia is a genus that is abundantly represented at Florissant as wood, cones, foliage, and pollen. The macrofossils show closer similarity to *Sequoia* than to *Sequoiadendron*, although there are various differences that distinguish the fossil species from modern *Sequoia sempervirens*. *Sequoia* had a widespread distribution throughout much of the midlatitude Northern Hemisphere during the Tertiary (Florin, 1963), although the genus is now endemic to a relictual range that extends inland only ~60 km along the coastline from central California to southernmost Oregon.

Abies is known from a single seed as well as abundant pollen at Florissant. The seed was assigned by MacGinitie (1953) to *Abies longirostris*, a species that was later synonymized by Axelrod (1987) with *Abies rigida* on the basis of material from the Oligocene Creede flora of Colorado. Although the genus *Abies* is widespread in the Northern Hemisphere today, this particular (megafossil) species is most similar to modern *Abies bracteata* (MacGinitie, 1953; Wolfe and Schorn, 1990), which is a rare, primitive species (Liu, 1971) that grows within a narrowly restricted range along the coastal mountains of southern California. This similarity and apparent relationship are also corroborated by a comparison of an *Abies* pollen type at Florissant with *Abies bracteata*, which is an unusually large and morphologically distinct type of pollen among *Abies* species (Leopold and Clay-Poole, 2001).

Other Florissant genera that are presently restricted to western North America include pollen that is provisionally assigned to *Xylonagra*, a genus presently endemic to Baja California. *Holodiscus*, known from leaves at Florissant (Schorn, 1998), is now restricted to western North America and northernmost South America (Colombia). *Cercocarpus* is known from leaves and fruits and is restricted to western and southwestern North America (MacGinitie, 1953; Lis, 1992).

Although the above-mentioned taxa survive in western North America today, changing climatic conditions resulted in extirpation, extinction, or dispersal of many of the other Florissant taxa. Some genera survive in other regions where climate remained, or became, more favorable.

Eastern North America

A large number of Florissant genera occur in the southeastern region of the United States, many of them growing in the southern Appalachians in the mixed mesophytic forest. Some are relictual there, such as *Pachysandra,* and *Torreya* is relictual in Florida. The genera *Quercus, Juglans, Carya, Ulmus, Platanus,* and *Acer* are important in the forests between the Ozark Plateau and the eastern seaboard, and are all deciduous trees that require adequate summer moisture. These all grew at Florissant, probably near the lake. Of special interest are the relictual occurrences of Appalachian forest genera in northeastern Mexico, representing a record of some former geographic connection between these areas. Some species of *Fagus*, *Liquidambar*, and *Cercis* and derivatives of eastern genera such as *Celtis (Mirandaceltis*) occur in the cloud forest areas along the eastern Sierra Madre (Sharp, 1958). Importantly, Boyle and others (this volume) find strong affinity for eastern deciduous forest taxa among the Florissant genera.

Mexico and the Caribbean

Clearly, some Eocene plants of mid-continental North America were distributed widely, including in Mexico. An exchange between midlatitude North America and Mexico occurred during parts of the Tertiary, and some of the taxa found in the Florissant flora attest to this exchange. The extinct Euro-American genus *Cedrelospermum* has distinctive fruits that have been recognized as far south as southern Mexico at localities dating from the middle part of the Tertiary (Magallon-Puebla and Cevallos-Ferriz, 1994b). Although *Eucommia* is no longer native to North America, it, too, extended into southern Mexico in the mid-Tertiary (Magallon-Puebla and Cevallos-Ferriz, 1994a). A number of Florissant genera occur today in the cloud forest of Northeastern Mexico (Boyle et al., this volume). Neotropical affinities are indicated by some of the legumes found at Florissant, including foliage very similar to that of *Arcoa*, which is found today only on the Greater Antilles island of Hispaniola (Dominican Republic and Haiti) (P.S. Herendeen, 2006, personal commun.).

The Florissant flora contains a diversity of Rosaceae. MacGinitie reported 11 species in seven genera, and in our list we have recognized eight genera of Rosaceae. Mostly shrubs, these are wide ranging from southern Mexico northwards, but one genus, *Vauquelinia*, occurs only in Mexico. Florissant also contained a wide range of Juglandaceous genera; of the seven living genera, six have been found at Florissant and four genera in the Juglandaceae grow today in Mexico.

South America

The category of South America had the lowest similarity (two species) in MacGinitie's (1953, p. 42) evaluation, and is actually somewhat more important on a generic level (20 taxa). One of his Southern Hemisphere taxa has been reassigned; although MacGinitie considered that "the identification of *Lomatia* in the fossil record is as valid as is possible for any paleobotanical determination to be," the fossil "seeds" (actually fruits) were later found in attachment with branches of the extinct ulmaceous genus *Cedrelospermum* and have a distinctive wing venation unlike the veinless wings of extant *Lomatia* seeds. Other Florissant genera with South American affinities (Tables 2 and 3) include *Tabernaemontana* identified from pollen, *Athyana*, and nine other taxa that are pantropical. The identification of the compound leaves of *Athyana* from Florissant seems reasonable given the characteristic winged rachises of the compound leaves, although it is difficult to rule out the possibility of affinity to some other more widespread genera of Sapindales that have similar foliage, such as *Rhus*.

Asia

As MacGinitie (1953) noted, many components of the Florissant flora are now mostly restricted to eastern Asia. *Ailanthus* (Simaroubaceae) is today distributed from India, through China, Malaysia, and to Australia, but is no longer native in North America or Europe. *Ailanthus* fruits of the same kind are known from the Eocene and younger sites in Europe, Asia, and North America (Corbett and Manchester, 2004). *Dipteronia* (Sapindaceae: Aceroideae) is restricted to central and southern China today, although it has an extensive fossil history in western North America (McClain and Manchester, 2001). Similarly, *Koelreuteria,* known from both fruits and foliage in the Florissant flora (MacGinitie 1953), is now native mainly in eastern Asia. Additional examples have been identified from pollen and are associated with the Chinese mixed mesophytic forest; these include *Cercidiphyllum*-type (*Cercidiphyllites* sp. of Wingate and Nichols, 2001), *Platycarya, Pteroceltis*, and Rhoipteleaceae (Leopold and Clay-Poole 2001). *Eucommia*, known from both fruits (Manchester, 2001) and pollen (Leopold and Clay-Poole, 2001; Wingate and Nichols, 2001, as *Tricolpopollenites parmularius*) at Florissant, is now restricted to central China, but it was present in both Asia and North America during the Eocene and has a good record in the Neogene of Europe (summarized in Manchester, 1999). This genus extended as far south as Puebla Province in southern Mexico during the middle part of the Tertiary (Magallon-Puebla and Cevallos-Ferriz, 1994a). The occurrence of these genera at Florissant serves to reinforce the recognition that many of the taxa now endemic to eastern Asia are remnants of groups that had broader distribution patterns in the past.

The Florissant flora also includes various genera that are disjunct today between North America and Asia, such as *Torreya* and *Carya*, based on megafossils that were recognized by MacGinitie (1953), and also *Pachysandra,* now known from pollen (as *Erdtmanipollis* in Wingate and Nichols, 2001). A subset of this group includes those that occur mainly in eastern Asia and eastern North America, including *Carya, Juglans*, and *Platanus*. Disjunct between eastern Asia and western North America is the oriental group of *Mahonia*, which is characterized by leaflets with palmate venation (Schorn, 1966).

Members of the Podocarpaceae characterized the Late Cretaceous floras in both the Old and New Worlds; *Podocarpus* records are found on both sides of the Pacific during the Paleogene (Rouse, 1962; Dilcher, 1969) and are mainly common as minor elements in the Neogene in eastern Asia. We are beginning to find some Neogene records of *Podocarpus* pollen in the western United States and Alaska (Reinink-Smith and Leopold, 2005). Today, although *Podocarpus* (sensu lato) is tropical and subtropical and its species are mainly in the Southern Hemisphere, it occurs in southernmost China and has a species that occurs in the temperate mixed mesophytic forest of the Yangtze River valley in China. A number of species exist in Mexico and a species of *Podocarpus* is prominent in northeastern Mexico in the cloud forest of Tamaulipas (Boyle et al., this volume).

Unexpected plant associations occur in the fossil record at Florissant. For example, the flora includes a fan palm, remains of *Picea, Abies*, and *Eucommia*, plus evidence of the warm-loving members of Juglandaceae. Though these may seem like unlikely associates, they also appear together in the Green River flora of Colorado (middle Eocene; MacGinitie 1969, p. 25). Some remarkable plant associations are found in modern forest plots in Tamaulipas, Mexico. For example, *Abies religioso* grows in the cool draws while nearby are a number of warm temperate and subtropical plants, such as *Podocarpus, Liquidambar,* and fan palms. Such modern associations in the subtropics are relevant to similar occurrences at Florissant.

Modern Affinities of the Florissant Genera

As a result of our reassessment of Florissant taxa we present a list of our identifications, which are primarily of genera (Table 1). It includes some 36 families and 62 genera or subgenera. In cases where we were able to recognize a family (e.g., Lauraceae and Ericaceae) but not the genus, these were excluded from the biogeographic analysis. Table 2 shows that many genera occur in more than one geographic area today.

Both the fossil record of where the Florissant genera first appear (Table 4) and the present-day geographic affinities of Florissant genera (Table 2) emphasize the connection with the present floras of eastern China. But many of these genera are shared with the eastern and southeastern deciduous forest of the United States. Thirty-six genera have a present distribution in central and southern China. Thirty-seven genera are found in Mexico, and the number in the eastern United States is 35, illustrating the even representation of present-day genera from these regions. Ten genera are pantropical in distribution, suggesting a mild winter climate for Florissant. In summary, the present relatives of the Florissant genera are now widespread and rather equally divided between south China and Japan, eastern United States, and Mexico. Nearly all now grow in summer-moist climates except those adapted to summer-dry areas such as *Sarcobatus* and *Xylonagra*, and perhaps *Abies bracteata.*

When we compare our generic tally with MacGinitie's species tally, we find a somewhat greater importance of affinities with central and southern China and the eastern United States, and a somewhat lesser role of southwestern interior taxa (Table 2). We find that the affinities with South American genera (20 taxa) are moderately important. Although that may be significant geographically, ecologically the meaning is unclear, as South America covers a myriad of environments. Several tropical genera fall in this group (*Tabernaemontana, Semeiandra,* and *Dioscorea*), but also temperate genera such *as Alnus*, *Juglans,* and other Juglandaceae are distributed there.

From our discussion on geographic affinities, it is clear that the Florissant flora included many taxa that do not coexist in any modern community. This raises the question as to whether these taxa actually coexisted in close proximity in the late Eocene Florissant community. First it is clear that many genera had much wider distributions in the Tertiary than they have today, which explains some of the associations and some presently disjunct populations (such as *Torreya,* which has endemic occurrences in Florida, California, and East Asia). Second, Boyle et al. (this volume) demonstrate that in modern cloud forest communities of Tamaulipas Province, Mexico, many temperate genera with southerly occurrences are found side by side with fully tropical genera; so the association of tropical and temperate groups in the subtropics of the past is not surprising.

Analysis of identified fossil floras and comparison with modern biogeographic distributions of taxa provide one important tool for inferring characteristics of paleoclimate; such comparisons may also be helpful in inferring possible evolutionary adaptations that reflect changed habitat distributions of particular taxa through time.

BIOGEOGRAPHIC IMPRINT: FLORISTIC PROVINCES OF THE PALEOGENE

Western and eastern North American pollen floras of the early Tertiary reveal two distinct and geographically separate land floras that apparently developed as a result of changed continental outlines and seaways in the Late Cretaceous and early Tertiary of North America. Tschudy (1980) and Srivastava (1994) mapped the distribution of the *Normapolles* province in northeastern North America, which extends from the southeastern United States north to Greenland, Iceland and northwestern Europe, and the *Aquilapollenites* province in western North America, which extends from Colorado northward across Alaska into northeastern Siberia. Each of these had separate component species that were unique or not common in the other province; for example, as a measure of their separateness, MacGinitie (1974) stated that the Eocene Claiborne/Puryear flora of the southeastern United States shared only five species with the Rocky Mountain Kisinger Lakes flora of the same age in Wyoming, and these species were all fern taxa. Tschudy (1980) showed that these floristic provinces corresponded to landmasses that were separated by the great north-south-trending epeiric sea in the Midcontinent (Fig. 2; a similar epeiric sea transected central Asia). This American seaway (the "Cannonball Sea") provided a barrier to plant migration during the latest Cretaceous until sometime in the late Paleocene. In this section, we are conjecturing whether the existence of these disparate floristic provinces of the Paleocene had an effect on the composition of a late Eocene flora such as Florissant. To explore this question we present data on former biogeographic connections and fossil occurrences.

A phytogeographic province is defined by Srivastava (1994, p. 197) as "an isolated land mass with its characteristic flora." The importance of this biogeographic information is that until the seaway shrank in the Midcontinent at the end of the Paleocene, there was little east/west interchange of species. Typical forms on each side of the epeiric seaway in Paleocene or Late Cretaceous floras are extinct forms, but some are assignable to vascular plant families, and some have known generic affinities. Characteristic forms are as follows:

1. Western North America, *Aquilapollenites* province:
   Mancicorpus, Proteacidites, Wodehouseia, Gunnera, Ulmipollenites, Ostryoipollenites, Myricaceoipollenites, Araucariacidites (= Araucaria-type).

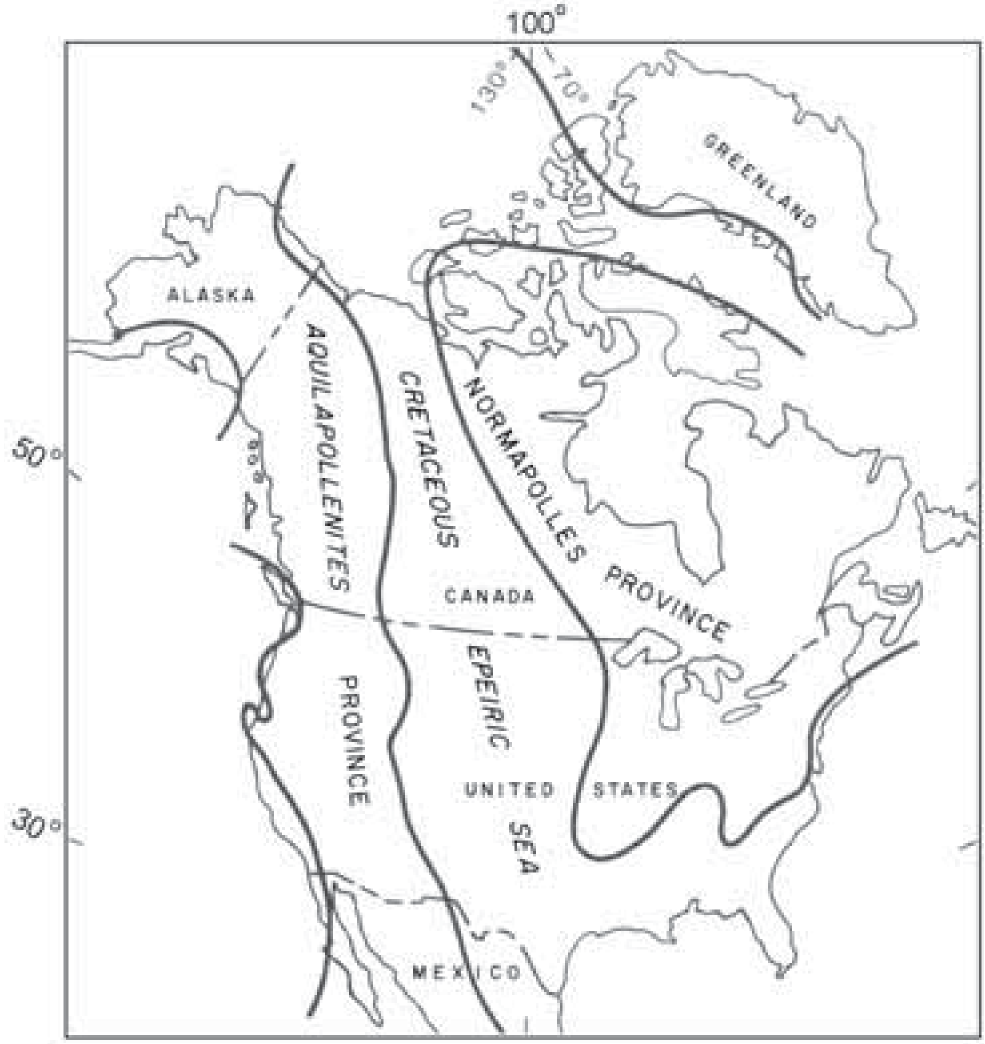

Figure 2. Map showing the floristic provinces of eastern and western North America during the Late Cretaceous and Paleocene, separated by the epeiric seaway (after Tschudy, 1980). Used by permission of New Mexico Bureau of Geology and Mineral Resources.

2. Eastern North America, *Normapolles* province: *Triporopollentites, Pseudocanalis, Extratriporopollenites, Momipites, Nyssapollenites, Rugubivesiculites* (= *Dacrydium*-type; Podocarpaceae).

Some crossing-over occurred, but fossil evidence of this is not abundant. For example, *Complexipollis* is common in the eastern U.S. sites and rare in Rocky Mountain sites. Some forms are known only on one side of the epeiric seaway, such as *Rugubivesiculites* (Podocarpaceae) and *Araucariacites* in southeastern floras. *Aquilapollenites* is virtually unknown in the Tertiary of the eastern United States.

These two floristic provinces bridged the present-day oceans by northern routes. The similarity at the species level of the Late Cretaceous pollen flora of northeastern Siberia with that in the northern Rocky Mountains flora is remarkable (Tschudy and Leopold, 1971; Leopold and Tschudy, 1964), and the Paleocene and Eocene floras of the eastern United States are very similar to those of northwestern Europe (Tschudy, 1971; Gruas-Cavagnetto, 1978; Leopold and Pakiser, 1964). The evidence from a myriad of Paleogene pollen floras at midlatitudes is very well founded. The similarity between the Paleogene floras of Germany (Krutzsch, 1957) and those of Mississippi, Arkansas, and Texas (Tschudy, 1973; Frederiksen, 1995) is compelling, whereas the contrast of these with the Paleogene floras of the northern Rocky Mountains (Tschudy 1971) is striking. Because of land bridges, which were in place during the Late Cretaceous and Paleocene, there are undoubtedly some remnant imprints that bear on composition of younger Tertiary floras through land connections with the Old World (e.g., Beringia in the North Pacific, and the Greenland-Iceland connection in the North Atlantic). In the overview by Manchester (1999) on biogeographical relationships, we can check the confidently identified genera of Florissant as to whether they crossed the North Atlantic land bridge; Manchester calls these presumed North Atlantic crossers, such as *Platycarya* and *Hydrangea*, "Euro-American" elements. *Platycarya* appears in England in the Bournemouth clay just before the Eocene, and it is recorded in the early Eocene both in the London Clay and in Colorado, Wyoming, and North Dakota (Hail and Leopold, 1960; Hickey, 1977; Nichols, 2006. Conversely, we can check Florissant genera that seem to have crossed the Bering land bridge, which Manchester calls "Amer-Asian" elements, indicating exchange between North America and Asia (e.g., *Acer* and *Eucommia).* Some elements that Manchester calls "endemic" are taxa not known outside North America during the Paleocene and Eocene. In our consideration of Florissant biogeographic occurrences, we indicate the term "endemic" for taxa that were apparently restricted to North America in the Paleocene and Eocene, e.g., *Sarcobatus*. Listed in Table 4 are our groupings for the Florissant flora.

It appears that there is a somewhat higher proportion of taxa at Florissant that were endemic to North America in the Eocene, e.g., those taxa not known to be present in other regions (nine taxa, Table 4). Four of the Florissant taxa show a Euro-American connection and four are Amer-Asian, showing early connections with Asia. These examples suggest that there was a greater contribution from groups endemic to western North America in the Florissant flora.

Some taxa that have Asian distributions today originated in the western United States and were present at Florissant. An example is *Cyclocarya*, which was endemic in the western United States in the Paleocene and Eocene but spread to the Old World in the Oligocene (Manchester, 1999 p. 508). Another example is *Pachysandra*, an American Eocene endemic. *Pachysandra/ Sarcococca* (Buxaceae pollen record) first appeared in the Paleocene of California and spread through the Rocky Mountains and Great Plains in the Eocene, to the West Coast and Idaho in the Oligocene and Miocene; Gray and Sohma (1964) showed that *Pachysandra* reached British Columbia in the Eocene, and it was recorded in Alaska by the Eocene and the Oligocene (Ridgway et al., 1995). A pollen record puts *Pachysandra* in the Pliocene Citronelle Formation of Alabama (Leopold, personal observ.), and it is represented today in a small area of the southern Appalachians by a single species, *P. procumbens*. The importance of North American endemic groups is especially interesting because many of these have strong records in the western United States, emphasizing American contributions to the old western floristic province, and later to other provinces.

Floras of the early and middle Eocene in the Rocky Mountains (Fig. 1) provide additional evidence for community evolution and changes in biogeography that preceded Florissant (Leopold and MacGinitie, 1972). Early Eocene floras such as the Kisinger Lakes flora were warm and humid, and there was a moderately strong affinity to both Old World and New World tropical taxa (MacGinitie, 1974; Leopold, 1974). The flora of the middle Eocene Green River Formation of Colorado, Utah, and Wyoming is strikingly different from the Kisinger Lakes flora, indicating a dry subtropical climate and only a minor biogeographic affinity to Old World taxa. Green River is warmer than Florissant and represents a lower elevation (MacGinitie, 1969; Wolfe, 1994). MacGinitie (1969) noted that 29 of the Green River species (41%) were closely related to those from Florissant, including similar or identical species of *Sequoia, Pinus, Populus, Salix, Quercus, Cedrelospermum, Mahonia, Prunus, Rosa, Vauquelinia, Ailanthus, Cedrela, Rhus, Dipteronia, Athyana, Cardiospermum,* and *Koelreuteria*. Pollen evidence from MacGinitie's Wardell Ranch flora locality in Colorado (USGS Paleobot. loc. D4480; middle to late middle Eocene) and a similar suite of samples from the Washakie Basin Laney Member (Roehler, 1991; USGS Paleobot. locs. D4479, D4475; early Eocene) also adds the following forms that occur at Florissant: *Lygodium* cf. *L. kaulfussii, Tsuga, Picea, Ephedra* cf. *E. nevadensis,* Arecaceae (Palmae type*), Carya, Pterocarya, Engelhardieae, Elaeagnus, Cardiospermum, Eucommia,* cf. *Ulmus, Alnus,* and *Betula.* Despite the similarities, Green River includes more tropical forms than Florissant, and Florissant has more temperate taxa. MacGinitie hypothesized that Florissant and Green River shared a common origin and that Florissant was a derivative of the Green River community. Although at least 10 m.y. older than Florissant, the plants present at Green River show that many of the Florissant genera had become well established in the continental interior.

BIOGEOGRAPHIC RESPONSES TO CLIMATIC COOLING DURING THE EOCENE-OLIGOCENE TRANSITION

Evolutionary changes within particular lineages appear to have resulted in ecologic/climatic shifts in particular taxa through time. The fossil record provides evidence for this, viz. the close comparison between fossil floras such as Creede (Wolfe and Schorn, 1989) and Florissant with the ecological distribution of those genera today.

Morphologic or reproductive similarities between modern and fossil taxa do not preclude the possibility of different ecological adaptations. Related to this is the question of community stability through time (Mason, 1947; Wolfe and Schorn, 1989). In this regard it is noteworthy that species that associate in particular communities today may have had ancestors that lived in dissimilar communities in the past, and likewise that species that lived together in the past may have descendants that live in different communities today. In this sense, communities such as Florissant can be considered as unique, "extinct" associations of species. Although modern communities can be found that are analogous to fossil communities, these modern communities are not homologous (Wolfe and Schorn, 1989).

Table 5 provides a climatic comparison of West Coast and interior U.S. floras of Paleogene age and illustrates the changing vegetation types. Because it is based on a mix of different authors, it includes data from different methods and different terminology for vegetation types. Table 6 illustrates the appearance of Florissant taxa at lower elevations and in younger floras, showing the sequence of the floras discussed and the Eocene-Oligocene transition.

The predominance of temperate taxa, when compared with the warmer subtropical to paratropical sea level floras of the same age, provides evidence that the Florissant flora represents an upland biotic community of at least moderate and possibly high elevation. Various estimates for mean annual temperature (MAT) at Florissant range from 11 to 18 ° C (see summary in Meyer,

TABLE 5. CLIMATIC COMPARISON OF WEST COAST AND INTERIOR U.S. FLORAS OF PALEOGENE AGE

	West Coast			Rocky Mountains			References
	Flora	MAT (°C)	Vegetation	Flora	MAT (°C)	Vegetation	
Late Oligocene	Yaquina	15.5	Broad-leaved evergreen	Creede	0–11.5	Mixed coniferous forest	Axelrod (1987); Wolfe and Schorn (1990); Wolfe (1981)
Early Oligocene	Bridge Creek, Lyons, Rujada, Willamette	9–13	Mixed mesophytic forest and mixed broad-leaved evergreen and coniferous forest	Ruby?	—	Temperate deciduous/coniferous forest & woodland	Meyer and Manchester (1997); Meyer (1973); Lakhanpal (1958); Wolfe (1981, 1992, 1994); Becker (1961, 1966)
Climatic cooling during the earliest Oligocene							
Earliest Oligocene	LaPorte Goshen	19–20	Notophyllous broad-leaved evergreen forest	Pitch-Pinnacle	11.2–14.2	—	Potbury (1935); Chaney and Sanborn (1933); Wolfe (1992, 1994)
Late Eocene	Comstock Kummerian, (Puget Group)	19–23	Notophyllous broad-leaved evergreen forest to paratropical rain forest	Antero Florissant	 11–18	— Warm temperate broad-leaved forest to subtropical cloud forest	Sanborn (1935); MacGinitie (1953); Wolfe (1994); Leopold and Clay-Poole (2001)
Middle Eocene	Lower Ravenian (Puget Group)	18–22	Paratropical rain forest	Green River Thunder Mountain	19	Savanna woodland and mixed coniferous forest	Wolfe and Wehr (1987); Wolfe (1994); MacGinitie (1969); MacGinitie (1974); Leopold (1974)
	Fultonian (Puget Group)	17–18	Broad-leaved evergreen	Kisinger Lakes	22	Semi-evergreen mesophyll forest	

Note: MAT—mean annual temperature.

TABLE 6. SIGNIFICANT FLORAS OF THE EOCENE-OLIGOCENE TRANSITION AND OCCURRENCE OF FLORISSANT GENERA

West Coast lowland floras				Rocky Mountains upland floras			
Flora	Age (Ma)	MAT (°C)	Examples of taxa shared with Florissant	Flora	Age (Ma)	MAT (°C)	Examples of taxa shared with Florissant
Oligocene							
Willamette	30.1	13	*Amelanchier* *Asterocarpinus* *Cedrelospermum* *Crataegus* *Mahonia* *Malus** *Pachysandra*† *Paracarpinus* *Ribes* *Rosa* *Rubus* *Sarcobatus*†	Creede	27.2	0–11.5	*Abies rigida** *Cercis* *Cercocarpus* *Holodiscus* *Mahonia* *Picea magna*-type *Pinus** *Populus* *Ribes*
Lyons		13					
Rujada		13					
Bridge Creek	31.8–33.62	9–12					
Earliest Oligocene							
LaPorte	32.3	22.1–23.0		Pitch-Pinnacle	29–32.9	11.2–14.2	
Goshen	33.4	19.0–20.1	—				
Latest Eocene				Antero	33.77–33.89		—
Comstock	39.7	19.1–21.2	*Carya** *Cedrelospermum* *Juglans*† *Podocarpus*†	Florissant	34.07	11–18	All

Note: MAT—mean annual temperature.

*Known from pollen.

†Known from pollen only.

2001; Boyle et al., this volume). Several recent studies using various paleobotanically based methods have derived relatively high estimates for Florissant's paleoelevation, ranging from 1900 to 4100 m (see summary in Meyer, 2001), although others have suggested warmer temperatures and hence lower elevation for the region during the late Eocene, followed by later Tertiary uplift (e.g., MacGinitie, 1953; Steven et al., 1997; Axelrod, 1998; Leopold and Clay-Poole, 2001). The warm temperature estimates are supported by a mix of fossil insects whose relatives inhabit tropical areas today.

In the highlands, within the same region but younger in age, the late Oligocene Creede flora (27.2 Ma) in Colorado provides a record of a cool temperate upland coniferous forest community that lacks many of the warm temperate and subtropical genera of Florissant. The Creede deposits are in an ancient caldera, located ~190 km southwest of Florissant (Fig. 1), and are interpreted to have been at high elevation. Estimates of the MAT of the Creede flora are from 0 to 11.5 °C (Wolfe and Schorn, 1989, based on CLAMP data; Axelrod 1987, based on nearest living relatives or NLR). The estimated temperatures differ depending in part on which method is used to infer these values.

Other nearby Colorado floras such as the Pitch-Pinnacle (Gregory and McIntosh, 1996) and Antero (Table 6; Wolfe, 1992; Prothero, this volume) occur very near the Eocene-Oligocene boundary, yet are not clearly resolved in terms of whether they occur before or after the climatic cooling. Pitch-Pinnacle is interpreted as 29–32.9 Ma in age and having a MAT of 12.7 ± 1.5 °C (Gregory and McIntosh, 1996). Antero is located in South Park, just west of Florissant, and dates of 33.77–33.89 Ma and a reversed magnetic polarity suggest a latest Eocene age slightly younger than Florissant (Prothero, this volume), and preliminary analysis of a very small collection of plants suggests a cool, post-deterioration flora (Wolfe, 1992). The few species known from Antero appear to show similarity to Creede (MacGinitie, 1953; Wolfe, 1992). Pitch-Pinnacle has conifers that are similar to Creede's, and angiosperm genera that are common to both Creede and Florissant (Gregory and McIntosh, 1996). The CLAMP paleotemperature estimate of 12.7 °C for Pitch-Pinnacle is close to the comparable CLAMP estimate of 12.8–13.9 °C for Florissant (Gregory and McIntosh, 1996).

In the lowlands preceding the cooling, West Coast floras of latest Eocene to earliest Oligocene age are subtropical to paratropical in character with MATs of ~19–23 °C (Table 6; Wolfe, 1994; see summary in Meyer, 2001). Notable examples of these floras include Comstock (Sanborn, 1935) and Goshen (Chaney and Sanborn, 1933) in western Oregon and LaPorte (Potbury, 1935) in California (Fig. 1), although others are summarized by Retallack et al. (2004). The ages for these floras are 39.7 Ma for Comstock and 33.4 Ma for Goshen (Retallack et al., 2004), and 32.3 Ma for LaPorte (from Wolfe, 1981). Better dating is needed for the LaPorte flora, which is based on K/Ar dating, whereas the others have Ar/Ar dates. These dates indicate that warm conditions persisted into the earliest Oligocene, based on calibration of the Eocene-Oligocene boundary at 33.9 Ma (Luterbacher et al., 2004). Mean annual temperatures estimated on the basis of CLAMP are 19.1–21.2 °C for Comstock, 19.0–20.1 °C for Goshen, and 22.1–23.0 °C for LaPorte (Wolfe, 1994; Gregory and McIntosh, 1996; Wolfe et al., 1998), indicating very warm conditions. Unfortunately, most of these lower-elevation late Eocene floras are in need of revision, and many of their taxonomic components are not clearly validated by critical analysis of morphological characters.

In the lowlands after the cooling, the early Oligocene floras near the West Coast contained many temperate elements suggesting MATs of only 9–13 °C (Table 6). Compared to the late Eocene and earliest Oligocene (pre-deterioration) low-elevation floras (Table 5), this indicates a temperature decline of at least 6–8 °C in the lowlands during the Eocene-Oligocene transition; the cooling according to Wolfe (1978, 1992, 1994) was due particularly to a decline in cold-month temperature. This climatic change may have occurred abruptly within <1 m.y. during the earliest part of the Oligocene (Wolfe, 1992), although other evidence suggests that it may have been a more gradual, fluctuating change over 6 m.y. during the early Oligocene (Retallack et al., 2004) associated with a decline in annual precipitation from ~1000 mm to ~700 mm. The Oligocene lowland floras are comparatively well understood taxonomically and include, for example, the Rujada (Lakhanpal, 1958), Lyons (Meyer, 1973), and Willamette floras, all located in western Oregon (Fig. 1). Willamette is dated as 30.1 Ma (Retallack et al., 2004). All of these floras indicate a MAT of ~13 °C (Wolfe, 1994). The slightly more interior Bridge Creek flora, which was probably at a low to moderate elevation of 500–1000 m above early Oligocene sea level, has dates ranging from 31.8 to 33.62 Ma and MATs of 9–12 °C (Meyer and Manchester, 1997). The vegetation types these floras record range from mixed broad-leaved evergreen and coniferous forest to mixed mesophytic forest to mixed northern hardwood forest (Wolfe, 1992; Meyer and Manchester, 1997), clearly more temperate than the earlier lowland sites.

Comparisons between these various late Eocene and early Oligocene floras representing both lowland and upland conditions provide the basis for inferring the responses of particular plant genera to climatic cooling (Wolfe, 1972, 1992; Meyer 2003, 2005). Some of the genera at Florissant are unknown in younger floras and apparently became extinct during the Eocene-Oligocene transition. For example, *Deviacer* and *Fagopsis* are unknown from well-dated post-Eocene floras. *Fagopsis* does occur in the Ruby flora of Montana, a flora very similar to that at Florissant (Becker, 1961, 1966); however, the Ruby flora is not confidently dated and may be as young as Whitneyan in the early Oligocene (Wing, 1987). Other examples of extinction/extirpation during the climatic cooling appear to be more abundant in lowland broad-leaved evergreen assemblages from the West Coast than they are in the Rocky Mountains, although more thorough taxonomic revision of the West Coast floras is needed in order to document confidently the genera that were affected. The timing and magnitude of the climate change in the Rocky Mountains are not as clearly defined (Prothero, this volume).

The Eocene and Oligocene floras near sea level from western Oregon (Fig. 1) indicate a maximum diversity of thermophilic taxa at 35–34 Ma, followed by plant extinctions or extirpations of 60% during the earliest Oligocene, after 33.4 Ma (Retallack et al., 2004). Following this initial Oligocene extinction, plant diversity recovered in this region by 31 Ma.

What was the fate of the Florissant genera during this time interval? Some of the genera that were present in the Florissant forest remained in the southern Rocky Mountain region into the Oligocene, as evidenced by comparisons with the Creede flora (Axelrod, 1987; Wolfe and Schorn, 1990), and are still in the Florissant area today. Examples include *Abies*, *Picea*, *Pinus*, *Mahonia*, *Populus*, *Ribes*, *Cercocarpus, Holdiscus,* and *Cercis*. Two species of *Cercocarpus* were found as fossils at Creede, one of which may be related to the Florissant species and is possibly an extinct genus ancestral to extant *Cercocarpus* (Wolfe and Schorn, 1990). *Abies rigida* is shared between Creede and Florissant and is most closely related to the modern *A. bracteata* in California, an observation that is also supported by pollen data. The *Picea* from Creede belongs to the same complex as the Florissant *Picea magna* and represents a type that is no longer extant in North America (Wolfe and Schorn, 1990). These genera persisted in the southern Rocky Mountains and were apparently well adapted to the changing climate or may have evolved in response to the cooling climate.

Some of the Florissant genera appear to have dispersed to regions of lower elevation or latitude where the temperate climate and mean annual temperatures following the climatic cooling may have approximated those of Florissant. Other taxa (e.g., *Cedrelospermum*) had been widespread during the late Eocene and, rather than dispersing, may simply have persisted in humid areas near the West Coast. Lower-elevation early Oligocene floras such as Bridge Creek, Lyons, Rujada, and Willamette represent a widespread midlatitude temperate hardwood forest that had developed at lower elevations and coastal localities during the early Oligocene.

The taxonomic affinities of the Bridge Creek and Rujada floras to that of Florissant were first noted by MacGinitie (1953), who considered that climate change during the interval of time separating these floras from Florissant may have resulted in "the migration of isotherms southward and downward." Indeed, many genera known from Florissant are lacking in West Coast lowland floras of late Eocene age, yet their appearance in early Oligocene and Miocene floras of the same region suggests they did disperse to lower elevations or coastward from late Eocene montane forests during the earliest Oligocene climatic cooling. Examples include *Pteroceltis, Pachysandra, Sarcobatus*, several genera in the Rosaceae, such as *Amelanchier*, *Crataegus*, *Malus*, *Rosa*, *Rubus*, as well as the extinct *Asterocarpinus/Paracarpinus* (Manchester and Crane, 1987) in the Betulaceae. *Ribes* also appears to have dispersed to lower elevations during this time, yet it also persisted in the southern Rocky Mountains (e.g., Creede). As climate fluctuated between warm and cool intervals during the middle and late Eocene (Wolfe, 1994), some of the genera common to Florissant (e.g., *Rosa, Acer,* and *Dipteronia*) may have dispersed between upland and lowland areas. Other Florissant genera existed at midlatitude low elevations in the Pacific Northwest since the Eocene and persisted there through the Miocene, including such examples as *Carya, Cercidiphyllum, Engelhardia, Juglans Platycarya, Podocarpus* (Rouse, 1962; Reinink-Smith and Leopold, 2005), *Pterocarya, Quercus,* and *Ulmus*. Hence they were simply widespread during and after the Eocene. The ultimate elimination of these genera may have been the result of lowered precipitation as well as cooling (Reinink-Smith and Leopold 2005; Axelrod and Raven, 1985), and paleosol evidence from central Oregon indicates that precipitation as well as temperature declined steeply at 33 Ma (Sheldon et al., 2002).

CONCLUSIONS

By utilizing a selected list of Florissant genera and subgenera that we consider to be confidently identified, especially those in which multiple organs are present, we have shown that some of the previously identified geographic affinities of the flora are changed. At least seven genera have been reassigned and cannot be used to support the original biogeographical analysis.

Taxonomic level of identification affects our results. Because our analysis focuses on the genera of Florissant and MacGinitie's analysis uses species identifications, one can expect a difference in geographic results. That is evident. MacGinitie's species analysis showed strongest relation to the western interior, the Edwards Plateau, Texas, northeastern Mexico, and central-east China, with only a few tropical species. Our generic list, tallied according to the same geographic categories used by MacGinitie (1953), suggests that the strongest relation is with genera of central and southern China, and that a very important and almost equivalent affinity exists with the flora of the eastern United States (the Ozark Plateau east to the southern Appalachians), similar to the findings of Boyle et al. (this volume). We find a stronger affinity with tropical genera; in some of these cases the Florissant species, such as *Semieandra* and *Dioscorea*, are represented by a northernmost taxon whereas the genus may be pantropical. We also find a larger number of genera at Florissant with modern distribution in South America than what was recognized by MacGinitie from species comparisons. About 20% of Florissant genera occur in the Tamaulipas highlands of northeastern Mexico today, suggesting a minor affinity with the forests of that area. In this regard the species analysis and the generic analysis share about the same top four geographic groups in common, but the emphasis is different (Table 3).

We have stated that a new comprehensive examination on the species level of these taxa would be more informative than a generic assessment, but such a review is beyond the reach of this study. However, the usefulness of our analysis is that it secures a wide number of generic identifications, and these are very useful in studying the pre-Eocene origin of the Florissant flora. The conservative list of genera also gives us a strong handle for tracking the dispersal or fate of the Florissant groups during the Oligocene deterioration after the time of Florissant's deposition.

Biogeographic analysis of early records of Florissant genera in North America (Manchester, 1999) suggests that a few taxa arrived on this continent before the late Eocene from Old World ancestors by way of northern routes, the Beringian corridor and the North Atlantic route. In some cases the American occurrences may have been ancestral to the Asian populations. Seven taxa were already widespread across Europe, North America, and Asia by the Eocene, and nine others were endemic to North America, occurring only here before the late Eocene and hence suggesting that they evolved here.

The Eocene-Oligocene transition records a pronounced cooling that was also a time of the first glaciation in East Antarctica (Ivany et al., 2006; Zanazzi et al., 2007). This cooling, which may have been global in extent, affected floras across western North America, and the composition of these plant communities was dynamically changed through processes of extinction, extirpation, dispersal, and persistence within regions owing to preadaptation or rapid evolution. At least nine broad-leaved genera dispersed to lower elevations during the Eocene and Oligocene transition. One Florissant genus, *Deviacer,* became extinct, as there are no further records of them after Florissant. Another (*Fagopsis*) became extinct during the Oligocene. At least nine genera are known to have remained in the southern Rocky Mountains at least well into the Oligocene, as evidenced by their occurrence at Creede, Colorado (Table 6). Evidence indicates that some taxa extended ranges southward into Mexico (e.g., *Eucommia* and *Cedrelospermum*), and these later became locally extinct.

The patterns reinforce the view that the species and genera of this flora responded independently to major climate change. The late Eocene Florissant flora, because of its upland interior occurrence just preceding a major change in global climate, provides crucial data for the interpretation of these biogeographic patterns through time.

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Magnetic stratigraphy of the Eocene-Oligocene floral transition in western North America

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ABSTRACT

Eocene and Oligocene floras of the western United States show a climatic deterioration from warmer conditions to much cooler and drier conditions. Recent ^{40}Ar/^{39}Ar dates and magnetic stratigraphy have greatly improved their correlation. In this study, the uppermost Eocene Antero Formation, Colorado, is entirely reversed in polarity, and is correlated with late Chron C13r, based on ^{40}Ar/^{39}Ar dates of 33.77–33.89 Ma. The early Oligocene Pitch-Pinnacle flora of Colorado is within rocks of normal polarity, and best correlated with Chron C12n (30.5–31.0 Ma), based on ^{40}Ar/^{39}Ar dates of 32.9–29.0 Ma (although correlation with Chron C11n is also possible). The late Oligocene (^{40}Ar/^{39}Ar dated 26.26–26.92 Ma) Creede flora of southwestern Colorado is correlated with Chron C8r. The early Oligocene (^{40}Ar/^{39}Ar dated at 31.5 Ma) Granger Canyon flora in the Warner Mountains, near Cedarville, northeastern California, is correlated with Chron C12r. These results are compiled with previously published dates and magnetic stratigraphy of the Eugene-Fisher floral sequence in western Oregon, the Bridge Creek floras in central Oregon, other floras in the Warner Mountains of northeast California, and the Florissant flora of central Colorado. In Colorado, the climatic change seems to have occurred between the Florissant and Antero floras, and is dated between 33.89 and 34.07 Ma, or latest Eocene in age, although the Pitch-Pinnacle flora suggests that the deterioration was less severe and took place in the early Oligocene. In northeast California, the dating is not as precise, so the climatic change could have occurred between 31.5 and 34.0 Ma (probably early Oligocene). In western Oregon (Eugene and Fisher Formations), the change occurs between the early Oligocene Goshen flora (33.4 Ma) and the early Oligocene Rujada flora (31.5 Ma). In the John Day region of Oregon, it occurs before the oldest Bridge Creek flora, dated at 33.62 Ma (right after the Eocene-Oligocene boundary). Thus, only two of these four floral sequences (Eugene, Oregon, and Cedarville, California) clearly show the early Oligocene climatic change consistent with that documented in the global marine record, whereas the climatic change was seemingly abrupt in the late Eocene in Colorado between 33.89 and 34.07 Ma, and also sometime during the late Eocene (before 33.62 Ma) in central Oregon.

Keywords: Eocene, Oligocene, magnetic stratigraphy, floras, Colorado, California.

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INTRODUCTION

The Florissant flora of Colorado provides one of our best windows on the fauna and flora of the late Eocene, the last pulse of warming before the "Oligocene deterioration" that was first documented by Wolfe (1971, 1978). Both the floras and the faunas provide evidence of relatively warmer and wetter conditions than prevailed in the Oligocene, just a million years later. However, to place this evidence in context, it is helpful to examine floras and faunas that occurred before and after Florissant, and also to look at regions outside the Colorado Rockies.

In recent years, the application of magnetic stratigraphy to the calibration of the faunal changes in Eocene-Oligocene land mammals (Prothero and Emry, 1996) and marine invertebrates and microfossils (Prothero, 2001) has made great strides. In most cases, we now have the stratigraphic resolution and chronostratigraphic precision to date most faunas to the nearest 100,000 yr, and correlate them all to a global time scale, allowing direct correlation of the global deep-marine climatic record with the land record and shallow-marine record of North America. However, fewer magnetostratigraphic studies have been conducted on important fossil plant localities, especially those near the Eocene-Oligocene transition. Important magnetostratigraphic studies of floras from the San Diego middle and late Eocene (Walsh et al., 1996), the Eocene-Oligocene sequence near Eugene, Oregon (Retallack et al., 2004), and the upper Eocene Florissant Formation in Colorado (Prothero and Sanchez, 2004) have now been published, but those results have not been summarized in one place. In addition, many new floras have been sampled, and two of those are reported in this paper. Studies such as those by Myers (2003) have updated the chronology of many of those floras, but the new results have refined the correlations even further.

Such a refined correlation is highly desirable, because the sequence of floras in western North America strikingly documents the details of climatic change in this region through the Eocene and Oligocene (MacGinitie, 1953; Wolfe and Hopkins, 1967; Axelrod and Bailey, 1969; Wolfe, 1971, 1978, 1992, 1994; Wing, 1987; Myers, 2003). Indeed, the dramatic cooling and drying near the Eocene-Oligocene boundary was the original basis for the term "Oligocene deterioration" of Wolfe (1971), renamed the "Terminal Eocene Event" by Wolfe (1978). According to Wolfe (1978), this floral change was the most dramatic of the entire Cenozoic, yet later work by Wolfe (1994) showed that the climatic change was not as extreme as originally suggested, and this has been corroborated by Retallack et al. (2004). In addition, there was confusion about dating in the earlier analyses published by Wolfe (1971, 1978). Most of those problems have now been resolved (Wolfe, 1992; Myers, 2003), but further refinement of dating is always valuable to test previous hypotheses.

This paper will summarize previous magnetostratigraphic chronologies of important middle to late Eocene and Oligocene floras in western North America, and provide new data for four important plant localities that have been recently sampled and analyzed. More stratigraphic sections and floras need to be studied, of course, but these results already point out some interesting problems that have not yet been resolved. The precise calibration of these floras, in turn, is important to assessing the magnitude and timing of paleotemperature change in North America during the Eocene-Oligocene transition.

METHODS

Four new sections were sampled for this study. The first was the classic upper Eocene Antero Formation and its floras from the South Park Basin, Park County, central Colorado (Figs. 1A, 1B). This formation was first named by Johnson (1937), and fully described by Stark et al. (1949, p. 63–66) and Epis and Chapin (1975) based on exposures north of Hartsel, Colorado. Although Stark et al. (1949) reported an aggregate thickness of the Antero Formation of over 200 m in some places, currently there are no continuous surface exposures that would allow collection of that much section. Instead, sampling was conducted in several isolated roadcuts northeast of Hartsel (sites 1–4, locations given in Table 1) and in the southern part of the South Park Basin, southwest of Hartsel (three sites spanning ~10 m of section, locations given in Table 1).

The second section was collected in the Pitch-Pinnacle Formation, on the western flank of the Sawatch Range just southwest of Monarch Pass, Saguache County, Colorado (Fig. 1B). Described in detail by Gregory and McIntosh (1996), our sampling followed the main section in their paper (Gregory and McIntosh, 1996, their Figure 5), concentrating on a large mine excavation ("Pitch-Pinnacle quarry" of Gregory and McIntosh, 1996, their Figure 2) which yields the main flora (lat 38°23.158′N, long 106°19.284′W), and on roadcuts uphill and down section from the mine pit. Seven sites, spanning ~14 m of section, were taken wherever exposures allowed (locations given in Table 1).

The third section studied was from the late Oligocene Creede flora (Axelrod, 1987; Wolfe and Schorn, 1989), in the Creede Formation in Mineral County, south-central Colorado (Fig. 1B). Reynolds et al. (2000) did an extensive paleomagnetic study of the subsurface portion of this formation obtained by drilling cores up to 703 m long, but they did not sample the surface sections of the uppermost part of the Creede Formation, which are the source of the well-known plant and insect fossils (Axelrod, 1987; Wolfe and Schorn, 1989, 1990). The best and most accessible exposure, which was sampled for this study, is the classic Bridsey Gulch section (UCMP PA 574) of Axelrod (1987), just north of Highway 149 (SE 1/4 SW 1/4 NW 1/4 Sec. 6, T. 41N., R. 1E., Creede 7.5 min quadrangle, Mineral County, Colorado; lat 37°49.769′N, long 106°55.087′W). Six sites spanning ~25 m of section were sampled, up to the point where the exposures were completely covered as the steep slopes gave way to a shallow bench. Fossil plants, insects, and other organisms are found in many levels in this section (Axelrod, 1987), although they are most abundant at the road level and at several quarries that were encountered during the traverse.

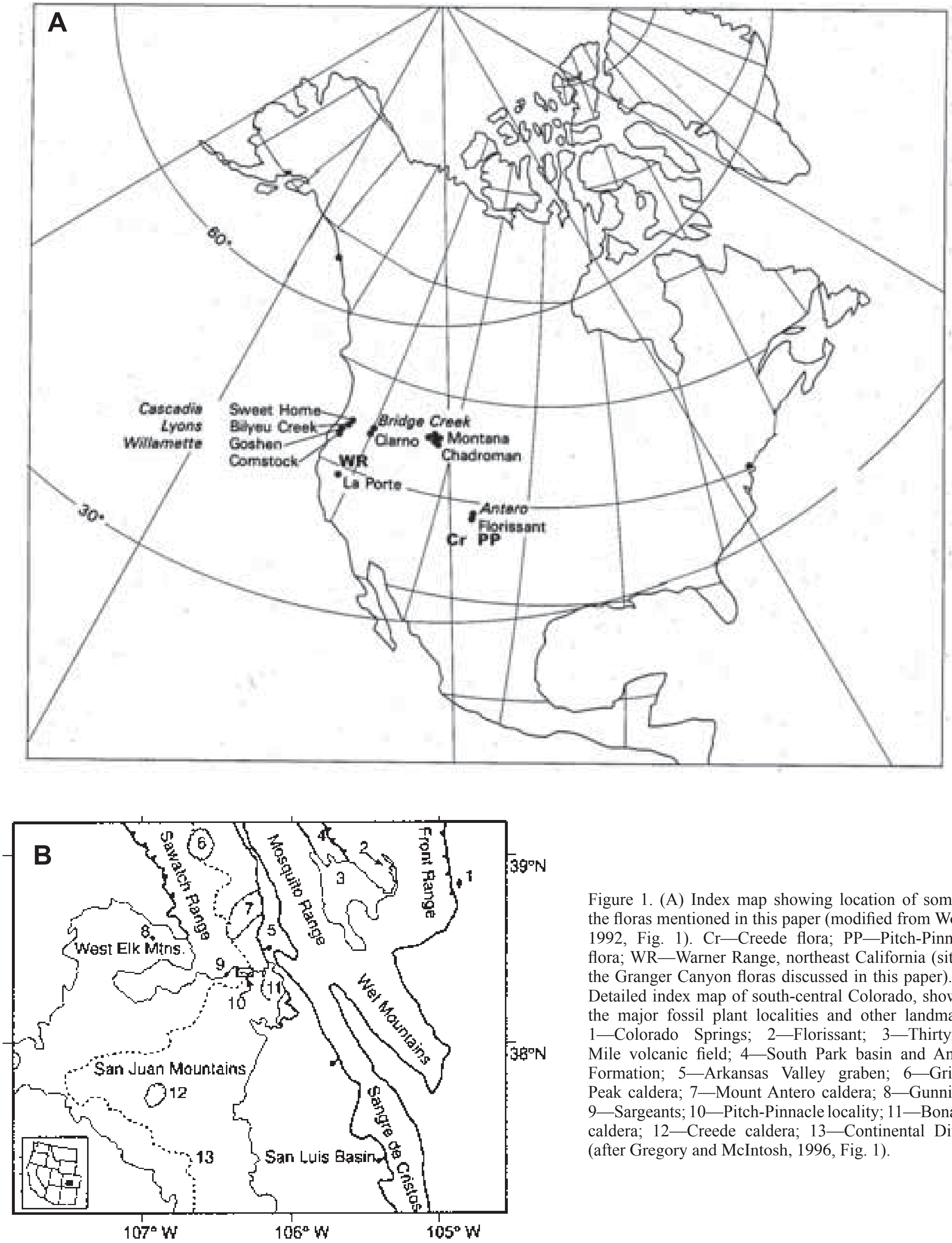

Figure 1. (A) Index map showing location of some of the floras mentioned in this paper (modified from Wolfe, 1992, Fig. 1). Cr—Creede flora; PP—Pitch-Pinnacle flora; WR—Warner Range, northeast California (site of the Granger Canyon floras discussed in this paper). (B) Detailed index map of south-central Colorado, showing the major fossil plant localities and other landmarks. 1—Colorado Springs; 2—Florissant; 3—Thirtynine Mile volcanic field; 4—South Park basin and Antero Formation; 5—Arkansas Valley graben; 6—Grizzly Peak caldera; 7—Mount Antero caldera; 8—Gunnison; 9—Sargeants; 10—Pitch-Pinnacle locality; 11—Bonanza caldera; 12—Creede caldera; 13—Continental Divide (after Gregory and McIntosh, 1996, Fig. 1).

TABLE 1. STATISTICS OF PALEOMAGNETIC SITES

Site	n/N	D	I	K	α_{95}	Lat	Long
Antero Formation							
1	4/4	160.0	–16.9	6.8	38.0	N39°09.704′	W105°45.050′
2	5/5	199.4	–43.8	10.3	25.0	N39°09.704′	W105°45.050′
3	6/6	187.8	–41.5	11.5	20.7	N39°09.907′	W105°45.200′
4	4/4	188.4	–23.7	4.4	49.8	N39°06.623′	W105°42.778′
5	4/4	195.1	–28.8	4.5	48.9	N38°50.718′	W105°48.851′
7	3/3	168.2	–43.8	4.8	63.5	N38°50.718′	W105°48.851′
Pitch-Pinnacle Locality							
1	4/4	353.9	39.6	4.3	50.2	N38°23.129′	W106°19.280′
2	4/4	22.9	62.0	23.6	19.3	N38°23.129′	W106°19.280′
3	3/3	46.0	56.1	7.4	49.1	N38°23.158′	W106°19.284′
5	4/4	28.0	38.5	2.8	67.9	N38°23.199’	W106°19.215′
6	3/3	21.8	57.5	25.8	24.8	N38°23.238′	W106°19.291′
7	3/3	23.5	41.0	6.9	51.2	N38°23.301′	W106°19.792′
8	3/3	178.8	–47.4	5.4	59.2	N38°23.360′	W106°18.801′
Creede Formation, Bridsey Gulch							
1	4/5	33.9	57.0	8.7	33.1	N37°49.769′	W106°55.087′
2	3/4	359.1	51.1	87.9	13.2	N37°49.769′	W106°55.087′
3	3/3	184.3	–57.9	3.5	78.8	N37°49.769′	W106°55.087′
4	3/3	188.6	–27.6	23.3	26.1	N37°49.769′	W106°55.087′
5	4/5	176.6	–33.8	5.1	45.4	N37°49.769′	W106°55.087′
6	3/4	253.7	–39.8	5.2	60.8	N37°49.769′	W106°55.087′
Granger Canyon							
1	2/5	179.8	–39.0	162.3	19.7	N41°28.470′	W120°11.207′
2	5/6	180.5	–18.1	35.7	13.0	N41°28.470′	W120°11.207′
3	1/4	348.1	–38.2	—	—	N41°28.470′	W120°11.207′
4	2/5	246.4	–28.3	431.4	12.1	N41°28.470′	W120°11.207′
5	2/5	22.8	11.2	7.8	107.8	N41°28.470′	W120°11.207′

Note: All directions are corrected for dip. n/N—total number of samples taken vs. interpretable samples; D—declination (in degrees); I—inclination (in degrees); K—Fisher's precision parameter; α_{95}—95% confidence ellipse around mean (in degrees); Lat—latitude; Long—longitude.

The fourth section was taken above and below the Granger Canyon plant locality (UCMP PA 760), in the Warner Range (Fig. 1A) near Cedarville, in northeast California (Myers, 1998, 2003). It is located at 1440 m elevation on the north slope of Granger Canyon (SE 1/4 SE 1/4 section 30, T. 42N., R. 16E., Warren Peak 7.5 min quadrangle, Modoc County, California; lat 41°28.470′N, long 120°11.207′W). The Warner Range contains a thick sequence of mostly volcanic rocks spanning a long interval of the Cenozoic (Duffield and McKee, 1986; Carmichael et al., 2006), but this particular fossil locality is a fine-grained lacustrine shale sandwiched between ignimbrites and volcanic agglomerates that yields an early Oligocene flora (Myers, 1998, 2003). Other important floras are known from the Cedarville area in the Warner Mountains, but they proved to be less accessible. I hope to return and sample those floras at a future date.

Samples were collected as oriented block samples in the field and subsampled with a drill press in the lab to produce a core. At least three samples were collected at each site, although for many sites where sampling was easier, four to six samples were obtained (Table 1). Poorly consolidated samples were hardened with sodium silicate in the field. Samples that were too fragile to drill were placed in plastic ring molds, into which I poured Zircar aluminum ceramic and which I then dried in the magnetically shielded room, to form core-sized cylinders. Samples were measured on the 2G Enterprises cryogenic magnetometer at Occidental College, using a Caltech-style automatic sample changer. After measuring natural remanent magnetization (NRM), each sample was treated with alternating field (AF) demagnetization at 2.0, 4.0, 6.0, 8.0, and 10.0 millitesla (mT) to determine the coercivity behavior of the sample, and to demagnetize any multi-domain grains before their remanence was baked in. Every sample was then thermally demagnetized at 50 °C steps from 200° to 680 °C to examine the demagnetization behavior in detail. This process removes any chemical remanent overprints due to iron hydroxides such as goethite (which dehydrates at 200 °C), and shows how the samples behaved as the Curie temperature of magnetite (578 °C) and the Neel temperature of hematite (680 °C) were approached.

Results were graphed on orthogonal demagnetization ("Zijderveld") plots (Fig. 2), and average directions of each sample were determined by the least-squares method of Kirschvink (1980). Mean directions for each site were then analyzed using Fisher (1953) statistics, and classified according to the scheme of Opdyke et al. (1977).

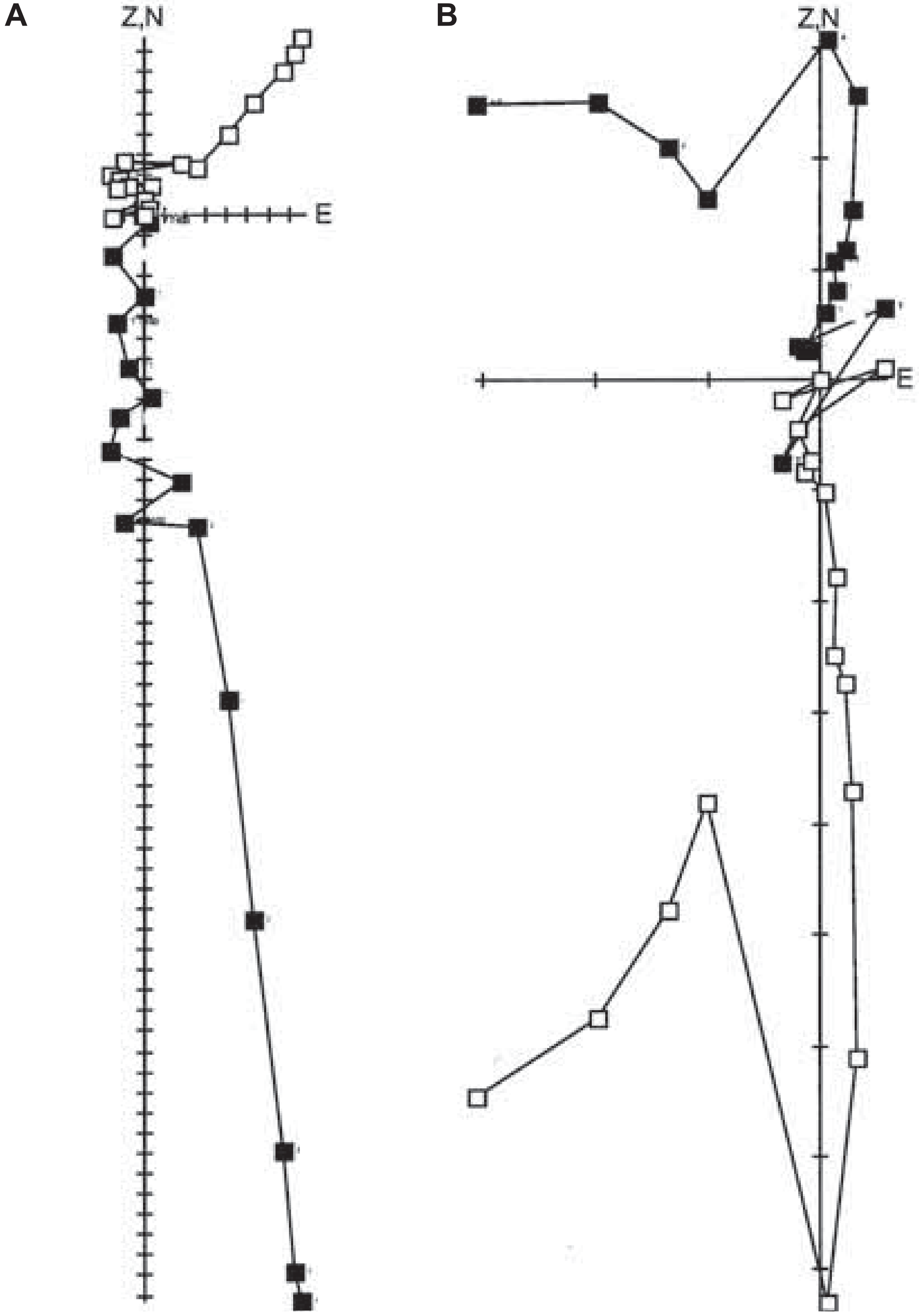

Figure 2. Orthogonal demagnetization (“Zijderveld”) plots of representative pilot samples. All directions are tilt-corrected. N—north-south axis; E—east-west axis; Z—axis of the vertical component (here superimposed on the north axis). Solid squares indicate declination (horizontal component); open squares indicate inclination (vertical component). First step is NRM, followed by AF steps of 2.0, 4.0, 6.0, 8.0, and 10.0 mT, then thermal steps from 200° to 680 °C in 50 °C increments. Each division equals 10^{-6} emu (electromagnetic units). (A) Typical results from the Antero Formation. (B) Typical results from the Pitch-Pinnacle plant locality.

RESULTS

Antero Formation, Colorado

A representative orthogonal demagnetization plot of the Antero Formation is shown in Figure 2A. All the sites taken in this study (Table 1) were reversed in polarity, consistent with results from the Antero tuff reported by McIntosh and Chapin (2004, Table 3, p. 227). As shown by Figure 2A, there was little overprinting of the magnetic signal, and only a single component of remanence appears to be present. Judging from the large response to AF demagnetization, the remanence must be held in a low-coercivity mineral such as magnetite. This is confirmed by the fact that the remanence completely disappeared above the Curie point of magnetite, 578 °C. The mean direction for all Antero samples was D = 184.2, I = –34.8, k = 6.5, α_{95} = 12.1, n = 26. The ^{40}Ar/^{39}Ar date of 33.77 ± 0.10 Ma (McIntosh and Chapin, 2004) for the Antero Tuff, or the ^{40}Ar/^{39}Ar date of 33.89 ± 0.25 Ma (Obradovich, 2003, personal commun.) suggest that these reversed rocks correlate with late Chron C13r, or latest Eocene in age.

Pitch-Pinnacle Formation, Colorado

A representative orthogonal demagnetization plot of the Pitch-Pinnacle rocks is shown in Figure 2B. Like most Pitch-Pinnacle sites, the sample shown in Figure 2B had a slight overprint to the northwest, which was removed by the first thermal step at 100 °C. The remanence of the sample then decayed steadily to the origin, and was almost completely gone by 600 °C. This suggests that it is largely held in magnetite, an interpretation that is corroborated by the large response to AF demagnetization (consistent with the remanence being held in a low-coercivity mineral). All the sites sampled through Gregory and McIntosh's (1996, Fig. 5) sequence were normal in polarity (see Fig. 3), except for the lowest site, up the road from the main locality and just outside the mine property entrance (near the "12" notation on the map of Gregory and McIntosh, 1996, Fig. 2; exact location given in Table 1). They were all Class I sites of Opdyke et al. (1977), so they were statistically removed from a random distribution at the 95% confidence interval. The mean of all normal sites was D = 20.7, I = 50.7, k = 6.5, α_{95} = 13.5, n = 21, and the mean of the single reversed site was D = 178.1, I = –47.4, k = 5.4, α_{95} = 59.2, n = 3. These directions are antipodal within error estimates, so this positive reversal test shows that the characteristic remanence has been obtained and overprinting has been removed. Inverting the reversed directions 180° and averaging them with the normal directions, the formational mean direction was D = 17.7, I = 50.5, k = 6.5, α_{95} = 12.6, n = 24 (Table 1).

Gregory and McIntosh (1996) interpreted ^{40}Ar/^{39}Ar dates from epiclastic sanidines in these rocks to indicate an age of deposition between 32.9 Ma and 29.0 Ma. These dates indicate that the best correlation of this normal polarity sequence is with earliest Oligocene Chron C12n (30.5–31 Ma), with the lowest reversed site (site 7) possibly correlating with latest Chron C12r. However, the imprecision of the younger age estimate allows the possibility of correlation with Chron C11n. Given that the flora seems to be intermediate in temperature estimate between Florissant and Creede, and most similar to that of Florissant, it seems more likely that the correlation with Chron C12n-C12r is correct.

Creede Formation, Colorado

Representative orthogonal demagnetization plots of the Creede Formation are shown in Figures 4A and 4B. Reynolds et al. (2000) obtained mixed results for their samples from the Creede drill cores, with some samples yielding stable results and others giving directions that were unstable or difficult to interpret. My analysis from the surface exposures of the uppermost Creede Formation at Bridsey Gulch produced both normal and reversed polarities (Table 1), with most samples yielding a stable interpretable result, typically with only a single component and no overprinting (Figs. 4A–4B). Nearly all samples showed minimal decreases in intensity during AF demagnetization, suggesting that a high-coercivity mineral overprinting (probably from iron hydroxides such as goethite) is present. However, samples decreased in intensity rapidly through thermal demagnetization above 200 °C (the dehydration threshold for goethite), and almost all remanence was gone by 600 °C, suggesting that most of the remanence is held in magnetite and not in hematite or some other high-coercivity mineral.

Averaging all the stable normal and reversed directions produced a normal mean of D = 17.1, I = 55.6, k = 12.5, α_{95} = 17.7, n = 7, and a reversed mean of D = 197.2, I = –42.7, k = 4.4, α_{95} = 22.2, n = 13. These directions are antipodal within error estimates (Table 1), yielding a positive reversal test and suggesting that the overprinting has been removed and the directions are primary (Fig. 5). Inverting the reversed directions through 180° and averaging all directions produces a formational mean of D = 17.4, I = 49.5, k = 5.7, α_{95} = 15.4, n = 20.

Magnetostratigraphic results of the Bridsey Gulch section are shown in Figure 6. All sites were Class I sites of Opdyke et al. (1977), meaning that they were significantly different from a random distribution at the 95% confidence level. Two sites spanning the lower 5 m of section are normal in polarity. The remaining four sites, spanning the upper 20 m of section, are all reversed in polarity.

Correlation of the Creede flora section is shown in Figure 7. Lanphere (2000) and Reynolds et al. (2000) indicated that the ^{40}Ar/^{39}Ar dates bracketing the Creede Formation range from 26.26 ± 0.04 Ma on the highest Fisher Dacite above the Creede Formation to 26.92 ± 0.07 Ma for the Snowshoe Mountain Tuff underlying the Creede Formation, suggesting that the entire 700+ m of the Creede Formation was deposited in 550,000–770,000 yr or less. The age of 26.26–26.92 Ma on the Creede Formation suggests that the reversed-normal sequence at Bridsey Gulch correlates with some part of Chron C8r–C9n, although the many

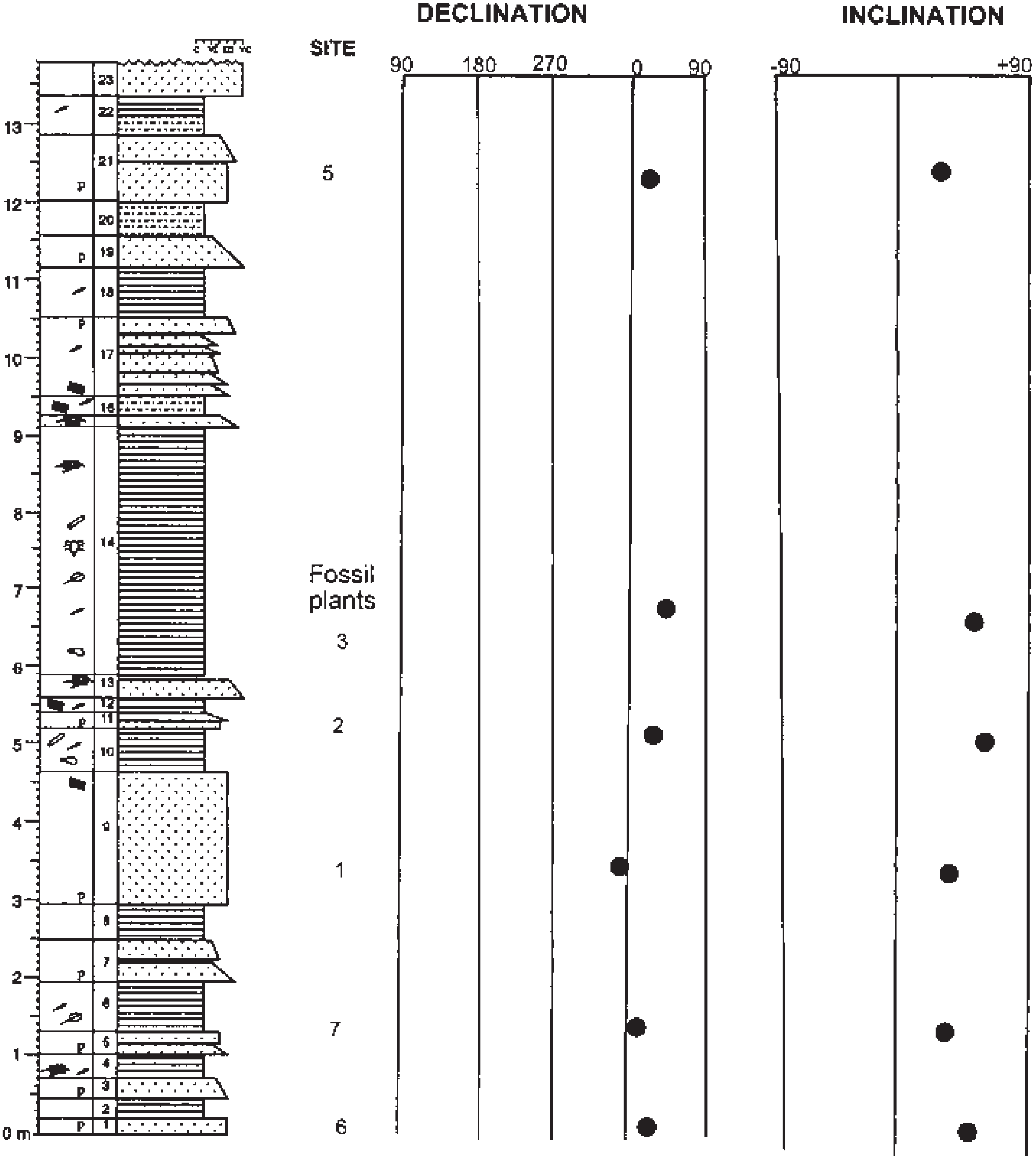

Figure 3. Magnetic stratigraphy of the Pitch-Pinnacle plant locality. Lithostratigraphy after Gregory and McIntosh (1996, their Fig. 5). Solid circles are Class I sites of Opdyke et al. (1977), which are statistically distinct from a random distribution at the 95% confidence level.

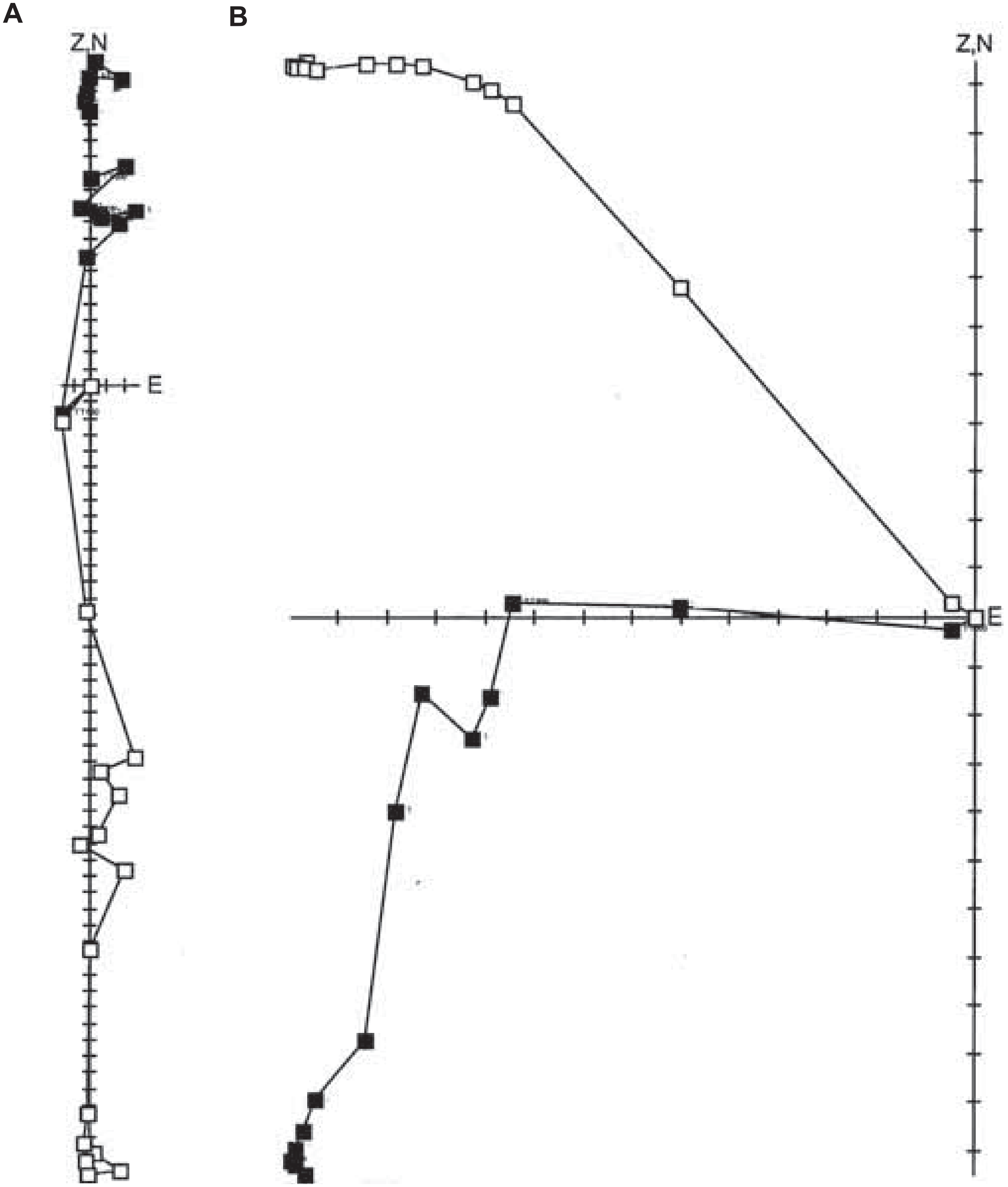

Figure 4. Orthogonal demagnetization (“Zijderveld”) plots of representative pilot samples. All conventions as in Figure 2. (A, B) Typical results from the Creede Formation.

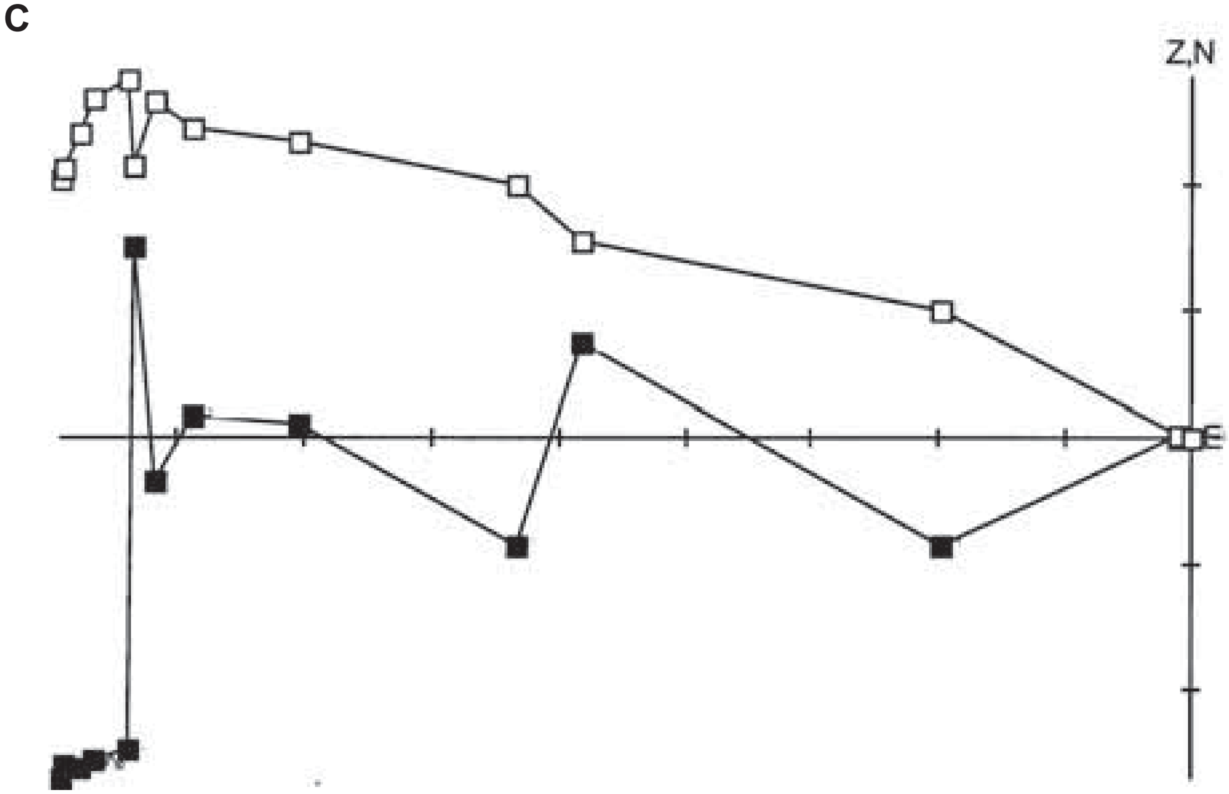

Figure 4 continued. (C) Typical results from the Granger plant locality.

polarity changes documented by Reynolds et al. (2000) for the lower 700 m of the section in the core samples apparently must also be accommodated within the narrow window of time of 550,000–770,000 yr spanning Chrons C8n–C9n (Fig. 7). Whatever interpretation is adopted, the tight age constraints from the ^{40}Ar/^{39}Ar dates clearly indicate that the Creede flora is earliest late Oligocene on the standard time scale.

Granger Canyon, Northeast California

The section at Granger Canyon (Fig. 8) was much shorter, because most of the exposures were thick ignimbrites and volcanic agglomerates that were very brittle and resisted hand sampling, and consequently most sites had only a few samples that survived the sampling process. Interbedded within this sequence is the thin shaly unit that produces the Granger Canyon flora (Fig. 8). Most of the sites produced an apparent reversed polarity (Fig. 4C) with a high-coercivity overprint probably held in goethite or other iron hydroxides. However, the remanence was completely gone by 600 °C, suggesting that magnetite was the primary carrier of the remanence, and little hematite was present. The single site in the lower agglomerate (Fig. 4D) produced a normal polarity, which seems to be held in both magnetite and hematite, given that significant remanence was present even at 680 °C.

Averaging all the stable normal and reversed directions produced a normal mean of D = 22.8, I = 11.2, k = 7.8, α_{95} = 107.8, n = 2, and a reversed mean of D = 193.5, I = –27.6, k = 8.1, α_{95} = 19.3, n = 10. These directions are antipodal within error estimates, yielding a positive reversal test and suggesting that the overprinting has been removed and the directions are primary. Inverting the reversed directions by180° and averaging all directions produces a formational mean of D = 15.4, I = 24.6, k = 8.3, α_{95} = 16.8, n = 12.

The magnetostratigraphic interpretation of the Granger Canyon is shown in Figure 8. As stated earlier, the lower ignimbrite-agglomerate apparently is normal in polarity, although this is based on a single site with only two surviving samples. The fossiliferous shale interval and the upper ignimbrite are entirely of reversed polarity, spanning at least 20 m of section sampled for this study. The total available section is much thicker in the field, because there are dozens of separate ignimbrites spanning hundreds of meters of section in the Warner Mountains.

Based on the ^{40}Ar/^{39}Ar date of 31.5 ± 0.4 Ma from a pebble breccia immediately below the floral locality (Myers, 1998, 2003), the best correlation seems to be with Chron C12r, or early Oligocene (Fig. 7). The single site of normal polarity in the lower unit does not appear to match the long interval of Chron C12r, which is reversed in polarity from 31 to 33 Ma (Fig. 7). However, during the early Oligocene there were numerous short events of

D

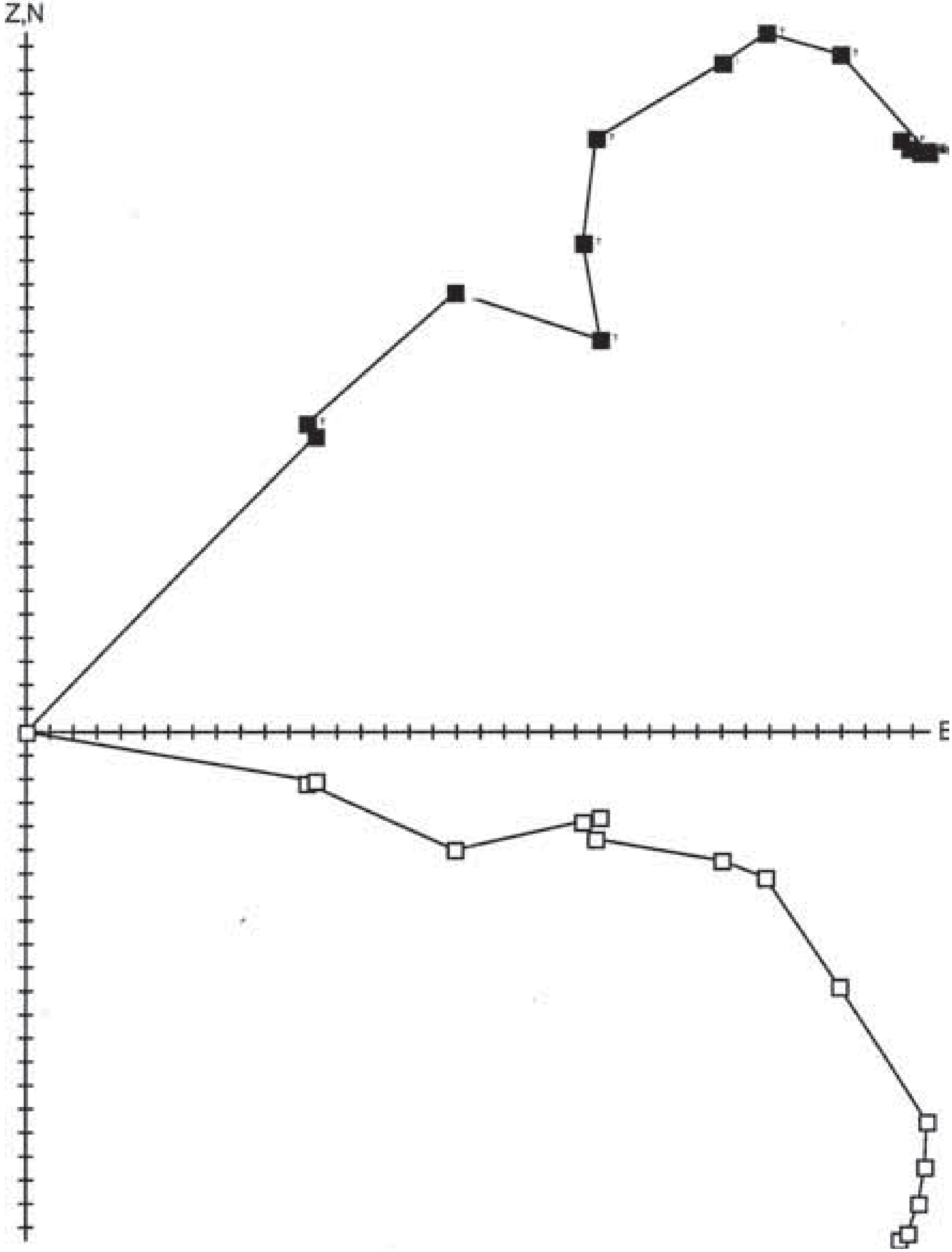

Figure 4 continued. (D) Typical results from the Granger plant locality.

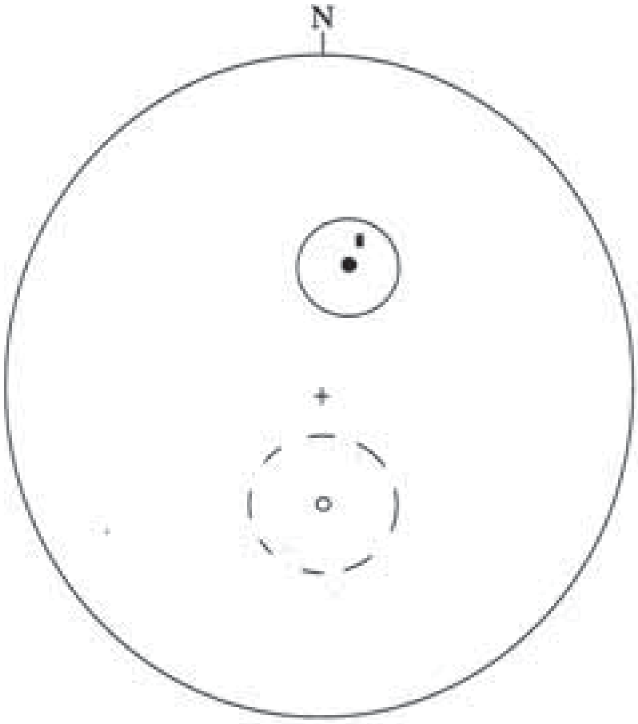

Figure 5. Stereonet showing the formational means (circles) and 95% ellipses of confidence of results from the Creede Formation. Solid circles indicate lower hemisphere projections; dashed and open circles indicate upper hemisphere projections. Solid rectangle shows the mean of the reversed sites inverted through the center of the stereonet to the lower hemisphere. The antipodal (within error limits) position of the means shows that they pass a reversal test and are primary or characteristic directions.

normal polarity in Chron C12r (Hartl et al., 1993) that might explain this behavior. Alternatively, the normal polarity is based on a single site with only two stable samples, so it is possible that normal overprinting was not removed from this high-temperature ignimbrite, and that the normal polarity is not a primary or characteristic direction. In any case, the reversed portion of the section (containing the flora) is consistent with the correlation with Chron C12r and with the 31.5 ± 0.4 Ma date just below the flora.

DISCUSSION

Correlation of some important Eocene-Oligocene floral localities is shown in Figure 7. In southwestern Colorado, four important floras are now calibrated by magnetic stratigraphy. The upper Eocene Florissant Formation (Evanoff et al., 2001; Prothero and Sanchez, 2004) is correlated with early Chron C13r, based on its reversed polarity and a ^{40}Ar/^{39}Ar date of 34.07 ± 0.10 Ma on the upper part of the section (Evanoff et al., 2001).

The Florissant flora (Meyer, 2003) is famous for its warm temperate characteristics, consistent with a warming trend in the late Eocene. A variety of temperature estimates (Table 2) have been calculated for this flora over the years (summarized by Wolfe, 1994, Table 2; Meyer, 2001, p. 210). Meyer (2001, p. 211) suggested that the mean annual temperature was ~13 °C, whereas Wolfe (1992) suggested 12.0–12.5 °C and later (1994) gave an estimate of only 10.8 °C. Gregory and McIntosh (1996, Table 7) gave estimates of mean annual temperature from 12.8 to 13.9 °C, with a warm-month mean of 30.0–33.3 °C. Gregory and McIntosh calculated a cold-month mean temperature of –2.0 to 1.3 °C, and a mean annual range of temperature of 27.7–29.1 °C.

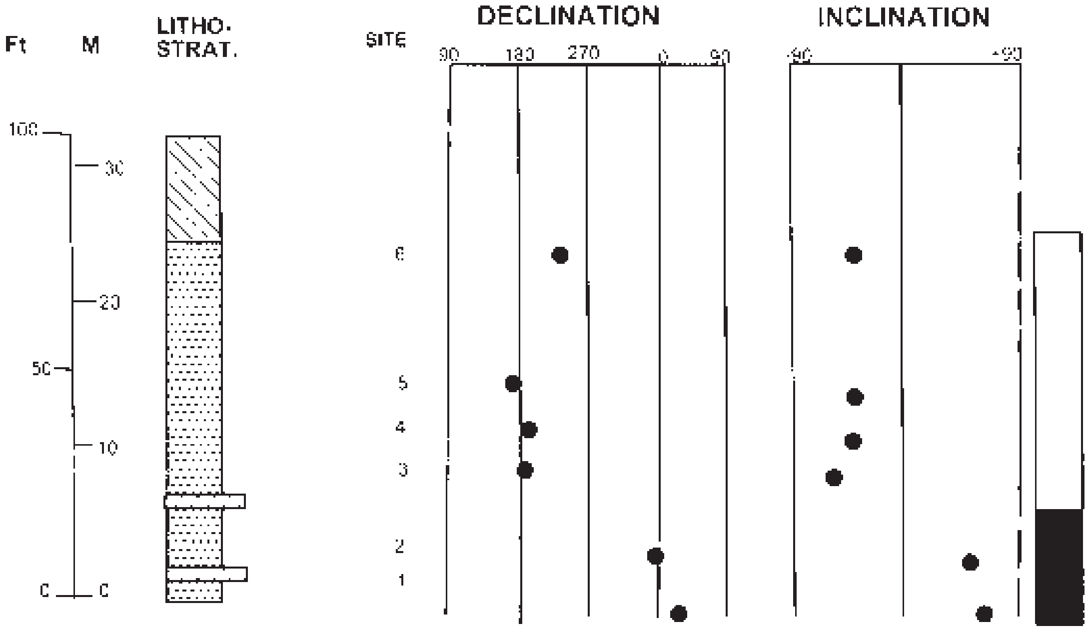

Figure 6. Magnetic stratigraphy of the Creede Formation at Bridsey Gulch. Stipples—sandstones; dashed lines—mudstones; diagonal hachures—covered interval. Solid circles are Class I sites of Opdyke et al. (1977), which are statistically distinct from a random distribution at the 95% confidence level.

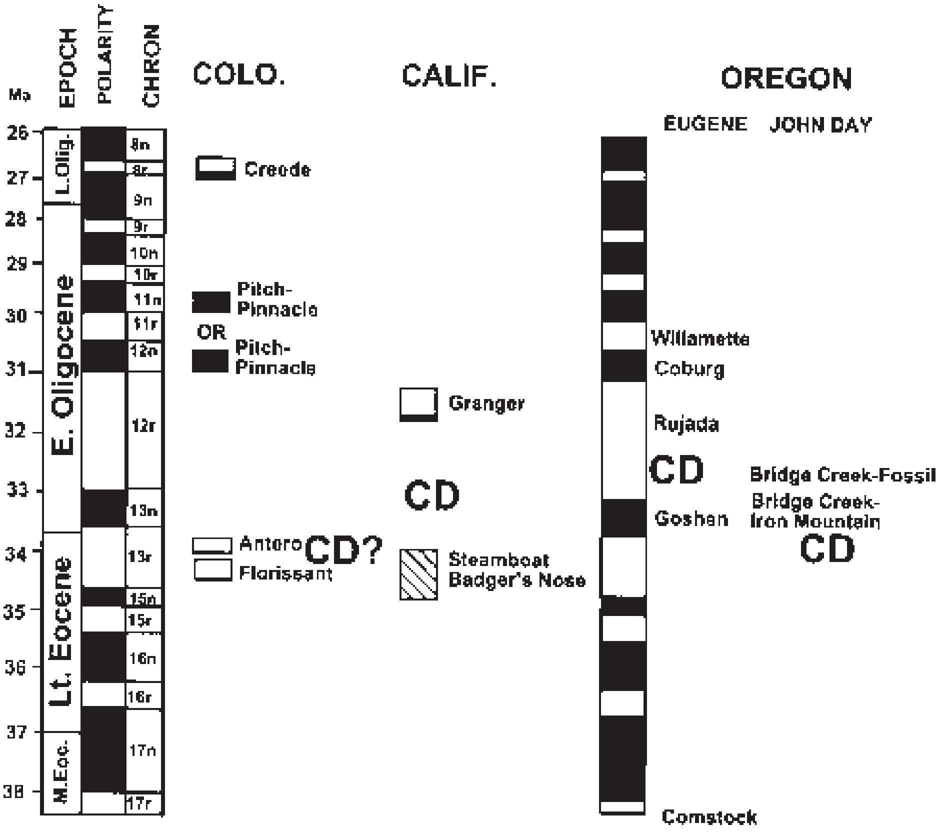

Figure 7. Chronostratigraphic correlation of major Eocene-Oligocene floras in Colorado, northeast California, and Oregon, based on data discussed in text. Time scale after Berggren et al. (1995). Magnetic polarity indicated by solid black bars (normal) and open bars (reversed); unknown polarity indicated by diagonal pattern. CD—geochronological age estimate of climatic deterioration event (see text for discussion).

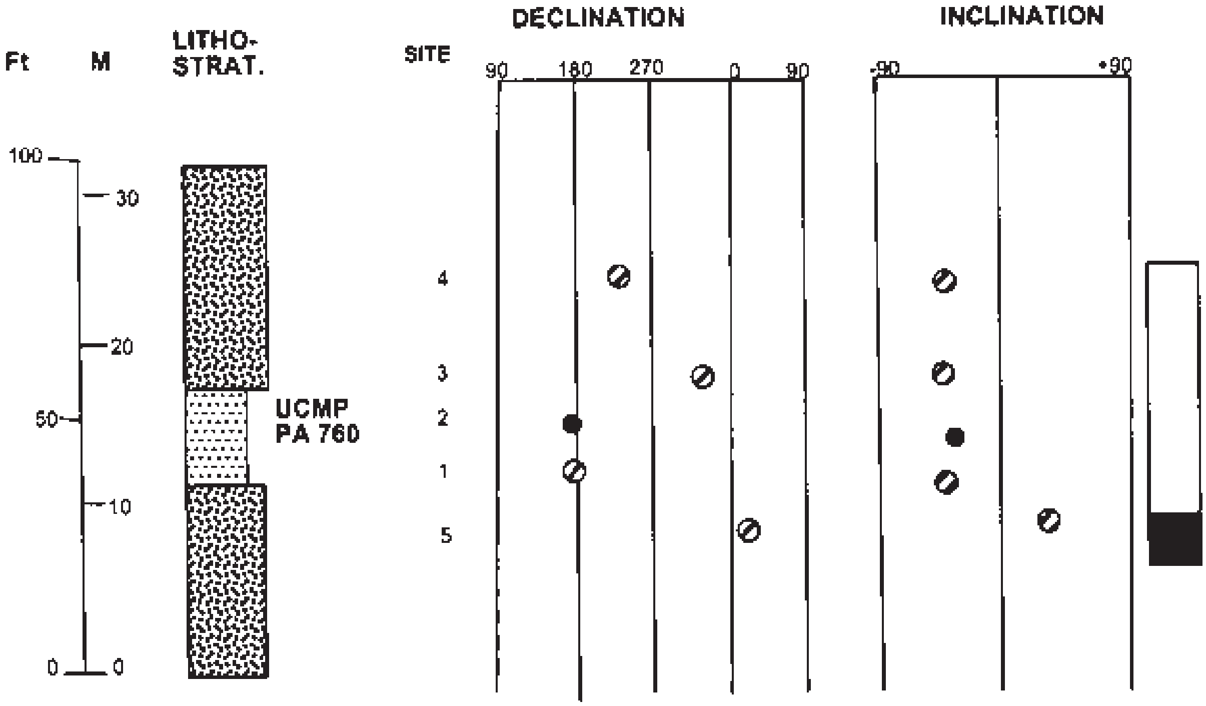

Figure 8. Magnetic stratigraphy of the Granger Canyon plant locality. Conventions as in Figures 3 and 6. Coarse stipple—volcanic agglomerates; dashed lines—shales. Hachured circles are Class II sites of Opdyke et al. (1977), in which fewer than three samples survived, so site statistics could not be calculated.

TABLE 2. AGE AND TEMPERATURE ESTIMATES OF KEY FLORAS MENTIONED IN THIS PAPER

Flora	Age (Ma)	MAT	CMMT	WMMT	MART	Source
Willamette, Oregon	30.1	13.2	6.2	20.8	14.6	Retallack et al. (2004)
Rujada, Oregon	31.3	13.9	2.4	23.6	21.2	Retallack et al. (2004)
Goshen, Oregon	33.4	19.7	6.8	25.1	18.3	Retallack et al. (2004)
Comstock, Oregon	39.7	22.4	7.0	26.5	19.5	Retallack et al. (2004)
Florissant, Colorado	34.07 ± 0.1	12.8	–2.0	30.0	27.7	Gregory and McIntosh (1996)
		13.9	1.3	33.3	29.1	Gregory and McIntosh (1996)
		10.8				Wolfe (1994)
Pitch-Pinnacle, Colorado	32.9–29.0	12.7	4.5	20.4	18.5	Gregory and McIntosh (1996)
Creede, Colorado	26.26–26.92	0–3				Wolfe and Schorn (1989)
		4.2				Gregory and McIntosh (1996)
Granger Canyon, California	31.5 ± 0.4	9.6	–0.4	21.1	21.5	Myers (2003)
Badger's Nose, California	34–35	12.5	2.6	21.1	18.5	Myers (2003)
Steamboat, California	34–35	17.1	5.6	24.3	18.7	Myers (2003)
Bridge Creek Fossil, Oregon	32.6	12.1	3.7	19.0	15.3	Myers (2003)
Bridge Creek Dugout, Oregon	33.6	10.3	0.9	17.7	16.8	Myers (2003)

Note: MAT—mean annual temperature; CMMT—cold-month mean temperature; WMMT—warm-month mean temperature; MART—mean annual range of temperature. All temperatures given in °C. Most temperature estimates based on the CLAMP method of Wolfe (1994).

However, these values for the cold-month and warm-month means are inconsistent with the values for mean annual temperature and mean annual range of temperature, and the mean warm-month temperature appears to be overestimated (Meyer, 2007, personal commun.).

The mammalian fauna of the Antero Formation (Stark et al., 1949, p.66) included large brontotheres, the rhinoceroses *Trigonias, Subhyracodon*, and *Hyracodon*, the horse *Mesohippus*, the oreodont *Agriochoerus*, the deerlike *Hypisodus,* plus the rabbit *Palaeolagus*. Although most of these mammal specimens are too fragmentary to be diagnostic of age, both brontotheres and *Trigonias* are known to have vanished at the end of the Chadronian (late Eocene). MacGinitie (1953) suggested a possibly Orellan or "middle Oligocene" (in the terminology of the time) age for the Antero, which would make the formation earliest Oligocene, according to modern mammalian biochronology. However, Kron and de Toledo (1994) confirmed the presence of brontotheres and other Chadronian mammals from the Antero Formation, making it latest Eocene. While sampling was being conducted for this study, additional brontothere lower teeth were observed at the outcrops that yielded paleomagnetic sites 5–7 (Table 1).

MacGinitie (1953, p. 75) and Wolfe (1992, p. 425) provided a very brief mention of the Antero flora (including *Pinus* cf. *crossii, Quercus* sp., *Vaccinium* sp., *Cercocarpus* cf. *C. henricksonii, Eleopoldia* cf. *E. lipmannii*), but no formal description was published. The original Wolfe collection was very limited and fragmentary and was thought to be lost, but it may be stored in the Smithsonian (G. Retallack, 2006, personal commun.). According to Wolfe (1992), the Antero flora is a post-deterioration flora representing cooler and drier climates and is very similar to the late Oligocene Creede flora. However, this interpretation is based on such a small sample of taxa (only six taxa and 16 specimens, according to Wolfe, 1992, p. 425) that it must be viewed with caution (H. Meyer, 2006, personal commun.). Durden (1966) provided a slightly longer list of plant taxa, including *Pinus, Quercus, Ulmus, Cercocarpus, Sequoia affinis, Chamaecyparis linguaefolia, Salix* spp., *Bidens* sp., "*Betula florissanti,*" *Mahonia marginata, Cardiospermum terminalis*, and *Abies* or *Pseudotsuga* sp. Several of these occur at Florissant and not at Creede, and this list is based on a larger sample than Wolfe (1992) reported. Durden (1966) deposited this collection at Yale. The paleotemperatures for the Antero flora shown in Figure 9 indicate the approximate conditions for both a "Creede-like" and "Florissant-like" interpretation, but these estimates have not been derived using a quantitative methodology applied specifically to Antero. During our sampling, it was apparent that many additional good plant fossils could be collected, so the flora really needs to be recollected on a larger scale and reanalyzed. If the new dates are correct and Wolfe's (1992) paleobotanical interpretation is valid, then this suggests that the climate change in the southern Rocky Mountains (Fig. 9) was very rapid (between 33.89 and 34.07 Ma) and occurred in the latest Eocene, not in the early Oligocene as all other global climatic records show (Miller et al., 1987; Miller, 1992; Prothero, 1994; Zachos et al., 1992, 2001). This is true whether one adopts the Eocene-Oligocene boundary age of 33.7 Ma (Berggren et al., 1995) or 33.9 Ma (Luterbacher et al., 2004). By contrast, Wing (1987) showed that the Chadronian and Orellan plant assemblages of southwest Montana showed no effect of the Eocene-Oligocene climatic change. However, if Durden's (1966) interpretation is correct, the Antero flora is only slightly different from that of Florissant. Clearly, the Antero flora requires further study to draw any confident conclusions.

According to Gregory and McIntosh (1996), the Pitch-Pinnacle flora yields a mean annual temperature of 12.7 ± 1.5 °C (compared to 10.8–13.9 °C for Florissant but only 0–4.2 °C for Creede; Antero is not mentioned). The cold-month mean temperature is estimated at 4.5 °C (warmer than Florissant) and the

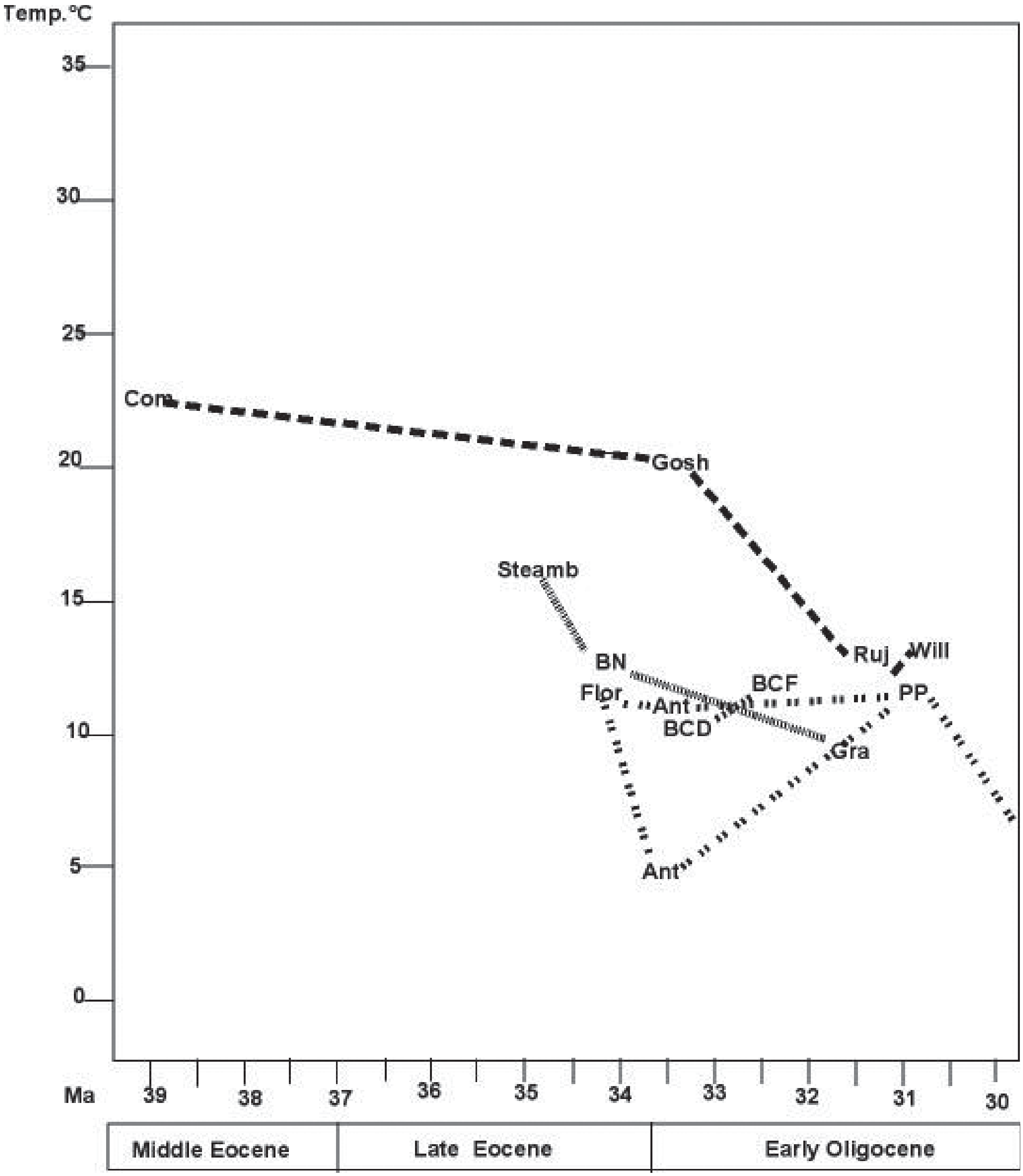

Figure 9. Diagram showing the change in temperature versus age as represented by the floras discussed in this paper. The abbreviations are plotted at the mean annual temperature of the flora. The coastal Oregon floras are connected by the long bold dashed lines; the northeastern California floras by the gray line; the Colorado floras by the light dashed line; the central Oregon floras are connected by the short-dashed line. The temperature estimates for the Antero flora are approximate and are considered to be provisional; there is evidence that the flora shows similarities to both Creede and Florissant, so both possible interpretations are shown here. Abbreviations: Com—Comstock flora; Gosh—Goshen flora; Ruj—Rujada flora; Will—Willamette flora; Steamb—Steamboat flora; BN—Badger's Nose flora; Gra—Granger flora; BCD—Bridge Creek-Dugout flora; BCF—Bridge Creek-Fossil flora; Flor—Florissant flora; Ant—Antero flora; PP—Pitch-Pinnacle flora. Sources of the data, and interpretations of the curves, are discussed in the text.

warm-month mean temperature is 20.4 °C (whereas Florissant gives values of 30.0–33.3 °C, according to Gregory and McIntosh, 1996), and the mean annual range of temperature is estimated at 18.5 °C (compared to 27–29 °C for Florissant, according to Gregory and McIntosh, 1996). The flora has angiosperm genera that are common to both Creede and Florissant, and conifers that are similar to those of Creede (Gregory and McIntosh, 1996). Clearly this is a warmer-climate flora only slightly cooler than Florissant, yet it is younger than the supposedly cool-climate (like Creede) Antero flora. Gregory and McIntosh (1996) argued that either it grew before the Oligocene deterioration at an elevation of 2–3 km or it could be a post-deterioration flora from an elevation of 1 km. However, because Antero and Florissant are from similar elevations, this does not explain why the cooler Antero flora occurs chronologically between warm-climate Florissant and Pitch-Pinnacle floras (Fig. 9). As mentioned above, the Antero flora is too poorly known to place much confidence in this conclusion. Because of this uncertainty, the deterioration may have occurred in the early Oligocene in Colorado, as it does in most other regions.

In the Warner Range of northeast California, Myers (1998, 2003) listed the pre-deterioration Steamboat and Badger's Nose floras of the Cedarville Flora as 34–35 Ma in age, or latest Eocene. The Steamboat floras produce mean annual temperature estimates of 17.1 °C, with a warm-month mean temperature of 24.3 °C and a cold-month mean temperature of 5.6 °C, and ~234 cm of annual precipitation. The Badger's Nose floras yield mean annual temperature estimates of 12.5 °C, with a warm-month mean temperature of 21.1 °C and a cold-month mean temperature of 2.6 °C, and ~178 cm of annual precipitation (Myers, 1998, 2003). The temperature values of the Badger's Nose flora are similar to those of the warm temperate late Eocene floras, such as Florissant (Wolfe, 1978, 1992). The early Oligocene (31.5 ± 0.4 Ma, Chron C12r) Granger Canyon flora (discussed above) yields a mean annual temperature of only 9.6 °C, with a warm-month mean temperature of 21.1° and a cold-month mean temperature of –0.4 °C, but with almost 260 cm of precipitation, so it appears to be a post-deterioration flora (Myers, 2003). However, the age constraints (Fig. 7) are insufficient to evaluate how much time elapsed for the climatic deterioration in this region. If the current dates are correct, it occurred between 34 and 31.5 Ma, so it could have happened any time in the latest Eocene or earliest Oligocene (Fig. 9).

The longest and most complete sequence of floras spanning the Eocene-Oligocene transition occurs in the Eugene and Fisher Formations near Eugene, Oregon. Recent high-resolution lithostratigraphy, biostratigraphy, tephrostratigraphy, ^{40}Ar/^{39}Ar dating, and magnetostratigraphy by Retallack et al. (2004) allowed fine-scale dating and correlation of the classic floras and marine invertebrate faunas in this sequence (Figs. 7 and 9). The middle Eocene Comstock flora was correlated with Chron C18n.2n (39.7 Ma), and the flora suggests a mean annual temperature of 22.4 °C with a warm-month mean of 26.5 °C, a cold-month mean of 7.0 °C, and a mean annual range of temperature of 19.5 °C, all suggestive of warm paratropical conditions. The late Eocene subtropical Goshen flora was one of the original bases for Wolfe's (1978) concept of a late Eocene warming event. It is now dated to occur within early Oligocene Chron C13n (33.4 Ma), and yields a mean annual temperature of 19.7 °C with a warm-month mean of 25.1 °C and a cold-month mean of 6.8 °C, and a mean annual range of temperature of 18.3 °C, only slightly cooler than the warm paratropical conditions of the Comstock flora. It should be noted, however, that under normal climatologic conditions, these estimates for Goshen and Comstock for mean warm-month temperature and mean cold-month temperature are not possible in combination with the mean annual temperatures that are estimated (H. Meyer, March 2007, personal commun.). The Rujada flora, dated at 31.5 Ma (Retallack et al., 2004), shows temperature estimates consistent with those of a post-deterioration flora (Fig. 9), with a mean annual temperature of 13.0 °C, a cold-month mean temperature of 2.4 °C, a warm-month mean temperature of 23.6 °C, and a mean annual range of temperature of 21.2 °C (Retallack et al., 2004). Stratigraphically above the Rujada flora are the early Oligocene Coburg and Willamette floras. They are dated at Chron C12n (30.9 Ma) and Chron C11r (30.1 Ma), respectively. The Willamette flora yields a mean annual temperature of 13.2 °C with a warm-month mean of 20.8 °C and a cold-month mean of 6.2 °C, and a mean annual range of temperature of 14.6 °C, and the much less well known Coburg flora is very similar (Retallack et al., 2004). These floras clearly suggest that the Oligocene deterioration had taken place by 31.5 Ma (Fig. 9) but was not as severe and abrupt as once suggested by Wolfe and Hopkins (1967) and Wolfe (1978). Thus, the Eugene-Fisher floral sequence places the climatic change in the earliest Oligocene (consistent with the global record), somewhere between 33.4 and 31.5 Ma. This 2-million-year gap between floras does not allow us to assess the rapidity of the change as well as for the closely spaced Antero and Florissant floras in Colorado, but the results are consistent with previous ideas that the climatic change occurred in the earliest Oligocene.

In the John Day region of central Oregon, the John Day Formation yields floras relevant to this discussion. The Iron Mountain assemblage of the Bridge Creek flora (Meyer and Manchester, 1997; Myers, 2003) is ^{40}Ar/^{39}Ar dated at 33.62 Ma. This is slightly younger than the Eocene-Oligocene boundary of 33.7 Ma according to Berggren et al. (1995), or 33.9 Ma according to Luterbacher et al. (2004). It yields a post-deterioration mean annual temperature of 10.3 °C, with comparable results for cold-month mean annual temperature of 0.9 °C and warm-month mean annual temperature of 17.7 °C (Myers, 2003). Just above this flora is the Fossil assemblage of the Bridge Creek flora, which is ^{40}Ar/^{39}Ar dated at 32.58 Ma, and yields a mean annual temperature of 12.1 °C with a warm-month mean of 19.0 °C and a cold-month mean of 3.1 °C, also suggesting a post-deterioration flora (Myers, 2003). These dates are from ashes directly interbedded with the floras (Retallack et al., 2004). Thus, the climatic event in central Oregon seems to have happened before 33.62 Ma (a date that is right after the Eocene-Oligocene boundary), not coincident with the early Oligocene Oi1 event of Zachos et al. (1992, 2001), which is dated at 33.0 Ma.

CONCLUSION

Available data suggest that the climatic cooling documented during the earliest Oligocene in the global climatic record seems to occur at different times in the floral records of the western United States (Fig. 9). In south-central Colorado, the age difference between the Florissant and Antero floras suggests that it occurred in the late Eocene, between 33.89 and 34.07 Ma, and was very abrupt (less than 200,000 yr). However, the occurrence of the 30.5–31.0 Ma (based on its preferred correlation with Chron C12n) Pitch-Pinnacle flora in Colorado suggests that the deterioration occurred in the early Oligocene; this in turn indicates that the Antero flora is anomalous and needs further analysis. In northeast California, the deterioration appears to have occurred in the early Oligocene, sometime between 34 and 31.5 Ma. In coastal Oregon, it occurred in the early Oligocene between the Goshen and Rujada floras, or between 33.4 and 31.5 Ma. In the Clarno Formation Bridge Creek floras of central Oregon, the available dates suggest that the deterioration was already in place by the beginning of the Oligocene, 33.62 Ma. Thus, the floras suggest some diachroneity of the climatic transition, with at least two regions (Colorado, central Oregon) providing possible evidence that the cooling had occurred before the global event in the early Oligocene (at 33.0 Ma), whereas two other regions (northeast California, coastal Oregon) document an early Oligocene deterioration that is consistent with the global record. Clearly, further work needs to be done on the paleobotany, geochronology, and chronostratigraphy of these floras, especially Antero and the Bridge Creek sequence, to test this hypothesis.

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A comparison of plant-insect associations in the middle Eocene Green River Formation and the Upper Eocene Florissant Formation and their climatic implications

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ABSTRACT

The fossil plants found in the Eocene Florissant Formation and Green River Formation are preserved with a level of detail that allows one to closely examine traces of insect feeding damage. Levels (amounts) and patterns (abundance of various types) of fossilized insect feeding damage from Florissant and the middle Eocene Green River Formation were compared. This allowed for a detailed examination of feeding damage and provided an opportunity to examine long-term patterns of change in insect herbivory during a period of climate fluctuation. Samples including 624 fossil leaves from Florissant and 584 fossil leaves from the Green River Formation were examined to document overall damage levels, the presence/absence of specific feeding guilds (i.e., hole-feeding, skeletonization, leaf-mining), and host-specific damage types.

Florissant insects show host specificity in their feeding preferences as evidenced through the distribution of feeding damage on plants and through the presence of identifiable host-specific interactions. Some of these interactions appear to be long lasting as they are also apparent on the same, or closely related, leaf species found in the Green River Formation. Insect damage levels declined from the middle to late Eocene. This decline is correlated with a cooling event during this time interval and is in concurrence with the findings of other authors who have examined fossilized herbivory and climate change patterns. There is also an increase in the abundance of galls during this same interval, which also may be related to climate change.

Keywords: Eocene, herbivory, insects, interactions, plants.

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INTRODUCTION

The early Cenozoic fossil record provides an ideal setting for examining the evolution of plant-insect interactions and for evaluating how climate change in particular affects ecosystems at basic trophic levels. The early Cenozoic is an important period because it provides a window into the early evolution of many insect and plant groups that make up our modern temperate ecosystems. As such, this period has begun to receive much attention from researchers interested in examining long-term patterns of change in plant-insect interactions.

Many researchers have been able to establish the presence of long-lasting associations between a variety of herbivorous insects and their host plants through an examination of the fossil record (Opler 1973; Hickey and Hodges 1975; Hickey and Doyle 1977; Larew 1986; Upchurch and Dilcher 1990; Labandeira et al. 1994; Wilf et al. 2000). Some studies have documented assemblage-level patterns of herbivory (Ash 1997; Beck and Labandeira 1998, Scott and Taylor 1983; Smith 1998), whereas others have also attempted to examine changes in herbivore damage over time (Wilf and Labandeira 1999; Smith 2000; Wilf et al. 2001). The latter studies examined changes in insect herbivory during periods of climate change in the Paleocene and Eocene and found evidence for an increase in herbivory as temperatures increased and a decrease in herbivory as temperatures decreased, suggesting that climate may have played an important role in the evolution of insect-plant associations.

Today, ~75% of all phytophagous (plant-feeding) insects are either monophagous (specialize on one species of plant) or oligophagous (specialize on a few species of plants in a single family) (Bernays and Chapman, 1994). It is likely that many of these associations originated during the Cenozoic, when the first appearances of many modern insect and plant genera occurred (Wing, 1987; Carpenter, 1992). However, insects possessed the mouthpart morphology to create the types of damage that we see on modern leaves prior to the Cenozoic (Labandeira and Sepkoski, 1993; Labandeira, 1997), and a few examples of modern associations have been documented from the Cretaceous (Labandeira et al., 1994).

Florissant fossil beds and the Green River Formation are deposits that are well known for their abundance, diversity, and excellent preservation of both insects and plants. Nearly 1500 species of insects and approximately120 plant species have been described from Florissant (MacGinitie, 1953; Manchester 2001; Meyer, 2003; Drummond, 2004) and nearly 300 insects and at least 157 plant morphotypes have been identified from the Green River Formation (MacGinitie, 1969; Barclay et al., 2003: Smith, 2000, pers. observation). But, what is known of the interactions between these two groups during this time interval? With the quality of preservation found in the Florissant and Green River Formations, it is possible to examine feeding guilds and learn whether insect feeding strategies and plant defensive strategies have changed over time. It is possible to determine the plants on which insects fed and whether this involved the most abundant plants, specific families, or no selectivity at all. Finally, the assemblages can be examined for evidence of stereotyped (recognizable, host-specific feeding damage) and long-lasting interactions between specific plant and insect groups.

In this study, I examined fossil leaves from the late Eocene Florissant Formation and the middle Eocene Green River Formation of Colorado, USA. I examined the insect-mediated damage that is found preserved on the leaf macrofossils and determined overall damage levels, the distribution of feeding guilds, and the presence of specialized damage types. The comparison of herbivory from the two fossil floras provides a rare opportunity to detect long-lasting associations (over a period of 9–13 m.y.) and to examine patterns of change in plant-insect interactions during a climatic cooling event.

MATERIALS AND METHODS

Florissant Fossil Beds

Geologic and Paleoclimatic Setting

Fossil plants were collected from Florissant Fossil Beds National Monument in Teller County, Colorado (Fig. 1). The Florissant Formation has been dated at 34.07 Ma (Evanoff et al., 2001) and the fossil beds were deposited in a lake that was formed by the volcaniclastic debris flow damming of the drainage basin (McLeroy and Anderson, 1966; Evanoff et al., 2001). On the basis of modern biogeographic affinities of the fossil plant assemblage MacGinitie (1953) interpreted the ancient lake setting as a warm-temperate environment. Subsequent studies, using consideration of physiognomic and floristic criteria (Meyer, 1992, 2001; Leopold and Clay-Poole, 2001), multivariate analysis of leaf characters using CLAMP (Wolfe, 1992, 1994; Gregory and McIntosh, 1996), comparison to modern forest communities (Boyle et al., this volume), and the mutual climate range of Diptera (Moe and Smith, 2005), have estimated mean annual temperatures (MATs) within a range of 10.8–17.5 C°. A mean annual precipitation (MAP) of 50 cm was estimated from the composition of the fossil flora (MacGinitie, 1953). MacGinitie also utilized floristic comparisons to estimate the paleoaltitude of the Florissant flora at 300–900 m. More recent studies have used foliar physiognomic techniques and lapse rates or enthalpy to estimate paleoelevations for Florissant ranging from 1900 to 4133 m (Gregory and Chase, 1992; Meyer, 1992, 2001; Wolfe, 1992, 1994; Gregory 1994; Forest et al., 1999).

Collection and Identification

Fossil plants were collected from two localities (FLFO-5 and FLFO-7) in the middle shale unit of the Florissant Formation (Fig. 1) within the boundaries of the national monument. These sites are located on the eastern margin of the paleolake and are interpreted here as nearshore environments on the basis of the distribution pattern of the Florissant Formation relative to the current topography, which is bounded by Precambrian Pikes Peak Granite and is thought to reflect ancient lake boundaries (Meyer,

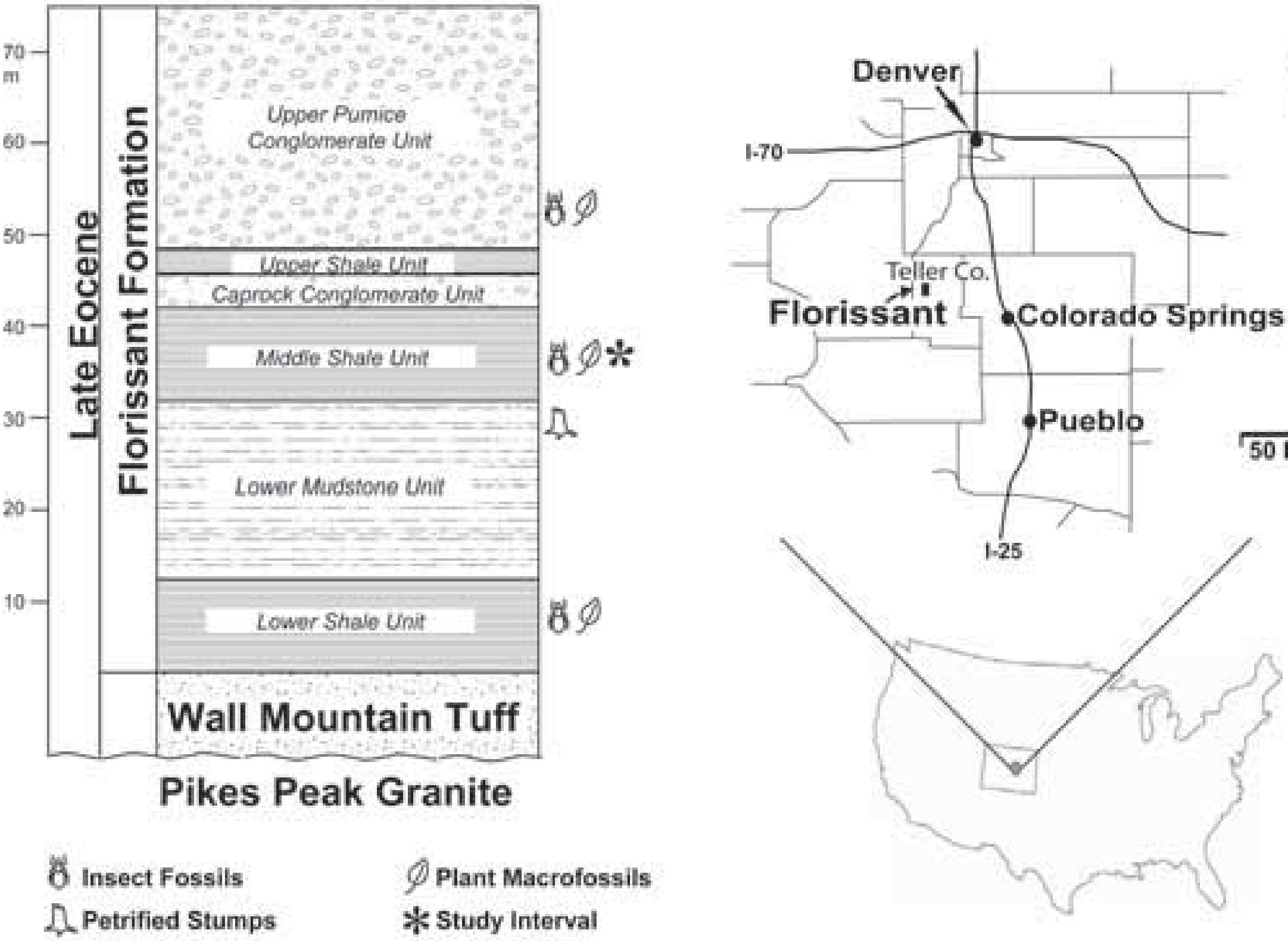

Figure 1. Stratigraphy of the Florissant fossil beds and general location of the Florissant Formation in Teller County, Colorado, USA (after Evanoff et al., 2001).

2003). Fossils from both localities are preserved as impressions and compressions in thinly laminated shale. The shale consists of couplets of diatoms and ash/clay (McLeroy and Anderson, 1966; O'Brien et al., this volume). Leaves are the main type of fossil found from the localities, but insects, mollusks, and fish remains also have been collected. Fossil specimens are sometimes found preserved among large amounts of organic debris and multiple leaf specimens are often found on the same piece of shale.

The collections were made by National Park Service staff, volunteers, and the author during the summers of 1997 and 1998. Specimens from both sites were combined into one Florissant sample for the purposes of comparative analysis. Because each locality samples only a small local area of the source forest and represents a short interval of time, pooling data from both localities provides a better representation of the source forest overall. Nearly 1200 fossil leaves were collected from Florissant, but only 624 angiosperm leaves were sufficiently preserved (preservation quality allowed for recognition of herbivore damage) to be used in this study. Leaf fragments smaller than 1 cm^2 were not included in the study. In neontological studies of herbivory, sample sizes range from ~200 to 10,000 leaves/sample, depending on the questions addressed (Bray, 1961; Nielsen, 1978; Coley, 1983; de la Cruz and Dirzo, 1987; Basset, 1991; Lowman and Heatwole, 1992; Filip et al., 1995; Barone, 2000; Williams-Linera and Herrera, 2003; Smith and Nufio, 2004). All dicotyledonous angiosperm specimens were identified to species when possible and non-angiosperm plants were not included in the analysis. MacGinitie's (1953) monograph and subsequent taxonomic revisions of the flora (Manchester and Crane 1983; Axelrod, 1986; Manchester 1987; Wolfe and Tanai, 1987; Manchester, 1989a, 1989b; Wolfe and Schorn 1990; Manchester 1992; Manchester and Donoghue 1995; Wang and Manchester, 2000; Manchester 2001; McClain and Manchester 2001) were used to identify the plants. Specimens that were not identifiable to the genus level but were identifiable at the family level were given a morphotaxon assignment. For the purposes of this study, a morphotaxon is a designation that is given to a specimen or group of specimens that are morphologically distinct from all other specimens but not yet assignable to a specific taxon. "Unidentified" specimens (17% of the specimens) were usually not identifiable because of poor preservation and/or the lack of distinguishing characteristics. All specimens are reposited in the National Park Service collections at Florissant Fossil Beds National Monument, Colorado (FLFO ACC 250–252 and 272).

Green River Formation

Geologic and Paleoclimatic Setting

Fossil plant material was collected from the Parachute Creek Member of the Green River Formation in Colorado (Fig. 2), which has been dated at 43–47 Ma (Roehler 1973; Remy, 1992; Hail and Smith 1997). MacGinitie (1969) interpreted the flora of the Green River Formation as representing a tropical to subtropical environment with a distinct dry season. Paleoclimate estimates based on nearest living relatives and leaf physiognomy characters give a MAT of 16–23 °C and MAP of ~45–86 cm for this portion of the Green River Formation (MacGinitie, 1969; Wolfe, 1994; Smith, 2000). MacGinitie (1969) estimated that the Green River flora grew at an elevation of no more than 300 m. However, foliar physiognomic techniques and paleoenthalpy yielded more recent paleoelevation estimates for the middle Eocene Green River Formation range between 1564–2900 m (Wolfe, 1994; Wolfe et al., 1998; Forest et al., 1999).

Collection and Identification

Fossil plant material was collected from four sampling areas spaced 35 m apart laterally within the same stratigraphic interval, from UCM locality 2001058, which is located near Long Point, in Garfield County, Colorado. Collections were made by the author and field assistants during the summers of 1997 and 1998. Data from the four sample areas were combined into one Green River sample of 584 leaves. Leaf fragments smaller than 1 cm^2 were not collected.

Located in the western Piceance Creek Basin, this portion of the lake has been interpreted as a marginal lacustrine environment (MacGinitie, 1969; Picard and High, 1972; Lundell and Surdam, 1975). Fossils are preserved as impressions and compressions in thinly laminated oil shale. The oil shale is dolomitic and interbedded with marlstone and claystone (Roehler, 1973; Hail and Smith, 1997). Leaf macrofossils are the predominant fossil found, but insects, seeds, and feathers have also been collected from the locality. Multiple specimens are usually found on the same piece of shale.

All dicotyledonous angiosperm specimens were identified to species using MacGinitie's (1969) classification and all subsequent revisions (Manchester, 1986; Manchester, 1989a, 1989b; Call and Dilcher, 1994, 1995, 1997; Lott et al., 1998;

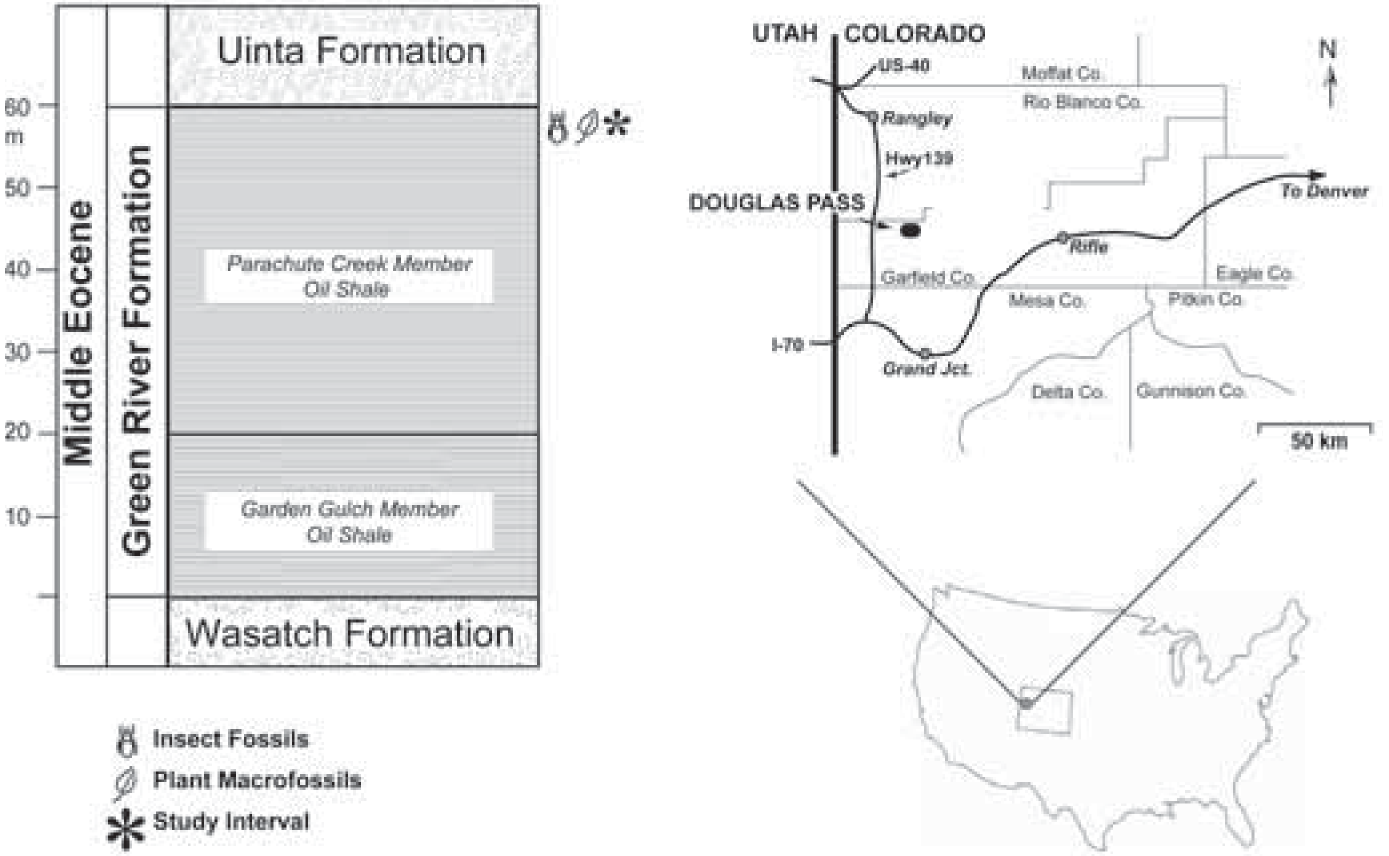

Figure 2. Stratigraphy of the Parachute Creek Member of the Green River Formation, adapted from Grande (1984), Remy (1992), Young (1995), and Cole et al. (1995), and a general location of the Green River locality in Garfield County, Colorado, USA.

Manchester et al., 1998; Wang and Manchester, 2000). Some legume leaflets were not identifiable to the genus level and are listed as "undetermined leaflets" from the family Leguminosae. Other "unidentified" specimens were not identifiable because they were either poorly preserved or because they were not identified or figured in any of the Green River plant publications. All specimens have been reposited in the paleontological collections of the University of Colorado Museum, Boulder, Colorado (UCM accession no. 348).

Comparison Between Fossil Sites

Certain aspects of the taphonomic character of leaves found in the Green River and Florissant floras appear to be very similar in terms of quality and detail of preservation, and in terms of size sorting of the leaves in both samples. Fossilized leaves were collected from relatively nearshore environments from both sites, and both assemblages appear to have an overrepresentation of small leaves derived primarily from the canopy of the source forest. This is based on the size of leaves from these assemblages and expectations from the plant taphonomy literature (Ferguson, 1985; Greenwood, 1992; Spicer, 1981).

According to floral lists, 68% of the families and 39% of the genera in the Florissant flora are also found in the Green River flora. MacGinitie (1969, p. 72–73) noted the similarities in taxonomy and preservation between the two floras and suggested that Florissant might contain some of the same species and/or descendants of species found in the Green River assemblage, including "29 identical or closely similar species."

Despite these similarities, there are definite differences between the two localities. For example, Florissant was a small lake relative to the lake environment of the Green River Formation. In addition, diatoms were present in Florissant and may have helped to facilitate preservation of the macrofossils (see O'Brien et al., this volume), whereas Green River has no record of diatoms and was a much more carbonate-rich environment.

Assessment of Herbivory

Each leaf was examined for the amount and type of insect damage using the criteria outlined by Labandeira (1998) and Beck and Labandeira (1998). Damage was categorized as belonging to one of five functional feeding groups (Fig. 3): (1) hole feeding—external foliage feeding in which an insect feeds through the leaf leaving behind a hole; (2) margin feeding—external foliage feeding in which an insect feeds on the margins of the leaf; (3) skeletonization—external foliage feeding in which an insect feeds on the soft tissues of the leaf, but does not feed on the veins (includes scraping leaf tissue layers); (4) leaf mining—internal feeding in which an immature insect lives and feeds within the leaf layers, leaving behind a blotch or serpentine shaped mine; and (5) galling—internal feeding in which an insect feeds and lives between the leaf tissue layers and the plant responds by developing histologically anomalous leaf tissue around the site. Plant galls can be induced by non-insect arthropods as well and sometimes it is difficult to distinguish between them. Specific gall types and potential inducers will be discussed in greater detail in the results section. Any distinguishable, stereotyped feeding damage found on leaves also was recorded. Insects that feed exclusively on one plant group often leave a pattern of damage that is unique to that insect and is consistent and clearly identifiable. This type of identifiable damage pattern is referred to as stereotyped feeding damage. All of the fossil leaves were photographed using a manual camera and stereo-microscope with a camera attachment. The photos were then scanned with a flatbed scanner and saved as digital images. All leaves and insect damage were measured using NIH *Image* software for the Macintosh (http://rsb.info.nih.gov/nih-image/).

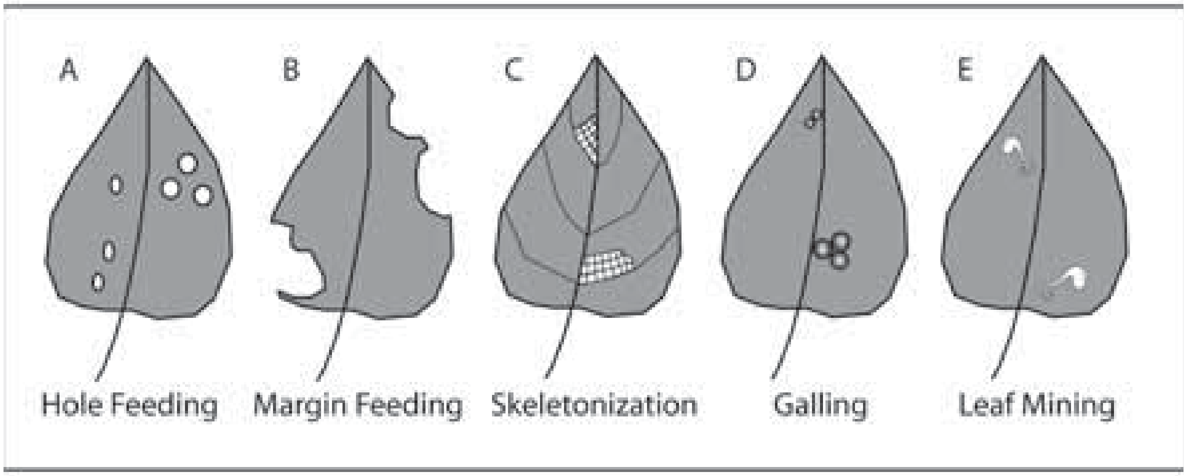

Figure 3. Illustrations of the five insect damage categories used in this study. Detailed descriptions can be found in the "Assessment of Herbivory" section within "Materials and Methods."

Statistical Analysis

All statistical analyses were performed with the use of JMP IN 3.2.1 (SAS Institute, 1996). Chi-square analysis of contingency tables was used to compare the relative abundance of plant taxa with the distribution of insect feeding damage in the Florissant assemblage. A *t*-test was used to compare the leaf area measurements between the Florissant and Green River floras. The amount of damage area was also compared between the two sites using a Wilcoxon signed-rank test. For families and genera that had at least ten leaves preserved in both localities, a Wilcoxon signed-rank test was used to compare the amount of damage made by insects between the two floras by family. Wilcoxon signed-rank tests were used because of the large number of leaves that had no feeding damage, necessitating the need for using a nonparametric test. Families that were compared are Anacardiaceae, Leguminosae, Salicaceae, Sapindaceae, and Ulmaceae. Genera that were compared are *Cedrelospermum, Populus*, and *Rhus*. Comparisons between Florissant and Green River with respect to overall incidence of herbivory, herbivore intensity, and feeding-guild structure were performed using chi-square analyses of contingency tables.

RESULTS

Florissant Formation

Of the 624 leaves from Florissant, 514 were identified to 48 plant species and morphotaxa within 17 families (Table 1). There were 110 unidentifiable specimens. The four most abundant plant species (*Cedrelospermum lineatum, Fagopsis longifolia, Staphylea acuminata,* and *Rhus* sp.) accounted for 50% of the leaves in the assemblage, and 44% of the insect damage in Florissant is found on these plants. The rank order of plant abundance and the rank order of plants with feeding damage are significantly different ($\chi^2 = 91.22$, $p < .0001$), indicating that insects were not feeding on plants in proportion to the plant's relative abundance. Twenty-two percent of the 48 plant species at Florissant have no insect-mediated damage. Four of five feeding guilds were present in the assemblage. No leaf-mining damage was found on the leaves observed in the study sample from Florissant.

Green River Formation

Of the 584 fossil leaves that were examined from the Green River Formation, 522 of the specimens were assigned to one of 22 plant species in 16 families and the remaining 62 specimens remain unidentified (Table 2). Four species (*Cardiospermum coloradensis, Cedrelospermum nervosum, Parvileguminophyllum coloradensis*, and *Syzigiodes americana*) accounted for 57% of the leaves in the assemblage, and 59% of the insect-damaged leaves were from these species. Nine species did not have any insect damage on them. These species occurred at low frequencies—only one to four specimens per taxon (Table 2).

Comparison of Florissant and Green River Formation

Overall leaf sizes in the Florissant and the Green River floras were not significantly different (F = 1.49, $p = .221$), but the amount of area damaged by insects was significantly greater (Wilcoxon signed-rank test, Z = 4.61739, $p < .0001$) in the Green River flora (2.5% of original leaf area) than in the Florissant flora (1.4% of original leaf area) (Table 3).

Comparisons of damage levels by plant family indicated significantly higher damage levels for Green River leaves from the Salicaceae (Wilcoxon signed-rank test, Z = –2.68160, $p = .0073$) and Sapindaceae (Wilcoxon signed-rank test, Z = –2.79887, $p = .0051$). All other plant families did not have significantly different damage levels (Wilcoxon signed-rank test, $p > .05$). When damage levels were compared by genus, only *Populus* had significantly different damage levels (Wilcoxon signed-rank test, Z = –2.17680, $p = .0295$), with herbivory being greater in the Green River Formation.

Only 23% of the leaves were damaged in the Florissant flora, compared to 34% in the Green River flora (Fig. 4A). This difference is statistically significant ($\chi^2 = 16.39$, $p < .0001$). There is no significant difference ($\chi^2 = 3.4$, $p = .183$) in the number of feeding types per leaf between the Florissant and Green River floras (Fig. 4B), and damaged leaves usually have only one type of feeding damage. No leaf from Florissant or the Green River has more than three types of damage.

Feeding-guild structure (Fig. 4C) is slightly different ($\chi^2 = 9.97$, $p = .041$) between the two floras. The main differences between the two are the dominance of leaves with hole-feeding damage and the greater proportion of leaves with galls in the Florissant assemblage.

Specialized Damage

There are several examples of feeding damage found on particular Florissant plants that appear to be created by an insect with a host-specific relationship with that plant. These damage patterns tend to be found on the rarer taxa in the assemblage. By contrast, *Fagopsis longifolia* is the most abundant plant at Florissant, but it has no specialized damage and very little generalized damage of any sort.

Cedrelospermum lineatum and *Staphylea acuminata* are the only abundant species with stereotyped, specialized feeding damage. *Staphylea acuminata* has two different examples of feeding damage that are likely produced by a specialist insect: distinctive skeletonization damage and gall damage (Fig. 5A). Distinctive galls and rounded hole-feeding patterns are also found on *Cedrelospermum lineatum* leaves (Fig. 5B). *Cedrelospermum* is an extinct genus; however, one of its closest living relatives, *Zelkova*, has gall damage on its leaves that is similar in appearance to the fossil galls. Galls on modern *Zelkova* are produced by aphids. Galls are also found on the leaves of the confamilial *Ulmus tenuinervis* at Florissant, including an example of two galls on a single leaf (Fig. 5C and 5D), and galls have been

TABLE 1. ABUNDANCE OF LEAVES AND DAMAGE LEVELS FOR PLANTS FOUND IN THE FLORISSANT FOSSIL BEDS SAMPLE

Family/Species	Leaves		Original leaf area (mm^2)	Damage area (mm^2)
	Total	Damaged		
Anacardiaceae				
Cotinus fraterna	3	0	2077.39	0
*Rhus sp.	29	4	6144.14	8.64
Schmaltzia vexans	1	1	489.58	24.70
Burseraceae				
* Bursera serrulata	5	0	1946.48	0
Celastraceae				
Celastrus typica	2	0	2818.63 0	
Fagaceae				
Castanea dolichophylla	1	1	532.23	2.55
Fagopsis longifolia	123	5	52,636.50	64.60
*Quercus sp.	24	3	6045.05	61.40
Taxon 1	1	1	733.87	26.20
Incertae Sedis				
Populites neeri	1	1	847.01	17.24
Juglandaceae				
Carya libbeyi	5	0	2396.20	0
Leguminosae				
*Caesalpinites sp.	2	0	491.41	0
Cercis parvifolia	1	1	842.62	3.09
Conzattia coriaceae	1	0	111.03	0
Prosopis linearifolia	2	0	876.89	0
Robinia lesquereuxi	9	3	1228.12	22.81
Leguminosae (continued)				
Taxon 1	7	2	1624.16	3.57
Taxon 2	5	1	247.72	1.08
Meliaceae				
Trichilia florissanti	4	4	3612.04	363.62
Myrtaceae				
Eugenia arenaceaeformis	4	3	3860.14	80.45
Oleaceae				
†*Osmanthus praemissa*	1	0	692.08	0
Rhamnaceae				
Rhamnites pseudo-stenophyllus	10	0	595.38	0
Ziziphus florissanti	1	0	115.57	0
Taxon 1	1	0	1271.36	0
Rosaceae				
Amelanchier scudderi	1	1	128.78	0.46
Cercocarpus myricaefolius	20	2	4261.27	16.28
Crataegus sp.	4	0	2246.72	0
Malus sp.	1	0	740.81	0
†*Rosa hillae*	8	0	1580.53	0
*Vauquelinia sp.	8	1	983.00	3.51
Taxon 1	3	1	217.25	4.96
Taxon 2	1	0	68.35	0
Taxon 3	1	1	395.86	1.94
Rosaceae (continued)				
Taxon 4	1	0	229.06	0
Taxon 5	1	0	296.53	0
Taxon 6	1	0	115.57	0
Salicaceae				
*Populus crassa	10	1	16,702.80	45.21
*Salix sp.	3	0	2750.90	0
Sapindaceae				
*Athyana haydenii	14	0	2701.11	0
*Cardiospermum terminalis	3	3	1512.69	21.53
*Koelreuteria alleni	5	2	1445.37	6.2
Sapindus coloradensis	19	1	9048.45	3.87
Staphylaceae				
Staphylea acuminata	31	21	34,170.70	1352.90
Ulmaceae				
†*Cedrelospermum lineatum*	127	34	35,116.80	374.11
†*Celtis mccoshii*	1	0	410.50	0
Ulmus tenuinervis	5	2	2094.98	63.89
Taxon 1	1	1	803.28	4.27
Unidentified	110	43	39,265.29	937.78
Total	**621**	**144**	**249,406.63**	**3516.86**

*Indicates genera also known from the Green River Formation.
†Indicates species also known from the Green River Formation.

TABLE 2. ABUNDANCE OF LEAVES AND DAMAGE LEVELS FOR PLANTS FOUND IN THE GREEN RIVER SAMPLE

Family/Species	Leaves		Original leaf area (mm^2)	Damage area (mm^2)
	Total	Damaged		
Anacardiaceae				
*_Rhus nigricans_	45	8	16,173.00	155.52
Araliaceae				
Araliophyllum quina	4	0	446.58	0
Burseraceae				
*_Bursera inaequalateralis_	3	0	1108.51	0
Euphorbiaceae				
Aleurites glandulosa	8	2	8072.65	217.52
Fagaceae				
*_Quercus_ sp.	1	0	290.16	0
Leguminosae				
*_Leguminosites_ sp.	9	1	1459.48	15.01
Parvilegum	46	8	8569.80	161.85
Undet. leaflets	21	4	3027.20	127.40
Myrtaceae				
Syzygioides americana	64	38	50,874.26	1862.46
Oleaceae				
†_Osmanthus praemissa_	1	0	176.97	0
Platanaceae				
*_Macginitea wyomingensis_	12	4	24,539.36	160.79
Rosaceae				
†_Rosa hillae_	3	0	427.43	0
Salicaceae				
*_Populus cinnamomoides_	20	9	18,908.55	486.57
*_Populus wilmattae_	16	10	10,676.37	524.56
*_Salix_ sp.	28	15	13,191.09	408.74
Sapindaceae				
Allophylus flexifolia	10	4	16,713.51	291.51
*_Athayana balli_	3	0	283.21	0
*_Cardiospermum coloradensis_	107	39	26,975.08	676.30
Sterculiaceae				
*_Sterculia coloradensis_	1	0	302.03	0
Styracaceae				
Styrax transversa	1	0	748.78	0
Symplocaceae				
Symplocos exilis	1	0	219.84	0
Ulmaceae				
*_Cedrelospermum nervosum_	115	31	29,304.48	738.65
†_Celtis mccoshii_	3	1	692.94	33.56
Unidentified	62	22	20,703.55	535.18
TOTAL	**584**	**196**	**253,884.87**	**6395.62**

Note: Parvilegum—_Parvileguminophyllum coloradensis_.
*Indicates genera also known from the Florissant Formation.
†Indicates species also known from the Florissant Formation.

TABLE 3. LEAF AREA MEASUREMENTS FROM FLORISSANT AND THE GREEN RIVER FORMATION

Site (N)	Mean leaf area (mm^2)	Standard error	Mean leaf area damaged (mm^2)	Standard error	Damaged (%)
Florissant (624)	399.96	16.97	5.64	1.02	1.4
Green River (584)	434.73	23.12	10.95	1.49	2.5

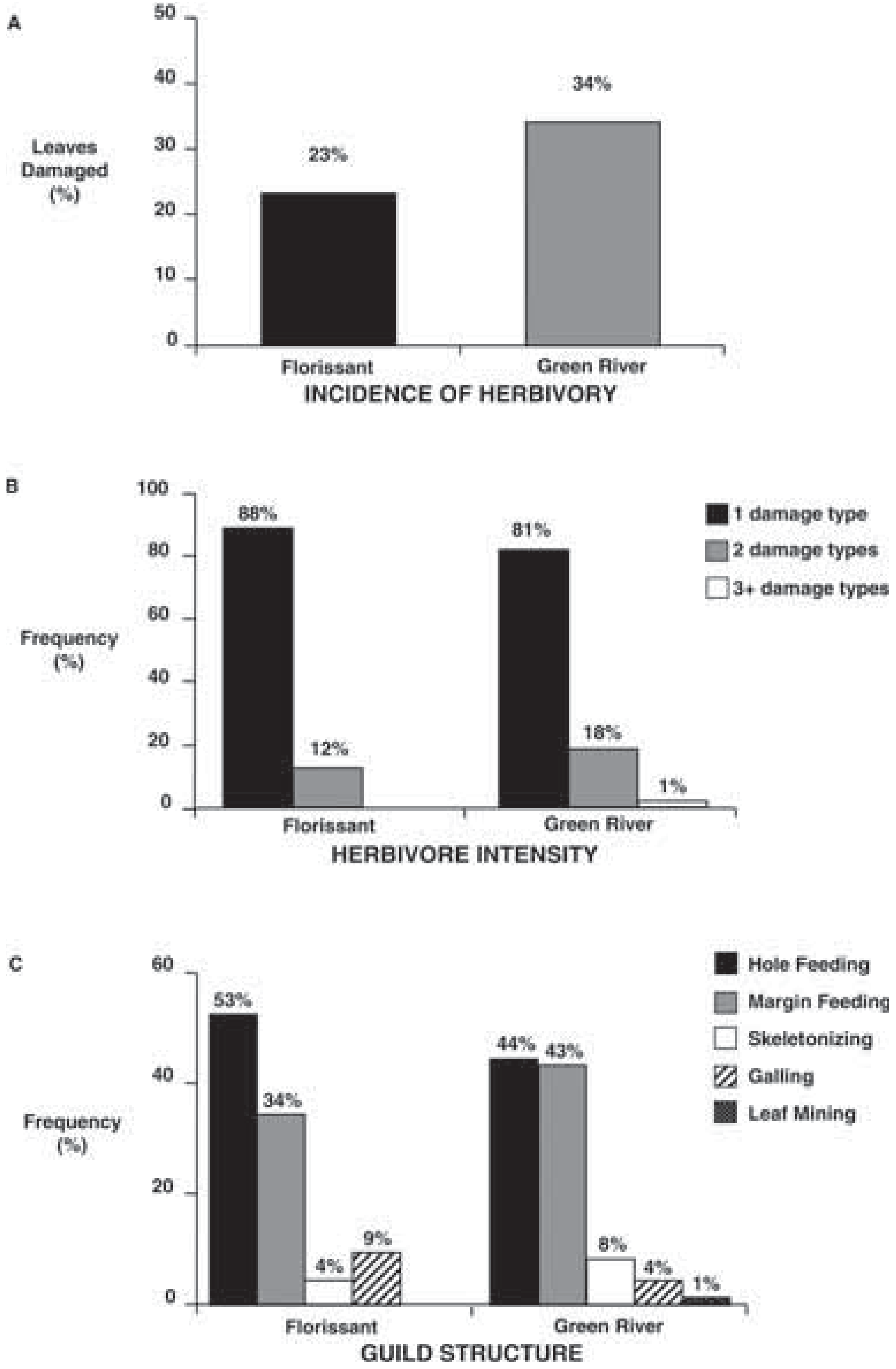

Figure 4. Comparisons of leaf damage in the Florissant and Green River floras. (A) Incidence of herbivory: percentage of leaves damaged in each sample was significantly different between localities ($\chi^2 = 16.39$, $p < .0001$). (B) Herbivore intensity: frequency of one, two, or three damage types per leaf in each sample was not significantly different ($\chi^2 = 3.4$, $p = .183$). (C) Guild structure: relative abundance of the different functional feeding groups at each site was significantly different ($\chi^2 = 9.97$, $p = 0.041$).

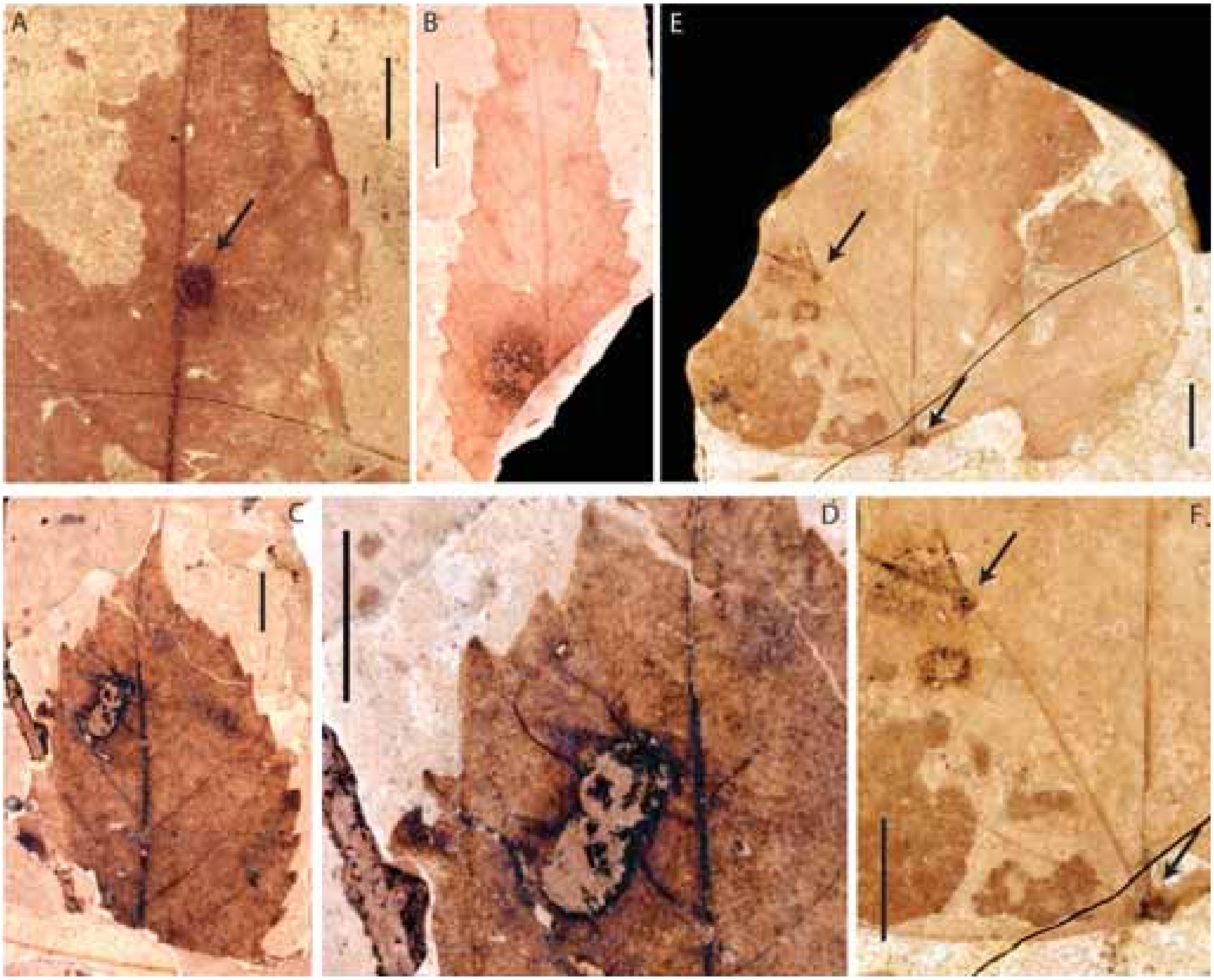

Figure 5. Examples of gall damage found from the Florissant Formation. (A) Gall damage found on *Staphylea acuminata* (FLFO 3175). (B) Gall damage on *Cedrelospermum lineatum* (FLFO 2795). None of the three dimensional features of the gall were preserved. (C) Two galls on *Ulmus tenuinervis* (FLFO 2791). (D) A close-up of the galls in Figure 5C. These galls were likely to have been made by aphids. (E) *Cercis parvifolia* leaf (FLFO 2723) with two distinct leaf galls, one positioned at the base of the leaf, and the second located on the left side where leaf veins branch. (F) Close-up of the two galls on *Cercis parvifolia*. Scale = 5 mm.

found on a specimen of *Rhus* and a specimen of *Robinia*. Aphids are known to produce host-specific galls on the leaves of *Ulmus* (Tribe Eriosomatini) and *Rhus* (Tribe Melaphini) in modern forests (Wool, 2005) and are good candidates for the producers of the galls found on the fossil leaves.

Two galls with a characteristic arrangement were found on a leaf of *Cercis parvifolia* (Fig. 5E and 5F). Specialist hole-feeding damage is found on leaves of *Trichilia florissantii* and highly specialized hole-feeding patterns are found on *Cardiospermum terminalis* (Fig. 6C). One *Populus crassa* specimen has distinctive skeletonization damage and one unidentifiable leaf has distinctive hole-feeding damage.

Three examples of specialized insect damage are found in both the Green River and Florissant floras. *Populus crassa* from Florissant has skeletonization damage that is also found on *Populus cinnamoides* (Fig. 6B) and *Salix* sp. leaves from the Green River Formation. The rounded hole-feeding patterns that are found on *Cedrelospermum nervosum* leaves in the Green River flora (Fig. 6A) are also found on the same species in Florissant. Finally, there are the distinctive, hole-feeding patterns with parallel-sided margins that are found on the leaves of *Cardiospermum terminalis* at Florissant and *Cardiospermum coloradensis* in the Green River Formation (Fig. 6C and 6D) This damage pattern is characterized by elliptical to slightly rounded holes. The holes typically occur between the second-order veins and have very well developed reaction tissue around the rim of damage. The holes range from 2 to 8 mm in length and are usually found in clusters of several elliptical holes.

DISCUSSION

Levels and Patterns of Herbivory

The majority of insect damage at Florissant was not found on the most abundant leaves in the assemblage. Some plant species seemed to have been avoided, whereas others seemed to have been preferred and included several examples of specialized feeding damage. This suggests that insects were exhibiting feeding preferences for specific host plants. This type of selectivity is common in modern insects (Bernays and Chapman, 1994) and could be due to a variety of factors, including differing phenology, varying physical and chemical plant defense, varying nutritive value of plants, and many other possibilities (reviewed in Coley and Aide, 1991). In addition, some of these interactions are likely to be examples of long-term associations between plants and insects and could be indicative of coevolved relationships (Ehrlich and Raven, 1964).

It is intriguing that no leaf miners were found on over 600 leaf specimens in the study sample. All leaf-mining families of insects had already made first appearances in the fossil record prior to the late Eocene (Labandeira and Sepkoski, 1993) and leaf mines have been documented from as early as the Late Triassic of South Africa (Scott et al., 2004; Labandeira and Anderson, 2005). In addition, eleven insect genera that are known to leaf mine on modern plants have been described from the Florissant deposits. Although not found in the study sample, there are two known examples of leaf mining damage at Florissant, one on a leaf of *Trichilia* (Fig. 4 *in* Meyer, 2003; specimen FLFO-3514) and another on a leaf of *Koelreuteria alleni* (pers. observation, one leaf mine found among ~1950 leaves examined; specimen UCM 34992). So, although leaf mining is rare, it did exist at Florissant. This also suggests that one must collect or examine very large sample sizes from assemblages in order to capture any evidence of leaf-mining. There are a few possible explanations for the rarity of leaf mining damage on Florissant leaves. The first

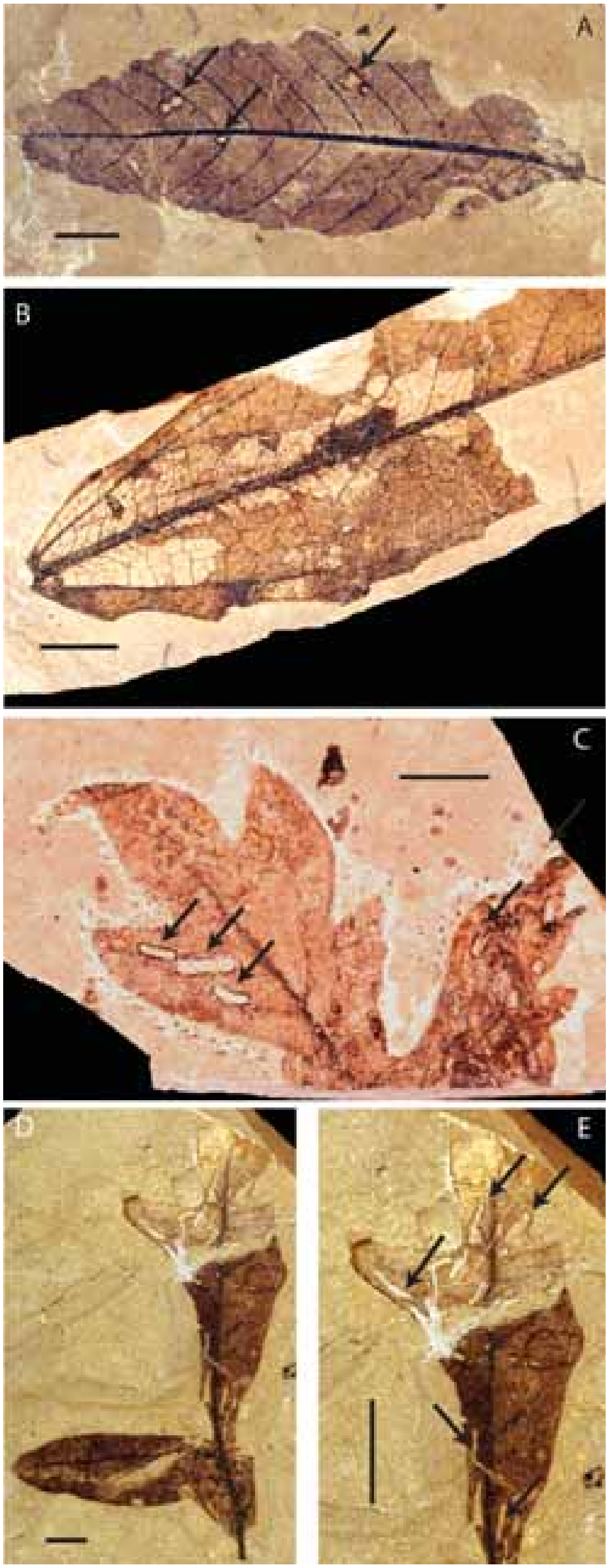

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Figure 6. Examples of insect feeding damage found on the same plant genera at both Florissant and Green River. (A) Hole-feeding damage found on the leaves of *Cedrelospermum nervosum* from the Green River Formation (UCM 38900). (B) An example of the skeletonizing damage found on the leaves of *Populus* and *Salix*. This is a *Populus cinnamoides* leaf from the Green River Formation (UCM 38759). (C) Parallel-sided hole-feeding damage on *Cardiospermum terminalis* from Florissant (FLFO 2890). (D) Parallel-sided hole-feeding damage on *Cardiospermum coloradensis* from the Green River Formation (UCM 38804). Scale = 5 mm. (E) A close-up of the feeding damage in 6D. Feeding damage in 6C and 6D are likely to have been made by the same type of insect.

possibility is that leaf miners were less common in the Eocene than in modern communities, where leaf-mining levels have been documented to be as high as 13.4–27% of leaves in a sample having leaf mines (Faeth et al., 1981; Basset, 1991). Second, it is possible that leaf mining insects had a preference for herbaceous plants. Lower levels of herbivory have been documented on canopy leaves than on understory leaves in some modern communities (Lowman and Heatwole, 1992; Barone, 2000). If this was the case, we might expect leaf mines to be rare to absent in fossil assemblages, because herbaceous, understory plants are known to be underrepresented in fossil assemblages (Spicer, 1981; Ferguson, 1985; Greenwood, 1992). Finally, leaf mines have been shown to be more apparent on the lower surface of modern leaves, (Smith, 2004) and even if fossil leaves are preserved in a 1:1 ratio of adaxial to abaxial surfaces (Gastaldo et al., 1996), this could decrease the sample of leaf mines in fossil assemblages by as much as 50% if both halves of specimens are not collected. However, at Florissant, where specimens typically have both parts and counterparts and often preserve both upper and lower surfaces of leaves, miners should be more fairly represented.

Florissant Compared with the Green River Formation

In the interior Rocky Mountain region of North America, levels of herbivory declined from the middle to the late Eocene. Not only did the amount of leaf area removed by insects decrease, but the number of leaves that were fed upon also declined. Further evidence of the decline in levels of herbivory can be found in the family and genus comparisons, where damage levels decreased over time in the families Salicaceae and Sapindaceae. However, changes in the Salicaceae are predominantly due to significant decreases in damage levels in the genus *Populus* over time. All other groups analyzed showed no significant difference in damage levels.

If many of the modern insect-plant associations were established, or were becoming established, in the middle Eocene, why were herbivory levels lower in the late Eocene Florissant flora? One possible explanation may involve differences in paleoelevation (which likely reflects differences in climate) between the two sites, although interpretation of this is complicated by differences in global climate between these times, as discussed below. As cited earlier, elevation estimates for Green River range from 1564 to 2900 m and for Florissant from 1900 to 4133 m, generally suggesting that Florissant was several hundred meters higher than Green River. Although not tested directly, modern herbivory levels may decline with higher elevation, as is seen in comparisons of high-elevation wet tropical sites, which have lower levels of herbivory (4.3% of leaf area removed), with low-elevation wet tropical sites, which have higher levels of herbivory (5%–10% leaf area removed) (Smith, 2000). An examination of the relationship between elevation and herbivory levels in modern forests would help to resolve this issue—although plant and insect diversity and temperature are usually correlated with elevation change as well. This may confound an understanding of the factors that most strongly influence herbivory.

Another related explanation for the differences in levels of herbivory between the Green River and Florissant floras may be cooling temperatures in the middle to late Eocene (Wolfe, 1994; Zachos et al., 2001). A correlation between climate change and herbivory levels has been documented for the Paleocene through the middle Eocene (Wilf and Labandeira, 1999; Smith, 2000; Wilf et al., 2001). These studies have documented an increase in levels and types of herbivory as temperatures increased and a decrease in levels and types of herbivory as temperatures decreased. A similar relationship has been identified in modern ecosystems, where decreases in latitude appear to be correlated with increases in temperature and increases in insect feeding damage levels (Coley and Barone, 1996).

Although climate is likely to play a role in plant-insect interactions, the simple pattern of increasing herbivory levels with increasing temperature is probably not the whole explanation. For example, modern increases in insect herbivory with decreasing latitude are correlated not only with changes in climate, but also with a general increase in insect (Erwin, 1982) and plant diversity (Chazdon and Denslow, 2002) and with changes in levels of plant defense (Coley and Aide, 1991). In the fossil record, we see a general increase in insect diversity from the early Cenozoic onward at both the familial (Labandeira and Sepkoski, 1993) and generic (Farrell, 1998) levels, with a corresponding general trend of increasing angiosperm diversity (Niklas et al., 1985). The interplay between insect herbivory and other biotic as well as abiotic factors (such as temperature, precipitation, seasonality, soil chemistry, and CO_2 levels) is likely to become clearer with the addition of other studies that focus on insect feeding damage in Cenozoic assemblages, and through a greater understanding of how these variables interact in modern ecosystems.

Specialist Interactions

In addition to helping clarify overall patterns of herbivory, long-term studies of herbivory in the fossil record allow us to track host-specific interactions in space and time. For example, the host-specific interactions seen at Florissant and Green River on *Cardiospermum*, *Cedrelospermum*, and *Populus* provide excellent examples of specialized interactions that existed for at least a 9 m.y. period. Ehrlich and Raven (1964) predicted that specialized plant-insect associations would be maintained for long periods of time. One must wonder, how long do these types of interactions last? Do any or all of the host-specific associations between Florissant and Green River plants and their insect herbivores still exist today? If not, how much longer did these association last? If plant and insect interactions promote the diversification of these groups as Ehrlich and Raven suggested, then should we expect to find an increase in specialized feeding damage that coincides with increases in plant and insect diversity? These questions can be answered through further investigation of the Cenozoic fossil record.

There were four examples of specialized plant-insect associations that were maintained from the middle to the late Eocene and there are several examples of host-specific associations in the Florissant assemblage. However, these values based on the fossil record should be viewed as underestimates, because more specialist associations were likely to have been maintained over these periods. Host-specific associations are probably underestimated in the fossil record because it is nearly impossible to identify specialist feeders that make non-stereotyped damage. Only the damage made by insects that feed in a consistent and distinctive manner, on the same or similar plant groups, can be recognized as specialist damage. Even though many externally feeding insects, especially margin feeders, specialize on only one plant species, they do not make a distinctive and recognizable damage pattern. For this reason, the number of specialists found in the fossil record is likely to be undercounted. Only highly stereotyped damage patterns, such as those made by galling and leaf-mining insects, should be compared through time.

The diversity of galling damage in the Florissant flora is higher than in the Green River flora. Today, there is a pattern of higher species diversity of galling insects in drier habitats that have nutrient-poor soils, and it has been hypothesized that galling insects have lower survivorship in wetter environments due to increased fungal and pathogenic attack (Fernandes and Price, 1991). The increase in the diversity of insect galls in the Florissant flora may be attributable to a relatively drier environment at Florissant than at Green River. Even very slight differences in precipitation levels or seasonality can result in dramatic differences in patterns and levels of insect herbivory (Smith and Nufio, 2004). One might therefore predict that galling insects would be even less diverse in the early Eocene, when conditions were comparatively warmer and wetter, than in the middle or late Eocene. Ongoing studies of middle Eocene insect assemblages (e.g., Green River Formation, Colorado, and Republic, Washington, USA; Messel, Germany) will make clear whether this prediction holds true.

SUMMARY

The quality of preservation in the Florissant and Green River Formations provides an excellent opportunity for studying plant-insect interactions. Cenozoic insects do appear to express some level of host-specificity in their feeding preferences. In addition, there is evidence for long-lasting associations between insect herbivores and their host plants, which may indicate coevolution between these groups. Comparisons of insect damage from the Florissant and Green River Formations show a decline in insect damage through time that may be attributable, in part, to global cooling. Evidence of an increase in galling diversity during the same time interval may also be related to climate changes that occurred during this time interval.

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An outline morphometric approach to identifying fossil spiders: A preliminary examination from the Florissant Formation

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ABSTRACT

Using available shape characters we conducted an outline morphometric analysis to make family-level identifications of fossil spiders from the Florissant Formation in Colorado. In this analysis we used carapace shape because it is a character that can be observed on most fossil spiders, and we also used linear leg characters. All measurements were first made on 202 modern spiders from eight families found in localities similar to the fossil lake environment. A multiple discriminant analysis (MDA) of the eigenshape axes was used to predict family placement among the modern data set to test the accuracy of the predictions. The modern spider families that were predicted correctly most often were the Salticidae (91.2%), Linyphiidae (80%), Dictynidae (76.5%), Tetragnathidae (68.2%), Clubionidae (66.7%), and Araneidae (65.5%). Families that produced less successful results were the Agelenidae (46.7%) and the Lycosidae (39.1%). Forty-three fossil spiders from Florissant were then added to

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the model to determine their family placement. All fossils were placed into modern families with varying degrees of accuracy. Only 42% of our identifications agree with those made by previous authors, but it is likely that these specimens were originally misidentified. With the addition of more taxa and characters, we believe that an outline morphometric approach shows great promise for helping to identify fossil taxa that are lacking traditional taxonomic characters.

Keywords: Araneae, spiders, morphometrics, Florissant.

INTRODUCTION

The anatomical completeness of fossil specimens is of great concern in studies of taxonomy and morphology. Finding preserved fossils with important identifiable characters is crucial to paleontologists, yet rare. Organisms with hard parts are more likely to be preserved as fossils, because they are more resistant to the biological, physical, and chemical processes that occur after death. However, even these fossils are susceptible to boring, chemical dissolution, and breakage (Menard and Boucot, 1951; Kidwell and Bosence, 1991; Best and Kidwell, 2000). As a result, only a subset of the fossil record may be relevant to taxonomic interpretation (Kidwell, 2001). Among the organisms that are composed of soft parts, researchers studying arthropods have found an even greater potential for disintegration and destruction (Schafer, 1972; Plotnick, 1986; Allison, 1988; Martinez-Delclos and Martinell, 1993; Briggs et al., 1998; Smith, 2000; Martinez-Delclos et al., 2004; Smith et al., 2006). Spider exoskeletons tend to be less sclerotized than other terrestrial arthropods, such as insects, thus contributing to their rarity in the fossil record.

Considering the difficulties associated with fossilization, it is no surprise that taxonomic work on fossils is so difficult (Kidwell, 2001). There are rare deposits, such as the Burgess Shale, where fossilization of soft parts has occurred and preservation is exceptional. However, diagnostic characters for these organisms are not always visible. This is especially true among the spiders (Order Araneae). Superfamily- and family-level diversity among fossil spiders have been based on a wide variety of available characters, including but not limited to leg length, leg width, and carapace shape (Penney, 2000, 2002; Penney and Selden, 2002). Making generic and specific placements of modern spider taxa typically relies on characters such as genitalia, minute cheliceral characters, and leg spine orientation are typically used (Chamberlin and Ivie, 1941; Chamberlin and Gertsch, 1958; Dondale and Redner, 1982; Levi, 1981; Roth, 1993; Ubick et al., 2005). These diagnostic characters are not usually visible on spiders preserved in shale, thus illustrating the need to find an alternative method for identifying fossil spiders. In this study we present a new method that uses a combination of outline morphometric analyses and linear characters to identify spiders to the family level.

Outline-based morphometrics is a technique used to quantify shape and size (Lohmann and Schweitzer, 1990). This method captures the available shape information, while reducing the amount of user input and potential bias when choosing distinguishing characters (Lohmann and Schweitzer, 1990), as the input is the complete shape. More importantly, the analysis allows for the discovery of covariation among the morphological variables (MacLeod, 1999), ultimately providing new variance-optimized axes summarizing the major aspects of shape variation in the fewest axes. Many workers have attempted to quantify morphological differences using shape characteristics to solve a variety of taxonomic questions (Kendall, 1984; Bookstein, 1986, 1991, 1996, 1997; Rohlf and Bookstein, 1990; Rohlf, 1993; MacLeod, 1999). This method has been useful in taxonomic and environmental studies of leaves (Jensen et al., 1993, 2002; McLellan and Endler, 1998; Premoli, 1996; MacLeod, 2002; Krieger et al., 2007), ontogenetic shape variation in fossil ostracod carapaces (Baltanas et al., 2000), and sexual dimorphism in isopods (Bertin et al., 2002). This technique has also been applied successfully to the classification of both modern (Warheit, 1992; MacLeod, 1999, 2002) and fossil taxa (Kowalewski, 1993; Baltanas et al., 2000).

The goals of this study are to (1) investigate whether morphometrics can be used to distinguish modern spiders at the family level; and (2) apply these methods to Eocene fossil spiders from Florissant.

FLORISSANT GEOLOGIC HISTORY

The Florissant Fossil Beds are an example of a fossil Lagerstätte in western Colorado that formed in an ancient lakebed 34.1 million years ago. This lake was formed by a large lahar, which dammed a stream drainage running through the Florissant valley. The Tertiary lacustrine strata of the Florissant Formation are composed of tuffaceous mudstone, fossiliferous shale layers comprising couplets with alternating layers of diatoms and ash-clay, and interbedded ash layers (Fig. 1). Estimates of climate at Florissant are varied, but it is generally agreed that the climate was warm temperate with mean annual temperature averaging ~13 °C, with a distinct dry season; estimates of the mean annual precipitation range from 50 to 80 cm (Meyer, 1992, 2001, 2003; Gregory, 1992). This area has been described as a transitional temperate environment on the basis of tropical and temperate insects that have been described from the area and leaf physiognomic studies (Scudder, 1890; Meyer, 1992, 2003; Gregory, 1992; Wolfe, 1992, 1994, 1995; Gregory, 1992; Leopold and Clay-Poole, 2001; Moe and Smith, 2005). Paleoelevation estimates for Florissant range from 1900 to 4100 m (Meyer, 1992, 2001, 2003; Gregory, 1992; Wolfe, 1992, 1994, 1995).

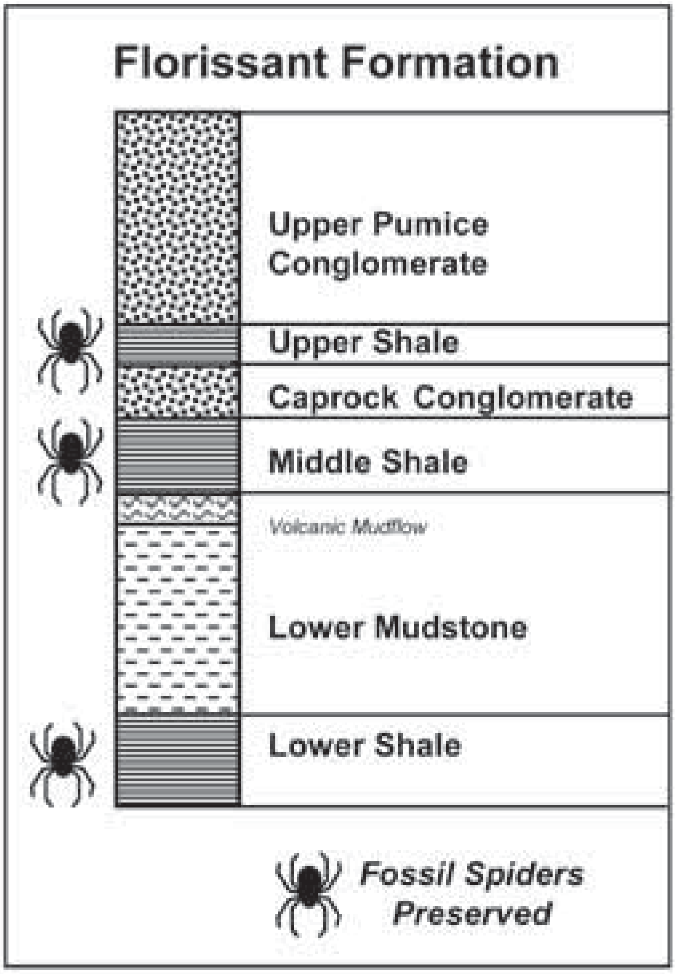

Figure 1. Columnar stratigraphic section of the Florissant Formation, adapted from Evanoff et al., 2001.

MATERIALS AND METHODS

Sources of Data

All modern specimens were from the spider collection at the Denver Museum of Nature & Science (DMNS). Fossil specimens were loaned from several institutions including the Florissant Fossil Bed National Monument (FLFO), the Museum of Comparative Zoology at Harvard University (MCZ), the National Museum of Natural History in Washington, D.C. (USNM), and the University of Colorado Museum in Boulder, Colorado (UCM).

Modern Material

The carapace shapes of modern spiders were studied by sampling 202 modern adult spiders from the eight most abundant families found around modern lake environments (Table 1 for families, Appendix for species examined). The genera and species examined were chosen to represent the range of morphological diversity within a family as recommended by experts in that group (B. Cutler for Salticidae, C. Dondale for Lycosidae, J. Miller for Linyphiidae, H. Levi for Tetragnathidae and Araneidae, D. Ubick for Clubionidae, 2004, personal commun.).

TABLE 1. FAMILIES USED IN THE MORPHOMETRIC AND MULTIPLE DISCRIMINANT ANALYSIS

Family	No. of specimens	No. of genera
Agelenidae	15	4
Araneidae	29	11
Clubionidae	12	3
Dictynidae	17	2
Linyphiidae	50	18
Lycosidae	23	6
Salticidae	34	17
Tetragnathidae	22	6
Unknown/Fossil	43	—

Although Florissant has been described as a transitional temperate environment (Leopold and Clay-Poole, 2001; Meyer, 2003), the eight spider families used in this study are also commonly found in tropical lake localities (Nentwig, 1993). For example, members of the Tetragnathidae are found almost exclusively along wetland habitats in both tropical and temperate environments (Aiken and Coyle, 2000). In addition, these families include the majority of families into which the fossil spiders had been placed by previous workers.

The morphological variability of carapace shapes within the families examined is extensive. This study focused on capturing as much of the variability in carapace shapes within families as possible by choosing multiple representatives from each of the families that captured the large-scale variation in shape. In addition, covariation among traits was also considered and taxa were chosen that would best differentiate among the smaller-scale aspects of morphology. Because this study is designed to be a first test of the viability of a morphometric technique using shape and linear characters, it is limited to the study of the eight most common families, as opposed to examining fewer representatives from more families.

Fossil Material

The first work on fossil spiders from Florissant began in the late nineteenth century with the large monograph *The Tertiary Insects of North America* by Samuel Scudder (1890), who placed many of the spiders into new species, within 11 extant families: Anyphaenidae, Amaurobiidae, Araneidae, Clubionidae, Linyphiidae, Salticidae, Segestriidae, Tetragnathidae, Theridiidae, Thomisidae, and Titanoecidae. Petrunkevitch (1922) reevaluated this work and corrected several taxonomic problems and classification mistakes that had been previously made. He added the Gnaphosidae, Lycosidae, Parratidae, and Theraphosidae to the families found at Florissant, but determined that the Anyphaenidae, Amaurobiidae, Salticidae, Theriidae, and Titanoecidae were not present. His revisions resulted in eight extant families being recognized from Florissant, and only one extinct family, the Parratidae.

Of the fossil specimens found at Florissant, only those spiders that were complete and preserved with the dorsal surface exposed were used in this study, and specimens that showed only the ventral surface or were preserved laterally were not included. In addition, specimens that appeared to have been distorted by the process of fossilization were excluded from the study. Forty-three fossil spiders were preserved dorsally with the carapace fully exposed, and these were used in the analysis. Of these, 24 had been identified by previous workers.

Morphometric Analysis

To generate the empirical morphospace of the modern families, we began by capturing images of the modern specimens using a Nikon 995 digital camera attached to a Leica MZ-6 microscope with a standard Leica 1× optical lens. A standard-scale TIFF image was captured of the carapace of each specimen. The TIFF images of the specimens were then placed into Photoshop 7.0 (Adobe Systems Incorporated, 1990–2002) and silhouettes were carefully made by increasing the amount of contrast in the picture. The automated thresholding approach to generating silhouettes is not always effective, and in some cases we manually captured the outline of specimens in Photoshop using the lasso tool. Silhouettes still need to be converted to a set of outline coordinates. The first step in this process is to select an initial starting point that can be repeatably located, which defines homology across specimens (Lohmann and Schweitzer, 1990). The exact midpoint of the anterior area of the carapace was chosen for this purpose, as it is a point that can be relocated along the form (Fig. 2).

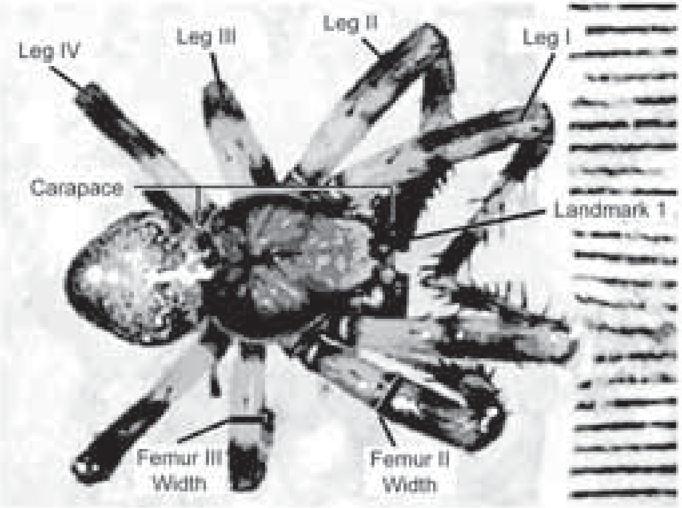

Figure 2. General spider body form depicting legs I–IV and femur widths II and III. The exact midpoint of the anterior area of the carapace was chosen to be landmark 1. This starting point for the outline is easy to locate on all of the specimens.

After selection of the outline starting point, the silhouetted images were converted to closed outlines using tpsDig 1.28 (F.J. Rohlf, http://life.bio.sunysb.edu/morph/). tpsDig represents the outlines as a series of boundary coordinate points from the starting point around the edge of the silhouetted object. Each outline consisted of 200 evenly spaced points placed around the circumference of the carapace shape. The x, y coordinate outlines were converted to phi functions using MacLeod's xy-phi program (available for download at http://life.bio.sunysb.edu/morph/). Phi functions describe the net angular change required to follow the outline around the carapace from the starting landmark (Zahn and Roskies, 1972). Conversion to phi functions removes position, rotation, and scale from the description of carapace shape; "shape" is what remains when these three quantities have been removed (Zelditch et al., 2004). The size of each carapace shape is calculated as the geometric area of the outline polygon, which is an additional independent character that is used to further place the spiders into family groups.

Once the shapes were standardized, the eigenshape analysis was performed with a covariance matrix using MacLeod's Eigenshape software (http://www.nhm.ac.uk/hosted_sites/paleonet/ftp/ftp.html). The analysis finds the vectors with the most comparable net angular change among all specimens, which is defined as eigenshape axis 1, and then proceeds in the same manner until all the shape covariation is analyzed (MacLeod, 1999). A 5% tolerance criterion was applied to the analysis, which reduced the number of data points from 200 points around the outline to 49 points. The first ten eigenshape axes (ES1–ES10) were examined, because they explain 99.08% of the shape variation (Table 2). After ES1 is removed, ES2-ES10 represents 87.06% of the remaining variance. The first axis represents the shape similarity among all the carapace shapes of all the specimens in the data set. Axes 2–10 represent a decreasing amount of variation among all the carapace shapes in the data set. Shape variation can be visualized along any axis in the morphospace by varying the amplitude of the eigenshape for that axis (a phi function) and averaging this with the phi function for the mean shape, a process termed "modeling" (Lohmann, 1983; MacLeod, 1999). The first ten axes were modeled using MacLeod's ESModel program (available for download at http://life.bio.sunysb.

TABLE 2. THE PERCENT VARIATION EXPLAINED BY EACH EIGENSHAPE AXIS

Eigenshape axis	Variation explained (%)	Cumulative variation (%)
ES1	(99.08)	—
ES2	33.47	33.47
ES3	19.02	52.49
ES4	12.50	64.99
ES5	5.87	70.86
ES6	5.11	75.97
ES7	4.02	79.99
ES8	2.72	82.71
ES9	2.39	85.10
ES10	1.96	87.06

edu/morph/), which generated three models corresponding to the maximum, mean, and minimum scores for each eigenshape axis. These shapes were then overlain and examined to look at carapace shape variation along each axis (Fig. 3).

Linear Measurements

Previous authors have determined the taxonomic identity of fossil spiders by using many different characters (Scudder, 1890; Petrunkevitch, 1922, 1958; Levi, 1980; Penney, 2000, 2002; Penney and Selden, 2002). In this study, we use linear characters in addition to the carapace shapes used in the outline analysis. In particular, we focus on linear leg measurements, or relative differences in the lengths and widths of legs I, II, III, and IV, as these characters are often diagnostic for spiders at the family level. For example, in the Araneidae and the Tetragnathidae (compared to the other six families used in the analysis), leg I is longer than leg II, which is longer than leg IV; leg III, in both families, is the shortest leg. And in the Tetragnathidae, leg I is considerably longer than leg II, whereas in the Araneidae it is only slightly longer (Levi, 2005a, 2005b). In the Salticidae, leg I or leg IV (depending on the species) is the longest leg (Richman et al., 2005). Finally, legs are often present on fossil spider specimens.

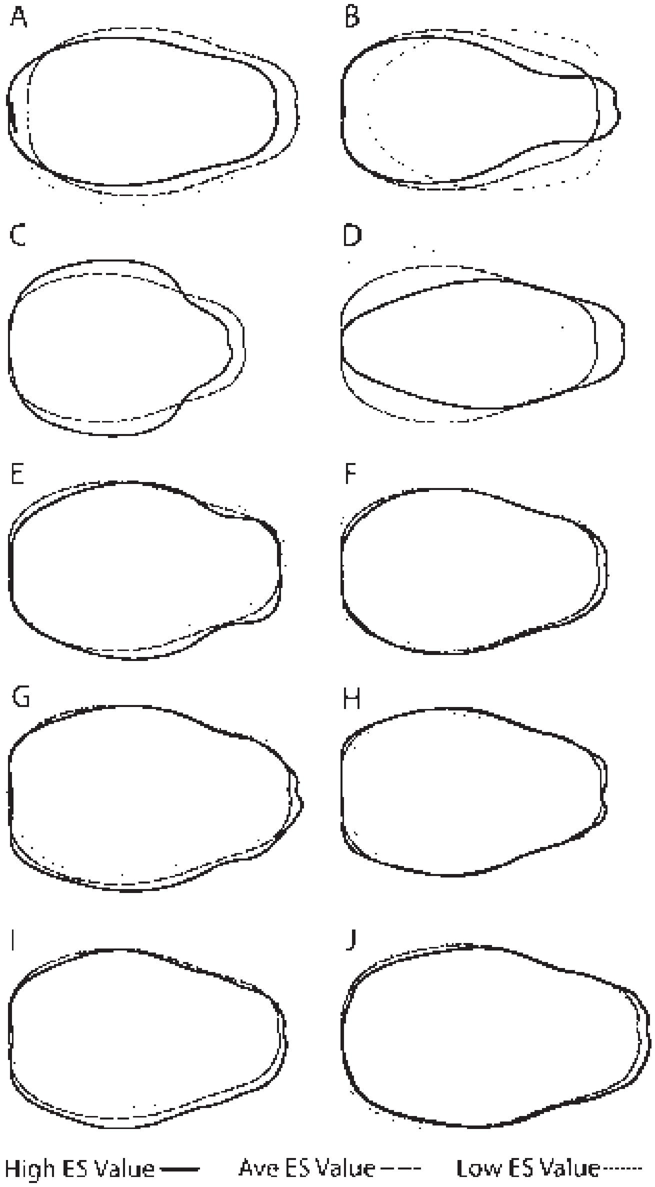

Figure 3. Modeled eigenshape axes 1–10. Each shape represents a dorsal view of the carapace. The lines represent the variability in carapace shapes most explained by that particular eigenshape axis. The left side of each axis is the distal end and the right side is the proximal end of the carapace. ES indicates the eigenshape axis being analyzed.

The first character that we used was the ratio of leg II length to leg III length (Fig. 2). This character should be helpful in separating the wandering spiders (Clubionidae, Lycosidae, and Salticidae) from the web-building spiders (Agelenidae, Araneidae, Dictynidae, Linyphiidae, and Tetragnathidae). Wandering spiders tend to have similar leg lengths, which aids in rapid movement on the ground. In contrast, web-building spiders tend to have legs of differing lengths to aid in web construction (Foelix, 1996). Ratios close to one would likely be a wandering spider and those ratios less than one would likely belong to a web-building spider family.

The width-to-length ratio of the femur of leg I was also used to further distinguish between spider families (Fig. 2), and several workers have argued that different families of spiders tend to have either long or short and either robust or thin first legs (Levi, 1980; Dondale and Redner, 1990; Foelix, 1996). For example, lycosids and agelenids have long robust legs I, whereas salticids and clubionids have short, robust legs I and lyniphiids have long, thin legs I. We also used the ratio of the femur width of leg I to the femur width of leg III. Leg thickness can vary across all the legs and change in thickness. For example, Araneidae tend to have much more robust femora on leg pairs I and II than on the other legs (Levi, 1980). The above characters were added because they were thought to be most useful in further defining family groups.

We recognize that there are likely to be exceptions to the general trends that we describe in the characters above. However, it is our belief that using a combination of such characters with the outline analysis will provide more useful results than using any single character on its own.

Statistical Analysis

A multivariate analysis of variance (MANOVA) test was performed to determine whether family designation was determined by carapace shape, carapace size, and the linear characters (SPSS 12.0, 2003). Because multiple comparisons are being made, a Bonferroni post hoc comparison test was used to examine the pairwise shape differences between the taxa.

A set of multiple discriminant analyses (MDA), with leave-one-out classification, were performed. We used leave-one-out classifications as means to test the quality of the modern data sets for prediction; leave-one-out classification removes one or more specimens from the initial analysis and treats the specimen(s) as "unknowns," which are then reprojected into the MDA and classified. This provides a way to perform a relatively conservative test of the efficiency of the MDA procedure. The first set of MDAs examined only modern spiders and the initial analysis used only eigenshape axes (ES1–ES10) to determine how well the carapace shape variation could differentiate families (SPSS 12.0, 2003). Linear characters and size were then sequentially added as independent variables to further differentiate the family groupings in additional MDA analyses.

Analysis of Fossil Specimens

After the MDAs based on the modern specimens were run, spider fossils from Florissant were examined. Seven of the eight families included in this analysis had been previously described from Florissant (all but Dictynidae) (Scudder, 1890; Petrunkevitch, 1922; Eskov and Zonshtein, 1990), and all of the families are known from deposits older than the Eocene, especially amber deposits (Petrunkevitch, 1958; Wunderlich, 1988; Selden, 1989; Penney, 2001, 2002; Penney and Selden, 2002; Selden 2002; Penney et al., 2003; Penney and Langan 2006; Penney and Ortuño, 2006).

The carapace shapes of the 43 fossil specimens were projected into the modern family shape space using Eigenshape Project (http://www.nhm.ac.uk/hosted_sites/paleonet/ftp/ftp.html), and another MDA using all the shape and size information (carapace shape/size and leg ratios) was run to make predictions concerning the family placement of the fossil specimens.

RESULTS

Shape Variations among Eigenshape Axes

The first ten axes were modeled to determine the carapace shape variation represented by each axis (Fig. 3). The mean shape of eigenshape axis 1 (ES1) represents the average shape of all spider specimens in the data set (Fig. 3A). This is a shape-similarity axis that represents all of the shape similarity. Wide carapace shapes score low on this axis. Carapace shapes that are narrower score high. The variation among families is slight, with the Dictynidae and Araneidae having the highest average scores, and the Agelenidae, Salticidae, and Linyphiidae having the lowest scores.

Eigenshape axis 2 (ES2) shows variation primarily along the anterior region of the carapace (Fig. 3B). Shapes that have little curvature along the posterior region and are narrow in the anterior region score high and include the Agelenidae and the Lycosidae. Shapes that have greater curvature along both the posterior and anterior regions score low and include the Salticidae. On Eigenshape axis 3 (ES3), carapace shapes that have a greater curvature in the posterior region while slighter in the anterior region score high, and carapace shapes that have a slighter curvature throughout the carapace score low (Fig. 3C). Families that score high include members of the Araneidae, whereas families that score low include Dictynidae, Clubionidae, and Salticidae.

Eigenshape axis 4 (ES4) represents the carapace curvature variation along the posterior region and the overall length (Fig. 3D). The carapace shapes that have little curvature score high and include members of the Linyphiidae, Agelenidae, and Lycosidae. Those carapace shapes that have a greater curvature in the posterior region score low and include Dictynidae, Araneidae, and Clubionidae.

Eigenshape axes 5–10 (ES5–ES10) represent variation along the lateral edge of the carapace shape (Fig. 3E–J). There is slight family-level variation along these axes. For example, on ES5 members of the Tetragnathidae score higher than all other families, whereas Linyphiidae score lowest (Fig. 3E). On ES6, members of the Dictynidae and Agelenidae score higher than all other families on this axis, and Araneidae and Clubionidae score lowest (Fig. 3F). Along ES7, members of the Dictynidae and Araneidae score high and Clubionidae score low (Fig. 3G). Along ES8, members of the Clubionidae and Dictynidae score high, and Agelenidae score low (Fig. 3H). On ES9, members of the Clubionidae score high and Araneidae and Salticidae score low (Fig. 3I), although it should be noted that family differences along this axis were not statistically significant. Finally, along ES10, members of the Tetragnathidae score high, and Salticidae score low (Fig. 3J).

Examining the Morphometric and Discriminant Analysis Tests

We found that family designation was defined by carapace shape (all axes but ES9), carapace size, leg length ratio of leg II to leg III, and the two femur ratios. The results of the MANOVA can be found in Table 3. The results of the MDA performed on the ten eigenshape axes and eight family groups are shown in Tables 4–8. Seven functions are given, which represent the variance of carapace shapes among all family groups. Only the first three functions will be reported, because they represent 87.06% of the variance (Table 2). In the first discriminant analysis, all eigenshape axes 1–10 were significant in their ability to distinguish family groupings (Function 1: Wilks' Lambda L = 0.12, $p < .0001$; Function 2: L = 0.309, $p < .0001$; Function 3: L = 0.494, $p < .0001$) (Table 5). However, the eigenshape axes were only able to place 41.6% of the modern spiders into the correct family (Table 6).

The second discriminant analysis, using the eigenshape axes, the leg length ratio, leg width ratios, and carapace size, also resulted in an ability to distinguish family groupings of the modern spiders based on all characters that was statistically significant (Function 1: Wilks. Lambda L = 0.015, $p < .0001$; Function 2: L = 0.055, $p < .0001$; Function 3: L = 0.166, $p < .0001$) (Table 7). The eigenshape axes, linear characters, and size accurately predicted the family membership of 70.3% of the modern spiders

TABLE 3. RESULTS OF MANOVA TEST WITH BONFERRONI CORRECTION

Dependent variable	Type III sum of squares	df	Mean Square	F	Signif.
Leg length II/III ratio	19.825	8	2.478	4.993	***
Femur width I/III ratio	4.802	8	0.600	21.503	***
Femur I W/L ratio	14352.799	8	1794.100	24.425	***
Size of carapace	5.226E+11n	8	6.53E+10	11.05	***
ES1	0.063	8	0.008	4.67	***
ES2	1.793	8	0.224	51.039	***
ES3	0.367	8	0.046	8.159	***
ES4	0.174	8	0.022	5.995	***
ES5	0.055	8	0.007	3.391	**
ES6	0.031	8	0.004	2.175	*
ES7	0.049	8	0.006	5.037	***
ES8	0.019	8	0.002	2.146	*
ES9	0.01	8	0.001	1.646	NS
ES10	0.02	8	0.002	3.975	***

Note: I, II, and III are leg numbers. W—width; L—Length; NS—not significant. * $p < .05$; ** $p < .001$; *** $p < .0001$. All variables are highly significant except for eigenshape axis 9.

TABLE 4. RESULTS OF MULTIPLE DISCRIMINANT ANALYSIS TEST INCLUDING ONLY THE MODERN SPECIMENS AS THE GROUPING VARIABLE AND ONLY EIGENSHAPE AXES 1–10 AS INDEPENDENT VARIABLES

Function	Eigenvalue	Percentage of variance	Cumulative percentage	Canonical correlation
1	1.567	52.6	52.6	0.781
2	0.600	20.1	72.7	0.612
3	0.449	15.1	87.8	0.557
4	0.235	7.9	95.7	0.436
5	0.083	2.8	98.5	0.277
6	0.040	1.3	99.9	0.196
7	0.004	0.1	100.0	0.065

TABLE 5. RESULTS OF STRENGTH TEST APPLIED TO THE MULTIPLE DISCRIMINANT ANALYSIS INCLUDING ONLY THE MODERN SPECIMENS AS THE GROUPING VARIABLES AND ONLY EIGENSHAPE AXES 1–10 AS INDEPENDENT VARIABLES

Test of function(s)	Wilks' Lambda	Chi-square	df	Signif.
1 through 7	0.120	406.631	70	***
2 through 7	0.309	225.644	54	***
3 through 7	0.494	135.444	40	***
4 through 7	0.716	64.264	28	***
5 through 7	0.884	23.688	18	NS
6 through 7	0.957	8.363	10	NS
7	0.996	0.822	4	NS

Note: NS—not significant. *** $p < .0001$. The results show that the first four functions are robust and highly significant.

TABLE 6. BOOT-STRAPPED PREDICTED GROUP MEASUREMENTS FOR THE EIGHT FAMILIES STUDIED

Family	Carapace only (%)	All characters (%)
Agelenidae	40.00	46.70
Araneidae	31.00	65.50
Clubionidae	41.70	66.70
Dictynidae	35.30	76.50
Linyphiidae	44.00	80.00
Lycosidae	17.40	39.10
Salticidae	85.30	91.20
Tetragnathidae	13.60	68.20
Mean	41.60	70.35

Note: Reported is the accuracy of the method for placing specimens in the correct family when using carapace shape data only and when using carapace shape in combination with all the remaining characters.

TABLE 7. THE RESULTS OF THE MULTIPLE DISCRIMINANT ANALYSIS TEST WITH ALL CHARACTERS

Function	Eigenvalue	Percentage of variance	Cumulative percentage	Canonical correlation
1	2.801	38.9	38.9	0.858
2	2.014	28.0	66.9	0.817
3	1.100	15.3	82.1	0.724
4	0.671	9.3	91.4	0.634
5	0.393	5.5	96.9	0.531
6	0.179	2.5	99.4	0.389
7	0.045	0.6	100.0	0.207

Note: The first three functions show significant eigenvalues over 1.

TABLE 8. RESULTS OF STRENGTH TEST APPLIED TO THE MULTIPLE DISCRIMINANT ANALYSIS WITH ALL CHARACTERS

Test of function(s)	Wilks' Lambda	Chi-square	df	Signif.
1 through 7	0.015	804.347	98	***
2 through 7	0.055	550.643	78	***
3 through 7	0.166	341.009	60	***
4 through 7	0.349	200.085	44	***
5 through 7	0.583	102.528	30	***
6 through 7	0.812	39.588	18	NS
7	0.957	8.337	8	NS

Note: NS—not significant. *** $p < .0001$. The results show that the first five functions are robust and highly significant.

sampled, and some groups in this analysis had very high rates of prediction when all the shape and size data sere used (Table 6). Tetragnathidae was most often confused with the Araneidae (3 of 15 spiders), Linyphiidae (2 of 15 spiders), and Dictynidae (2 of 15 spiders). The Clubionidae were also confused with the Linyphiidae (3 of 12 spiders), although when these two families are combined there is 75% accuracy between these two groups. Agelenidae were most often confused with Lycosidae (6 of 15 spiders) and Lycosidae was most often confused with Agelenidae (6 out of 23 spiders). Once combined, there is 78.2% accuracy for these two groups.

In the final discriminant analysis, fossils were placed into one of the eight families analyzed. There were no fossil spiders identified as Agelenidae. When specimens were identified as Salticidae, Linyphiidae, or Dictynidae there was a greater than 76.5% chance that these groupings were correct and that the specimens were placed into the appropriate family.

DISCUSSION

The goal of this study was to test a method that could be used with the types of characters that are typically preserved in the fossil record to identify spiders to the family level. By using a morphometric study of the carapace of extant spiders, subtleties of the shape could be analyzed and used to help identify modern spider families. Combining the morphometric analysis with linear leg measurements greatly improved the method. The results of this analysis provide a starting point for family-level identification of two-dimensional fossils. Even for families with low prediction rates, it is possible to assess whether the fossil may represent one of two or three families commonly confused in the analysis.

Character Combinations

The combination of carapace shape and the leg length ratio character helped to distinguish many of the families, especially between the major spider feeding guilds. These feeding guilds, the web-spinning spiders and the wandering spiders, have very different leg sizes depending on their feeding strategy (Chamberlin and Ivie, 1941; Levi, 1980, 1981, 1986). For example, many of the web builders like Agelenidae, Araneidae, and Tetragnathidae were separated from the wandering spiders like Lycosidae and Salticidae. Carapace shape further separated family members within each feeding guild. Subtleties in the shape that were likely to have remained unnoticed by casual observation became clear and usable through an outline morphometric approach.

Popular identification keys for spider families reflect unique character suites (Nentwig, 1993). Using a combination of outline and linear characters, represented by eigenshape axes and leg characteristics in this study, was found to be more useful than using any one of those characters alone. As a result, any character combination (carapace shape, size, and leg characters) gives a much higher prediction rate than do those characters analyzed separately. This character suite strengthens the overall prediction rate of each family, showing that the signals produced by each individual character increase the tendency for correct family placement.

Misidentified Families

Some of the spiders were consistently misplaced into a family. Among these were the Agelenidae, Clubionidae, and Lycosidae. However, when some of these families were grouped into combinations, the prediction rates increased. For example, when the Agelenidae and Lycosidae were combined, there was an 86.7% prediction rate that a fossil belonged to one of these two families. When Clubionidae was grouped with the Linyphiidae, the prediction rate jumped to 91.7%. The similarity in form of these families cannot be explained by phylogeny, because they are distantly related (Coddington and Levi, 1991).

Although the results do not attest to a complete success of the method, it is nevertheless useful in its capability to determine a specimen's identification to one of two groups, which is far superior to trying to rule out multiple groups. At the very least, for those taxa with low prediction rates, this method allows one to narrow the list of suspects and focus on specific characters.

Additions to Improve the Analysis

Although there was high overall accuracy for distinguishing family groupings, the potential accuracy was highly variable depending on the family. There are several ways the methods could be further improved to increase accuracy and make the model more useful to future researchers.

In addition to carapace shape, the carapace size was a useful character for identifying modern taxa. For example, Dictynidae and Linyphiidae tend to be composed of taxa that have relatively small bodies—most species are less than 4 mm as adults (although there are some genera with large body sizes worldwide that were not included in this analysis) (Chamberlin and Gertsch 1958). Because all the modern specimens used in the analysis were adult, this is a reliable character. However, size is not likely to be a character that is useful for the placement of fossil specimens. With fossil spiders, unless genitalia are preserved it can be difficult to determine whether a small spider is actually just a juvenile. Therefore, other morphological characters, in addition to size, must be included in an analysis to validate family placements for fossil specimens.

The inclusion of additional characters should also help better distinguish between family groups. We found that increasing the number of characters used in the analysis greatly increased the accuracy of family-level placement and we expect that improvements would continue with the addition of more characters. However, we realize that finding more characters that are consistently available on fossil specimens can be a challenge. In addition to the number of characters, expanding the number of families (and the representative genera within these families) to be included in the analysis should make the method much more applicable to a wider range of fossil deposits. The families used in this analysis were chosen because of their abundance in modern temperate lake environments. Other families common to lake environments and other climate regions should also be included, such as the Theridiidae, Thomisidae, and Philodromidae.

Fossil Family Placements

Every fossil spider was placed into a modern family, but the predicted accuracy of these placements was highly variable. Only ten of the previously identified specimens (42%) were placed in the family to which they had been assigned by the previous author. We believe that many of the identifications made by previous authors are, in fact, incorrect (Roberts 2004). However, we had greater confidence in our identification of fossil spiders when we placed them into families whose modern representatives had prediction rates of over 70%. Although nearly all of the spider families described from Florissant are extant, there is one specimen that has been attributed to the extinct family Parratidae. This specimen was not included in the present analyses because we focused on modern families. However, including this specimen in future morphometric analyses with a larger data set of extant families should yield interesting results. Given the modern composition of the Florissant spider assemblage and the large number of misidentifications made by previous workers, we would not be surprised to learn that the placement of this specimen within an extinct family is also erroneous.

Implications

Obtaining fossils that possess the characters needed for identification is often difficult. Some paleontologists believe that more fossils would be identifiable if better characters were available (Schopf et al., 1975; Schopf, 1981; Kowalewski et al., 1997). Workers interested in fossil spiders have had a difficult time understanding familial diversity and evolutionary rates because of the scarcity of characters preserved in shale (Eskov and Zonshtein, 1990; Coddington and Levi, 1991). It is, therefore, important to capture as much morphological information from a fossil as possible, as this increases the likelihood of a correct identification.

The scarcity of preservable characters has especially been a problem for identifying the fossil spiders of Florissant, and past researchers have painted a picture of spider diversity based on a much more limited data set. The use of this new methodology provides a view of the taxonomic diversity of spiders at Florissant that is dramatically different from previous interpretations. Morphometrics has allowed for the use of additional characters in making objective family placements. The results here suggest that we can make accurate predictions based on a combination of both non-traditional and traditional morphological characters that are commonly preserved in fossil shale deposits.

The methods used here are likely to be extendable to other arthropod groups. For example, insects are abundant in shale deposits and can be difficult to identify without adequate preservation of important characters (e.g., genitalia, color patterns). Diptera and many Hymenoptera, for example, can be identified to species by wing venation characters (Leach, 1815; Macquart, 1835; Newman, 1835) and wings are common in many fossil deposits (Scudder, 1890). Morphometric analysis allows shape characteristics to be quantified and has the potential to aid in identification. In short, this technique has great potential and appeal to any paleontologist in situations where character preservation among fossils is problematic.

Most importantly, approaches like the one detailed here move paleobiologists away from subjective identifications and toward more objective methods for taxonomic placement, and allow one to evaluate the uncertainty involved in such placements. Having some measure of accuracy when using morphology for the placement of modern families gives us the ability to assess the validity of our placements. This is a positive step toward recovering the baseline biodiversity information necessary for almost all paleobiological inferences.

APPENDIX. MODERN SPIDER SPECIES USED IN THE MORPHOMETRIC ANALYSES. NUMBER IN PARENTHESES INDICATES NUMBER OF SPECIMENS, IF MORE THAN ONE WAS USED FROM A PARTICULAR SPECIES

Family Agelenidae
Agelenopsis aperta
Agelenopsis emertoni
Agelenopsis naevia
Agelenopsis oklahoma
Agelenopsis pennsylvanica
Agelenopsis spatula
Agelenopsis utahana
Calilena arizonica
Hololena dana
Hololena hola
Hololena nevada
Hololena oquirrhensis
Tegenaria agrestis
Tegenaria domestica
Tegenaria duellica

Family Araneidae
Acanthepeira stellata
Aculepeira carbonaria
Aculepeira packardi
Araneus marmoreus
Araneus normandi
Araneus ocellatulus
Araneus pegina (2)
Araneus pratensis
Araniella cucurbitina (2)
Araniella displicata (2)
Araniella sp.
Argiope argentata
Argiope aurantia (2)
Mangora mobilis
Mangora passiva
Mangora placida
Mastophora bisaccata
Metepeira arizonica
Metepeira minima
Neoscona arabesca (2)
Neoscona crucifera
Neoscona domiciliorum
Verrucosa arenata
Zygiella x-notata

Family Clubionidae
Cheiracanthium inclusium
Cheiracanthium mildei
Clubiona abboti
Clubiona canadensis
Clubiona johnsoni
Clubiona kastoni
Clubiona kulczynskii
Clubiona maritima
Clubiona riparia
Clubiona sp.
Clubiona spiralis
Elaver exceptus

Family Dictynidae
Dictyna foliacea (2)
Dictyna idahoana
Dictyna longispina
Dictyna nebraska
Dictyna sancta
Dictyna terrestris
Dictyna tridentata
Dictyna volucripes
Emblyna borealis
Emblyna completa
Emblyna completoides
Emblyna palomara
Neoantistea agilis
Neoantistea crandalli
Neoantistea magna

Family Linyphiidae
Bathyphantes latescens
Ceratinopsis purpurea (2)
Collinsia holmgreni (2)
Eperigone contorta
Eperigone maculata (2)
Erigone acanthagnatha
Erigone aletris
Erigone atra
Erigone blaesa
Erigone dentigera (2)
Erigone ephala
Erigone psychrophila
Erigone sp. (2)
Frontinella huachuca
Frontinella pyramitela
Grammonota gentilis
Grammonota inusiata (2)
Grammonota trivittata
Helophora insignis (2)
Hilaira proletaria
Hilaira vexatrix (2)
Hypselistes florens
Linyphantes pualla (2)
Microlinyphia mandiblulata
Microlinyphia pusilla
Neriene clathrata (2)
Neriene variabilis (2)
Neoantistea oklahoma
Oedothorax trilobatus
Pityohyphantes brachygynus
Pityohyphantes costatus (2)
Pityohyphantes phrygianus (2)
Scotinotylus pallidus
Walckenaeira communis
Walckenaeria clavicornis
Walckenaeria directa
Walckenaeria karpinskii
Walckenaeria vigilax

Family Lycosidae
Arctosa alpigena
Arctosa littoralis
Arctosa virgo (2)
Geolycosa missouriensis
Geolycosa wrighti
Hogna antelucana (2)
Hogna coloradensis
Hogna sp. (2)
Pardosa lapidicina (2)
Pardosa mercarialis
Pardosa mulaiki
Pardosa ourayensis
Pardosa sternalis
Pirata insularis
Pirata minutus
Pirata piraticus
Pirata sedentarius (2)
Traebacosa marxi

Family Salticidae
Ghela canadensis
Habrocestum pulex (2)
Habronattus brunneus
Habronattus clypeatus
Habronattus venatoris
Habronattus viridipes
Marpissa lineate
Marpissa pikei
Metaphidippus iviei
Neon nelli
Peckhamia scorpionia
Pelegrina aeneola
Pelegrina flavipes
Pelegrina peckhamorem
Pelegrina proterva
Pellenes jucundus
Pellenes levii
Phidippus arizonensis
Phidippus borealis
Phidippus pulcher
Phidippus rimator
Phidippus whitmani
Phlegra fasciata
Platycryptus californicus
Platycryptus undatus
Salticus scenicus
Sassacus papenhoei
Sassacus vitis
Sitticus pubescens
Sitticus ranieri
Thiodina sylvana
Tutelina harti
Tutelina similis

Family Tetragnathidae
Glenognatha emertoni
Glenognatha foxi
Leucauge argyra (2)
Leucauge mandibulata (2)
Leucauge sp.
Leucauge venusta (2)
Metellina curtisi (2)
Nephila clavipes (2)
Pachygnatha autumnalis
Pachygnatha brevis
Pachygnatha tristriata
Pachygnatha xanthostoma
Tetragnatha elongata
Tetragnatha extensa
Tetragnatha laboriosa
Tetragnatha straminea
Tetragnatha versicolor

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The Chadronian mammalian fauna of the Florissant Formation, Florissant Fossil Beds National Monument, Colorado

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ABSTRACT

During the past five years, renewed prospecting and collecting of mammalian fossils in the Florissant Formation within Florissant Fossil Beds National Monument in central Colorado has nearly tripled the known diversity of fossil mammals from this rock unit. Taxa first recorded here from the Florissant Formation include the eomyid rodent *Paradjidaumo trilophus*, the lagomorph *Palaeolagus*, and the rare artiodactyl *Pseudoprotoceras longinaris*. We also describe an isolated deciduous premolar of a protoceratid. We update the mammalian faunal list of the Florissant Formation, which includes some 16 species in 13 families and 6 orders. The mammalian fauna corroborates the Chadronian (latest Eocene) age determined by others. Geographic ranges of *Pelycomys*, *Palaeolagus*, and *Paradjidaumo trilophus* are extended slightly southwest from northeastern Colorado, and the range of *Pseudoprotoceras longinaris* is extended southwest from Wyoming and Nebraska. Based upon comparison with nearest living relatives and plausible analogs, the mammalian taxa represented in the Florissant Formation seem to be consistent with the moist, warm temperate, relatively high elevation wetland and woodland habitats that have been inferred by others for the area in and around late Eocene Lake Florissant.

Keywords: Eocene, mammals, Florissant, Chadronian, Colorado.

INTRODUCTION

The Florissant Formation is a late Eocene series of lake shales, volcanics, and fluvial deposits exposed mostly within Florissant Fossil Beds National Monument in central Colorado (Fig. 1). The vertebrate fossil record dates back to Cope's discoveries in the 1870s (Cope, 1873, 1874, 1875, 1879) and is composed mainly of fish and a few birds preserved in the lacustrine shales, but fossil mammals have been rare discoveries.

Our discoveries in 2003–2005 within Florissant Fossil Beds National Monument nearly triple the known diversity of fossil mammals from the Florissant Formation. Before 2003, the known documented mammalian fauna from Florissant consisted of a single crushed partial opossum skeleton from the lake shales (Gazin,

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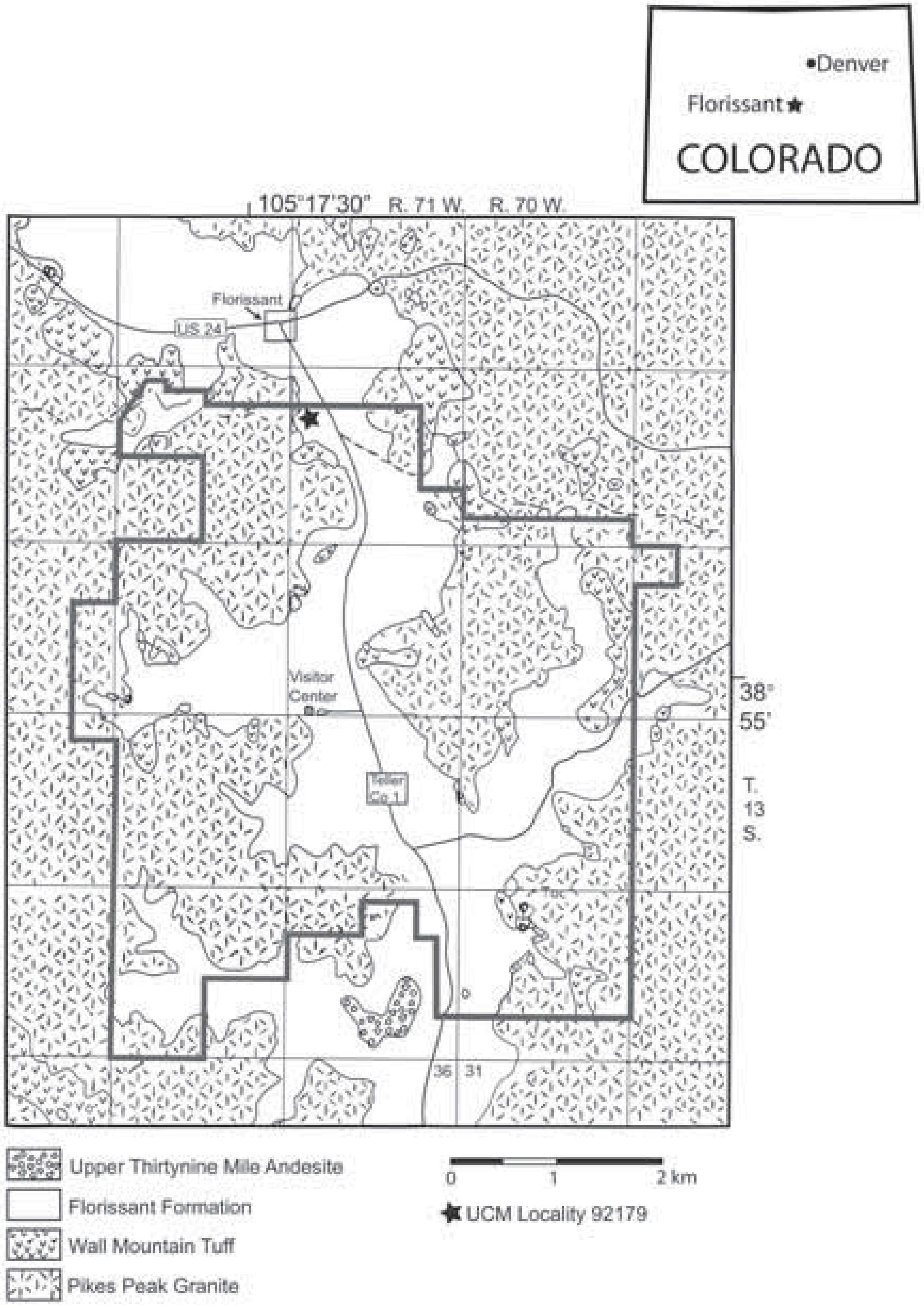

Figure 1. Geologic map of Florissant Fossil Beds National Monument, modified from Evanoff et al. (2001, Fig. 1). Areal extent of the monument is outlined by the thick gray line. Star indicates the location of UCM locality 92179 from which the specimens described here were recovered.

1935), and from the lower mudstone unit, fragmentary fossils of a merycoidodontid oreodont (MacGinitie, 1953), another small artiodactyl (?*Leptomeryx*), brontothere tooth enamel fragments, and a *Mesohippus* jaw. Additionally, a vertebral fragment of a large brontothere and other miscellaneous bone fragments were recovered from the arkosic conglomerate adjacent to the middle shale unit (Evanoff et al., 2001).

The first records at Florissant of the lipotyphlans *Centetodon* and *Domnina*, the lagomorph *Megalagus*, and the rodents *Pelycomys*, *Eutypomys*, *Ischyromys*, and *Adjidaumo* were discovered in 2003 and were described by Worley-Georg and Eberle (2006). We build upon that research by providing systematic description of several more members of the Florissant mammalian fauna, including the first records here of protoceratid artiodactyls and eomyine rodents. We conclude with an updated list of the Florissant mammalian fauna and a discussion of its biostratigraphic, biogeographic, and paleoecologic implications. Our faunal list should be considered a working list that will require periodic updating as we continue to sort the many kilograms of sedimentary matrix collected from the Florissant Formation and describe more members of the fauna.

GEOLOGIC AND BIOSTRATIGRAPHIC SETTING

First coined the Florissant Lake Beds by Cross (1894), the principal fossil-bearing strata in Florissant Fossil Beds National Monument, comprising lake shales, volcanic sediments, and fluvial deposits, were redefined as the Florissant Formation by Evanoff et al. (2001), who recognized six informal subdivisions. UCM localities 92179 (the most productive locality), 2004197, and 2005138 are at approximately the same stratigraphic level within the lower mudstone unit, just below the famous petrified forest area of the national monument and at the 29 m level of the stratigraphic section measured by Evanoff et al. (2001, Fig. 4). The lower mudstone unit occurs between the lower shale unit, which has produced most of the fish and bird fossils from the Florissant Formation, and the middle shale unit, where most of the famous plant and insect localities occur. The opossum skeleton initially described by Gazin (1935) is from the lake shales, although its exact locality is unknown. Whereas the shale units represent lacustrine environments, the lower mudstone unit is composed of stream deposits and, in its top few meters, a lahar deposit that buried the petrified forest (Evanoff et al., 2001).

The mammalian fauna of the Florissant Formation represents the Chadronian North American land mammal age (NALMA), which is defined by the first appearance of the oreodontid *Bathygenys*. Its termination (and onset of the next younger Orellan NALMA) is marked by appearance of the artiodactyl *Hypertragulus calcaratus* (Prothero and Emry, 2004 and references therein). The last appearance of the Brontotheriidae plays a secondary role in defining the Chadronian-Orellan boundary, which falls within magnetochron C13r. An ^{40}Ar/^{39}Ar date for a tuff near Douglas, Wyoming that approximates the Chadronian-Orellan boundary falls very close to the Eocene-Oligocene boundary of 33.7 Ma (Prothero and Swisher, 1992). The Chadronian is further subdivided into earliest Chadronian, late early Chadronian, middle Chadronian, and late Chadronian intervals (Prothero and Emry, 2004).

The ^{40}Ar/^{39}Ar analyses of sanidine crystals from four pumice samples in upper parts of the Florissant Formation ranging from 16 to 45 m stratigraphically above the mammal localities yielded a weighted mean age of 34.07 ± 0.10 Ma (Evanoff et al., 2001), which indicates a latest Eocene age, late in the Chadronian NALMA (Prothero and Emry, 2004). Paleomagnetic analyses place the Florissant Formation within Chron C13r (33.7–34.7 Ma; Prothero and Sanchez, 2004).

MATERIALS AND METHODS

Specimens described here were recovered as float from UCM locality 92179 within Florissant Fossil Beds National Monument during the summer of 2003 and fall of 2005. Nearby, and stratigraphically equivalent, fossil mammal localities include UCM locality 2004197, which produced a worn brontothere premolar (Worley-Georg and Eberle, 2006), and UCM locality 2005138 from which additional specimens of *Mesohippus* were collected. Detailed locality information is on file in the Paleontology Section at the University of Colorado Museum (UCM) and at Florissant Fossil Beds National Monument, Florissant, Colorado.

In 2003, the loose surface sediment at UCM 92179 was dry-screened from an area of ~13.5 m^2 and sorted on site (larger fraction) or at UCM. Approximately 2.5 cm below the surface, the mudstone is so well cemented that attempts to break down the rock with water were unsuccessful. However, the site remains productive, as a return visit in 2005 recovered more mammalian fossils.

Only mammalian teeth and jaws are included in this systematic study. However, several undiagnostic mammalian bone and tooth fragments were recovered, as were a limb bone and astragalus attributed to Perissodactyla and tentatively referred to *Mesohippus*. Notably, there have been no known discoveries of reptilians.

Identifications were made via comparison with specimens and casts at the University of Colorado Museum and the Royal Saskatchewan Museum, and with descriptions in the literature. Specimens were measured using a Spot camera attached to a microscope and calibrated Spot version 3.5.8 for Windows XP software. Cusp terminology for lagomorphs follows Dawson (1958), and terminology of protoceratid artiodactyl teeth follows Patton and Taylor (1973). Classification and cusp terminology for rodents follows Korth (1994). All other taxonomic classification follows McKenna and Bell (1997).

Specimens described here are dually catalogued in the Florissant Fossil Beds National Monument (FLFO) collection and UCM fossil vertebrate collection, and are deposited in the UCM collection. Several specimens were molded and cast in a UCM Paleontology Section lab, where the molds and original casts remain. A second set of casts is held at Florissant Fossil Beds National Monument.

Abbreviations

***Institutional abbreviations*—**FLFO, Florissant Fossil Beds National Monument, Florissant, Colorado; UCM, University of Colorado Museum, Boulder, Colorado; UW, University of Wyoming.

***Dental Terminology and Measurements*—**Lowercase letters (e.g., m1) designate teeth from lower jaws; uppercase letters (e.g., M1) designate teeth from upper jaws; L, left tooth (e.g., Lm1); R, right tooth (e.g., Rm1); M/m, molar; P/p, premolar, dP/dp, deciduous premolar; A-P length, anteroposterior length; AntW, anterior width; PostW, posterior width.

SYSTEMATIC PALEONTOLOGY

Order RODENTIA Bowdich, 1821
Family EOMYIDAE Depéret and Douxami, 1902
Genus PARADJIDAUMO Burke, 1934
PARADJIDAUMO TRILOPHUS (Cope, 1873) Wood, 1937
Figure 2A, Table 1

Gymnoptychus nasutus Cope, 1873 (in part)
Gymnoptychus trilophus Cope, 1873
Adjidaumo trilophus (Cope) Hay, 1899
Adjidaumo nasutus (Cope) Hay, 1899
Eumys minor Douglass, 1902
Gymnoptychus minor (Douglass) Matthew, 1903
Gymnoptychus liolophus Matthew, 1903
Adjidaumo minor (Douglass) Hay, 1930
Paradjidaumo minor (Douglass), Burke, 1934
Paradjidaumo nasutus (Cope) Burke, 1934
Paradjidaumo trilophus (Cope) Wood, 1937

Referred Specimen—FLFO 5976 (UCM 99590), dentary fragment with right p4–m1 from UCM locality 92179, Florissant Formation, Florissant Fossil Beds National Monument, Florissant, Colorado (Chadronian).

Known Occurrences—Renova Formation, Pipestone Springs, Montana; Yoder Member of the Chadron Formation, Wyoming; Toston Formation, Montana (all Chadronian); Cedar Creek Member, White River Formation, Colorado; Orella Member, Brule Formation, Nebraska; Scenic Member, Brule Formation, South Dakota; Toston Formation, Montana (all Orellan).

Description and Discussion—FLFO 5976 (UCM 99590), a right dentary fragment with worn p4–m1, is most similar in size and morphology to *Paradjidaumo trilophus.*

The p4 of FLFO 5976 (UCM 99590) has two distinct, closely appressed anterior cusps joined by a small anterior cingulid, characteristic of *P. trilophus* but contrasting *P. hansonorum*, which lacks the anterior cingulid (Russell, 1972). At its buccal margin, the ectolophid joins the proto- and hypoconids. About halfway along the ectolophid, the mesolophid extends toward the lingual margin of the tooth. The posterolophid extends toward the entoconid, and the hypolophid passes from the entoconid to about the midpoint of the posterolophid, as in *Paradjidaumo trilophus* (Black, 1965).

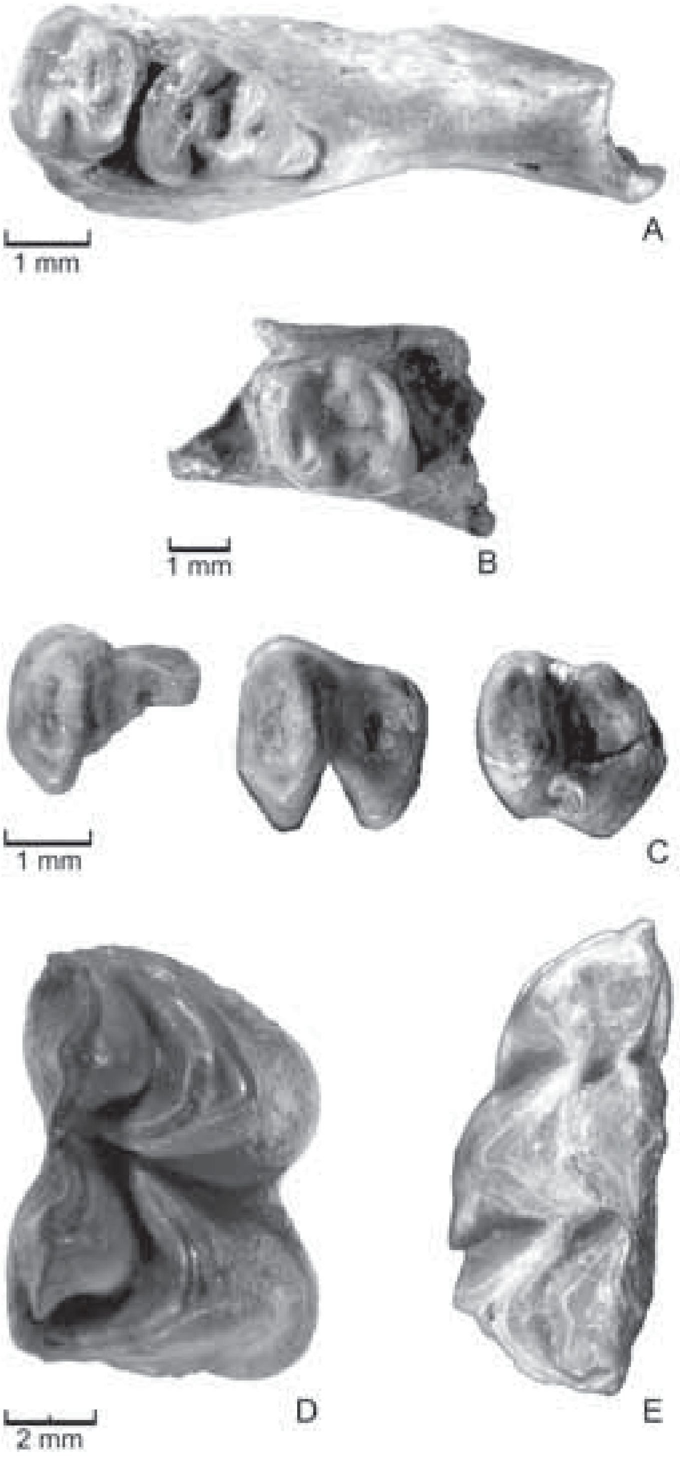

Figure 2. Dental material of mammalian specimens described here from UCM 92179 in the Florissant Formation. (A) *Paradjidaumo trilophus*, UCM 99590, right dentary fragment with p4–m1. (B) *Pelycomys* sp., UCM 99575, Lm2. (C) *Palaeolagus* sp., UCM 99576, associated left p4–m2. (D) *Pseudoprotoceras longinaris*, FLFO 5809 (UCM 99565), probable right m2. (E) Protoceratidae, gen. et sp. indet., UCM 99581, left dp4. (D and E have the same scale.)

TABLE 1. MEASUREMENTS (IN MM) OF UCM 99590, LOWER RIGHT P4 AND M1 OF *PARADJIDAUMO TRILOPHUS* FROM UCM LOCALITY 92179 IN THE FLORISSANT FORMATION

Tooth	A-P Length	AntW	PostW
p4	1.74	1.28	1.66
m1	1.51	1.50	1.75

Note: A-P—anterior-posterior; Ant—anterior; Post—posterior, W—width.

The m1 on FLFO 5976 (UCM 99590) is worn, and its anterior cingulid is broken. Its trigonid is higher and narrower than its talonid, as in *Paradjidaumo trilophus* (Russell, 1972). The mesolophid is long and joins with the entoconid, and the hypolophid has been worn away. In unworn molars of *Paradjidaumo* (Wood, 1980), a basic three-lobed, "omega" pattern is formed from the metalophid and mesolophid. Although there is considerable intraspecific size variation (Korth, 1980), m1 of FLFO 5976 (UCM 99590) falls at the high end of ranges of *Paradjidaumo trilophus* published by Black (1965, p. 30).

Occurrence of *Paradjidaumo trilophus* in the Florissant Formation represents a geographic range expansion southwestward from northeastern Colorado.

Family APLODONTIDAE Trouessart, 1897

Subfamily PROSCIURINAE Wilson, 1949

PELYCOMYS Galbreath, 1953

Pelycomys sp.

Figure 2B, Table 2

Referred Specimens—FLFO 5977 (UCM 99575), Lm2, and FLFO 5814 (UCM 99561), Lm2, both from UCM locality 92179, Florissant Formation, Florissant Fossil Beds National Monument, Florissant, Colorado (Chadronian).

Description and Discussion—FLFO 5977 (UCM 99575), a mildly worn left m2, exhibits diagnostic characters of *Pelycomys.* As in *Pelycomys brulanus* (Korth, 1986), the metalophulid II is complete and lower than the anterior cingulid; the hypolophid is complete and connected to the entoconid; there is a well-defined mesostylid and a relatively wide trigonid basin; and the hypoconulid is lacking. As in both *P. brulanus* (Korth, 1986) and *P. placidus* (Galbreath, 1953), FLFO 5977 (UCM 99575), bears a large mesoconid and hypoconid. A small swelling occurs on the anterior cingulid, as in *P. brulanus,* but is absent in *P. placidus* and *P.* cf. *P. brulanus* reported by Korth (1986).

FLFO 5814 (UCM 99561), a left m2 initially referred to *Pelycomys* sp. A by Worley-Georg and Eberle (2006), is similar in size and morphology to FLFO 5977 (UCM 99575). The Florissant specimens are not as wide as m2s of *P. brulanus* and *P. placidus*. In fact, they are longer than they are wide, in contrast to these Orellan species of *Pelycomys*, which typically have molars that are wider than they are long (Korth, 1986, 1989).

The only documented Chadronian species of *Pelycomys* is *P. rugosus,* whose m2s are at least 25% larger than the Florissant specimens, have a more rugose enamel, and lack a mesoconid (Galbreath, 1953). However, as in the Florissant specimens, m2s of *P. rugosus* are relatively narrow, and their length is greater than their width (Galbreath, 1953, Table 7).

The Florissant specimens share characters with both Chadronian and Orellan species of *Pelycomys* and this makes species-level identification level difficult. Given their overall similarity to *P. brulanus*, they may represent an early variant of this species.

TABLE 2. MEASUREMENTS (IN MM) OF LOWER MOLARS OF *PELYCOMYS* SP. FROM UCM LOCALITY 92179 IN THE FLORISSANT FORMATION

Specimen	Tooth	A-P Length	AntW	PostW
UCM 99575	Lm2	2.52	2.19	2.27
FLFO 5814	Lm2	2.37	2.28	2.32

Note: Abbreviations as in Table 1.

Order LAGOMORPHA Brandt, 1855

Family LEPORIDAE Gray, 1821

Genus PALAEOLAGUS Leidy, 1856

Palaeolagus sp.

Figure 2C, Table 3

Referred Specimen—FLFO 5973 (UCM 99576), associated left p4–m2 with dentary fragment, from UCM locality 92179, Florissant Formation, Florissant Fossil Beds National Monument, Florissant, Colorado (Chadronian).

Description and Discussion—FLFO 5973 (UCM 99576), left p4–m2 with an associated dentary fragment, is most similar in size and morphology to *Palaeolagus* from the White River Formation. The p4 has two columns, although the posterior column has been broken and the talonid basin is missing. The m1 and m2 also have two columns that are separated by a thin layer of cement. Isolated lakes indicate that the teeth belonged to an older individual. As in *Palaeolagus* (Dawson, 1958), the trigonid is united to the talonid by a lingual bridge of enamel and dentine.

Characters used to differentiate species of *Palaeolagus* are present in the lower third premolar (Dawson, 1958), which is not present in the specimen described here. As such, FLFO 5973 (UCM 99576) cannot be assigned to a species. FLFO 5973 (UCM 99576) is ~40% smaller than *Megalagus brachyodon* (Wood, 1940), also known from the Florissant Formation (Worley-Georg and Eberle, 2006). FLFO 5973 (UCM 99576) represents the first occurrence of *Palaeolagus* in the Florissant Formation and extends the geographic range of the genus southwestward from northeastern Colorado.

TABLE 3. MEASUREMENTS (IN MM) OF UCM 99576, LOWER MOLARS OF *PALAEOLAGUS* SP. FROM UCM LOCALITY 92179 IN THE FLORISSANT FORMATION

Tooth	A-P Length	AntW	PostW
m1	2.38	2.17	1.91
m2	2.24	1.92	1.98

Note: Abbreviations as in Table 1.

Order ARTIODACTYLA Owen, 1848
Suborder TYLOPODA Illiger, 1811
Family PROTOCERATIDAE Marsh, 1891
Genus *PSEUDOPROTOCERAS* Cook, 1934
PSEUDOPROTOCERAS LONGINARIS Cook, 1934
Figure 2D

Pseudoprotoceras longinaris, Cook, 1934, page 149

Referred Specimen—FLFO 5809 (UCM 99565), probable Rm2 from UCM locality 92179, Florissant Formation, Florissant Fossil Beds National Monument, Florissant, Colorado (Chadronian).

Known Occurrences—White River Formation, Flagstaff Rim, Wyoming; Yoder Member of the Chadron Formation, Wyoming; Chadron Formation, Nebraska (all Chadronian).

Description and Discussion—FLFO 5809 (UCM 99565) is morphologically most similar to m2s of *Pseudoprotoceras.* The anterior arm of the hypoconid is slightly deflected by the posterior arm of the protoconid and terminates before making contact with the entoconid. This contrasts with molars of the Camelidae, in which the anterior arm of the hypoconid extends inward to join with the anterior end of the entoconid, and the posterior end of the protoconid unites with the posterior end of the metaconid (Honey, 2004). On FLFO 5809 (UCM 99565), anterior and posterior cingulids are strong, but there is no buccal cingulid. Two low cuspules, equivalent to the "accessory column" of Emry and Storer (1981), occur in the buccal valley between the proto- and hypoconids. According to Emry and Storer (1981), this feature is usually present on m1 but absent on m2 and m3 of *Pseudoprotoceras*, although there is considerable intraspecific variation. Ribs are present on the lingual margin of the meta- and entoconids, and a distinct entostylid occurs. The posterior arm of the metaconid overlaps with the anterior arm of the entoconid and the lingual wall forms a *V* between the two cusps, contrasting with primitive camelid molars, whose lingual cusps do not overlap and have a relatively flat lingual wall (Honey, 2004). The posterior arm of the hypoconid is strong and terminates behind the entoconid, resulting in the appearance of a slight bulge, as in *Leptotragulus* (Black, 1978).

Species of *Pseudoprotoceras* are differentiated from one another primarily by size (Emry and Storer, 1981). The anteroposterior length and transverse width of FLFO 5809 (UCM 99565) are, respectively, 9.62 mm and 7.13 mm, and the tooth is ~20% smaller than early Chadronian *Pseudoprotoceras semicinctus* and late Chadronian *P. taylori* (Emry and Storer, 1981), but 26%–40% larger than morphologically similar *Leptotragulus* (Black, 1978). Although lower molars of *P. longinaris* are sparsely documented, FLFO 5809 (UCM 99565) is only ~3% longer than the largest m2s of *P. longinaris* reported by Kihm (1987) from the Yoder Member of the Chadron Formation.

Pseudoprotoceras is common throughout the Chadronian of the Great Plains (Emry and Storer, 1981), and is known from Duchesnean strata of Saskatchewan (Storer, 1996). *Pseudoprotoceras longinaris* made its first appearance during the middle Chadronian and survived into late Chadronian time (Prothero, 1998; Prothero and Emry, 2004). Its occurrence in the Florissant Formation represents a geographic range expansion southwestward into the central upland of Colorado.

Protoceratidae, gen. et sp. indet.
Figure 2E

Referred Specimen—FLFO 5975 (UCM 99581), left dp4 from UCM locality 92179, Florissant Formation, Florissant Fossil Beds National Monument, Florissant, Colorado (Chadronian).

Description and Discussion—FLFO 5975 (UCM 99581), a nearly complete left dp4, is a molarized three-lobed tooth similar in morphology to dp4s of *Pseudoprotoceras semicinctus* figured by Emry and Storer (1981) and *Leptotragulus* (i.e., UW 11325). As in protoceratid dp4s, FLFO 5975 (UCM 99581) tapers anteriorly, its anterior lobe bears subequal lingual and buccal cusps, and the anterior buccal cingulid is narrow.

FLFO 5975 (UCM 99581) has an anteroposterior length of 10.44 mm, which is ~25% smaller than the dp4 of *P. semicinctus* and ~5% smaller than the dp4 of *Leptotragulus.* Because of incompleteness, the transverse width was not measured.

On FLFO 5975 (UCM 99581), the enamel is missing from the cusp apices, and irregular pits expose the dentine along the lingual side of the tooth. The pattern of enamel loss may have more than one cause, including abrasion through transport, which affects the topographically highest points on the tooth (i.e., cusps), and decalcification by plant acids, which manifests as shallow grooves and irregular pitting (Fisher, 1981b). What appears to be ruled out is digestion by crocodilians, which results in completely enamel-less teeth (Fisher, 1981a), and by mammalian carnivores, which generally defecate (or, in some species, regurgitate) seemingly unaltered teeth and bones (Fisher, 1981b). Notably, neither crocodilians nor mammalian carnivores are documented from the Florissant Formation.

FLFO 5975 (UCM 99581) may belong to *Pseudoprotoceras longinaris,* also known from the same locality. However, given its incompleteness and the fact that dp4s of the Protoceratidae are not diagnostic at the species level, we simply assign it to this family. Protoceratids are common throughout the Chadronian in the Great Plains region of North America, although this specimen represents only the second occurrence of the family in the Florissant Formation.

DISCUSSION

Biostratigraphy and Biogeography

The mammalian fauna from the Florissant Formation (Table 4) corroborates the Chadronian or latest Eocene age for the Florissant Formation that has been suggested by others. *Paradjidaumo trilophus*, *Adjidaumo minimus* (Emry, 1992), *Pelycomys* (McKenna and Bell, 1997), *Ischyromys typus* (Heaton, 1996), and *Palaeolagus* (Dawson, 1958) made their first appearance in the Chadronian, whereas the brontothere *Megacerops* became extinct at the end of the Chadronian (Prothero and Emry, 2004). Restricted to the Chadronian are *Eutypomys parvus* (Storer, 1996; Tabrum et al.,

TABLE 4. MAMMALIAN FAUNAL LIST FROM THE FLORISSANT FORMATION

Cohort Marsupialia		
	Order Didelphimorpha	
		Nanodelphys cf. *N. hunti*
Cohort Placentalia		
	Order Lipotyphla	
		Centetodon magnus
		Domnina sp. cf. *D. thompsoni*
	Order Rodentia	
		Pelycomys sp.
		Eutypomys parvus
		Ischyromys (Ischyromys) sp. cf. *I. typus*
		Ischyromys (Titanotheriomys) sp. cf. *I. douglassi*
		Adjidaumo minimus
		Paradjidaumo trilophus
	Order Lagomorpha	
		Megalagus brachyodon
		Palaeolagus sp.
	Order Artiodactyla	
		Leptomeryx sp.
		Pseudoprotoceras longinaris
		Protoceratidae, gen. et sp. indet.
		Oreodontidae gen. et sp. indet.
	Order Perissodactyla	
		Mesohippus sp.
		Megacerops sp.

Note: Higher taxon classification follows McKenna and Bell (1997). Data compiled from Worley-Georg and Eberle (2006), Gazin (1935), MacGinitie (1953), and this report.

1996), *Ischyromys douglassi* (Black, 1968; Heaton 1996; Tabrum et al. 1996), *Domnina thompsoni* (Tabrum et al., 1996), *Megalagus brachyodon* (Emry et al., 1987; Wood et al., 1941), and *Pseudoprotoceras longinaris* (Emry and Storer, 1981). Occurrence of *M. brachyodon* and *P. longinaris* in the Florissant fauna suggests an age no older than middle Chadronian (Prothero and Emry, 2004), which is consistent with the late Chadronian age proposed by Evanoff et al. (2001) on the basis of an ^{40}Ar/^{39}Ar weighted mean age of 34.07 + 0.10 Ma for pumice samples from upper parts of the Florissant Formation.

In addition to those reported by Worley-Georg and Eberle (2006), the taxa described above represent geographic range extensions. Ranges of *Pelycomys*, *Palaeolagus*, and *Paradjidaumo trilophus* are extended slightly southwest from northeastern Colorado, and the range of *Pseudoprotoceras longinaris* is extended southwest from Wyoming and Nebraska. As in the fossil flora from Florissant (see Becker, 1961), the mammalian fauna shows greater taxonomic affinity to more northern Chadronian faunas, particularly western Montana and Nebraska, than to coeval faunas to the south (Worley-Georg and Eberle, 2006).

Paleoecology

Although recent paleoelevation estimates of Florissant vary considerably (and are controversial), many indicate that this region was at quite high elevation during late Eocene time, ranging from 1900 m to more than 4100 m (see summary in Meyer, 2001). Leaf physiognomy and evidence of nearest living relatives suggest that late Eocene Florissant probably experienced a seasonally equable, moderately moist, warm temperate climate with a distinct dry season; estimates of mean annual temperature range from 11 to 18 °C. Lush forests grew alongside Lake Florissant, while woodlands and scrublands dominated by genera of *Pinus* (pine), *Quercus* (oak), *Vauquelinia* (rosewood), and *Cercocarpus* (mahogany) covered the hills and ridges surrounding the lake basin (MacGinitie 1953: Meyer, 2003 and references therein). Although it should be used with caution, comparison with nearest living relatives is a preliminary means of inferring how and where some of the mammals may have fit into the late Eocene Florissant ecosystem. However, it should be noted that some taxa, such as the extinct eomyid rodents, occupied a number of niches (Korth, 2006, personal commun.), and consequently cannot be used effectively in paleoenvironmental reconstruction. We discuss some living relatives and plausible analogs of Florissant taxa below.

A plausible extant analog to *Pelycomys* from Florissant may be *Aplodontia rufa* (mountain beaver), the only living aplodontid rodent. Among the most primitive living rodents, *A. rufa* is a small, herbivorous burrower adapted to cool, moist habitats of broad-leaved deciduous and coniferous forests in the high montane regions along the west coast of North America (Macdonald, 1987), an environment not unlike Eocene Florissant.

Palaeolagus and *Megalagus* are extinct members of the Leporidae, which today includes some 44 species of rabbits and hares and has nearly worldwide distribution. Leporids occupy a variety of habitats, including montane shrublands, woodlands, riparian lands, and semi-desert shrublands, and are generalized herbivores. Most of today's rabbits are burrowers (Macdonald, 1987).

Mesohippus was a medium-sized (~60 cm high at the shoulder), functionally tridactyl horse that ranged throughout western North America in late Eocene–Oligocene time (MacFadden, 1998). *Mesohippus* is hypothesized to have been a generalized herbivore, having a mixed diet of browse and grass, similar to today's elk (MacFadden, 2004).

Considered close relatives of camels within the Suborder Tylopoda (Prothero and Schoch, 2002), the Protoceratidae were relatively rare members of Chadronian faunas of western North America. *Pseudoprotoceras* was a small, hornless, browsing artiodactyl that inhabited a mixed environment of forest and grassland (Prothero, 1998). Because of their retracted nasal bones, Janis (1982) suggested that protoceratids had a broad, mooselike snout adapted to feeding on soft, semiaquatic vegetation. Today's tylopods include camels, vicuña, llama, alpaca, and the guanaco. With the exception of camels, they are naturally restricted to South American montane regions and upland plateau, browsing and grazing on low grass (Macdonald, 1987).

Judging from our comparisons, some of the mammalian taxa represented in the Florissant Formation seem consistent with paleobotany-based interpretations of moist, warm temperate, montane wetland and woodland habitats for the area in and around Lake Florissant during late Eocene time. Continued recovery of vertebrate fossils from the Florissant Formation as well as stable isotope analyses of mammalian tooth enamel (in progress; see Barton and Fricke, 2006) should provide further insight into the latest Eocene climate and ecology of Florissant.

SUMMARY AND FUTURE RESEARCH

Our discovery of a Chadronian mammalian fauna in the Florissant Formation provides a more vivid picture of the ancient Lake Florissant ecosystem that to date has been inferred largely from its abundant plant and insect fossils. From a broader perspective, the mammalian fauna, combined with ^{40}Ar/^{39}Ar ages (Evanoff et al., 2001) and paleomagnetic analyses (Prothero and Sanchez, 2004), affords high-resolution dating of the Florissant Formation and correlation of the Florissant Formation to other regions of North America. That the mammalian fauna appears comparable to Chadronian faunas of Montana, Nebraska, Wyoming, Saskatchewan, and northeastern Colorado corroborates paleobotanical evidence for a northern biotic province during late Eocene time (Worley-Georg and Eberle, 2006). However, as a cautionary note, our interpretations are preliminary in that they are based on a relatively small number of diagnostic specimens (~40) predominantly from one locality in the Florissant Formation, whereas other documented Chadronian faunal assemblages comprise hundreds (e.g., Texas; see Wilson, 1986) and thousands (e.g., Montana; Tabrum et al., 1996) of specimens. Consequently, a high research priority is simply recovery of more mammalian fossils from the Florissant Formation, which would refine correlation to other North American localities and allow us to test more adequately hypotheses concerning late Eocene North American mammalian biogeography.

Strata in the nearby, correlative Antero Formation (in the South Park Basin west of Florissant) and small patches of White River Formation to the north in the North Park Basin are largely unexplored by paleontologists, despite preliminary discoveries of Chadronian mammals in these units (e.g., McGrew, 1953). A thorough paleontologic investigation of the Florissant Formation and these nearby correlatives would go a long way toward understanding late Eocene faunas and environments of upland Colorado.

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Mineralogy and geochemistry of late Eocene silicified wood from Florissant Fossil Beds National Monument, Colorado

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ABSTRACT

Silicified stumps preserved within a late Eocene lahar deposit have diverse mineralogy, ranging from opal-CT to chalcedony. In specimens that contain both silica polymorphs, the minerals appear to have originated independently, rather than from diagenetic transformation of an opaline parent material. This petrifaction process is unlike the progressive transformation of opal-A→opal-CT→chalcedony that has long been accepted as a general model for wood silicification. At the Florissant fossil forest, petrifaction occurred in several stages, beginning with precipitation of amorphous silica on cell wall surfaces. Cell lumina later became filled with opal-CT and chalcedony. A final phase of silica deposition is evidenced by chalcedony-filled fractures that crosscut permineralized tissues in some specimens. Spaces between adjacent tracheids commonly remain unmineralized, causing the silicified wood to remain permeable to water, and to readily cleave radially and tangentially. To a lesser degree, the fossilized wood is subject to transverse fracturing. This combination of structural characteristics causes Florissant fossil stumps to be susceptible to damage from freeze-thaw weathering.

Keywords: chalcedony, opal-A, opal-CT, petrified wood, silicification.

INTRODUCTION

The late Eocene Florissant Formation provides a notable example of an ancient depositional environment that preserved an assemblage of fossilized stumps and logs. Located within a single 5-m-thick volcaniclastic debris flow, these silicified trunks range in diameter from 0.5 to 4 m, with heights of 1–4 m. Although petrified forests are known throughout the world (Dernbach, 1996; Daniels and Dayvault, 2006), decades of careful paleontologic research combined with the well-defined stratigraphic and geologic characteristics of the deposit make the Florissant fossil forest an invaluable site for studying the petrifaction processes. The 70-m-thick Florissant Formation is composed of tuffaceous lacustrine, fluvial, and lahar sediments that were deposited in a paleovalley on the high-elevation, low- to moderate-relief erosion surface of central Colorado, during the late Eocene (Gregory and Chase, 1994; Evanoff et al., 2001). A detailed stratigraphic column was published by Evanoff et al. (2001) and reproduced with minor alterations by Gregory-Wodzicki (2001) and Meyer (2003). Single crystal laser-fusion ^{40}Ar/^{39}Ar analyses of sanidine crystals from pumice near the top of the formation yielded a mean age of 34.07 ± 0.10 Ma (Evanoff et al., 2001).

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Compressed remains of plants, insects, and fish in thinly bedded lacustrine shales of the Florissant Formation have received considerable attention from researchers (see bibliography in Meyer, 2003). Although the fossil forest began attracting tourists in the 1860s, many decades passed before the silicified stumps were studied by paleontologists. Andrews (1936) described *Sequoia*-like wood that he named *Sequoioxylon pearsalii*, now known to be the most common taxon in the fossil forest. Evanoff (cited in Gregory-Wodzicki, 2001) mapped 31 fossil stumps, of which 91% were vertical, leading him to conclude that the fossils represent a single forest that was buried in situ. Gregory-Wodzicki (2001) speculated that the trees died because the mudflow prevented oxygen from reaching their roots. Portions of the trunks exposed above the level of the mudflow were susceptible to rapid decay. Wheeler (2001) described five dicot wood types, and Gregory-Wodzicki (2001) investigated ring width and variability in 28 *Sequoioxylon* stumps to cross-date the trees and to evaluate paleoclimatic conditions.

My investigations focused on the mineralogic and geochemical characteristics of an assemblage of specimens chosen by National Park Service personnel as being representative of various types of fossil wood preserved at Florissant Fossil Beds National Monument. These samples include material from some of the best-known specimens exposed near the visitor center. Analytical data obtained from these fossils are important for several reasons. Determining the mineralogy, chemical composition, and microscopic characteristics of Florissant fossil wood is an important step for increasing our understanding of how wood becomes petrified. In particular, the discovery that some of the silicified wood specimens contain both opal-CT and chalcedony provides new insights into the petrifaction process, hinting that silicification may proceed along more than one geochemical pathway. In addition, understanding the mineralogic composition and physical properties of silicified wood is essential for developing effective strategies for protecting the fossil stumps from weathering, a major conservation challenge facing the personnel responsible for conserving this magnificent fossil forest.

WOOD SILICIFICATION: AN OVERVIEW

Petrified wood is abundant in the fossil record, and a multitude of researchers have described taxonomic and paleoenvironmental aspects of fossil forests. In contrast, the subject of how wood becomes petrified has received much less attention. Indeed, the most comprehensive studies date back more than two decades (e.g., Murata, 1940; Buurman, 1972; Mitchell and Tufts, 1973; Leo and Barghoorn, 1976; Stein, 1982; Scurfield and Segnit, 1984). Although new data continue to be added, the basic hypotheses regarding the petrifaction process have largely remained unchanged. As discussed later in this report, new evidence from Florissant fossils challenges some of these long-held ideas.

Two mechanisms have been proposed to explain how wood becomes petrified. *Replacement* describes precipitation of minerals in spaces formerly occupied by organic matter (Correns, 1950). *Permineralization* results when cell material remains at least partially intact and open spaces become filled with minerals. In support of the latter hypothesis, Schopf (1971) noted that the success of the acetate peel method is clear evidence that intact cellular tissues are sometimes preserved. However, St. John (1927) noted that when 25 petrified wood specimens from a variety of localities were treated with hydrofluoric acid, some samples contained no visible traces of plant tissue, whereas other specimens preserved detailed cell structures—evidence that wood petrifaction may result from replacement, permineralization, or a combination of the two processes.

The most-studied aspect of wood petrifaction has been the initial infiltration of dissolved silica into plant cells. Schopf (1971) suggested that silica is precipitated from groundwater as a replacement for water molecules in the cell walls, a process that entombs organic matter. The most widely accepted hypotheses is that of Leo and Barghoorn (1976), who postulated that silicification occurs because the original organic materials have an affinity for dissolved silicic acid molecules, causing petrifaction to begin with the accumulation of amorphous silica as a film on cell walls. Porous silica preserves the cell morphology, while allowing organic matter to degrade slowly. This organic templating process has been confirmed in subsequent studies (e.g., Karowe and Jefferson, 1987; Wang et al., 2001). In a general sense, the process can be thought of as “replacement,” because as minerals are precipitated, organic components are simultaneously lost through microbial or chemical attack. However, on a cellular level the templating process does not involve a molecule-by-molecule replacement of organic polymers by silica. The end result is petrified wood that may preserve much microscopic detail, but which typically contains only a small fraction of the original organic matter.

Organic templating may begin the process, but complete petrifaction requires a series of events. Scurfield (1979) and Scurfield and Segnit (1984) described a five-step sequence: (1) silica-bearing groundwater penetrates via splits and checks; (2) silica-laden water enters individual cells via reticulated micropores, which gradually enlarge as organic components of the cell wall break down, increasing permeability; (3) petrifaction results only if the deposition of silica occurs at a rate that exceeds decay, preserving the dimensional stability of the wood; (4) deposition of silica in cell lumina and intercellular voids may occur as a separate episode of late-stage mineralization; (5) lithification is accompanied by loss of water from hydrous silica. Transformation of one form of silica to another may occur.

Scurfield and Segnit (1984) recognized four forms of silica that may be present in petrified wood: (1) highly disordered, nearly amorphous hydrous SiO_2 (opal-A); (2) a disordered interlayering of tridymite and cristobalite (opal-CT); (3) chalcedony (microcrystalline quartz); and (4) quartz, characterized by individual crystals large enough to be easily visible under a light microscope.

Mineralogic transformation of silica during wood petrifaction has become a widely accepted hypothesis, even though the supporting evidence is largely indirect. Petrified wood composed of opal-A is rare (perhaps because it rapidly transforms to opal-CT), and X-ray diffraction patterns typically show that opalized woods contain opal-CT as the major constituent (Mitchell and Tufts, 1973). The alleged transformation of opal-CT to chalcedony has been based in part on the abundance of opalized wood in Cenozoic deposits, in contrast to the predominance of wood mineralized with chalcedony and microgranular quartz in Mesozoic deposits (Felix, 1897; Stein, 1982).

Indirect evidence of mineral transformation comes from siliceous sediments and hot spring sinters. The diagenetic change of opal-A→opal-CT→chert in siliceous biogenic deposits is well documented in both marine and nonmarine environments (Davis, 1918; Ernst and Calvert, 1969; Mizutani, 1970, 1977; Murata and Nakata, 1974; Kastner et al., 1977; Iijama and Tada, 1981; Williams and Crerar, 1985; Williams et al., 1985), and in siliceous hot spring sinters (White et al., 1964, 1992; Herdianita et al., 2000; Smith et al., 2001; Guidry and Chafetz, 2003).

Mineralogic transformation may be an important process, but it may not be the only mechanism responsible for silicification of wood. Buurman (1972) believed that the presence of lignified organic remains in chalcedonized wood was evidence of direct precipitation of quartz. Observations of agates and silica geodes show that opal-CT and chalcedony can be directly precipitated as alternating layers within a single specimen (Augustithis, 1982). Experimental evidence of silica precipitation under simulated hydrothermal conditions has yielded conflicting results. Flörke et al. (1990) found that cristobalite could form directly without requiring an amorphous opaline precursor. White and Corwin (1961) reported that chalcedony did not precipitate from synthetic hydrothermal solutions, but chalcedony was observed to have crystallized directly from experimental solutions (Oehler, 1976).

Polymineralic silica assemblages have been reported in petrified wood from Antarctica (Jefferson and McDonald, 1981) and New Zealand (Sutherland, 1994), but in both instances the silica mineral paragenesis was not resolved. The Florissant petrified forest provides a particularly good opportunity for studying the silicification process. Fossils are preserved in a single stratum deposited during a rapid geologic event, but the mineralogy of the silicified wood is surprisingly diverse, ranging from pure opal to pure quartz, with some stumps consisting of a mixture of the two minerals.

ANALYTICAL METHODS

Data were obtained from specimens selected from six silicified stumps (Figs. 1 and 2) by National Park Service personnel. Samples comprised one example of *Chadronoxylon* (a dicot) and 14 specimens of *Sequoioxylon* that span a range of colors and textures. Locality data are shown in Figure 1; sample numbers refer to the National Park Service Inventory and Monitoring of paleontological sites. Data for each sample consisted of density and loss on ignition values, major element composition, mineral identification, and microstructure as revealed by optical and scanning electron microscopy. Analytical methods were chosen on the basis of several factors. Developing new analytical methods or instrumentation was not a goal of this research, and data were obtained using well-established protocols for laboratory instruments that are commonly available to geologists. This strategy will, I hope, encourage other investigators who wish to attempt to replicate this study, or to apply these analytical techniques to their own research. In addition to determining basic physical properties such as density, color, and loss on ignition, silicified wood samples were analyzed using a combination of X-ray diffraction, X-ray fluorescence, scanning electron microscopy/energy-dispersive X-ray spectrometry (SEM/EDX), and optical microscopy.

The density of each specimen was calculated using a Sartorius Model 2000 electronic analytical balance equipped with a Model 6069 hydrostatic weighing device. Loss on ignition (LOI) values were obtained by heating powdered samples at 900 ºC. For silicified wood, this weight loss is the result of loss of structural water and combustion of organic carbon. For quartz-permineralized wood, the amount of structural water is low, and LOI values provide an indication of the amount of relict organic carbon. For fossil woods permineralized with opal, weight loss primarily represents loss of structural water from hydrous silica. Colors of powdered samples were described using the Munsell Soil Color Chart (McBeth Division of Kollmorgen Instrument Corporation, New Windsor, New York, 1994). Major element compositions were determined with a Rigaku Model 3070 X-ray fluorescence spectrometer from glass discs prepared by fusing 3.5 g of powdered petrified wood and 7 g of lithium tetraborate at 1000 ºC, using analytical protocols developed by Johnson et al. (1999). Scanning electron photomicrographs were made using a Tescan Vega SEM equipped with an EDAX nondispersive X-ray spectrometer. Samples were attached to aluminum stubs with epoxy adhesive and sputter-coated with palladium. Optical photomicrographs were made with a Spot Infinity digital camera, using a Wild model 420 stereo microscope for bulk specimens and a Zeiss Photomicroscope for thin sections. X-ray diffraction patterns were obtained from packed powders using a General Electric XRD-5 diffractometer operated at a 2θ scan rate of 2º/min using Cu $K\alpha$ radiation. Index of crystallinity values for quartz-mineralized specimens were determined using the method of Murata and Norman (1976), using diffraction patterns obtained from a Rigaku Geigerflex diffractometer operated at a step increment of 0.02º and a dwell time of 10 s.

RESULTS

Mineralogy and Geochemistry

Major element compositions of Florissant fossil wood (Table 1) indicate that silica is the dominant constituent of all samples. Siliceous volcanic rocks are a likely source of dissolved silica for wood petrifaction (Murata, 1940), and the local abun-

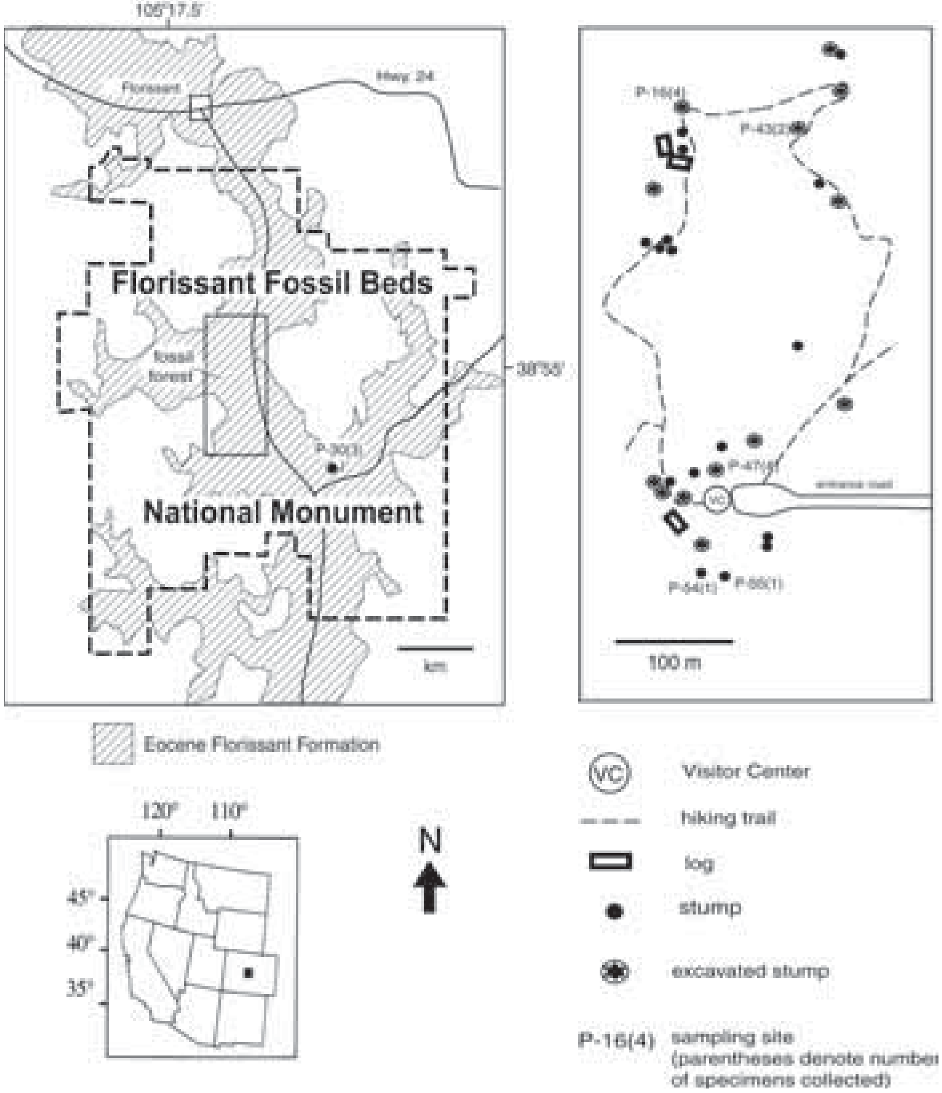


Figure 1. Location map, modified from Evanoff et al. (2001) and Gregory-Wodzicki (2001). Petrified stumps are labeled using Florissant Fossil Beds National Monument inventory numbers.

dance of ash and pumice in the Florissant Formation was an important geologic factor during preservation of the fossil forest. The abundance of diatoms in lacustrine strata are evidence of dissolved silica in surface waters during deposition of the Florissant strata (Harding and Chant, 2000; O'Brien et al., 2002, this volume). Diagenetic alteration of the host rocks would have released a diverse variety of elements, but only silica was precipitated in large quantities within the buried trees, an observation consistent with the Leo and Barghoorn (1976) hypothesis that organic constituents of cell walls have a strong affinity for silicic acid molecules.

The mineralogy of silicified trees within a single lahar deposit is surprisingly diverse. X-ray diffraction patterns reveal that *Sequoioxylon* stumps P-43 and *Chadronoxylon* stump P-30 are composed of nearly pure opal-CT. Specimens from *Sequoioxylon* stumps P-54 and P-55 consist of pure quartz, whereas *Sequoioxylon* stump P-47 contains appreciable amounts of both opal-CT and quartz. Stump P-16 is of particular interest. With an estimated mass of 60 metric tons and a basal diameter of 5.9 m (3.7 m at breast height), "Big Stump" (Fig. 2A) is one of the largest fossils at Florissant Fossil Beds National Monument (Meyer, 2003). Five samples collected from different color zones have mineral compositions that include pure opal-CT, a mixture of opal-CT and quartz, and pure quartz (Fig. 3).

Murata and Norman (1976) used X-ray diffraction to quantify the degree of crystallinity of quartz samples, using the resolution of the 1.3820Å (67.74° 2θ) X-ray peak to calculate a crystallinity index (C.I.) for individual specimens. Index numbers are obtained by determining the peak height above background level for the 67.8º 2-theta (1.38Å d-spacing) diffraction peak measured for a powdered quartz crystal (Fig. 4). The pure quartz is arbitrarily considered to have a C.I. index of 10.0, and indices for

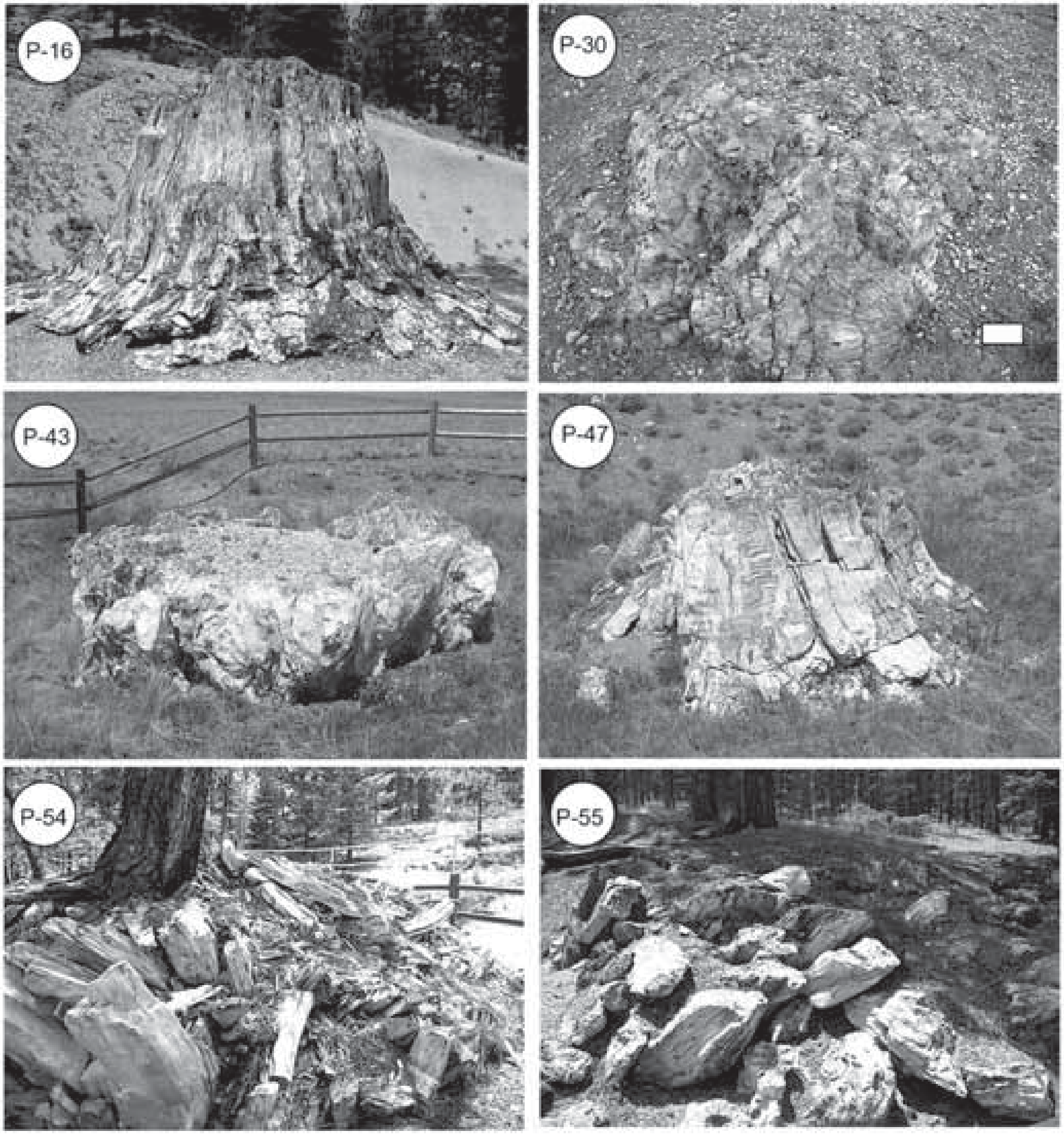


Figure 2. Samples used in this study were collected from six silicified stumps, labeled here with Florissant Fossil Beds National Monument inventory numbers. Specimen P-30 is *Chadronoxylon,* a dicot. Scale bar = 10 cm. All other specimens are *Sequoioxylon*. Photos by Melissa Barton.

TABLE 1. MAJOR ELEMENT COMPOSITION OF FLORISSANT SILICIFIED WOOD

Sample:	P-16a	P-16b	P-16c	P-16d	P-30	P-43	P-47	P-54	P-55
Mineralogy:	Opal and trace quartz	Quartz	Opal-CT	Opal-CT	Opal-CT	Opal-CT	Quartz and opal-CT	Quartz	Quartz
Oxide wt%									
SiO_2	86.61	97.49	94.66	95.81	88.71	93.39	96.08	96.60	97.07
Al_2O_3	0.00	0.00	0.00	0.00	0.40	0.10	0.09	0.06	0.14
TiO_2	0.09	0.02	0.04	0.04	0.03	0.02	0.02	0.01	0.01
Fe_2O_3*	0.10	0.45	0.43	0.56	2.12	0.33	0.09	0.00	0.09
MgO	0.02	0.03	0.10	0.00	0.07	0.00	0.00	0.03	0.04
MnO	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
CaO	0.13	0.10	0.35	0.06	0.27	0.18	0.16	0.27	0.13
K_2O	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Na_2O	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
P_2O_5	0.04	0.07	0.05	0.00	0.84	0.10	0.04	0.04	0.08
LOI at 900°C	13.41	2.71	3.96	3.58	5.65	4.34	2.57	2.62	1.52
Total	100.40	100.89	99.59	100.05	98.09	98.46	99.05	99.63	99.08
Density g/cm^3	2.03	2.32	1.84	2.13	1.82	2.04	2.38	2.47	2.34
Munsell color	7.5YR3/3 dark brown	10YR6/3 pale brown	10YR6/3 pale brown	7.5YR5/2 brown	10YR4/3 brown	7.5YR7/2 pinkish gray	10YR8/1 white	10YR8/1 white	67.5YR8/2 pinkish white

Note: LOI—loss on ignition.
*Total iron calculated as Fe_2O_3.

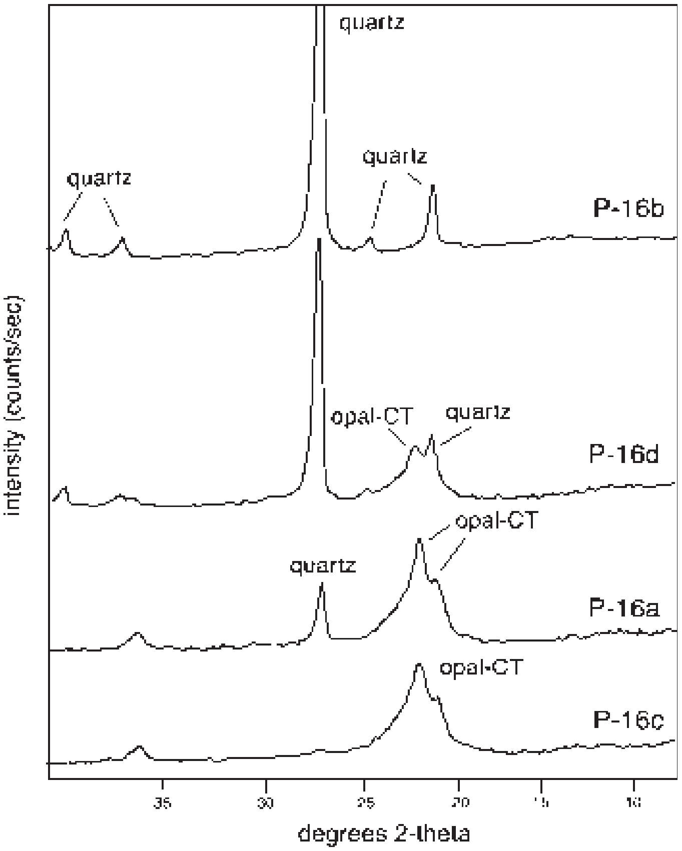


Figure 3. X-ray diffraction patterns of four samples from *Sequoioxylon* stump P-16. Patterns are offset along the y-axis for clarity.

silicified wood samples are calculated as ratios of their peak heights to this calibration standard. Florissant samples that yielded pure quartz X-ray diffraction patterns have C.I. values of <1.0, evidence that quartz is present as chalcedony, consistent with microscopic evidence from thin sections. From a geochemical point of view, one measure of the uniqueness of the Florissant fossil wood is that crystallinity indices are the lowest values that I have measured from quartz-mineralized wood from 29 localities worldwide (C.I. numbers from these localities range from 1.3 to 9.0).

Mineralogic characteristics are related to density and LOI values (Table 1). Woods mineralized with opal have densities of 2.04 g/cm^3 or less, in contrast to densities of 2.34 g/cm^3 or greater for quartz-mineralized wood. For opalized samples, relatively high LOI values (3.96–13.41 wt%) are primarily caused by loss of water from opal and to a lesser extent from combustion of relict organic matter. Quartz-mineralized woods yielded LOI values of 2.34–2.47 wt%, probably mostly representing organic matter.

In unweathered specimens, opalized woods vary from dark brown to gray in color. Brown colors are caused by relict organic matter, as evidenced by bleaching that occurs during natural weathering and in the laboratory when powdered samples are

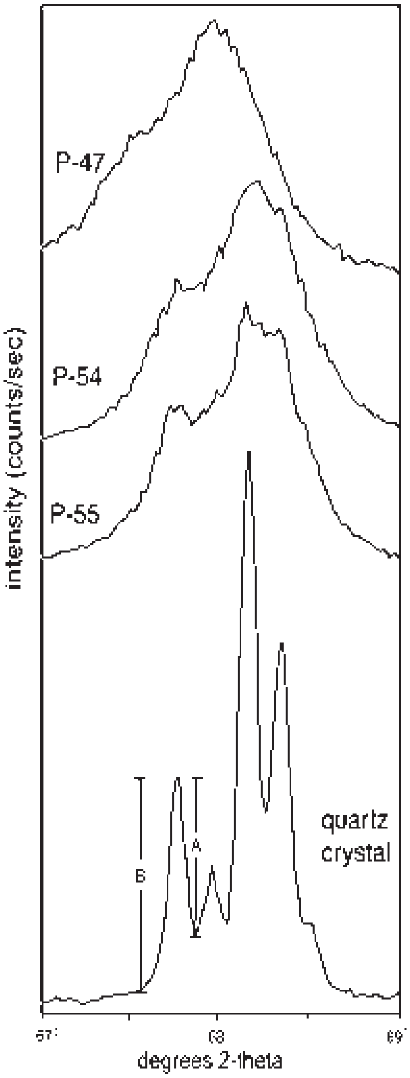


Figure 4. Crystallinity index values for Florissant specimens that contained only quartz were calculated relative to the A/B ratio measured for the 67.8° 2-theta X-ray diffraction peak for a pure powdered quartz crystal. See "Analytical Methods" for details.

heated at 450 °C. Samples that contain quartz as the major constituent are typically tan or cream colored in hand specimen and white when powdered. These results indicate that as a quick field test, mineral composition of Florissant fossil wood can be estimated simply by looking at color.

Iron-rich minerals play a minor role in determining color, producing variegated reddish-brown areas on some fossil stumps. Iron oxide contents range from <0.1 wt% for quartz wood to 0.33–2.12 wt% for opalized specimens. SEM/EDAX analysis suggests that this iron was originally present as disseminated grains of iron pyrite that oxidized to limonite during weathering. The variation in iron content was not studied in detail, and several factors may be involved. A higher iron concentration was observed for the *Chadronoxylon* (dicot) wood as compared to *Sequoioxylon* specimens, but the significance of this observation is not clear. Iron is typically an element that is transported into plant tissues during fossilization, rather than accumulating during the life of the tree. Perhaps *Chadronoxylon* wood was more permeable to iron-bearing groundwater than wood of *Sequoioxylon*. An alternative possibility is the fact that the *Chadronoxylon* stump is located in a different part of the fossil bed than the other specimens (Fig. 1), and the differences in iron content may simply reflect local variations in the dissolved element content of groundwater.

Microscopy

SEM images primarily show topography, and relict anatomical features are most likely to be observed when cell lumina and intercellular spaces remain unmineralized, so that cell wall surfaces are exposed when specimens are fractured (Mustoe, 2004). Topographic features of cell surfaces are preserved with great fidelity in both opalized and chalcedony-mineralized specimens (Fig. 5).

With optical microscopy, the visibility of relict cell architecture in silicified wood is largely determined by the transparency of silica minerals and the presence of opaque or colored inclusions that delineate relict tissue structure (Figs. 6 and 7). Preservation of relict organic matter causes cell structures to be readily visible in most Florissant petrified wood specimens (Fig. 7). Carbonaceous material causes the brownish color characteristic of fossilized cell walls, in contrast to the colorless silica that fills cell lumina and intercellular spaces. SEM/EDAX spectra show a distinct carbon X-ray peak (Fig. 7E); silica is a major constituent of relict cell walls, consistent with the organic templating hypothesis (Leo and Barghoorn, 1976). The quality of anatomical preservation is variable, and cells in some specimens have been deformed or destroyed by biogenic decomposition, but in many specimens the preservation of anatomical detail is excellent (Figs. 6 and 7).

A variety of instrumental methods have been used to map the distribution of elements in permineralized fossils. Analytical techniques include conventional X-ray microprobe (Dietrich et al., 2000), synchrotron-based X-ray microprobe (Kuczumow et al., 2001), electron microprobe (Boyce et al., 2001), and SEM/EDX (Kuczumow et al., 2001; Scott and Collinson, 2003). For some samples, elemental distributions can be correlated with microscopic anatomical features (e.g., cell walls). Elemental mapping has proved to be most successful when fossils contain several mineral phases, such as fossil woods that are permineralized with a combination of silica and calcium carbonate (Scott and Collinson, 2003; Siurek et al., 2004), and carbonaceous fossils preserved as inclusions in chert (Boyce et al., 2001). Studies in our laboratory indicate that elemental mapping is less useful for petrified wood that contains silica as the only major inorganic constituent. SEM/EDX maps of Florissant fossil wood specimens are relatively featureless. Silicon and oxygen tend to be ubiquitous in these silicified fossils. EDX analyses commonly

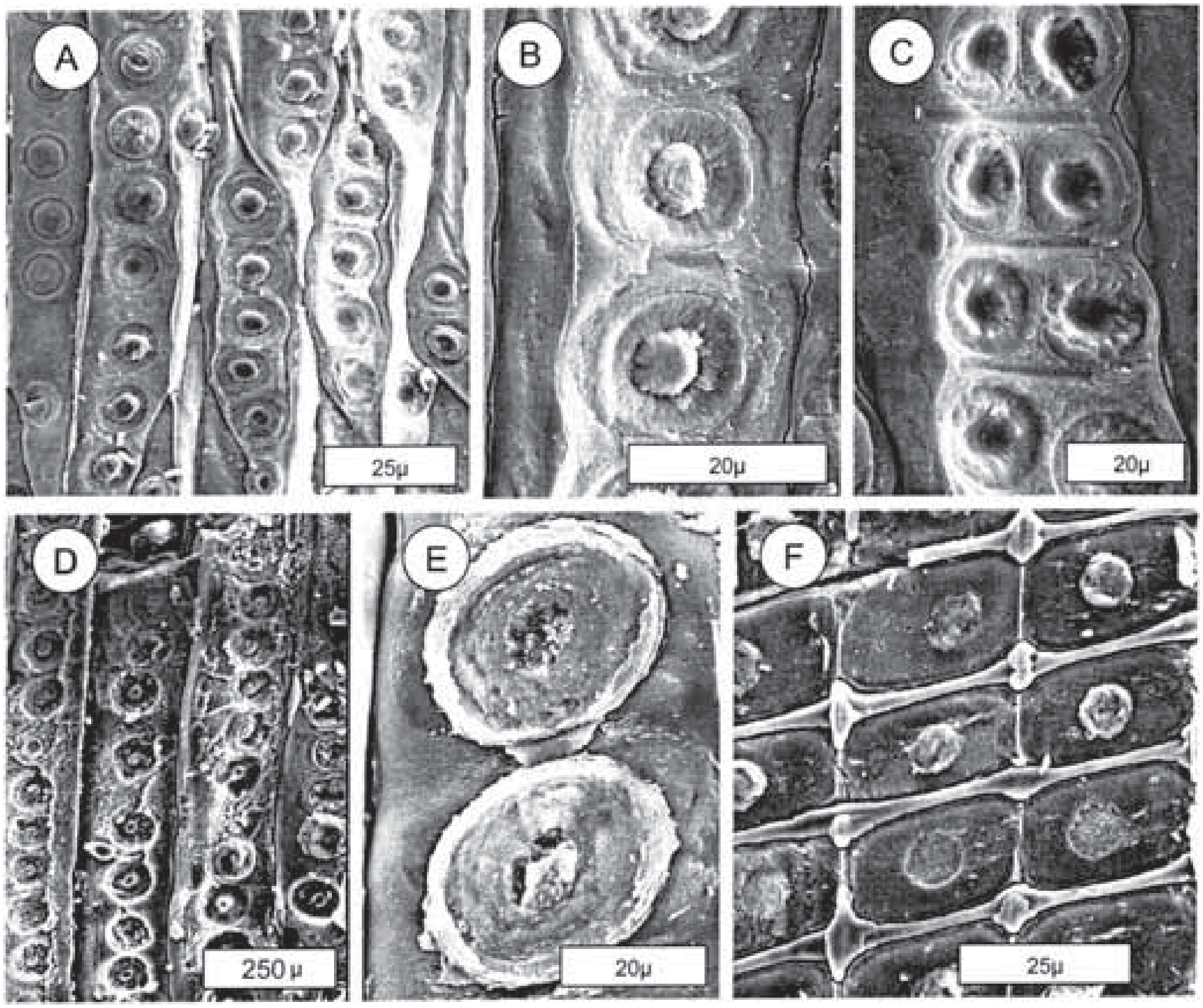
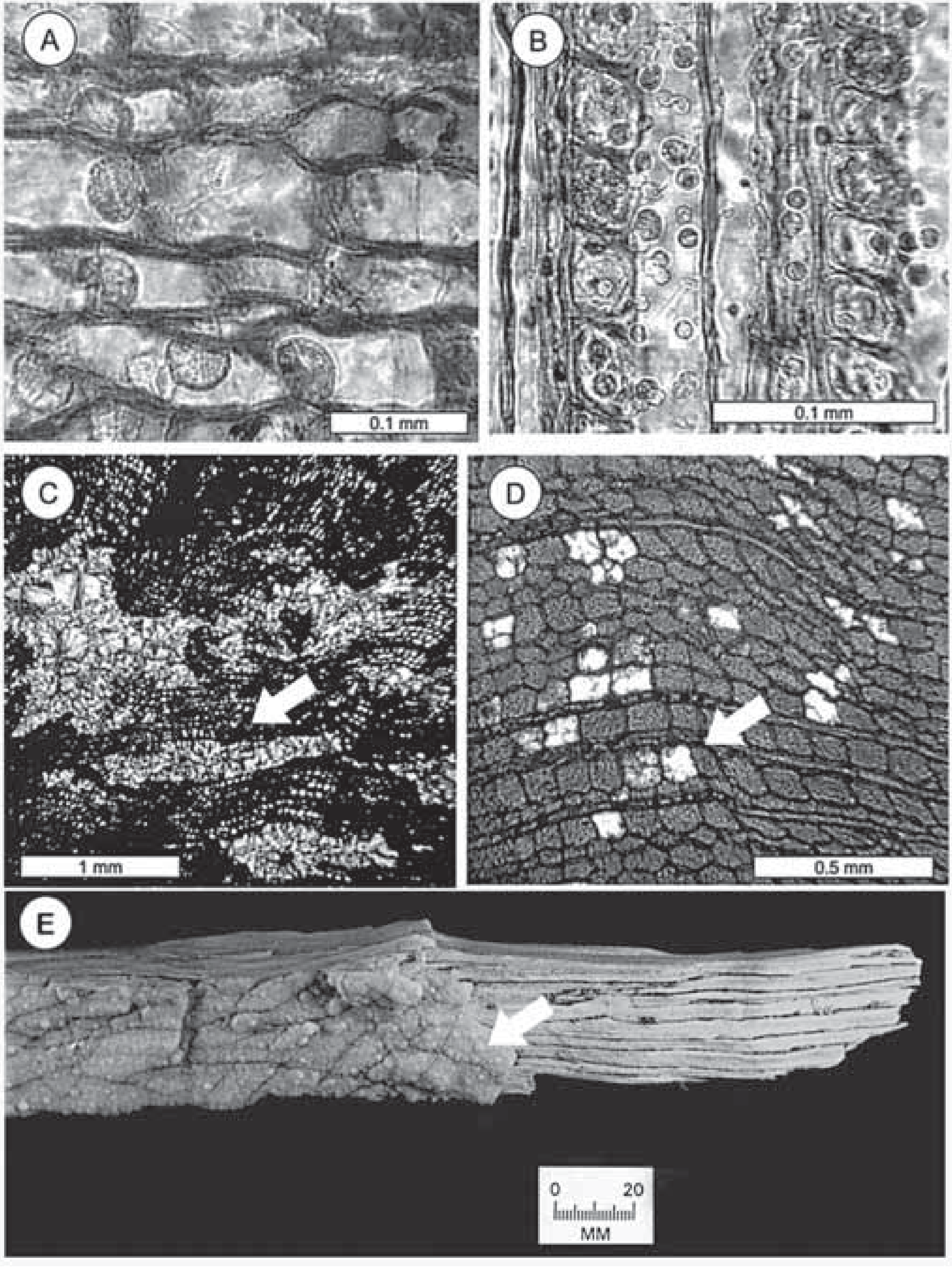


Figure 5. SEM radial views of Florissant fossil *Sequoioxylon* wood showing tracheids with bordered pits. (A–C) Opalized specimen P-16c. (D, E) Chalcedonized specimen P-55a. (F) Parenchyma cells with cross-field pits, specimen P-55a.

detect the presence of carbon, and when the scan area of the electron beam is minimized, the EDX spectra usually show that carbon is enriched in relict cell walls relative to silica-filled lumina. However, cell walls were not visible in X-ray maps of polished silicified wood samples. The failure of X-ray mapping to reveal variations in carbon content results from a combination of factors. The EDX detector uses a supercooled silicon wafer to detect X-rays emitted when atoms in the specimen are energized by the incident electron beam. These X-rays are processed one photon at a time, a very demanding challenge for the electronic detecting system. The very-low-energy (0.277 KeV) X-rays emitted by carbon atoms are particularly difficult to detect and quantify, lying very close to the light element detection limit of the EDX analyzer. Analysis is further complicated by the fact that carbon has a very low fluorescence yield, causing EDX spectra to have poorer detection limits for this element compared to elements having higher atomic numbers. Figure 8 provides an illustration of these problems, depicting X-ray maps of carbon, oxygen,

Figure 6. Transmitted-light thin-section photomicrographs of *Sequoioxylon* specimens that contain both opal-CT and chalcedony. (A, B) Transverse and radial views of sample P-16a show lepispheres of opal-CT attached to cell walls, surrounded by clear chalcedony. (C) Transverse view of P-16d reveals chalcedony filling fractures. (D) In specimen P-16c, cell lumina are filled with opal-CT, but in one area of this transverse section a few of the tracheids are mineralized with chalcedony. (E) Botryoidal chalcedony crusts are present in fractures in opalized wood from stump P-47.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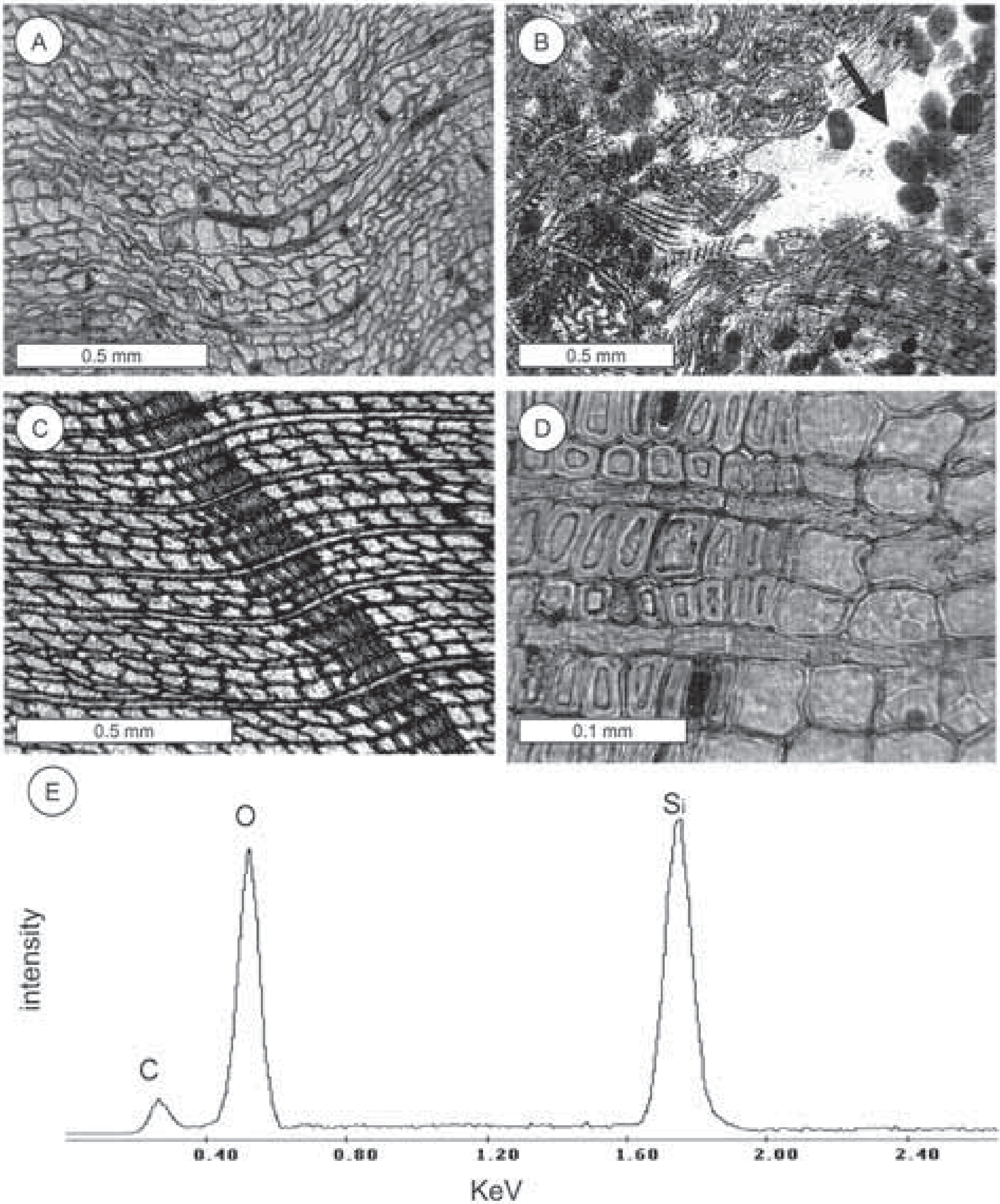

Figure 7. Transmitted-light thin-section photomicrographs showing transverse views of Florissant petrified *Sequoioxylon* wood. (A, B) Specimen P-16b contains chalcedonized wood in a region of the stump where the cells were distorted and locally decayed prior to petrifaction. Note the preservation of probable insect fecal pellets (arrow in B). (C) Undamaged wood in parts of this same specimen is mineralized with a mixture of chalcedony and opal-CT. (D) Chalcedonized wood typical of specimen P-55. In photos C and D, the thin-walled earlywood and thick-walled latewood of successive growth rings are consistent with seasonality in the local paleoclimate. (E) SEM/EDX spectrum of P-16d shows a strong carbon peak, indicative of the preservation of relict organic matter within the dark-colored cell walls.

and silicon in a polished slab of silicified wood that contains two ovoid inclusions, presumed to be fossilized insect fecal pellets. Their dark brown color under transmitted light suggests a carbonaceous composition, and microbeam analysis reveals the presence of carbon as a constituent of these particles. However, X-ray mapping of the full field of view fails to reveal variations in carbon content. The EDX maps show a deficiency of both oxygen and silicon in the ovoid regions, as compared to the abundance of both elements in the adjacent matrix. Note that as the atomic number increases, elements are mapped with greater precision. Thus, carbon (atomic number 6) was not detected, and compositional boundaries are less sharply defined for oxygen (atomic number 8) than for silicon (atomic number 14). As noted above, X-ray maps are most likely to be successful when samples contain a combination of elements that have markedly different atomic numbers, a characteristic not typical of Florissant silicified wood. Boyce et al. (2001) successfully mapped carbon distributions in several types of permineralized fossils by taking advantage of the higher electron beam currents and greater resolution of the electron microprobe, but at present ordinary transmitted light microscopy remains the simplest method for observing the distribution of relict carbon in silicified wood.

Optical microscopy also provides a valuable tool for studying the relationship between opal-CT and chalcedony in specimens where both minerals are present. Cross-polarized light views show opal-CT to have very low interference colors, in contrast to the brighter colors typical of chalcedony. In thin sections prepared for this study, no samples showed evidence of transformation of opal-CT to chalcedony. Instead, when they were present together the two minerals showed very well-defined boundaries. Most often, chalcedony is present as a vein material in fissures that penetrate opalized wood, providing evidence of late-stage silica deposition that occurred after the wood had been petrified (Fig. 6E). A very different type of opal/chalcedony association occurs in samples where tiny hemispheres (“lepispheres”) are attached to the interior surfaces of cell walls, where they are enclosed within clear chalcedony that later permineralized the cell lumina (Fig. 6A

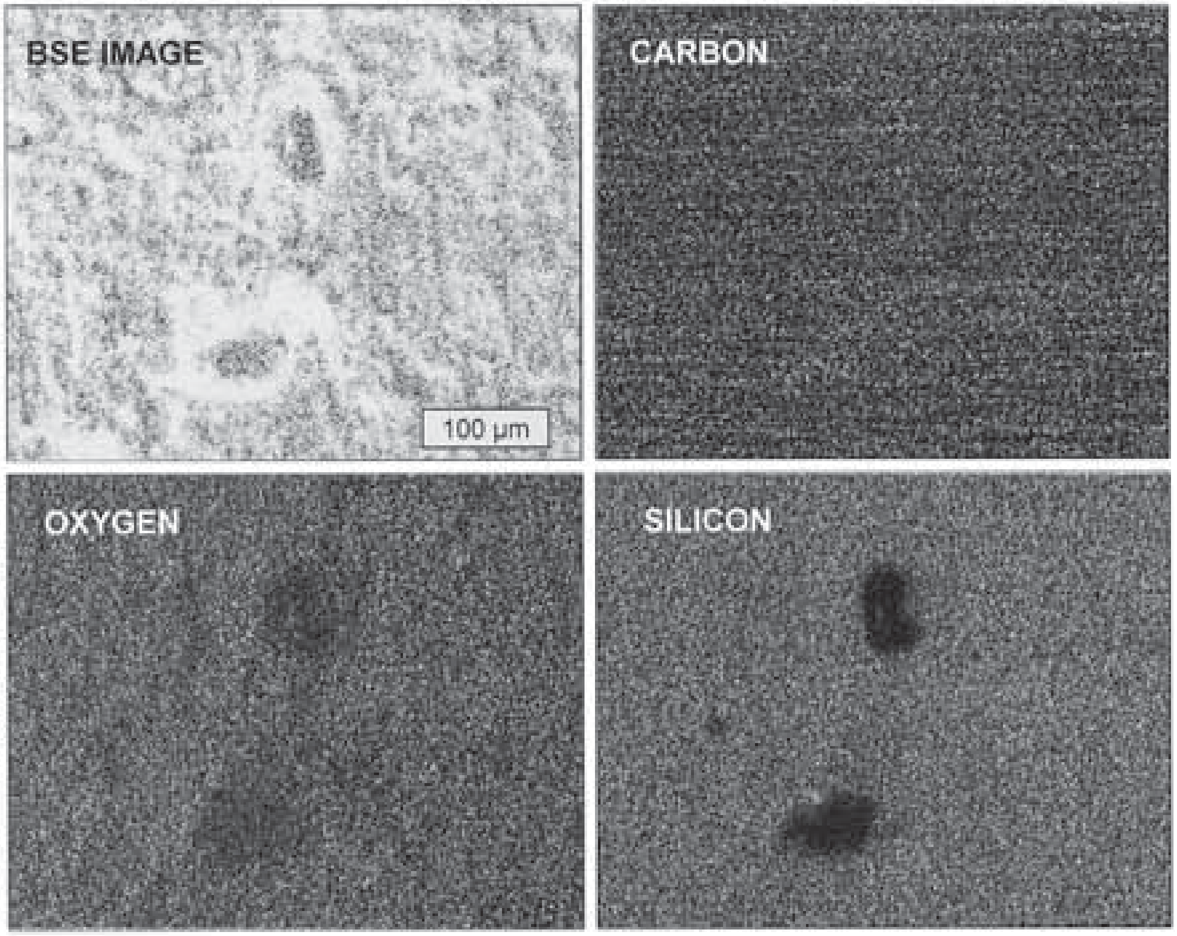

Figure 8. Back-scattered electron SEM image and EDX element distribution maps for carbon, silicon, and oxygen obtained from a polished slice of silicified wood from stump P-16 that contains two ovoid inclusions, possibly fossilized insect fecal pellets. Dark zones in each EDX image represent areas of the specimen where a particular element either is absent or is present only at undetectable levels. (Fig. 7B shows an optical photomicrograph of this specimen; see text for discussion.)

and 6B). These opal masses show no evidence of alteration at their contacts with the adjacent chalcedony, suggesting that the chalcedony did not originate from transformation of an opal-CT precursor, and that the two polymorphs instead developed independently during successive stages of silicification. In a few specimens, chalcedony is sparsely present as a filling material in individual cells within opalized wood (Fig. 6d), but this texture is uncommon.

DISCUSSION

Florissant specimens have great importance for helping geoscientists to understand the nature of the petrifaction process energy better. Unfortunately, some aspects of the early stages of fossilization are enigmatic. To have a complete understanding of the silicification processes that caused wood specimens at Florissant to become permineralized, it would be helpful to know the physical state of silica in the mineralizing fluid, and the environmental conditions that existed at the time of silicification. Was the silica a colloid or sol? Did silica form short or long-chain polymers? Was temperature an important factor in determining the physical state of silica, and the resultant mineralogy? Unfortunately, none of these questions can be answered by presently available evidence, though perhaps one day additional evidence may shed light on these mysteries.

Although the initial silicification processes remain imperfectly understood, other mineralogic features can be interpreted with greater certainty. The presence of tree trunks mineralized with opal-CT, chalcedony, or a mixture of the two is a particularly important and previously unrecognized feature of the Florissant fossil forest. One possible explanation for the presence of both minerals is that the silica mineralogy is evidence of local variations in the rates of diagenetic transformation. This hypothesis assumes that all of the wood was initially permineralized with opal, and that some of the specimens later became at least partially converted to chalcedony.

Mizutani (1970, 1977) described the successive transformation of amorphous biogenic silica (opal-A) to opal-CT and quartz as primarily being a function of geologic age and burial temperature. Neither factor can account for differences in silica mineralogy at Florissant, where stumps were buried within a single stratum of very limited geographic extent. Instead, mineralogic heterogeneity might have been produced by highly localized conditions, e.g., variations in permeability or chemical composition of groundwater. A particularly vexing problem for the mineralogic transformation hypothesis is the apparent absence of “missing link” specimens, where opal is in the process of being altered to chalcedony. Instead, in specimens where both minerals are present, the two phases appear to be coexisting as primary minerals.

Rather than supporting the transformation hypothesis, evidence from Florissant specimens suggests that some buried trees were directly mineralized with chalcedony, without an opal-CT precursor. Under epithermal conditions, opal is precipitated when concentrations of dissolved silica are relatively high, but lower silica concentrations may result in direct precipitation of chalcedony. Crystalline quartz precipitates only from extremely dilute solutions (Iler, 1979; Fournier, 1985). These geochemical characteristics may explain the mineralogy of Florissant fossil wood.

Initial silicification of cell walls probably followed the organic templating model, as evidenced by the presence of silicified cell walls that retain appreciable amounts of relict organic matter (Fig. 7C). Subsequent steps in the silicification process may have followed more than one pathway. Opalized specimens may have originated in woods that were exposed to solutions containing relatively high levels of dissolved silica, allowing cell lumina and intracellular voids to become impregnated with opal-CT (or perhaps opal-A that was later transformed to opal-CT). In contrast, wood mineralized with pure chalcedony may have originated in areas in the deposit with lower silica concentrations, perhaps as a result of small scale hydrologic or lithologic effects within the sedimentary matrix that caused concentrations to vary as groundwater passed through the deposit. Also, permeability and moisture content variations within the wood may have influenced silica mineralogy. Given the large diameters of the buried trees, seepage of silica-bearing groundwater through the tissue may have produced a concentration gradient, by which precipitation of silica in the outer tissues led to a reduction in dissolved silica in the remaining solution, affecting the type of silica that was subsequently deposited in inner regions of the same tree. Anatomical variations among different tree genera may have played a role during fossilization, and within a single trunk differences in physical properties between earlywood and latewood may have led to geochemical differences. Kuczumow et al. (2001) reported microspectrometric evidence of compositional variations in silicified wood from Poland that correlated with relict annual rings, and it would not be surprising to find similar characteristics in specimens from other localities. Although data obtained from the present reconnaissance study are insufficient for recognizing subtle compositional variations that may occur within individual stumps, the Florissant fossil forest is an excellent site for more detailed future research.

Geochemical and mineralogic characteristics are important factors to be considered during development of strategies for mitigating weathering damage to the silicified stumps that are a major feature of Florissant Fossil Beds National Monument. Microscopic observations are particularly useful for explaining why the silicified wood is so susceptible to weathering. Regardless of whether they are mineralized with opal-CT or chalcedony, Florissant fossil woods are typically composed of cells that are separated from each other by narrow (<1 µm) open spaces, causing the fossilized tissue to have cleavage characteristics much like that of modern wood. Florissant specimens readily cleave along radial planes because of the weak interface between longitudinal tracheids and latitudinal rays. Tangential fracturing also occurs because of parting along growth ring boundaries where there is a marked difference in texture between the wood of successive rings. Unlike modern wood, specimens of Florissant fossil wood are prone to fracture in the cross-grain (transverse) direction. Although Florissant fossil stumps are resistant to chemical decomposition because of their siliceous compositions, they are susceptible to damage by frost wedging because of the blocky fracture. These phenomena are discussed in detail by Young et al. (this volume).

CONCLUSIONS

The mineralogic, microscopic, and geochemical properties of Florissant silicified wood are significant for several reasons. From a conservation standpoint, these characteristics are important factors to be considered during development of possible conservation strategies for reducing weathering rates of the petrified stumps. In addition, data from this reconnaissance study shed new light on the fossilization processes that produced these spectacular specimens. The coexistence of opal-CT and chalcedony in some fossil stumps conflicts with the widely accepted hypothesis that chalcedonized wood results from transformation of an opaline precursor. Instead, wood silicification appears to have resulted from a combination of processes rather than following a single transformation pathway. This discovery demonstrates that the Florissant fossil forest is an important locality for studying the petrifaction process. The data presented here, based on analyses of only 15 specimens collected from six fossil stumps, provide only a tantalizing glimpse into possible geochemical processes that caused tree remains to become silicified. Perhaps the greatest significance of this investigation is that it points the way for possible future research. Analyses of a larger number of samples are needed to clarify the range of mineralogic and compositional variation among the more than 30 known fossil logs and stumps. Possible causes of these variations include local differences in groundwater flow rates and dissolved-element concentrations, and environmental factors such as pH and burial temperature. Within an individual stump, mineralization may be related to anatomical characteristics (e.g., cell diameter, presence or absence of open vessels) and to structural features (e.g., voids caused by decay or fissures produced from desiccation or mechanical damage). More extensive microscopic study is needed to understand better how these factors influence petrifaction. Do woods from different tree species become fossilized in the same manner? Present data are inadequate to address this issue.

Florissant Fossil Beds National Monument provides an ideal location for resolving these paleontologic uncertainties. Fossil wood occurs in an ancient lahar deposit that has been the subject of considerable past study, and this research has produced detailed geologic maps and stratigraphic columns, as well as a wealth of paleoenvironmental information. Silicified tree remains have been carefully surveyed, and many of them have been identified taxonomically. Furthermore, the protection efforts by the National Park Service ensure that the site will remain accessible for future scientific research, an important consideration given the sad reality that many other petrified wood localities have suffered from the effects of overzealous collecting, unskilled excavation, or access restrictions related to changes in land ownership or commercial development.

Florissant Fossil Beds National Monument is also an excellent location for studying possible strategies for reducing damage to silicified fossils caused by exposure to natural weathering. As discussed earlier in this report, the mineralogic compositions and microscopic physical characteristics of this silicified wood help to explain why Florissant specimens are susceptible to rapid freeze-thaw weathering in the harsh cold-season climate. Analytical information obtained in this study provides a starting point for developing conservation procedures aimed at reducing weathering rates, and the data and the analytical methods used to obtain them set a helpful precedent for establishing research protocols for conducting future research at fossil sites in other regions.

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Conservation of an Eocene petrified forest at Florissant Fossil Beds National Monument: Investigation of strategies and techniques for stabilizing in situ fossil stumps

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ABSTRACT

Silicified stumps at Florissant Fossil Beds National Monument are subject to degradation from a variety of causes, including freeze-thaw weathering. In the past, noninvasive measures have been taken to conserve selected fossils, including use of metal bands for reinforcement and construction of shelters. Our study had two goals. The first was to document the temperature and relative humidity to which petrified stumps are exposed at Florissant. The second was to conduct a preliminary examination of the feasibility of using consolidants and adhesives to reinforce fossil wood and reduce its susceptibility to weathering.

Electronic data loggers were used to monitor temperature and relative humidity both internally and externally for one exposed and one sheltered fossil stump, and results indicated that over 289 days of the cold season, there were 119 freeze-thaw events for the surface of the exposed stump and 95 events for the surface of the stump protected by a roof. Temperature and humidity variations were markedly lower for the subsurface sensors.

Seven organosilicate formulations were field tested as consolidants on samples of petrified wood. Adhesives used to repair fractures included two polyvinyl butyral (PVB) formulations, two casein adhesives, and one epoxy. After eight months of exposure, fractures repaired with epoxy remained well bonded. Specimens repaired with PVB remained intact, but outer regions were visibly damaged, presumably from UV radiation. Of the two casein products that were tested, one had poor bond strength and the other was difficult to apply because of its low viscosity. Evaluating the effectiveness of organosilicate emulsions as consolidants to reduce weathering rates will

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require more research. Preliminary results of our field tests have identified goals for future efforts and established performance criteria for adhesives and consolidants used for silicified wood.

Keywords: adhesives, conservation, consolidants, Florissant, petrified wood.

INTRODUCTION

Florissant Fossil Beds National Monument in central Colorado (Fig. 1) was established in 1969 to protect fossil beds that contain two major paleontological features: diverse plant and animal remains in shale, and a petrified forest that contains some of the largest-diameter petrified trees in the world. These silicified stumps measure as much as 4.1m dbh (diameter at breast height). Most of the fossil wood represents an extinct species of redwood, *Sequoioxylon pearsallii* (Andrews, 1936). Five taxa of dicotyledonous woods have also been identified (Wheeler, 2001), although specimens are comparatively rare. The fossil stumps are preserved in situ in a volcanic lahar deposit within the lower mudstone unit of the late Eocene Florissant Formation (Evanoff et al., 2001). This lahar deposit consists of a 5-m-thick stratum of volcanic sediment derived from the Thirtynine Mile volcanic field southwest of the current national monument (Evanoff et al., 2001; Meyer, 2003). The trees are interpreted to have died following deposition because the roots could no longer absorb sufficient oxygen (Gregory-Wodzicki, 2001).

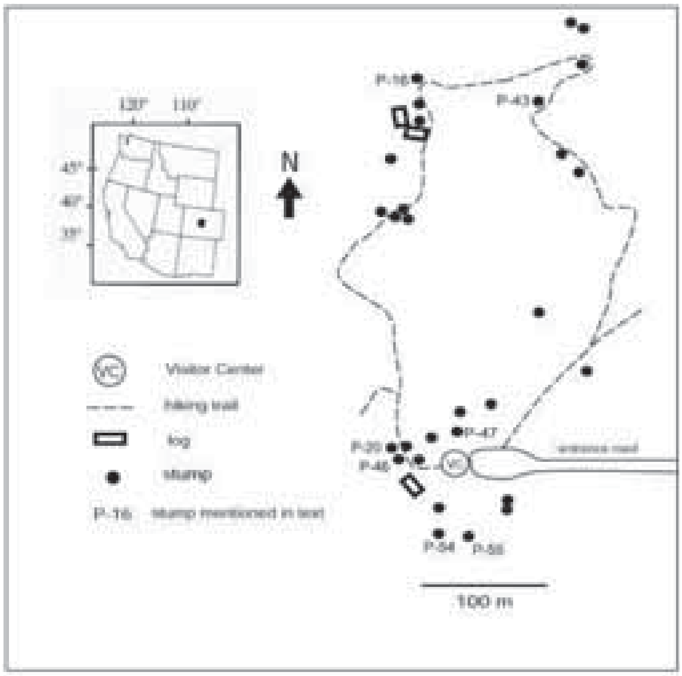

Figure 1. Map of Florissant outcrops and National Monument boundaries. Map on right corresponds to filled-in box in the map on the left.

Fossil stumps at Florissant have diverse mineral compositions that range from pure common opal (opal-CT) to pure chalcedony, and include specimens that contain both minerals (Mustoe, this volume). Relict organic matter is also present. Regardless of whether wood has been mineralized with common opal or chalcedony, spaces between adjacent cells typically remain open (Mustoe, this volume). In a few specimens, incomplete silicification causes fossilized wood to be soft and friable (Fig. 2). More commonly, the wood is well lithified and high magnification is required to see the open intercellular spaces (Fig. 3). This mode of petrifaction makes Florissant fossil stumps vulnerable to fragmentation for two reasons. First, open intercellular spaces cause the silicified wood to retain the splitting characteristics of

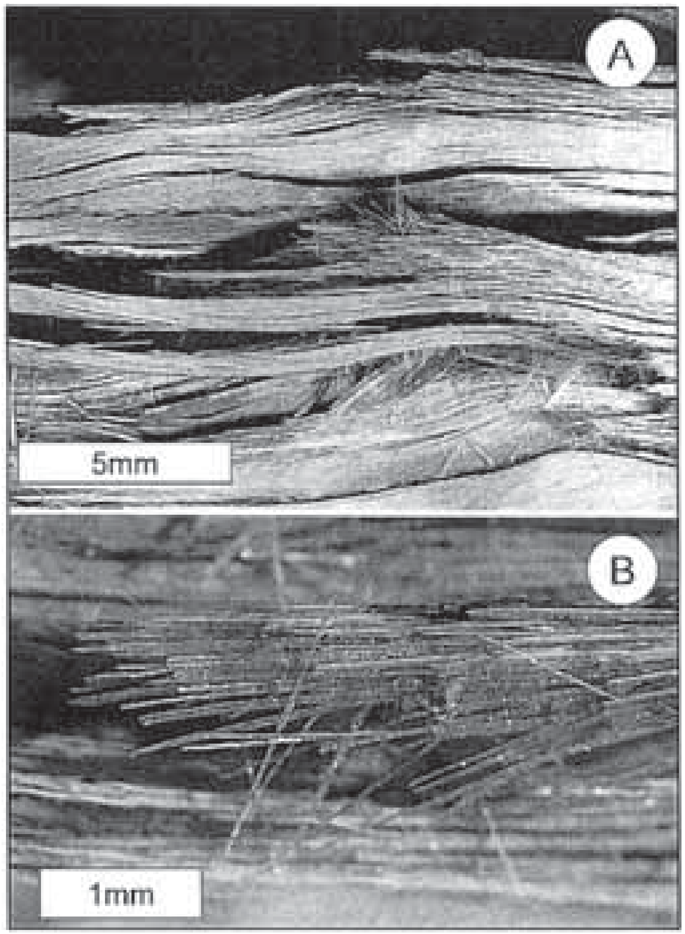

Figure 2. (A, B) Optical photomicrographs of soft, friable silicified wood from FLFO P-43. Individual tracheids have been mineralized with opal-CT, but spaces between adjacent cells remain unmineralized.

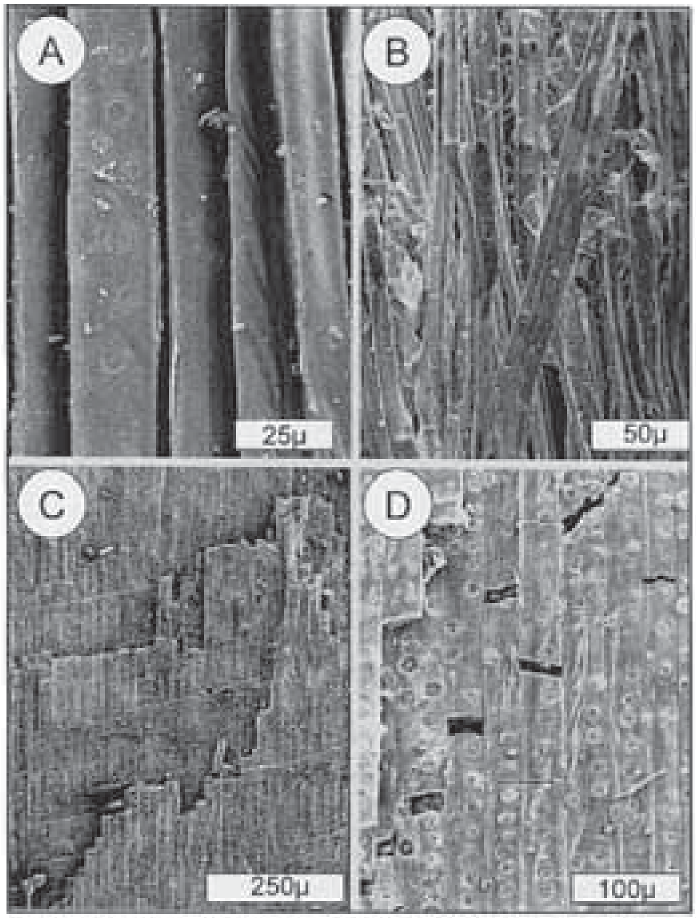

Figure 3. SEM photomicrographs of radial views of silicified wood show how the microstructure affects weathering characteristics: (A, B) FLFO P-43. Spaces between silicified tracheids remain unmineralized, allowing the fossil wood to cleave along radial and tangential planes. (C, D) FLFO P-55. The brittle silicified cells are vulnerable to planar transverse fracture, causing weathered petrified stumps to break into blocky fragments.

the original tissue, cleaving readily along radial and tangential planes. Second, unlike modern wood, the permineralized tracheids have a brittleness that allows the fossil wood to break in the cross-grain direction (Fig. 3D). As a result of these characteristics, wedging from frost or biogenic processes caused Florissant stumps to fracture into a myriad of blocky fragments (Fig. 4).

The petrified trees show evidence of damage and fragmentation from a variety of causes, particularly due to decades of exposure in the harsh climate of the area. These fossil stumps are the most visible and impressive attraction for visitors to the national monument, and preserving their integrity well into the future is a primary concern of the National Park Service. This paper provides an overview of causes for the damage and examines possible strategies for reducing the rate of deterioration, focusing particularly on the feasibility of using chemical consolidants and adhesives to treat silicified wood.

CONSERVATION ISSUES

There are at least 30 known in situ stumps in the Florissant valley within the boundaries of Florissant Fossil Beds National Monument. Additional stumps have been located during construction of nearby housing developments, particularly south of the monument. Several of the most impressive stumps exposed in the monument were uncovered decades ago when the site was being developed as a tourist attraction. Many other petrified stumps within the monument are exposed only along their top surfaces at ground level, whereas others remain completely buried. In an effort to prevent further deterioration from weathering, the National Park Service buried the tops of six partially exposed stumps in 1987. Temporary shelters were assembled over two of the fully excavated stumps in 1997, and permanent shelters were constructed in 2001 to replace the temporary shelters and also cover one additional stump, providing partial protection from weathering. Of particular concern to the present study are the excavated stumps (Fig. 5) that are fully or partially exposed to weathering, including the Big Stump (FLFO P-16) and the Redwood Trio (FLFO P-20).

Causes of Deterioration

Effects of Human Activity

The Florissant fossil beds were publicly reported in the 1860s, and tourists began arriving in increasing numbers with the coming of the railroad in 1887. The area remained under private ownership for many decades, and by the 1920s two adjacent land parcels within the petrified forest were being operated as commercial enterprises (Meyer, 2003; Veatch and Meyer, this volume). During this period the condition of the fossil site markedly deteriorated because of specimen removal, including entire stumps, and from few restrictions of access to the fossils (e.g., old photographs commonly show tourists sitting and standing on the Big Stump; Fig. 5A). Other causes of deterioration included excavation by early land owners. Anecdotal accounts suggest that dynamite was used to remove the rock matrix that enclosed large petrified stumps (FLFO P-20, P-31, and 46) located in two deep pits behind the present visitor center. This blasting may have contributed to the blocky fragmentation of these stumps. In contrast, Big Stump (FLFO P-16) is more cohesive, perhaps because of more careful excavation techniques; however, this stump has its own record of damage from human activity, and it contains a remnant of a broken steel saw blade that was used in an unsuccessful attempt more than a century ago to cut the 60 metric ton specimen into pieces so that it could be transported to the eastern United States for public exhibit (Meyer, 2003). Even the most careful excavations expose the stumps to increased weathering. Although the creation of Florissant Fossil Beds National Monument has dramatically reduced threats to the fossils from human activities, illegal collecting by park visitors remains a cause of concern.

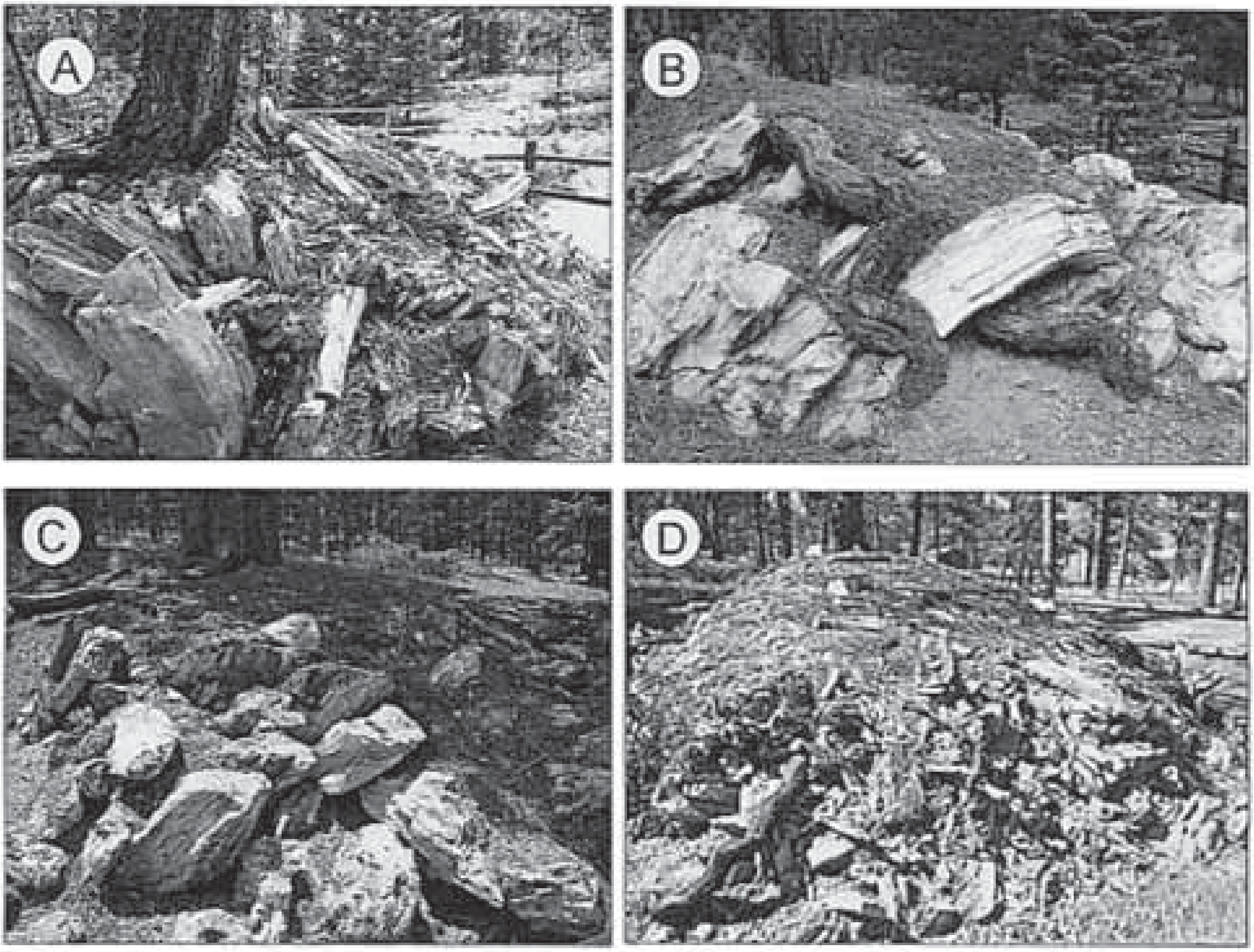

Figure 4. Florissant fossil stumps affected by severe deterioration. (A) FLFO P-54. (B) FLFO P-55, with trunk and roots of a ponderosa pine growing in weathered stumps. (C) FLFO P-55. (D) FLFO P-54, showing blocky fracture related to transverse fracturing of silicified wood cells.

Another challenge in conserving the fossil stumps is determining whether unknown specimens occur in areas designated for construction activity. Ground-penetrating radar (GPR) has not proven to be reliable for locating buried stumps at Florissant (R. Young, 1998, unpublished report for the National Park Service). A subsequent preliminary analysis by the U.S. Geological Survey in 2001 determined that an abundance of clay in the upper soil layers prevented obtaining useful results. During recent planning for construction of an administrative building and new visitor center, the National Park Service used an auger to probe vertically to a depth of about 1 m and horizontally in a grid spaced at 1 m intervals, and this has proven to be moderately effective as a means for locating buried petrified wood. When a large specimen is located, construction plans can be modified to avoid damaging the material.

Physical Weathering

The Rocky Mountain region experiences harsh weather conditions that include extreme temperature fluctuations and abundant precipitation. Florissant's silicified stumps are regularly exposed to atmospheric precipitation and to ground moisture from wet soils and snow cover. These conditions make freeze-thaw weathering a likely cause of major structural damage to the stumps.

Meteorological factors that influence frost weathering rates include rainfall, snowfall, and temperature. Freezing can occur during any month, but even during the coldest month (January) temperatures often warm well above freezing. Climate data collected from a standard meteorological station at Florissant Fossil Beds National Monument since the 1980s show January daily high/low temperatures that fluctuate from −16 °C to 10 °C. Mean annual precipitation is 39 cm, 87% of which falls from March through September, primarily as summer rainfall. The ground surface is often barren during the winter, with only 1.5 cm of precipitation falling during the three-month period from December through February. Greatest snow accumulations are usually in November and March, with March snowfall averaging 35 cm (= precipitation value of 3 cm).

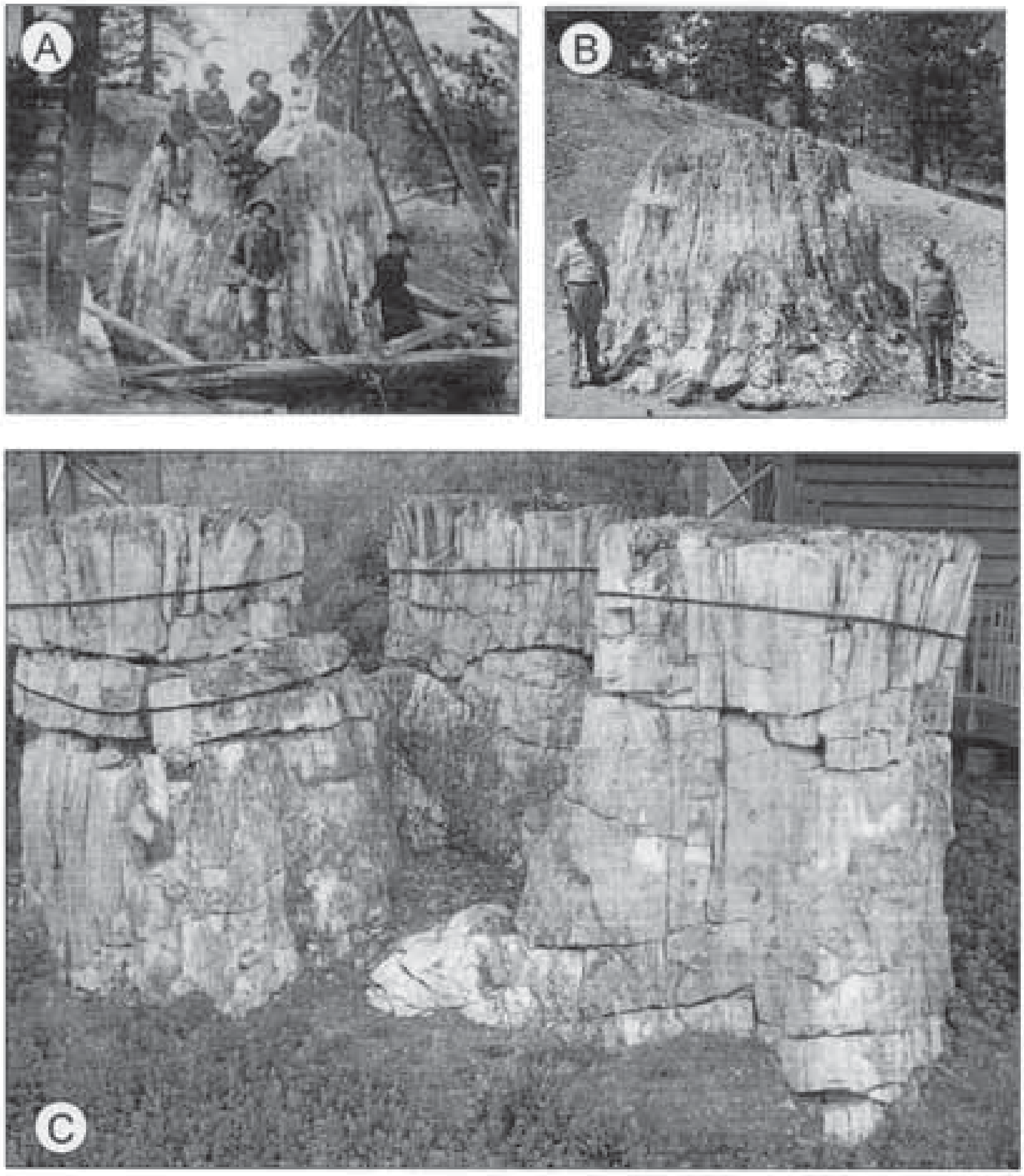

Figure 5. (A, B) Archival photographs of the Big Stump (FLFO P-16). (C) Modern photo of Redwood Trio (FLFO P-20), reinforced with steel cable bands.

Moisture that infiltrates fractures in the stumps can potentially freeze, thaw, and refreeze within a matter of hours. This phenomenon is most pronounced during the spring and fall, and is exacerbated by the fact that silicified trunks are large enough that the south side may thaw while the north side remains frozen. As discussed below, detailed microclimate data were obtained from several fossil sites during the 2003–2004 cold season in the hope of enhancing understanding of the frost-weathering process. The formation of ice within a porous rock appears to provide a simple explanation of frost weathering, but a combination of physical processes is involved (Powers, 1955; Winkler, 1968, 1975; Larsen and Cady, 1969). In addition to the pressure generated when water freezes, accompanying displacement of unfrozen water may generate hydraulic pressure. Severity of frost damage is influenced by the amount of absorbed water that is present and by the size and shape of the pores. Under laboratory conditions, coarse-grained and coarse-pored rocks generally withstand freezing well, and for fine-grained rocks the susceptibility to frost weathering is related to the pore size, with smaller pore sizes experiencing less weathering. Walker et al. (1969) found that rocks that contain more than 5% water by volume are very susceptible to frost damage, particularly when mean pore

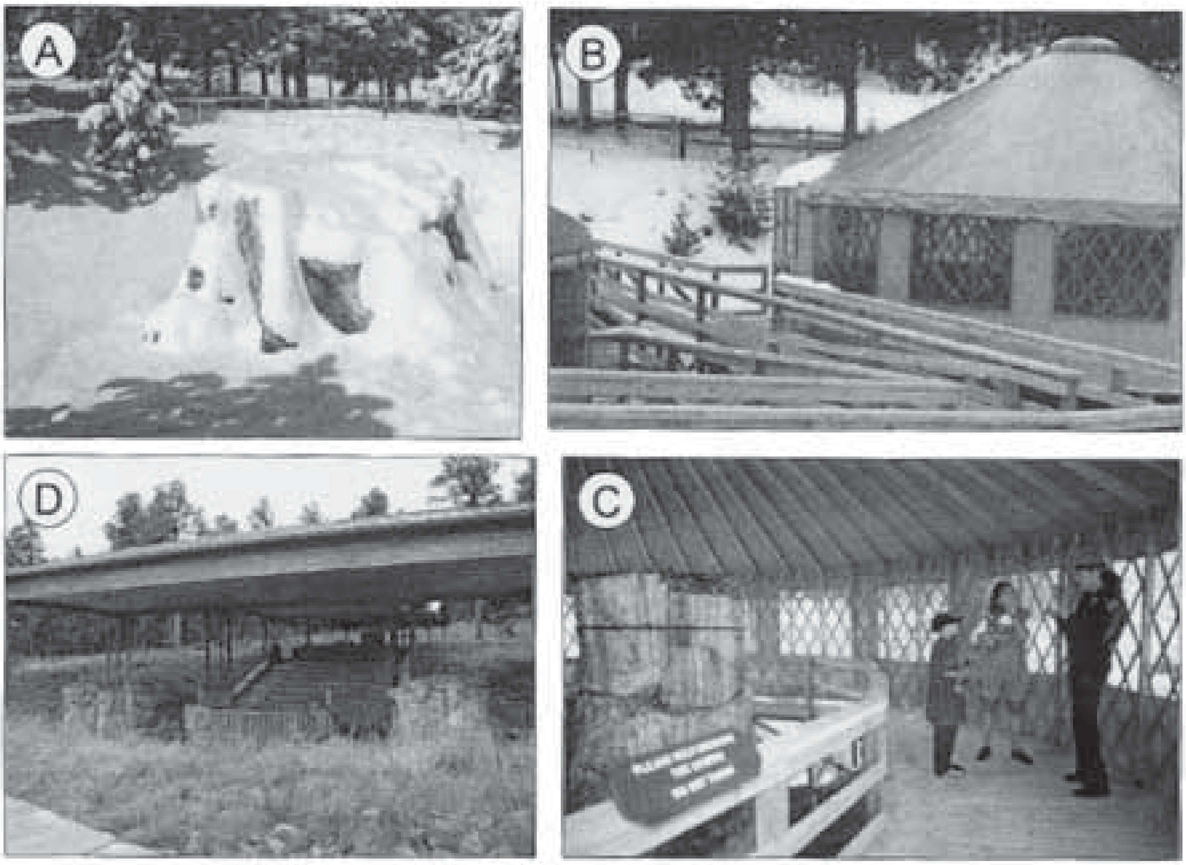

Figure 6. (A) Snow accumulation on unprotected stump (FLFO P-46). (B, C) Yurts used to shelter several stumps between 1997 and 2001. (D) Amphitheater constructed in 2001 shelters two stumps (FLFO P-20 and P-46).

diameters are >5 µ. These large pores allow liquid to escape as the frost line advances through the rock. Hudec (1978) conducted laboratory tests that showed the susceptibility of carbonate rocks used for engineering aggregate was directly related to the tendency of the materials to become water saturated from adsorption. Because absorbed water in these rocks was observed to be highly resistant to freezing, Hudec concluded that deterioration of certain "frost sensitive" rocks may instead be the result of pore pressure effects rather than ice formation. These experimental observations suggest that freeze-thaw weathering is a complex phenomenon. However, past studies have been devoted to porous sedimentary rocks composed of approximately equant grains, and to carbonate rocks, concrete, and other materials of engineering importance. The siliceous and carbonaceous composition and the fibrous texture of Florissant silicified wood may cause its weathering characteristics to be different from other lithotypes.

Biological Weathering

Biotic factors that can cause deterioration of the fossils include growth of modern plants that live on the top surfaces of the petrified stumps. These plants range in size from lichens, herbs and shrubs to a moderate-size ponderosa pine tree (Fig. 4A and 4B). Root growth penetrates the stumps along existing fractures, increasing their width. Animal activity is a much less important source of deterioration, but damage can be caused by nesting birds, burrowing rodents, and trampling of the top surfaces of exposed stumps by herds of elk. As these effects are thought to be minimal, biotic weathering processes are not a focus of this study.

Conservation History

Past conservation strategies at Florissant Fossil Beds National Monument have included use of metal bands to reinforce fractured stumps and installation of shelters to reduce exposure to precipitation. Before 1997, the excavated stumps were fully exposed to weather, including winter snowfall (Fig. 6A) and heavy rain and hail during the summer. In 1997, the National Park Service purchased and assembled two large yurts (circular canvas tents modified from the design of the traditional dwellings of central Asia) as temporary shelters to enclose two of the stumps, including the Redwood Trio (FLFO P-20) and another stump adjacent to it (FLFO P-31). These shelters provided protection from precipitation and reduced temperature fluctuations. In 2001, the yurts (Fig. 6B and 6C) were replaced by two large permanent shelters (Fig. 6D) that

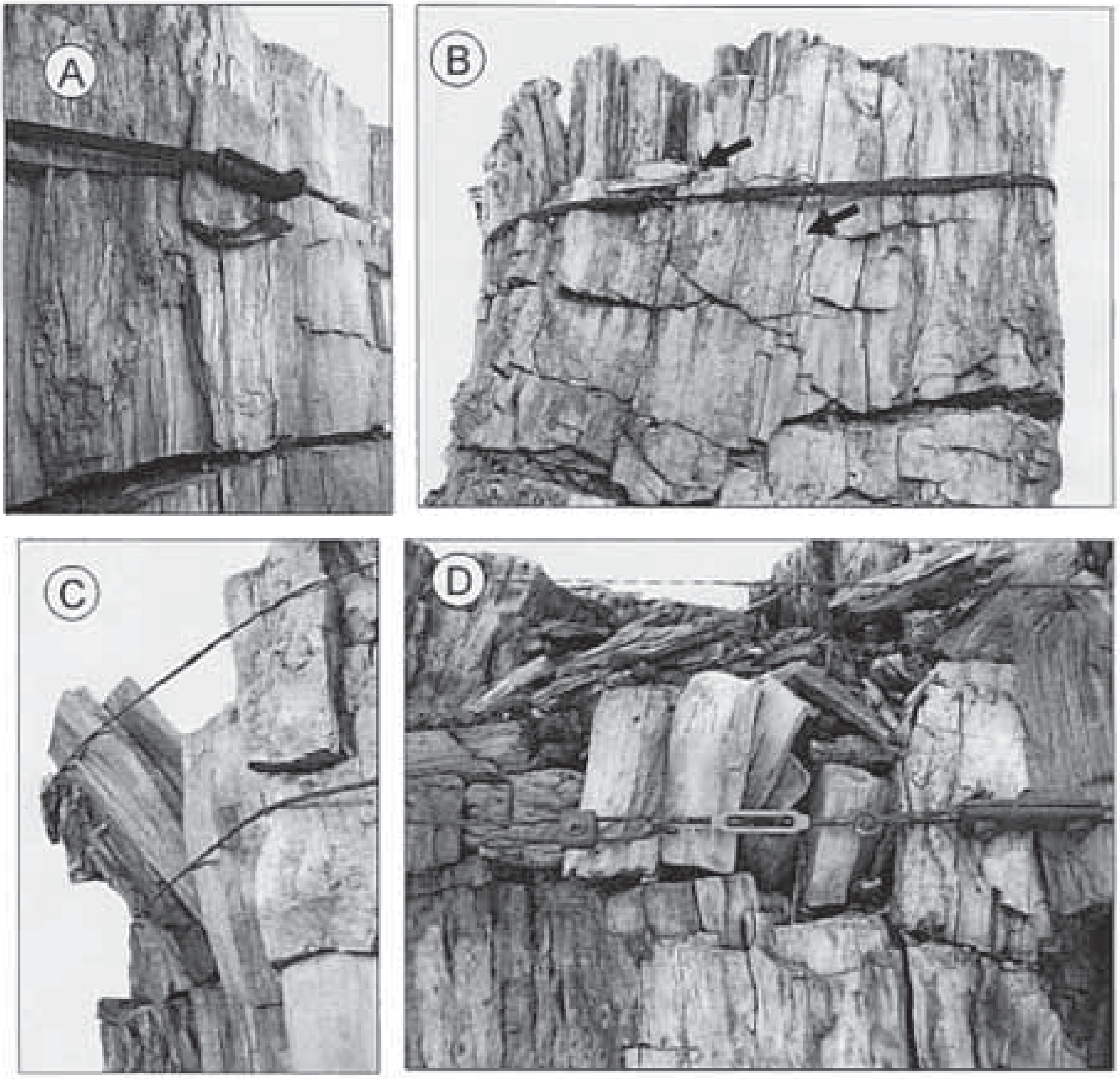

Figure 7. Flat metal bands (A, B) and flexible steel cables (C, D) were installed in an early attempt to reinforce petrified stumps. HOBO® Micro Station data-logging module and sensor mounted on surface of FLFO P-20 are shown with arrows on B. A second sensor (not visible) was placed in a 25 cm deep crevice and sealed with plasticine clay.

provide a roof, but no walls, to protect three of the most spectacular stumps: FLFO P-20, P-31, and P-46, the last being the park's largest stump, with a dbh of 4.1m. Although much less effective than the yurts for providing a protective environment for the fossils, the open-sided permanent shelters are a compromise to help reduce exposure to precipitation while fulfilling the desire of park management to provide a new amphitheater with an unobstructed view. Wind-blown snow, direct exposure to outdoor temperature fluctuations, and poor drainage are problems inside these structures, and the stumps remain susceptible to weathering, creating the need for further stabilization treatment.

Sometime before the 1950s, metal bands were installed around the circumference of several petrified stumps near the present visitor center. These bands remain in place today. Two types of reinforcements were used: rigid steel bands that were bent around the stump and tightened using an adjustable threaded bolt (Fig. 7A and 7B), and flexible steel cable bands (Figs. 5C, 7C, 7D). These reinforcements were inspected during this study, and both types were found to offer only minimal support to the petrified trees. The bands do not conform to the uneven stump surface, offering only point-to-point contact around the circumference. Threaded bolts used to secure rigid metal bands have rusted into locked positions. In response to force, the flexible cable bands shift their position instead of providing firm support. Large pieces of the stumps have broken and fallen at places where gaps exist between the bands and adjacent fossil wood (Fig. 7C and 7D). The bands and cables do serve to hold large fragmented blocks of wood in place, and their removal would allow many loose pieces to fall.

New Conservation Strategies

Two basic strategies could be used to reduce weathering damage to fossil wood at Florissant Fossil Beds. One technique would be to use an adhesive or joint filler to join adjacent fragments and to fill open voids and fractures, blocking the entry of water. A second possibility would be to apply a low-viscosity consolidant capable of infiltrating intercellular spaces to reduce permeability and increase mechanical strength.

The ideal adhesive or joint filler would have a bond strength that is equal to or greater than the strength of the material being bonded, have acceptable aesthetic qualities (e.g., repairs should not be visually obvious), and be effective in the environmental conditions of the site in terms both of application characteristics and permanence of bond. As examples, an adhesive designed for bonding dry surfaces will not be effective for repairing damp, porous specimens, and products that require warm temperatures for polymerization may be impossible to apply in cool weather.

A successful consolidant must be able to penetrate the stone prior to setting. The depth of penetration ideally reaches an unweathered substrate, binding adjacent granules in a manner that prevents further decay. The ideal consolidant would not substantially affect either the stone's chemical composition or its aesthetic qualities, and this consolidant would be removable without damaging the stone at any later time if problems developed or a better product became available. Finally, the consolidant should be easy to apply under field conditions.

At present, no adhesives or consolidants possess all of these characteristics. Although some products have been used successfully for architectural and archaeological conservation projects (Horie, 1987; Grisafe, 1996, 2000; Jerome et al., 1998; Grissom et al., 1999; Oliver, 2002), geologic and environmental conditions at Florissant are very different from conditions found at most of the archaeological sites. For example, according to their manufacturers, some silicon-based consolidants allow the escape of water vapor, but these observations are mostly based on sandstone and other clastic sedimentary rocks that have high permeability. In these materials, equant mineral grains are surrounded by intergranular spaces that allow aqueous solutions to penetrate deeply. The fibrous structure of Florissant silicified woods may cause consolidants to perform differently. Because most of these products cannot be removed once they have been applied, it is critical to field test adhesives and consolidants to evaluate their performance.

A particular concern is that the introduction of adhesives or consolidants might retard the evaporation of moisture that is absorbed into the stumps from their contact with moist ground or from precipitation that enters along unsealed fractures, thus increasing weathering rates. Winkler (1975) and Gauri and Appo Rau (1978) noted that consolidants could accelerate weathering rates by producing a relatively impermeable outer layer, causing stresses to accumulate at this boundary zone. Subsequent weathering may cause the treated layer to peel away as a unit, unlike the gradual pitting that occurs on natural surfaces. Oliver (2002) reported highly variable results from tests of organosilicate consolidants used in attempts to retard weathering of sedimentary rocks at three national monuments in the southwestern United States. When underlying causes of deterioration (e.g., subsurface moisture, presence of soluble salts, and freeze-thaw cycles) could not be ameliorated, consolidants had very limited effectiveness. These observations are a warning that the possible use of chemical treatments at Florissant requires careful preliminary testing.

EXPERIMENTAL METHODS

Weather Data Logging

In order to quantify environmental conditions that influence weathering at the Florissant fossil forest, HOBO® Micro Station data loggers were installed on two fossil stumps, and temperature and relative humidity values were recorded at 3 h intervals between August 2004 and June 2005. One unit was placed on the Redwood Trio stump (FLFO P-20), which is protected by a covered shelter. The other was placed on an exposed stump (FLFO P-47) located ~60 m east. Each unit had two sensors; one was placed on the exposed stump surface and the other was lodged into a crevice ~25 cm deep. The crevice sensor was enclosed with a plasticine clay seal that served as a barrier to external atmospheric conditions. Unfortunately, data from the subsurface sensor in the outdoor stump were rendered unusable because the enclosing clay was removed by an animal at an unknown time during the measurement period.

Field Testing of Consolidants and Adhesives

We conducted a preliminary study to lay the groundwork for future scientific examinations. Our cursory investigation involved a descriptive analysis using four types of adhesives and consolidants that could possibly be used at Florissant: organosilicates, solvent-dispersed polyvinyl acetyl adhesives, an epoxy resin, and casein-based adhesive and joint filler. These products were applied to samples of petrified *Sequoioxylon* wood that were collected during construction of the stump shelter and amphitheater in 2001. Field observations were made of specimens at the time of product application, at occasional intervals during the course of the experiment, and after eight months of exposure to outdoor weathering conditions.

Consolidants

Organosilicate consolidants. Ethyl silicate (tetraethoxysilane) formulations were selected for testing because these organosilicates have been used as consolidants for architectural and archaeological applications, with varying degrees of success (Torraca, 1970; Grisafe 1996, 2000, 2001). Ethyl silicate can be dispersed in ethanol or organic solvents such as acetone and methyl ethyl ketone to form a low-viscosity liquid that penetrates deeply into porous stone. Polymerization involves the formation of siloxane (Si-O-Si) bonds that provide great strength while having little impact on the treated stone (Schmidt-Thomsen, 1969). A unique characteristic of ethyl silicate solutions is that during solidification, amorphous silica gel is deposited as a coating on individual mineral grains, leaving void spaces open. This binding action increases the physical strength of the stone without rendering it impermeable or changing its thermal expansion characteristics. Ethyl silicates are sometimes combined with hydrophobic silicone resins. In addition to increasing mechanical strength, these products are intended to reduce the stone's permeability to prevent absorption of moisture. To be successful, these consolidants must still allow passage of water vapor to reduce the threat of spalling (the fragmentation or separation of the surface layers) that is often associated with water-repellent coatings.

Precipitation of amorphous silica is a nonreversible chemical reaction, and the consolidant cannot be removed if problems develop later. Although these organosilicates have been on the market for more than 30 years, knowledge of their stability over very long periods is lacking. The performance characteristics of these products are known primarily from their use on porous rocks (e.g., sandstone and clastic limestone), which are materials that have petrologic characteristics that are significantly different from those of silicified wood.

Our study tested the effectiveness of a variety of ethyl silicate products that ranged from pure ethyl silicate consolidants to silane-based crèmes and emulsions. Complimentary samples were provided by Wacker Silicones, the American division of the German Wacker Chemical Corporation, Silbond Corporation, and PROSOCO Corporation. Silbond Condensed® and Wacker Silres® BS OH100 are ethyl silicate monomer dissolved in ethanol. PROSOCO Conservare® H100 is ethyl silicate in ethanol, with the addition of an organic tin compound as a catalyst to speed solidification. Silbond ESP-E® contains ethyl silicate polymer in alcohol, formulated as a medium for the manufacture of zinc-rich coating products. Wacker Silres® BS Creme-C is a thixotropic emulsion of silane and water, designed as a penetrating water repellent for concrete. Wacker Silres® BS 2001 is an aqueous liquid emulsion of silane/siloxane, marketed as a water repellent for concrete, brick, and tile. PROSOCO Conservare® H100 consists of ethyl silicate and silane dissolved in a mixture of organic solvents, with an organic tin compound as a catalyst.

Application of consolidants. Seven silicified wood samples, numbered one through seven and prefaced with a "C" for consolidant, each having an approximate volume of 1200 cm^3, were used for outdoor testing of the various organosilicate consolidants. One sample was left untreated as the control sample. Organosilicate products were applied to the exterior surfaces of the seven samples, so we could test each formulation on all sides and top of a single specimen. Smaller (50–100 g) specimens were immersed in consolidant and air dried, but not exposed to weathering, to provide reference samples. Prior to application of consolidants, all samples were cleaned using scrub brushes, sponges, and water. Because of the fragile nature of the petrified wood, it was not possible to remove all soiling agents. The outdoor testing area was set up in a remote, secure area of the monument. Treated samples were emplaced vertically in the soil to serve as miniature proxies for silicified stumps (Fig. 8A). Consolidants were applied following industrial protocols specified by the manufacturers, in sufficient quantities to saturate the specimen surfaces. Unstable weather proved to be a complication; product applications started in the morning and were completed in the early afternoon. Because of afternoon showers, the testing area was covered with tarps to protect the specimens from rainfall and avoid a negative effect on the results, although the change in ambient humidity levels could not be regulated. Per manufacturer specifications, environmental changes such as these can affect the performance of the consolidants. No obvious problems were detected, but the experiment provided a reminder that unpredictable meteorology needs to be considered during the selection and use of these products.

Adhesives

Polyvinyl acetyl adhesives. Polyvinyl acetyl adhesives have long been used during preparation of vertebrate fossils, as well as in a wide range of industrial applications. Members of this chemical family include polyvinyl formal (PVF, trade name Formvar®), and polyvinyl butyral (PVB, trade name Butvar®). Both compounds can also be dissolved in certain organic solvents, and subsequent solidification occurs as a result of evaporation (Farmer and Jemmott, 1990). This mode of application makes these vinyl polymers useful for strengthening porous materials. In solid form, polyvinyl acetyl compounds melt and flow when they are heated, and this thermoplastic behavior is utilized for many industrial applications. PVF has long been used as an insulating coating for electric wire, whereas PVB is the variety usually selected for use with wood, textiles, paper, and other porous materials. PVB has been widely used as a treatment for fossil bones and archaeological materials that require conservation treatment during excavation and subsequent preparation. Common PVB solvents include acetone, ethanol, isopropanol, and toluene.

The fast evaporation of organic solvents can be an asset for application, although the flammability and potential inhalation hazards of these solvents require careful safety procedures. A wide range of viscosities can be achieved by varying the concentration of solvent, and polyvinyl acetyl compounds are reasonably inexpensive. A particular advantage of PVB for conservation applications is that it can be removed at a later time by flushing the treated material with solvent, although this would be destructive if applied to the fossil stumps and therefore should be considered only for localized and not large-scale applications. When evaluating localized application, a potential aesthetic disadvantage is that the evaporation of solvent prior to complete

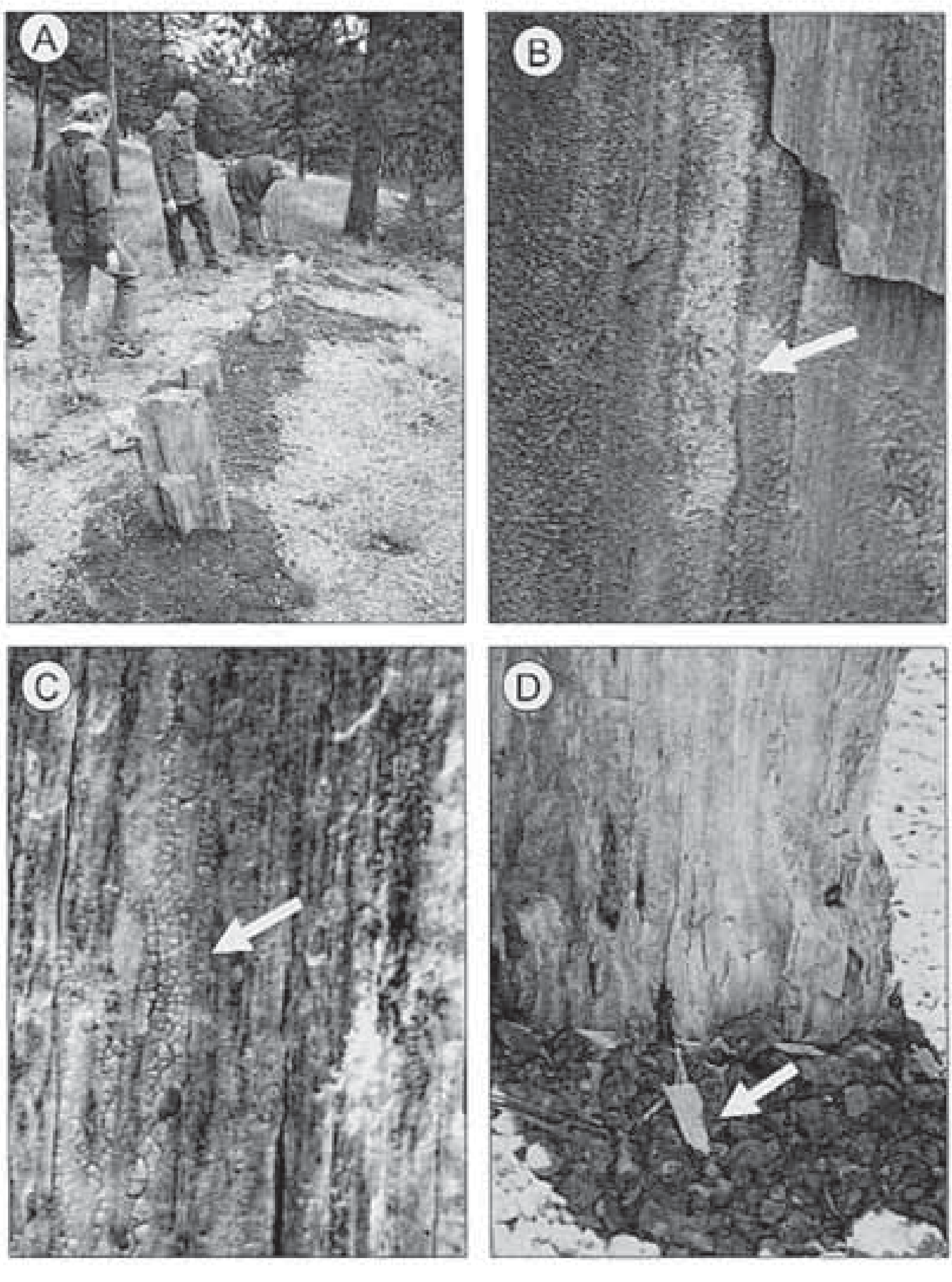

Figure 8. (A) Outdoor area used for testing adhesives and consolidants. (B) Example of the white silica residue (arrow) left after initial curing of several organosilicate formulations. (C) Flaky crust (arrow) formed after curing of Silbond ESPE®. (D) Specimens treated with organosilicates showed basal spalling (arrow) after eight months of outdoor exposure.

absorption may leave PVB as a glossy surface residue. This residue could be removed with a solvent wash of the area. One long-term consideration is the possibility that these products may gradually become less soluble with age because of the development of crosslinks between the polymers; conversely, bond strengths may decrease because of breaks in the polymer chain. Two PVB products were selected for testing at Florissant, both of which are produced by Solutia (formerly Monsanto Corporation): Butvar B-76® and Butvar B-79®.

Epoxy. Epoxy adhesives require mixing resin and a hardener that crosslink to produce a strong, irreversible bond (Meath, 1990). After hardening, epoxies are waterproof and resistant to acids and alkalis, but they soften at high temperatures and have slight solubility in acetone, alcohol, and some other organic solvents. A wide range of resins and hardeners can be used to vary viscosity, minimum curing temperature, and setting time. Unlike solvent-based adhesives that solidify by evaporation, epoxies do not significantly change in volume as they cure, making them perform well as gap fillers. Epoxies may adversely affect the appearance of the specimen because of their color and gloss. Cleanup of excess adhesive prior to curing with organic solvents reduces these aesthetic problems. Solidified epoxy is nearly impossible to remove. The epoxy tested at Florissant was Huntsman's Araldite 2015 A/B®, a translucent thixotropic adhesive.

Casein adhesive. Casein adhesives date back at least to ancient Egypt, when milk curd and lime were mixed to produce waterproof glue. Once an industrial mainstay, casein adhesives have largely been replaced by synthetic resins. Presently they remain in use as stabilizers in latex-based finishes and adhesives, and as binding and surface-coating agents for paper (Bye, 1990). For conservation purposes, casein products have the advantage that they can be applied under a wide range of temperature conditions (4–40 ºC), they are nontoxic, and water can be used to clean up uncured excesses. After the powder casein product is mixed with water, a chemical reaction produces calcium caseinate, a strong, hard, brittle bonding agent with high moisture resistance and an off-white opaque color that can readily be modified by addition of pigments. In modern formulations, plasticizers and fungicides are commonly added to increase flexibility and retard microbial degradation (Horie, 1987). Our study investigated two formulations that were recommended by technical consultants for Jahn Products (distributed in the United States through Cathedral Stone Products): Jahn M30® (marketed as a microinjection grout) and Jahn Restoration Adhesive®.

Application of adhesives. Seven silicified wood specimens were used to test the effectiveness of adhesives for repairing fractures. For these tests, the samples were broken, usually along existing cracks, to provide clean fracture surfaces. Each fractured sample was repaired with one of the following products: Solutia Butvar-76® or B-79® PVB, Araldite 2015® epoxy, Jahn M30® casein injection grout, or Jahn Restoration Adhesive®. The PVB adhesives were both diluted to honeylike consistency with methyl ethyl ketone and acetone. These liquids were applied to fracture surfaces and the specimens were allowed to remain undisturbed while the solvent slowly evaporated. After solidification of the adhesive, more dilute PVB solutions were brushed on the specimen surface. For the injection grout specimen, surface cracks were dammed using water-miscible clay, and the injection grout was forced into an opening using a large-gauge syringe. Application of the injection grout proved challenging because of the low viscosity of the product selected—the product seeped out of unnoticed, micro-cracks—and required extensive post-application cleaning and removal of the product from the sample surface. Repaired specimens were exposed to the same weathering conditions as the consolidant-treated samples.

Laboratory Analyses of Mineralogy and Physical Properties

A variety of analytical methods were used to study the mineralogy and physical properties of silicified wood samples that had been selected by National Park Service personnel for field tests. Mineral compositions were determined on packed powders by X-ray diffraction, using a general Electric XRD-5 diffractometer with nickel-filtered copper radiation, at a scan rate of 2°/min. Density was measured using a Sartorius model 1700 electronic analytical balance equipped with a model 6080 hydrostatic weighing accessory. Weight losses ("loss on ignition") were measured after heating 1 g each of powdered samples for 30 min at 900 °C, after first drying the samples overnight at 100 °C. After eight months of field exposure, the absorption characteristics of samples treated with organosilicates were determined to help evaluate the performance of these products. A diamond blade was used to trim away the outer 5 mm layer from one surface of each specimen, and absorption of liquid water was observed by placing a drop of water on the cut surface. Quantitative data came from measuring the weight change when a slab having a volume of ~0.5 cm^3 was cut from the 5–10 mm depth zone of each specimen, and immersed in distilled water for 1 h.

Major element compositions of untreated samples (Table 1) were determined by X-ray fluorescence (XRF), using a Rigaku model 3070 XRF wavelength dispersive spectrometer. Samples were prepared by fusing 3.5 g of powdered petrified wood with 7 g of lithium tetraborate to produce a glass disc. These elemental analyses were undertaken to provide an indication of compositional variations among individual Florissant fossil wood specimens. This information was not obtained until after field tests had begun, but the data provide a useful baseline for designing future studies.

Optical photomicrographs (Fig. 2) were taken with a Wild Photomakroscope equipped with a Spot Infinity digital camera. A Tescan Vega scanning electron microscope operated at a beam voltage of 10 KeV was used to obtain the images show in Figure 3.

RESULTS AND DISCUSSION

Weather Data

Temperatures expressed as the number of freeze-thaw cycles recorded by the HOBO® data loggers are summarized in

TABLE 1. PHYSICAL AND CHEMICAL CHARACTERISTICS OF FLORISSANT FOSSIL BEDS SILICIFIED WOOD SAMPLES USED FOR TESTING CONSOLIDANTS

Sample	C1	C2	C3	C4	C5	C6	C7
Mineralogy	Opal-CT & trace of quartz	Quartz & opal-CT	Opal-CT	Opal-CT	Opal-CT	Opal-CT	Opal-CT
Treatment	Silbond Condensed®	Silbond ESP-E®	Wacker Silres® BS 2001	Wacker Silres® BS Creme-C	Wacker Silres® BS OH100®	PROSOCO Conservare® H100®	PROSOCO Conservare® OH100®
Major element composition by XRF							
SiO_2	78.87%	93.71%	85.27%	85.91%	87.60%	83.99%	84.85%
Al_2O_3	0.14	0.30	0.27	0.10	0.44	0.82	0.95
TiO_2	0.05	0.12	0.06	0.03	0.14	0.06	0.06
Fe_2O_3*	0.762	0.14	1.66	1.75	2.86	6.40	4.81
MnO	0.00	0.00	0.00	0.00	0.00	0.00	0.00
MgO	0.00	0.00	0.00	0.00	0.00	0.00	0.03
CaO	0.21	0.32	0.70	0.60	0.70	0.39	0.38
K_2O	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Na_2O	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Loss on ignition	20.01	3.59	12.42	11.12	8.82	9.02	8.33
Total	100.00[†]	98.18	100.38	99.51	100.56	100.68	99.41
Physical properties							
Color of powder	dark brown 7.5YR 3/2	very pale brown 10YR 8/2	brown 7.5YR 4/2	brown 7.5YR 5/2	brown 7.5YR 5/3	light brown 7.5YR 6/3	brown 7.5YR 5/3
Density g/cm^3	1.83	1.99	1.66	1.68	1.70	1.72	1.68
Absorption (untreated)	ND	8.8%	12.4%	19.1%	ND	8.9%	ND
Absorption (treated)	2.7%	7.5%	9.2%	4.1%	10.4%	7.8%	11.8%

*Total iron calculated as Fe_2O_3.

[†] oxide% values to 100% to adjust for high loss on ignition.

Figure 9. The greatest variations were measured by the outdoor exposed sensor on stump FLFO P-47, which recorded a total of 119 freeze-thaw events over a period of 289 days. The sensor mounted on the surface of FLFO P-20, a stump sheltered by the amphitheater roof, measured 95 freeze-thaw events during the same time period. Only 21 freeze-thaw events were recorded by the sensor embedded within this stump.

March 2005 was the month that had the largest number of freeze-thaw events as recorded by the surface sensor on unprotected stump FLFO P-47 and the surface and subsurface sensors on sheltered stump FLFO P-20 (Fig. 10). These data provide insights into the performance of the shelters in regards to freeze-thaw weathering.

The surface sensor on stump FLFO P-47 recorded a wide range of daily temperature fluctuations, as expected for a stump that is directly exposed to the elements. The external sensor on sheltered stump FLFO P-20 recorded temperature variations that were nearly as great (range) as those of the unsheltered stump, indicating that the shelter had little effect on the frequency of

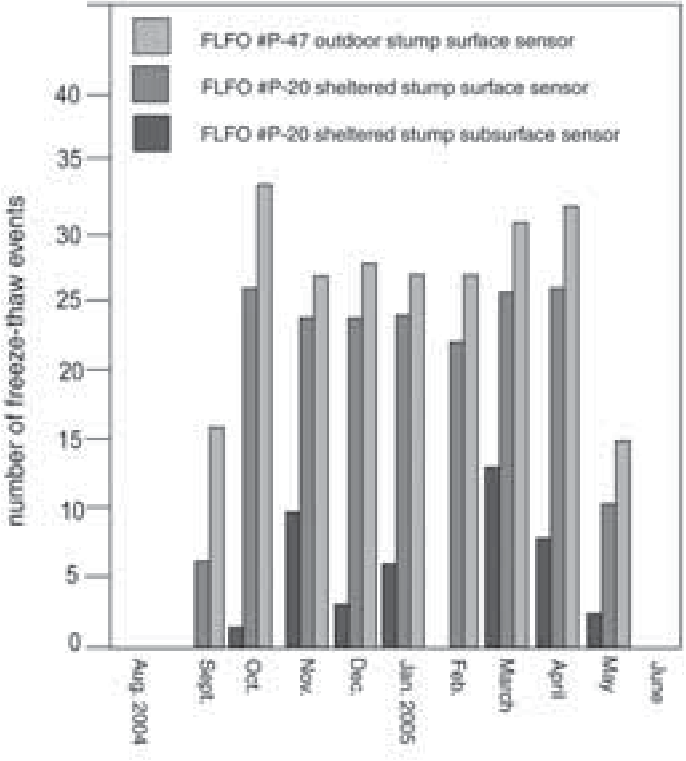

Figure 9. Temperature data expressed as the number of freeze-thaw cycles recorded over 289 days during the 2004/2005 cold season. The subsurface sensor for stump FLFO P-20 was embedded in a crevice ~25 cm below the surface.

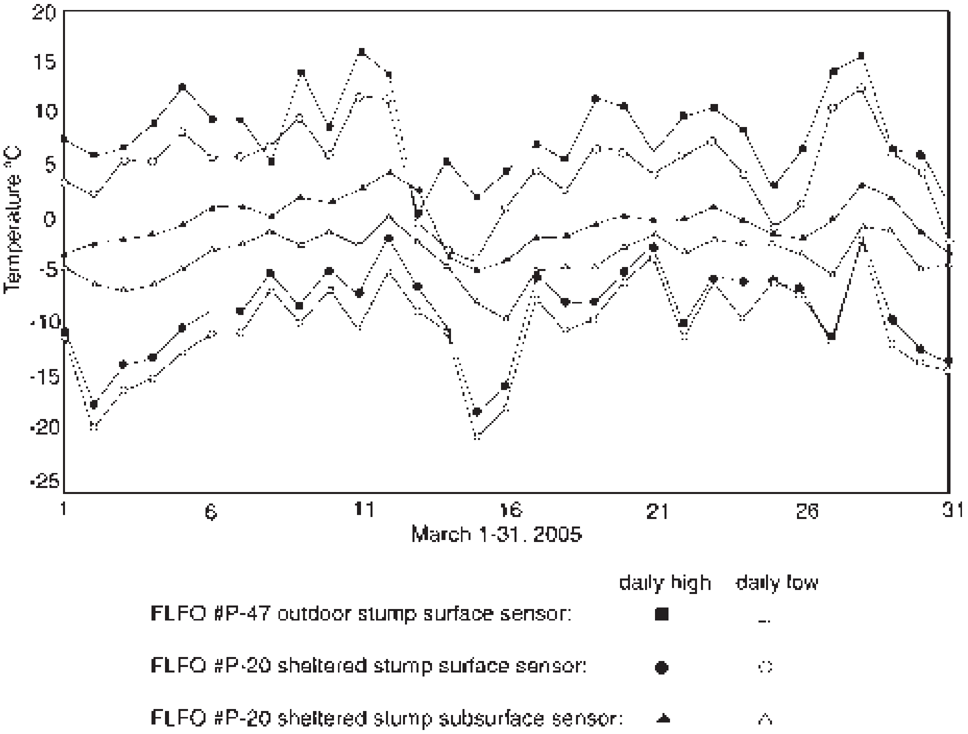

Figure 10. Daily high and low temperatures recorded by surface and subsurface sensors during March 2005, the month that had the greatest temperature variability during the 2004–2005 cold season.

freeze-thaw cycles. Observations based on daily high and low temperatures are consistent with temperature data recorded at 3 h intervals. The sensor on stump FLFO P-47 recorded 16 freeze-thaw events, with <0 °C temperatures measured for up to 18 continuous hours. The sensor on the surface of stump FLFO P-20 recorded 13 freeze-thaw events, with continuous <0 °C temperatures persisting for as much as 78 h. Only seven freeze-thaw events were recorded by the sensor embedded in FLFO P-20, with up to 153 continuous hours <0 °C temperatures. Thus, it appears that damage from freeze-thaw cycles is most likely to occur only in a shallow outer zone of each stump, an interpretation that is supported by field observations that indicate near-surface spalling and flaking to be the most common form of structural damage.

Freeze-thaw weathering only occurs in materials that contain moisture. Although open-sided shelters do not greatly reduce the number of freeze-thaw events, they may retard weathering rates by protecting the stumps from rain and snow. Sheltered stumps may also absorb moisture from the atmosphere during periods of elevated humidity. Relative humidity values recorded at the surface of stump FLFO P-20 during March 2005 ranged from 15.75% to 94.25%, similar to the 16.25% to 96.75% variation measured by the exposed sensor on stump FLFO P-47. The low range of relative humidity values recorded by the sensor embedded in stump FLFO P-20 (e.g., 51.25% to 61.75% measured during March 2005) presumably resulted from the barrier provided by the plasticine clay used to seal this sensor.

Damage from freeze-thaw weathering is most likely to occur during the cold season when sunny days alternate with cold nights. Relative humidity (RH) values show a diurnal cycle, as illustrated in Figure 11. Nighttime RH values were typically much higher than at midday. Daytime RH values show a strong negative correlation to temperature; i.e., the warmest days were the driest, a statistical pattern that is consistent with the high frequency of sunny days during much of the winter. This weather pattern is also evident in the wide range of temperature variation measured by the two sensors that were exposed to atmospheric conditions.

The sensor in stump FLFO P-20 showed that the subsurface of this stump remained below 0 °C for long time periods, in contrast to the frequent freeze-thaw events measured at stump surfaces. Daily high temperatures measured for sheltered stump FLFO P-20 were only slightly different from temperatures measured by the unprotected sensor, suggesting that sun-shading effects of the shelter are largely offset by the fact that the roof acts as a solar collector that warms the air beneath it. Additional weather observations would be helpful for formulating conservation strategies, but at present no definite conclusions can be made.

Mineralogy and Geochemistry of the Samples

Major element compositions of silicified wood specimens (Table 1) that were used for testing and evaluating the application of consolidants and adhesives are similar to results obtained from fossil stumps at other sites in Florissant Fossil Beds National Monument, consisting primarily of silica present as opal-CT and chalcedony (for a detailed description see Mustoe, this volume). Density values of 1.66–1.72 g/cm^3 were measured for samples C3–C7 that contain opal-CT as the only silica mineral. Density

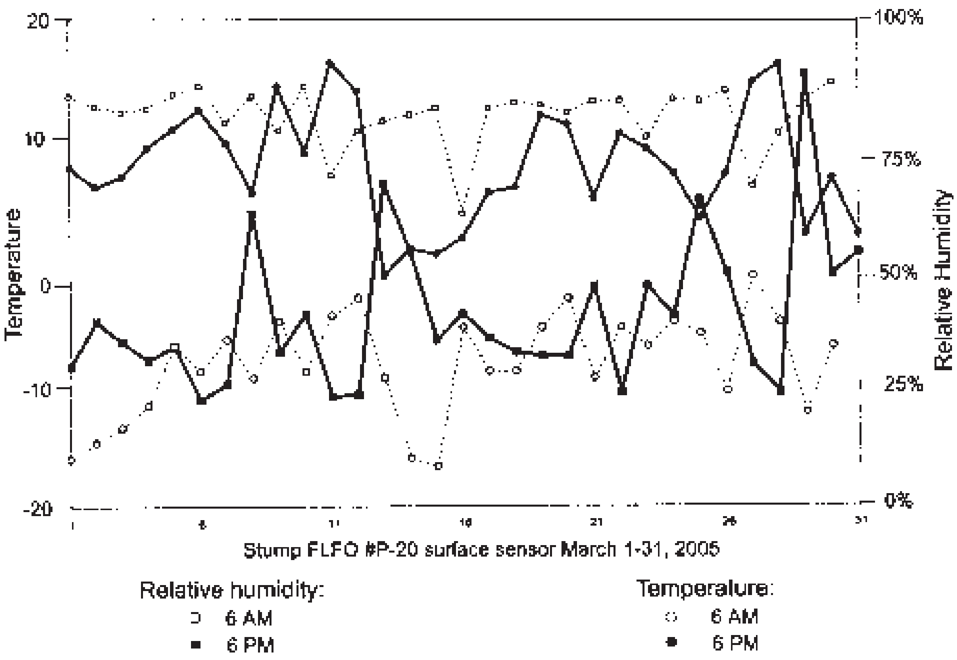

Figure 11. Temperature and relative humidity values recorded by sensors on stump FLFO P-20 from March 2005 show diurnal variation.

values of 1.83 and 1.99 g/cm^3 measured for samples C1 and C2 are consistent with X-ray diffraction patterns that indicate these specimens contain a mixture of opal-CT and chalcedony. Some Florissant fossil stumps contain chalcedony as the only form of silica (Mustoe, this volume), but the specimens used for field testing consolidants did not include examples of this lithotype.

Consolidants and adhesives

The results of field tests are described below and summarized in Table 2.

Consolidants

White patches of silica were visible shortly after application on most specimens that were treated with organosilicate products (Fig. 8b) This phenomenon was observed with formulations that contain monomeric ethyl silicate as the active ingredient (Wacker Silres® BS OH100®, Silbond Condensed®, and PROSOCO Conservare® OH100), and for the thixotropic product Wacker Silres® BS Creme-C, which contains additional silane as a water repellent. The polymerization process of ethyl silicates incorporates traces of water from the specimen and atmosphere, and hydrolysis results in the condensation of a silica gel (Horie, 1987). White patches may have been caused by high ambient humidity at the time of application. In the future, cleaning specimen surfaces with methyl ethyl ketone or ethanol to remove the unabsorbed product prior to curing may avoid this problem. The sample treated with Silbond ESPE® developed a flaky surface crust (Fig. 8C), possibly related to the presence of a catalyst that caused solidification of the product before it was completely absorbed. Surface silica deposits were not visible on specimens treated with Wacker Silres® BS 2001 and PROSOCO Conservare® H100.

After eight months of outdoor exposure, the appearance of each sample was compared with photographs taken shortly after the products had been applied. During episodes of wet weather during the course of the experiment, water was observed to bead or pool on surfaces of specimens treated with Wacker Silres® BS 2001 and Wacker Silres® BS Creme-C, two of three products that contain water-repellent additives. Hydrophobic phenomena were not observed in the sample treated with the third product containing a water repellent, PROSOCO Conservare® H100.

In the sample treated with Silbond ESP-E®, after eight months the flaky crust had been washed away and a slight hazy zone remained as a remnant of the consolidant application; in all other samples surface silica deposits were no longer visible. No discolorations were evident for any treated specimens. The basal zones of samples treated with Silbond Condensed®, Wacker Silres® BS Creme-C, Wacker Silres® BS OH100, and PROSOCO Conservare® H100® showed small splayed fractures and small amounts of petrified wood debris around the base of the specimen (Fig. 8D). However, there was also an increase in wood debris at the base of the untreated control sample. Because of this, and the facts that each product was tested on only a single silicified wood sample and weather conditions varied during application, additional testing is needed to accurately compare the performance of the various organosilicate formulations. Surface damage and basal debris were not observed for every treated sample, but the degree of specimen deterioration did not appear to be related to the product type (e.g., pure ethyl silicate emulsions versus products containing hydrophobic additives). Overall, the preliminary evidence suggests that organosilicate consolidants may not be effective for reducing weathering rates for Florissant fossil wood.

TABLE 2. SUMMARY RESULTS FOR FIELD TESTS OF CONSOLIDANTS AND ADHESIVES

Product	Active ingredient	Application characteristics	Comments	Results after 8 months of exposure to weathering
Organosilicate Consolidants				
Wacker Silres® BS OH100 Silbond Condensed PROSOCO Conservare® OH100 Wacker Silres® BS Creme-C	Ethyl silicate + catalyst	All formulations are organic solvent-based emulsions applied with a brush	White patches of silica residue were visible on most treated specimens after initial curing	Silica residues were nearly invisible. Treated specimens commonly showed small fractures and surface feathering, with traces of weathering debris at the base of the specimen
Wacker Silres® BS2 001 PROSOCO Conservare® H100	Ethyl silicate + hydrophobic silane		No visible impact to specimen	
Silbond ESP-E	Hydrophobic silane		Silbond ESP-E produced a flaky surface crust	Surface crust had faded to a hazy appearance
Adhesives				
Butvar B-76 Butvar B-79	Polyvinyl butyral	Solid dissolved in acetone/MEK to a honeylike viscosity	Flammable; requires good ventilation	Repaired fractures remained intact, but outer layer had deteriorated (from UV exposure?)
Araldite 2015A/B	Epoxy	2-part mix, 1:1 ratio	10 min. pot life	Repaired fractures remained intact. Excess adhesive on specimen surface remained glossy.
Jahn Restoration Adhesive	Casein	Powder mixed with water for use	Water cleanup of excess adhesive; can be applied at low temperatures	Low bond strength; repaired joints failed with minimal applied pressure
Jahn m30 microinjection grout	Casein	Powder mixed with water for use	Poor gap filling because of low viscosity	Repaired fractures remained intact

Laboratory data provide a partial explanation of the field observations. Absorption tests indicate that none of the organosilicate products penetrated deeply into the silicified wood. In every treated specimen, the outer surface was water repellent, but when a 5 mm layer was removed by sawing, a water drop placed on the cut surface was almost immediately absorbed. Quantitative measurements (Table 1) showed that although absorption was reduced in treated samples, the reduction was typically rather small. The only exception was sample C4, where surface treatment with Wacker Silres® BS Creme-C caused absorption to decrease, as indicated by a weight gain of 19.1% after fossil wood was immersed in water, compared to a gain of only 4.1% for treated material. Sample C4 appeared under the microscope to have much higher porosity than the other specimens. Although Wacker Silres® BS Creme-C possibly has greater effectiveness as a moisture sealant than other products tested, a more likely explanation is that the high porosity of the specimen merely facilitated deeper penetration. Test samples were not tested for absorption and mineralogy prior to application of adhesives and consolidants. Results of laboratory analyses post application revealed that the samples did not share absorption values or mineralogy.

Adhesives

Samples used for testing adhesives were examined after weathering exposure for visible evidence of bond failure and changes in appearance. Spontaneous joint failure was observed in one specimen repaired with the casein-based adhesive from Jahn Restoration; all other specimens remained intact. When arm strength was used to apply tensile stress, other samples repaired with the casein-based adhesive suffered joint failure, apparently because the adhesive failed to bond strongly to the silicified wood. The other casein-based product, the Jahn M30® injection grout, performed much better. Despite the challenging application of this product, injection grout strengthened the specimen to which it was applied and attempts to pull apart the specimen were unsuccessful.

Joints repaired with Araldite 2015 A/B® epoxy also resisted manual attempts to break the bond. Small traces of epoxy that remained on the surface from initial application remained slightly glossy, with no visible evidence of deterioration.

Fractures repaired with PVB remained well bonded, but the outer PVB coating layer became extremely brittle, and could easily be peeled away, along with a thin layer of silicified wood. This deterioration was probably caused by exposure to UV radiation. Marker tape had been wrapped around the circumference of one specimen at the time of product application, and removal of the tape after eight months of weathering exposure revealed a cohesive glossy PVB coating, in contrast to the faded flaking material on adjacent surfaces.

CONCLUSIONS

Data loggers proved to be very effective for providing a detailed record of temperature and humidity conditions at individual sites. Additional monitoring at Florissant would be desirable to understand better how microclimatic factors influence the effectiveness of shelters for protecting stump fossils from weathering. Because the effectiveness of adhesives and consolidants is not yet definitive, until more information is available these shelters appear to be the best option for attempting to minimize weathering damage. Addition of walls or adjustable drapes would probably improve the effectiveness of the shelters in mitigating temperature fluctuation.

PVB adhesives and the Jahn Restoration Adhesive did not perform adequately when they were used for Florissant silicified wood because the outer coating became brittle (PVB) or the joints failed (Jahn Restoration Adhesive). However, the performance of the casein-based joint filler (Jahn M30®) was sufficient to warrant further investigation into casein products that have higher viscosity, reducing the difficulty of application. Araldite 2015 A/B® epoxy performed well as a bonding agent. However, a wide selection of epoxies is presently being marketed, and it would be advisable to field test additional epoxy formulations and application techniques before selecting a particular product for full-scale application to a petrified stump. Because epoxy remaining on specimen surfaces is a potential aesthetic problem, application demands careful attention.

The effectiveness of organosilicate solutions as consolidants for the Florissant wood cannot be adequately evaluated on the basis of current evidence. Our field tests indicate that organosilicate emulsions can perhaps be applied in a manner that meets aesthetic requirements, but the effectiveness of these products for reducing frost weathering remains questionable. One of the most appealing properties of the organosilicate consolidants is that the principal end product is pure silica, a material that would be expected to be very stable over time, in contrast to organic constituents, which are the main ingredient of all other tested products. This potential asset is countered by the worrisome possibility that organosilicates might increase weathering rates by preventing evaporation of trapped moisture, or that pore spaces between silica-coated grains would allow entry of liquid water. In either scenario, this water would likely cause continued vulnerability of treated silicified wood to freeze-thaw weathering.

No final decisions can be made regarding conservation strategies until more data are available. Longer periods of observation are of critical importance, although the amount of time that is required remains uncertain; laboratory tests using an environmental chamber (e.g., Sleater, 1978) possibly could simulate the effects of long-term weathering in a relatively short time period. Despite the brief duration of our field tests, it appears that PVB can be eliminated from consideration as an adhesive. Preliminary observations indicate that much more detailed research will be required to evaluate adequately the performance of organosilicate consolidants on petrified wood. Additional products should also be considered, including a more diverse selection of epoxy and casein adhesives. The list of possible consolidants might be expanded to include acrylic and fluorocarbon/acrylic solutions. If experiments are conducted in the future, consideration needs to be given to compositional variations within the fossil stumps, and it would be helpful to test each product on multiple samples. Evaluation of results could be improved by using engineering tests to quantitatively evaluate bond strength, moisture resistance, and penetration depth.

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Development of an integrated paleontological database and Web site of Florissant collections, taxonomy, and publications

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ABSTRACT

A detailed survey of collections and publications for the Florissant fossil beds (Colorado, USA) forms the basis for developing a new relational database and Web site that documents information that had become widely scattered following 130 years of scientific study at Florissant. More than 1700 species that remain valid, mostly of plants, insects, and spiders, had been described in more than 300 publications, and these published specimens had been dispersed among ~15 museums. Some of these specimens were not well documented in original publications and many of the type specimens had never been illustrated.

Catalog data were compiled on-site at museums, specimens were photographed, and all of the publications referring to Florissant specimens were located. Taxonomic classification of the fossils was updated to modern concepts. A relational database incorporates the data into five core tables for specimens, bibliography, references to specimens in publication, taxonomy, and images. The database allows for complex searches to interrelate these categories, enabling new research and facilitating collections management. Examples show that the largest number of scientific publications and new species descriptions appeared from 1890 to 1920 and that most of the originally described insect species, but only about half of the plant species, still remain valid and unrevised. Digital images of the fossils and digital files for pre-1923 publications form an archive that is linked to the data records. A Web site makes the database publicly accessible for technical use, and also provides a less complex application for the layperson as well as a new college-level curriculum.

Keywords: Florissant, Eocene, paleontological database, museum collections.

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INTRODUCTION

The paleontological site at Florissant, Colorado, is world renowned for its high taxonomic diversity, primarily of fossil plants, insects, and spiders. The fossils occur in lacustrine, fluvial, and lahar deposits of the Florissant Formation, which is dated at 34.07 Ma and represents the end of the late Eocene (Evanoff et al., 2001). Tremendous scientific attention by numerous paleontologists for more than a century resulted in the description of hundreds of species, and this information was documented in publications and collections that were so widely dispersed both in the literature and between different museums that it became very difficult for researchers to access easily.

In order to locate all published specimens and to create a taxonomic inventory that facilitates specimen-based research at Florissant, the National Park Service (NPS) initiated a project in 1995 to survey all of the existing museum collections and bibliographic references and to integrate these into a single relational database that includes museum collection, publication, and updated taxonomic information (Meyer, 1998; Meyer et al. 2002; Wasson and Meyer, 2004). Scanned photographic images for almost all of the published specimens, and digitized copies of many of the relevant publications, are also included. This database is accessible as a public Web site (http://planning.nps.gov/flfo) that primarily serves the needs of researchers, although other applications are being developed to better accommodate educators, students, and the layperson (once completed, these Web sites will be available by link from the Web site for Florissant Fossil Beds National Monument at www.nps.gov/flfo).

This paper discusses the methods by which the Florissant database was developed, as well as its applications to research, education, and interpretation. It is hoped that this will provide a guideline for similar projects that seek to develop databases for other significant fossil sites with similarly complex publication and collection histories.

BACKGROUND AND PURPOSE

Most of the existing collections of Florissant fossils were made during the late 1800s and early 1900s, long before the establishment of Florissant Fossil Beds National Monument in 1969 (Meyer, 2003; Veatch and Meyer, this volume). These collections consist of at least 40,000 specimens that are now accessioned into more than 25 museums, ~15 of which include the published type specimens that define new species. About 1700 megafossil species that are still considered valid in the literature have been described, and many more species were described but later placed into synonymy in subsequent publications. These specimens have been referenced in more than 300 publications. Almost all of the species represented by these type specimens are unique to Florissant. As the size and dispersal of collections, the number of described taxa, and the body of scientific publications grew over the decades, so too did the complexity and challenge of easily finding this information.

There were many reasons for developing an integrated database to document fully the museum data, citations in publications, and taxonomic placement of the fossils:

1. A complete compilation of all published specimens listing the museums in which they were housed did not exist, and often the original or subsequent publication of a specimen did not indicate the repository and/or catalog number.
2. Only a partial bibliography documenting the publication of Florissant specimens had been compiled.
3. Many specimens had been cited in multiple publications, with the later publications sometimes assigning new taxonomic combinations. These later publications included taxonomic monographs that were not specific to Florissant, yet contained one or more citations of Florissant specimens.
4. Some museums lacked database programs and relied upon old paper catalog records that had no search capability.
5. Museum records or specimen labels often included erroneous data, but such inconsistencies frequently could be resolved by comparison with publication data.
6. Entire collections had moved from one museum to another, and new catalog numbers had been assigned in the process. For example, the entire Princeton University collection from Florissant, which included many type specimens, had moved to the National Museum of Natural History and Yale Peabody Museum.
7. Corresponding halves (i.e., part and counterpart) of the same specimen in many cases had become disassociated and were in different museums with different catalog records and no cross-referencing to document the existence of the other part.
8. Half of the 5190 published specimens had never been illustrated in the original publications, including 444 holotypes and 1179 syntypes (although these numbers were unknown until the database was completed). Those that had been illustrated often were depicted only with line drawings or artistic renditions. Photographic documentation was needed in order to provide a consistent format for illustration, including close-up details.
9. No complete species list had been compiled to assess taxonomic diversity, which is fundamental to understanding the composition of the paleocommunity.
10. Many taxonomic concepts had changed since the most recently published taxonomic assignments for some of the Florissant species, yet there had been no compilation to update this information. For example, many of the genera and some of the families to which Florissant fossil species were assigned decades ago subsequently had been subsumed under other names, based upon the taxonomic classification of extant organisms, yet this was not documented in the literature pertaining specifically to Florissant.

These various factors had resulted in a widely scattered body of data, both throughout the literature and among different museums, making it difficult for paleontologists to easily locate, access, and correlate the basic information about Florissant's paleontology.

Although many databases were in use by different repositories at the time we began this project, none of these had a structural format that could be easily adapted for our effort. For that reason, it was necessary to create a customized structure for the Florissant database.

DEVELOPMENT OF THE DATABASE

Development of the database involved two separate phases. The first of these was to acquire data and photographs at the museums where the Florissant collections are housed, and to locate and copy the publications in which those specimens had been referenced. A later, second phase was to develop a relational database in order to simplify the organization and housing of these data and to serve this information via the internet.

Acquisition of Data

Compilation of Specimen and Publication Data

The purpose of the database was defined at the outset to include *all* of the previously published specimens from Florissant, including type specimens and specimens that had been figured or specifically mentioned in publication. Also included was a selection of unpublished specimens that were unusual or particularly well preserved, as well as specimens that could potentially represent currently undescribed new species.

Development of the museum specimens table for the database involved on-site collection inventories at all of the museums known to house published Florissant specimens in order to compile collection data and complete the photography of all published specimens. This collections-first approach was used instead of surveying the literature as the primary step because, in many instances, the publications did not indicate the whereabouts of the specimens that were described therein. In most cases, a copy of each publication in which a located specimen had been referenced was obtained while on-site (usually in the museum's or university's library), and specimens were compared in-hand with the information and illustrations in those publications. Photocopies of these publications were added to the library at Florissant Fossil Beds National Monument, and many of these were later digitized for the database archive.

Each specimen was correlated to every scientific publication in which it had been referenced, and in many cases specimens had been referenced in multiple publications. These were differentiated by defining a field for publication status (see "status" under Reference Table in Appendix), which indicates the sequence of a specimen's publication history by the terms *original* (indicating that the record shows the first publication in which the specimen was cited), *most recent* (indicating that the record shows the most recently published taxonomic assignment for the specimen), and *intermediate* (indicating that the record shows a published treatment of the specimen between its original and most recent publications). Frequently, each of these various publications assigned the specimen to a different taxonomic name, either by placing it into synonymy or by creating a new combination. In some cases, it was necessary to follow the International Codes of Botanical and Zoological Nomenclature in order to resolve particular nomenclatural problems that resulted from inconsistencies in the publication history for a specimen.

Specific data fields were defined for compiling the data (see Appendix), and records were made on-site using paper worksheets. Each specimen was assigned an inventory number as a unique identifier to provide a means for sequentially tracking specimens in the database and in the photo log. This method proved to be more effective than using catalog numbers for several reasons: (1) some specimens already had multiple catalog numbers; (2) some catalog numbers needed to be changed as problems were discovered during the course of the inventory for this project; and (3) some specimens had different non-sequential numbers for parts and counterparts of the same specimen in the same museum, yet the objective of the inventory was to combine these. Only when corresponding halves of the same specimens were in different museums were separate inventory numbers assigned.

The collection size for each museum was estimated by extrapolating from specimen counts in several representative drawers that were categorized according to variations in specimen sizes and arrangement. This estimate totals ~40,000 specimens. Estimates for each museum are shown in Table 1.

The organizational arrangement of collections varied from one museum to another in the way that specimens were grouped. For example, published specimens in the fossil plant collections at the U.S. National Museum of Natural History (USNM) and the University of California Museum of Paleontology (UCMP), and the fossil insect collection at the American Museum of Natural History (AMNH), were arranged according to the publication in which those specimens had been first described and included both type and other referenced specimens. The Museum of Comparative Zoology at Harvard (MCZ) had a collection of fossil insects that grouped all published specimens and was arranged taxonomically; in many instances, however, this secondarily resulted in a correlation with publications that had dealt with particular taxonomic groups, and although these were not always the original publications in which the fossils had been first described, it usually was easy to trace back from these secondary publications to locate the original description. The University of Colorado Museum (UCM) and the National Museum of Natural History had type collections of fossil insects that were arranged alphabetically by genus with no correlation to publication, yet other published (non-type) specimens were difficult to recognize because they were intermixed and unmarked in the general collections. Some collections, such as the fossil plant type collection at the National Museum of Natural History, had specimen labels that traced an individual specimen through multiple publications, and this greatly facilitated the inventory process. Because of the variability in collection organization, the approach to inventorying the Florissant collections had to be customized for each

TABLE 1. FLORISSANT COLLECTION SIZE AT MUSEUMS INCLUDED IN DATABASE

Museum	Total Florissant collection size (estimated)	Specimens included in database
Museum of Comparative Zoology, Harvard University	8000	2298
National Museum of Natural History, Smithsonian Institution	10,400	1120
University of Colorado Museum of Natural History	5500	468
University of California Museum of Paleontology	>1000	333
American Museum of Natural History	1000	313
Museum Unknown	n/a	249
Peabody Museum of Natural History, Yale University	1600	181
The Natural History Museum, London	>1100	173
U.S. Geological Survey, Denver Palynology Collection	N/C	142
University of Washington	N/C	94
Denver Museum of Nature & Science	>3200	70
Waynesburg College	>3000	65
Field Museum of Natural History	>1200	43
Milwaukee Public Museum	1000	41
University of Florida Museum of Natural History	500	24
Carnegie Museum of Natural History	100	22
Florissant Fossil Beds National Monument	3000	15
National Museums of Scotland	18	5
University of Michigan Museum of Paleontology	175	3
University of Minnesota	N/C	2
California Academy of Sciences	N/C	1
San Diego Natural History Museum	N/C	1
TOTAL	~40,800	5663

Note: Ranked according to number of specimens included in the database. Total collection size includes both published and unpublished specimens and is estimated by extrapolation from representative drawer counts (see text for explanation). N/C—small collections and palynomorph collections that were not counted.

particular museum. In some cases the on-site surveys resulted in an inventory that was closely associated with the publication histories of the specimens, and in other cases the surveys resulted in data entries for genus, species, and type status, but the correlation with publications remained unknown.

After all of the specimens from the collection inventory had been entered into the developing database, the publications were checked again in order to correlate the unmatched type specimens (i.e., those that had been entered only as genus, species, and type status) to the appropriate publications in which they had been described, and to search for specimens that had not been located on-site. Those specimens that were documented in publication but had not been located in the collections were incorporated into the database and are indicated in the field for *catalog number* as “unknown [specimen has not been located]” and in the field for *object status* as “apparently missing [specimen has not been located in any of the museum surveys].” In most cases, these were probably originally in the collections of the same museums that were surveyed, but have since been lost. We recognize that our method could have missed some specimens and/or publication records altogether, although considering the wide scope of the museum inventory and the number of museums included, it is unlikely that more than a few such specimens still exist among major museum collections.

The inventory of collections was done primarily by the first author between 1995 and 2003, and involved a total of ~250 days spent at 17 museums to examine and photograph nearly 5200 specimens and to record accompanying catalog and accession records (i.e., at a rate of ~20 specimens per day). An additional 250 specimens that are referenced in publication but that are currently missing from collections or could not be located were also included in the database. Further, ~250 palynomorphs were included based upon previous photographic documentation in publication, and ~500 unpublished specimens were included. Currently, the database includes a total of 5663 specimens (Table 1), ~5200 of which have been referenced in publication. Of these, more than 3750 had been designated as various type specimens (e.g., holotype, lectotype, syntype, paratype) in the original publications, but ~325 of these were subsumed by synonymy in subsequent publications.

Compilation of Bibliography and Library

At the outset of the project, a substantial bibliography of many of the scientific publications dealing with Florissant’s paleontology already had been compiled from sources such as the GeoRef database and the archive collection of the late F. Martin Brown (housed at Florissant Fossil Beds National Monument). Photocopies of these references were acquired through interlibrary loans or from the library of the U.S. Geological Survey in Denver. As the museum survey progressed, other relevant publications were located and copied from various sources, including (1) information on specimen labels or reprints filed with collections; (2) citations in various related publications, such as the *Treatise on Invertebrate Paleontology* (Carpenter, 1992); (3) the late Frank M. Carpenter's taxonomic card file and reprint collection, as well as part of the reprint collection of the late Samuel H. Scudder, in the MCZ at Harvard University; (4) research in the Ernst Mayr Library at Harvard University; and (5) reprints and specialized knowledge of the literature provided by museum curators. Whenever possible, these reprints were in-hand as a source of verification when each individual fossil specimen was examined.

Compilation of Updated Taxonomy

Data from the survey of collections and publications provided the basis for compiling the first complete species list for Florissant. This list was derived from the taxonomic treatment of type specimens in the most recent publications in which they had been cited, although many of these most recent publications were more than a century old, and many taxonomic concepts, particularly at the levels from genus to family, had been modified over the years. The taxonomic component of the database was developed to update the taxonomic classification into more contemporary, consistent terminology, and in many cases this supersedes the taxonomic information from the older publications.

All of the fossil plants described by early workers such as Lesquereux (1883) were thoroughly revised by MacGinitie (1953) and many of these revisions were examined again by Manchester (2001). Because these treatments were relatively recent, almost no updating of generic names was needed for the plants. Generic names were verified according to Mabberley (1997), and compilation of names for higher taxonomic ranks followed Takhtajan (1997) for the flowering plants. By contrast, many of the fossil insects and spiders had not been treated in publication since some of the early workers such as Scudder (1890, 1893, 1900). Taxonomic classification of many of the insects at the generic level and higher had been revised since these early works, and some of the names had been changed on the basis of more recent taxonomic studies of extant members of these groups. It was therefore necessary to examine each generic assignment for the insects (Boyce Drummond, unpublished report for the National Park Service) and to update some of these generic names according to sources such as *Nomina Insecta Nearctica* (Poole and Gentili, 1996–1997; www.nearctica.com/nomina/main.htm), and higher taxonomic ranks according to Borror et al. (1989). In such cases, the names are based on revisions of extant material, yet the Florissant fossils were not individually reevaluated to determine with certainty whether or not they necessarily possess the characters that conform to those generic changes. Such work on the fossil insects, comparable to MacGinitie's (1953) revision of the plants, will take years of detailed research to complete. The resulting updated taxonomic list for Florissant incorporating these changes was reported previously (Meyer, 2003). Our conservative approach to higher taxonomic rankings in the database follows the widely recognized classifications of Takhtajan (1997) and Borror et al. (1989), although of course it is probable that the database will be revised in the future to incorporate newer phylogenetic approaches to systematics as these become better established.

Compilation of Digital Archive

At the time the project began in 1995, the technology for digital photography was still new and developing rapidly, and it was decided instead that all images would be taken as photographic transparencies using Kodak Kodachrome film. Kodachrome 40, a tungsten balanced film, was used initially, but when Kodak discontinued this product, Kodachrome 64 was substituted in conjunction with an indoor tungsten light filter. Kodachrome was selected because of its known longevity for color stability, which far exceeds that of other transparency films. All photographs were taken in duplicate, and in some cases, the duplicates were taken on separate rolls of film as a security measure, which proved to be beneficial. All of the original transparencies from this project, totaling ~12,000 mounted slides, including the set of duplicates, are in the collection at Florissant Fossil Beds National Monument. All of these were scanned with a Polaroid Sprintscan® slide scanner, and these digital images were incorporated into the database archive. Because of limitations on the capacity for storage of numerous large digital files at the time the scanning was done, most of the images were scanned at low resolution and are ~500 × 300 pixels.

As required by several of the individual museums, permission was needed to use images of the specimens and to make the collection data available on a Web site. For many specimens, this permission does not extend to reuse of images or data by users of the Web site. For that reason, it always remains the legal responsibility of the Web site user to contact the individual museum for any subsequent use of an image or data, including use in scientific publications. A clear statement of warning to this effect appears on every page within the Web site. Inclusion of all museums was critical, because if even one museum's specimens were excluded, it would compromise the integrity of the database and limit its utility. It has been mutually beneficial, however, and the museums have been able to access their own data from the Florissant database in ways that their own databases may not have provided. Exports of the Florissant data and images have been provided to several museums to aid them in developing or expanding their own databases.

Almost all of the publications in which the Florissant specimens were referenced were obtained as originals or copies for the library at Florissant Fossil Beds National Monument. As a component project for the Colorado Digitization Project, more than 186 publications were digitized (~4000 of the 12,000 pages of relevant publications about Florissant paleontology), and these range in size from large monographs such as those of Scudder (1890) and MacGinitie (1953) to the many very short contributions of Cockerell. The publications that were incorporated into the database archive are those that were free of copyright restrictions (primarily those pre-dating 1923) or that were used by permission. A large portion of the scientific work at Florissant was done in the late 1800s and early 1900s, however, and hence the archive captures many of the most significant publications. It is noteworthy that these pre-1923 publications included more than 1500 original descriptions of Florissant's new species, although many of these species were subsumed by synonymy in the later publications.

Design of the Database

Structural Design and Functionality

In order to synthesize the widely dispersed information about Florissant specimens and publications and make it more accessible to researchers, a relational database management system (RDBMS) was developed. This database was designed to facilitate the kinds of complex searches that are needed to document the collections and their associated literature, which in turn provides a census of the taxonomic diversity at Florissant.

In this context, a RDBMS is defined as a series of data tables with defined relationships among the tables, and among the queries, forms, and programming code that are used for data entry, management (e.g., quality assurance and control), analysis, and reporting. Readers are referred to Hernandez (2003) and Riordan (1999) for an introduction and overview of such systems. This section focuses primarily on the underlying tables and their relationships, and describes how this information is served over the Internet. The tables are the core of the system, whereas the Web interface is what most users will see. The desktop forms and code that are used for data entry are of lesser importance because they frequently change to accommodate hardware, software, and user needs.

The Florissant database addresses five information elements: (1) museum specimens, (2) the bibliography of publications, (3) references to specific citations of specimens in those publications, (4) current taxonomy, and (5) a digital archive of the specimen photographs and copies of scientific publications. By housing all of the five elements in one system, it is possible to link and manage all of the information efficiently. The design of this relational database was entirely customized to accommodate these information needs, and therefore was not modeled after any other system that existed at the time this project began in 1995.

The table structure of a relational database for a particular application could potentially take various forms, although the ideal database design is normally one that closely reflects the real-world system that it is attempting to describe. The design and success of this database system therefore depended on five core tables that we believe provide a sound conceptual and functional model for the information elements that were needed to make this an effective paleontological database. These tables, their attributes (or fields), and the relationships between them are shown in Figure 1.

The database framework illustrated by Figure 1 utilizes basic relational database theory, design, and symbology. This framework emphasizes that the power and efficiency in a relational database comes in part from storing each information element in only one location, where tables are linked together using primary keys (unique identifiers) and foreign keys (references to the unique identifiers), and "**1**" and "**∞**" represent cardinality between tables, or one-to-many respectively.

Contents of the Tables

The data fields that make up each of the five tables are shown in Figure 1. These fields are defined in the Appendix.

Specimens. The museum specimens table (tblSpecimen) contains information inherent to each individual specimen as an object, such as the name of the museum where it is housed, current and past catalog numbers, accession number, collector, locality, and object status. These data are similar to those in other paleontological collections databases, including the University of California Museum of Paleontology (http://bscit.berkeley.edu/ucmp/, February 2006) and the Florida Museum of Natural History (http://www.flmnh.ufl.edu/databases/, February 2006). The unique inventory number that was assigned during the museum collections inventory was used as the primary key in the specimens table, and as a linked foreign key in the images and references tables (Fig. 1).

Bibliography. The bibliography table (tblBibliography) contains standard bibliographic information for almost all of the scientific publications pertaining to Florissant. These fields include author, year, title, journal name, volume number, book reference, and page numbers. A list of topical keywords is included to facilitate search capabilities.

References to specimens in publications. The reference table (tblReference) serves as a linking table between the stand-alone specimen and bibliography tables (Fig. 1). As such, it contains foreign keys that link to the primary keys in both of these other tables. It also describes the many-to-many relationship between the specimen and bibliography tables, where one specimen can be referenced in multiple scientific publications, and/or one publication can refer to many different specimens. The table holds information that documents the description or citation of each specimen in a particular publication, the taxonomic classification that is used in that publication, and the status of the specimen in that publication (i.e., original, intermediate, or most recent). Each specimen is correlated to every scientific publication in which it has been referenced, and the table then links to these publications in the bibliography table. Many specimens are referenced in multiple publications, and often these various publications assign the specimen to a different taxonomic name.

Taxonomy. The content of the taxonomy data table is conceptual in nature and is based on updated classification schemes as discussed previously. The table contains hierarchical names for various taxonomic ranks of the Florissant organisms, and it is linked to the actual specimens in the specimen data table (Fig. 1). These names sometimes differ from those to which a specimen may be linked in the reference table if the updated taxonomic name is more recent, and previous taxonomic names to which a specimen was referred in publication must be searched

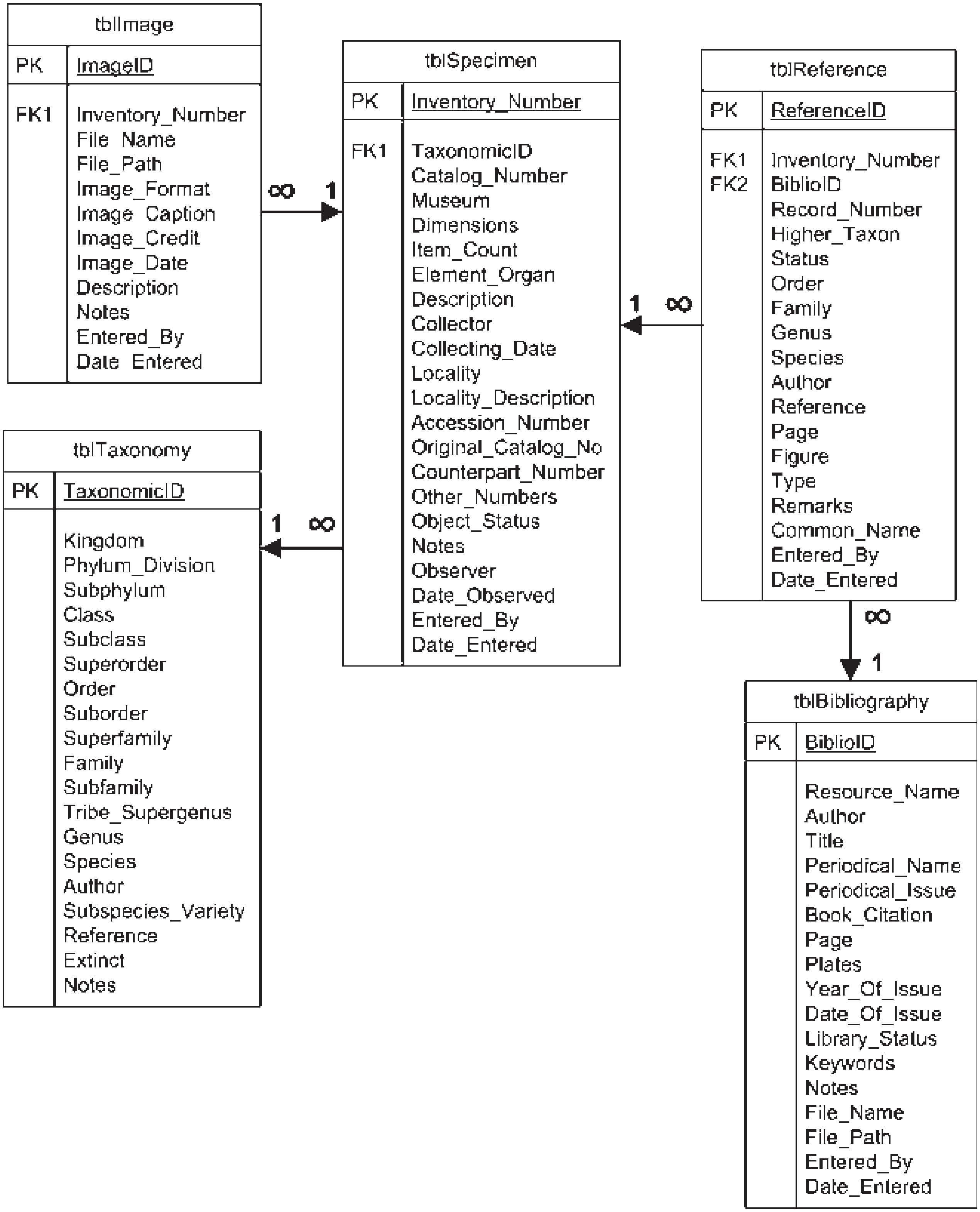

Figure 1. Diagram displaying the core tables in the database system and their relationships to one another. Each of the tables and their corresponding relationships are described in the text, and field definitions are given in the appendix. PK—primary key; FK—foreign key.

from the reference table. The taxonomy data table is linked to all of the museum specimens, and each specimen has one taxonomic record.

Digital archive. The digital archive is composed of two types of digital files: images of specimens, and copies of the publications. Each specimen can have one or many related images. To accommodate this, the image table (tblImage) contains the name of each image, the file path to where it is located, and information about when the photo was created and by whom. Images are stored in a subdirectory on the same server as the database. The images that are accessible by Web site are jpeg files at low resolution, and this is intended to limit third parties from using them for high-quality reproduction, in accordance with the conditions of the permission from some of the museums whose specimens are included. Researchers can request a high-resolution image from Florissant Fossil Beds National Monument once they have obtained permission for use from the appropriate museum. In total, the database contains more than 6000 photographic images of fossils.

Digital copies of scientific publications, as documented in the bibliography, are stored in portable document format (pdf). There is always a one-to-one relationship between the bibliographic citations and the digital document (except for one very large document that needed to be divided into three separate parts), and therefore the link to the digital document is maintained in the bibliography table.

Keeping Pace with Advances in Technology

One obstacle to the optimization of the database during its development, particularly with the desktop application used for data entry, was the rapid change in software, hardware, and NPS standards regarding information systems. Various programs were used throughout the development of the desktop database application owing to the changing needs of the project and in particular the internet compatibilities of the different programs. Initially, the database was assembled using Blackwell Idealist® because of its ease of data entry and simple database structure. As the information needs became more complex and the data were to be served over the internet, the data were migrated to Microsoft Access® using a customized modification of a natural resources management system application known as IRMS (Integrated Resource Management System). Although this application proved to be useful through the inception of the Web site in 2002, changes in versions of Access and the discontinued support of the IRMS system by the NPS forced another revision of the database to its current relational data structure in Access. Further modifications are currently under way, as discussed below.

APPLICATIONS OF THE DATABASE

The database has been adapted into several levels to allow for a variety of users. The desktop version of the database accommodates technical users at the NPS while the Web interface (http://planning.nps.gov/flfo/) is available to the general public. This Web site provides tools for simple searches to obtain data for research and collections management, and it has been instrumental in developing a non-technical interpretive Web site and an educational curriculum (which will be available by link from www.nps.gov/flfo). The database also provided the basis for a book about Florissant paleontology (Meyer, 2003). It should be noted that the tabulation of data for tables and figures presented in this paper is based on the January 2006 version of the database.

Functionality

This section describes our current configuration of the database system. It is intended to provide the reader with a basic understanding of our desktop application and Web interface, realizing that this configuration is dynamic and will evolve as technology and software continue to change.

Desktop Version

The desktop version of the database has two primary functions: data entry, and specialized searching and reporting. Data entry is facilitated through Microsoft Access® forms, coded using Visual Basic for Applications (VBA), which enables the user to add information about publications, specimens, and taxonomy. The most versatile part of the desktop application is the ability to accommodate highly focused, multilevel queries. These are capable of showing complex interrelationships between the various fields, including the specimens and their cataloging data, the scientific literature that cites these specimens, the varying taxonomic treatment of these specimens in multiple publications over time, and the naming of these specimens into currently recognized taxonomic ranks. These complex queries are not pre-programmed and require a basic knowledge of how to use the Microsoft Access® query interface.

Web Site

The Web site is currently served from an NPS server in Washington, D.C. Presently, the database tables (Fig. 1) are housed in Microsoft Access® and served using Web pages coded in Macromedia Cold Fusion®. This Access-Cold Fusion combination is suitable for small-scale Web applications that rarely experience more than a few concurrent requests for information. Since its inception in 2002, the first page of the Florissant Web site has received ~20 hits per day.

Unlike the desktop application, which has the ability to create customized queries as needed, search options on the Web interface had to be pre-programmed. Thus, the current Web site design provides three search portals based on taxonomy, bibliographic citations, and museum specimens. Following an initial search, the output can be refined further by using more detailed search criteria, and it also allows the user to link between the taxonomy, museum specimens, and bibliography databases (Fig. 2). This provides a flexible framework that helps to accommodate more focused questions, although not to the same level of complex refinement that the desktop database enables. This is the first implementation of the Web site, and future modifications may allow Web users to conduct even more detailed searches. The current Web site address is http://planning.nps.gov/flfo/, or it can also be located by a link from the Web site for Florissant Fossil Beds National Monument.

Currently, plans are underway to migrate the data into Specify, which is a customizable collections-based research database (Specify Software Project, 2007). This conversion will enable the development of a revised Web site that will be hosted as a partnership between the NPS and the University of Colorado at Boulder.

Data Sharing with Other Paleontology Databases

Since the inception of the Florissant database, similar databases such as Paleoportal (www.paleoportal.org), CHRONOS (www.chronos.org), and the Paleobiology Database (paleodb.org/cgi-bin/bridge.pl) came into existence around 2000. These projects are joint ventures among various scientific institutions and organizations, and all share the objective of compiling and synthesizing paleontologic, geologic, and biologic data about fossil species into a single, easily searchable Web site. The approaches to these Web sites vary from creation of large databases housing information provided to them by researchers and professionals, to creation of electronic infrastructures that provide access to a multitude of other internet databases. They provide a single portal for searching the wealth of information from these other sites.

We are pursuing the potential for integrating with these other paleontology data clearinghouses. In addition, we will consider alternative means for sharing and integrating the data, including the use of extensible markup language (World Wide Web Consortium, 2006), Web services, and service oriented architectures (He, 2003). Connecting or incorporating data from the Florissant database would help to minimize the need for these other databases to acquire the information independently from widely scattered and poorly updated sources. Paleoportal already recognizes Florissant as an example of “famous floras and faunas,” and although the Paleoportal Web site includes a brief explanation of Florissant and a link to the Florissant database Web site, it does not yet serve the full body of Florissant collection data.

Potential problems in sharing the database with these sites include providing additional server space for the link, extending the permission for use from the various museums, and creating a filtering mechanism by which the sites could avoid duplications of data in those cases where particular museums with Florissant collections are already linked to these sites. An additional problem in serving so many diverse databases through one portal is that the ability of these larger, servicing databases to continually provide data can rely entirely on the sustained functionality of the databases to which they link. Whatever the solution, we hope to minimize user confusion and reduce the time spent searching, yet still address concerns regarding data compatibility, sensitivity, and ownership. One promising option is to use the Distributed Generic Information Retrieval (DiGIR; Specify Software Project 2007) protocol, which is one type of XML-based Web service developed specifically for the sharing of taxonomic information. DiGIR allows numerous database systems to be simultaneously queried from one Web interface and overcomes the issues that arise when attempting to merge incompatible database systems.

Applications to Research

The database and Web site provide ready access to information and materials that previously were difficult to find because they were widely dispersed among different museums and publications. The specimen component of the database enables direct searches of collections and specimen data including links to all of the publications in which a specimen was referenced. The associated archive of specimen photographs provides images that can be used to examine the general morphology of the fossil organism and assess its state of preservation. Many of these fossils, even the type specimens, were never illustrated in publication and are available exclusively in the Florissant database (Fig. 3). These images can aid a researcher in deciding which specimens would be the most useful to request on loan, and in some instances can provide the needed research information in themselves.

The taxonomic component of the database provides a consistent conceptual framework that updates the taxonomic position for the fossil organisms and in some cases supersedes the older taxonomic information from the most recent publication of the fossil specimens. Researchers with an interest in certain taxonomic groups can use the database to readily compile and tabulate an inventory of these groups and to locate the museums in which the type specimens are reposited. The database provides the first comprehensive census of the taxonomic diversity at Florissant, thus enabling more accurate reconstructions of the paleocommunity and its paleoenvironment. A summary count of the major taxonomic groups is shown in Table 2.

The bibliographic component of the database readily facilitates literature searches to locate publications in which the fossils were described, generate lists of species for each publication, and document nomenclatural changes. Many of these publications are instantly available in the database’s digital library archive, which includes many holdings of older, obscure publications. Some of these are difficult to obtain otherwise, even from large libraries.

The combined components of the database also enable research into the history of paleontology at Florissant (Veatch and Meyer, this volume). Figure 4, for example, shows the number of publications about Florissant during each decade; Figure 5 shows the number of new species described in these works per decade; and Table 3 shows the publications in which most of these specimens were referenced. This clearly shows the emphasis of the earlier publications on describing new species, particularly during the period from 1890 to 1920. It also reflects the fact that new species descriptions were concentrated into a few lengthy monographs during the 1890s (e.g., Scudder, 1890, 1893), whereas the numerous publications of Cockerell, Rohwer, Brues, and Wickham during the 1900s and 1910s each included fewer descriptions of new species.

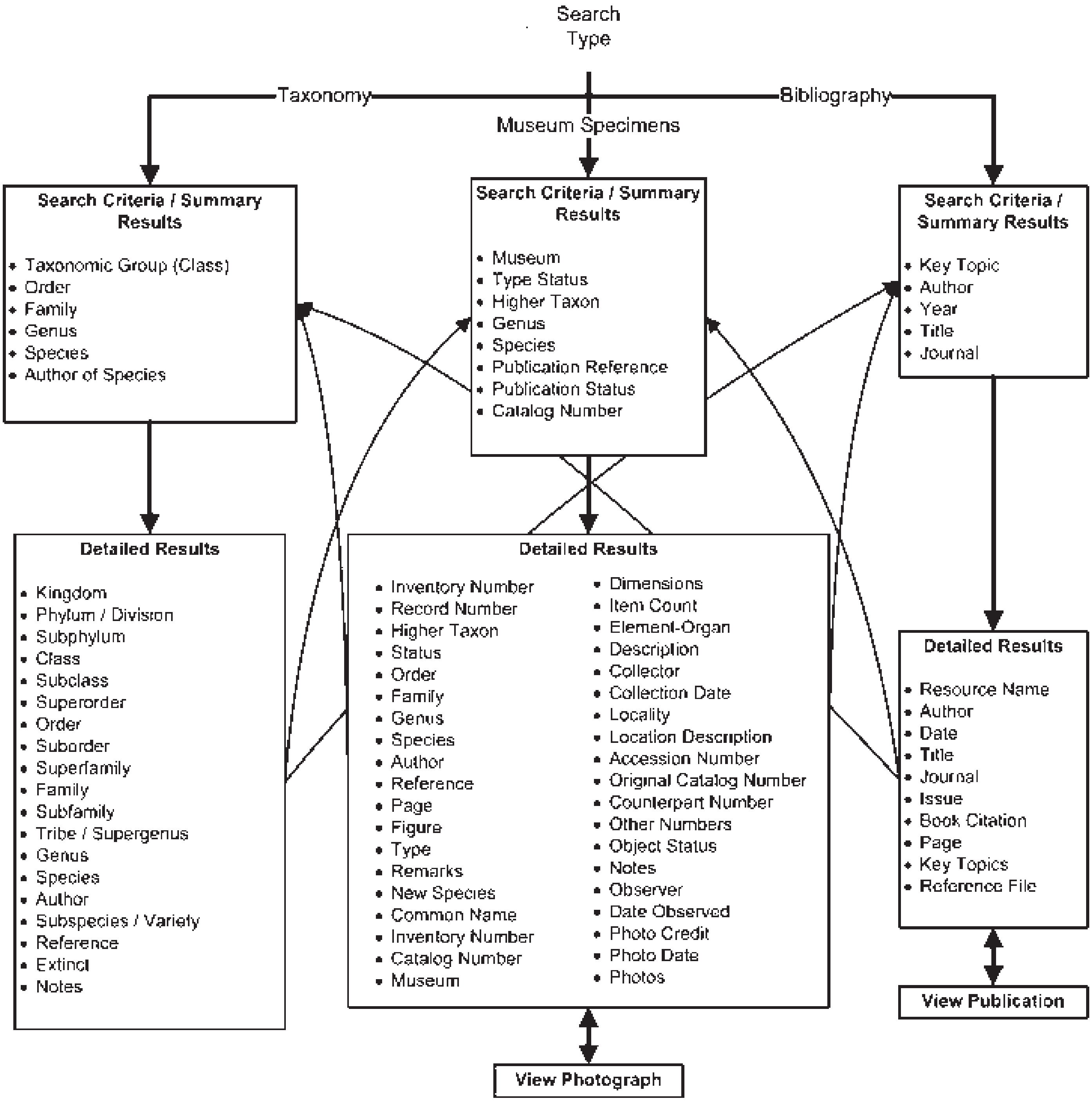

Figure 2. The Web site provides three primary search pathways for taxonomy, museum specimens, and bibliography. The user can submit queries for selected fields in each pathway to obtain summary lists for all records matching the combined search criteria. Any particular record from these lists can be selected to obtain detailed results. The detailed results for museum specimens and bibliography link to the digital archives of specimen images and publications, respectively. The detailed results within any search pathway provide a link to obtain the list of related summary results in either of the other two pathways.

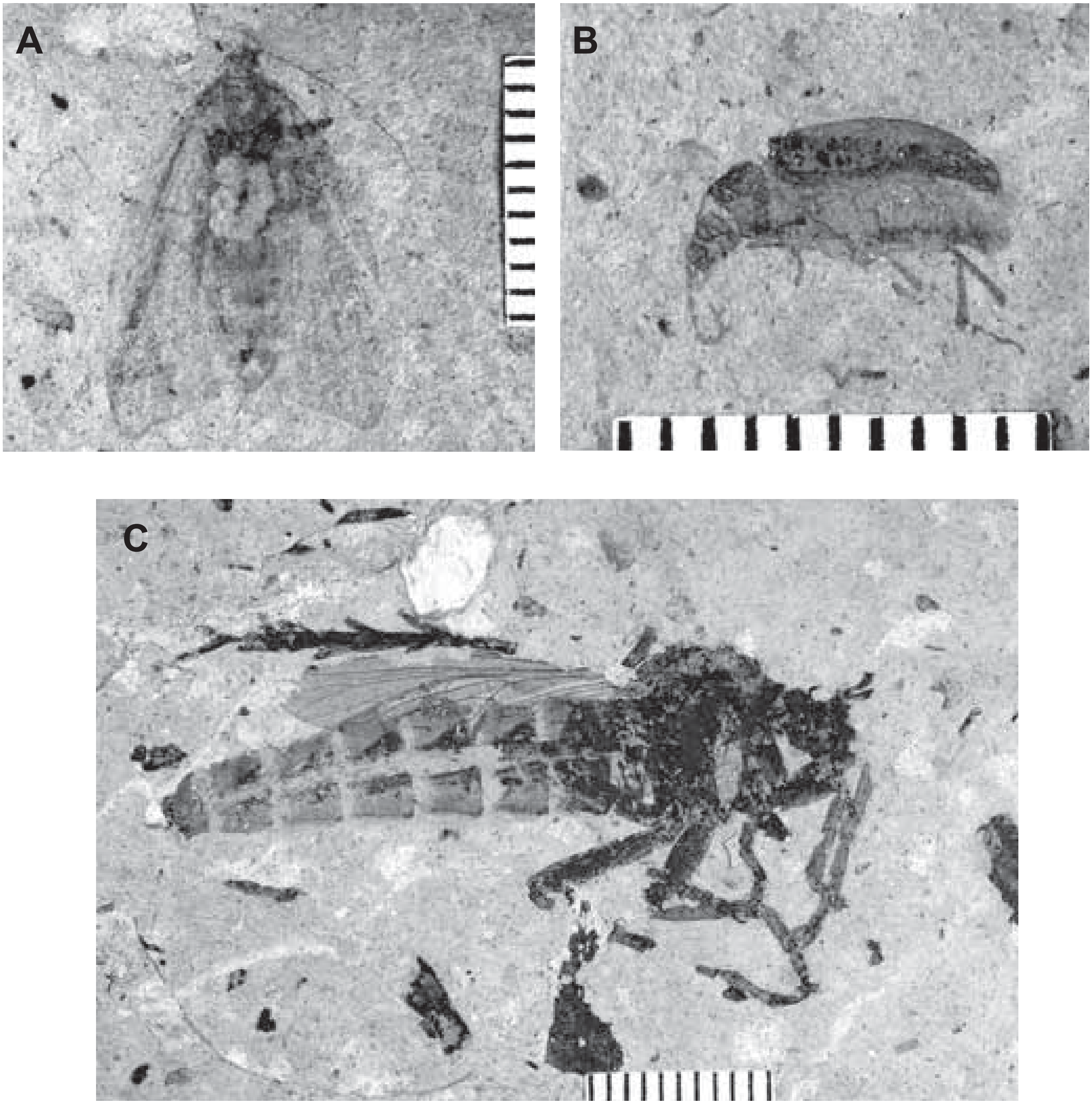

Figure 3. Many of the original holotype specimens that were designated to characterize the new species from Florissant were never illustrated. New photographs of these are available in the image archive of the database. (A) Fossils of Lepidoptera are extremely rare in the fossil record, yet Cockerell (1907) never figured this holotype specimen in his original description of the moth *Tortrix florissantana*. This specimen is in the collection of the University of Colorado, and as a consequence of the development of the database, it was correlated with its other half at the Natural History Museum, London. Specimen UCM-8579. (B) Previously unfigured holotype of the chrysomelid beetle *Colaspis aetatis* described by Wickham (1911). Specimen UCM-8219. (C) Cockerell (1908b, p. 173) referred to this as "the finest fossil insect found at Florissant by the expedition of 1906," yet he did not illustrate it when he designated it as the holotype for the new species *Microstylum wheeleri* (Cockerell, 1908b), a robber fly. Specimen UCM-4522. All scale bars are 1 cm, with increments of millimeters. Images of specimens used courtesy of the University of Colorado Museum of Natural History.

The database contributes information for broader research topics such as assessing global biodiversity through time. For example, because the Florissant database tracks the taxonomic treatment of particular specimens through different publications, it is capable of documenting nomenclatural changes to taxonomy and therefore of contributing to an assessment of the "flux ratio" that compares historical rates of invalidation and revalidation (Alroy, 2002). One simple assessment of this is shown in Figure 6, which illustrates the number of species originally described at Florissant compared to the number that are still valid in the most recent publications. In this regard, an analysis of the species described from Florissant during the 1800s and early 1900s (see Fig. 5) shows that many of the original binomial names for the plant megafossils have been invalidated or placed into synonymy (Fig. 6), resulting in nearly a 50% reduction by the work of MacGinitie (1953) alone, whereas a similar analysis for the Florissant insects indicates that many of the original names remain unchanged by the lack of subsequent critical studies. Thus the diversity of insect species at Florissant, based on the previously published names documented in the database as most recent, is probably misleading and may be significantly inflated if the insect names are invalid or need to be synonymized to a level comparable to that of the plants. If this is true and if the Florissant database is incorporated along with other databases in developing a global paleontological database, then biodiversity estimates for the Florissant fossil insects based on previously described specimens could be considerably overestimated relative to the fossil plants, particularly for those insect genera that were highly split into different species by the original workers.

TABLE 2. NUMBER OF SPECIES-LEVEL CLASSIFICATIONS FOR EACH CLASS

Class	Species entries in database
Hexapoda	1516
Magnoliopsida	180
Arachnida	53
Liliopsida	13
Pisces	9
Pinatae	8
Gastropoda	7
Mammalia	6
Aves	5
Diplopoda	2
Bivalvia	1
Crustacea	1
Not specified	193
TOTAL	1994

Note: Species entries include some taxa unnamed at the species level and denoted by original authors as "sp.," particularly among palynomorphs. Classes not specified are mostly pollen and spore morphotypes or incertae sedis plant macrofossils. All numbers are based on the January 2006 version of the database.

Applications to Collections Management

Curators at museums with Florissant collections often can find more complete and more searchable information from the Florissant Web site than in their own records. In part this is because the compilation of the database resolved various catalog inconsistencies, correlated all specimens with publications, and provided photographic documentation. For example, the database is used by the University of Colorado Museum (UCM) to (1) confirm type specimens and matching them with their references, (2) determine whether specimens indicated in publications as UCM types are in fact elsewhere, *not* in that museum, (3) locate specimens in the collection that are the counterparts of type specimens in other museums, (4) update old taxonomic names on labels to the currently valid name,

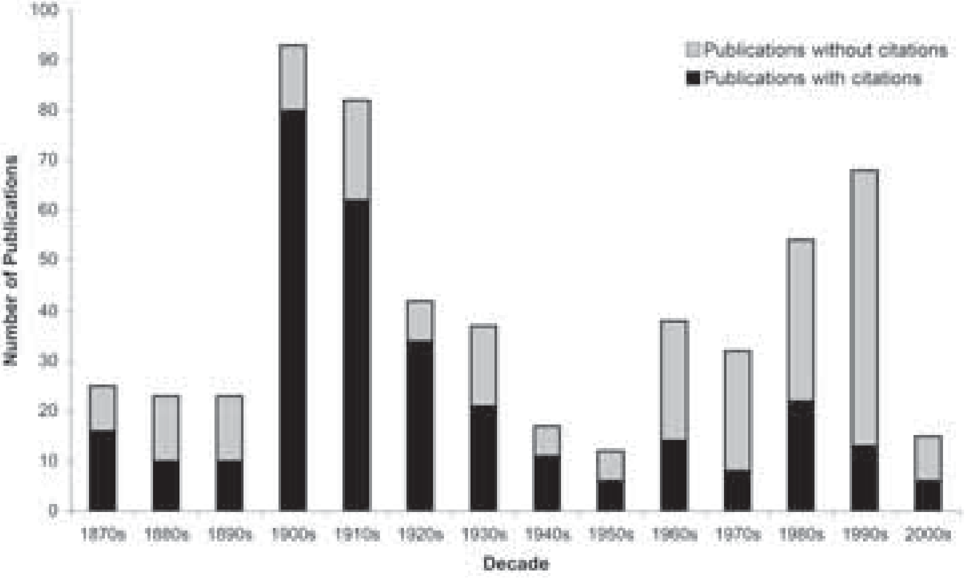

Figure 4. Number of publications per decade showing those that referenced specific fossil specimens (denoted as "with citations") as well as those that did not reference specimens (e.g., general references to Florissant paleontology and geology; denoted as "without citations"). Results are based on the January 2006 version of the database.

(5) locate bibliographic citations for specimens that have been lost over the years and are no longer in the collection, and (6) taxonomically identify non-type specimens in the general collection by comparing them to photographs in the database (Amy Moe, January 2006, written commun.). The American Museum of Natural History (AMNH) uses the database to compare actual specimens against the database photographs in order to establish a specimen's condition when it goes out for loan and comes back in, and also to refer potential collection users to a source for browsing the AMNH collection (Bushra Hussaini, January 2006, written commun.). The Natural History Museum, London (NHM) has used the database to access data and images for particular specimens in their collection, because the Florissant specimens are not in their database (Andrew Ross, January 2006, written commun.). The MCZ at Harvard University houses the largest number of specimens included in the database (Table 1), yet during the time of our collections survey, the museum did not have its own database for managing these collections. An MCZ fossil insect database was developed subsequently, and many of the data fields were populated using an export from the Florissant database (Phil Perkins, February 2006, written commun.).

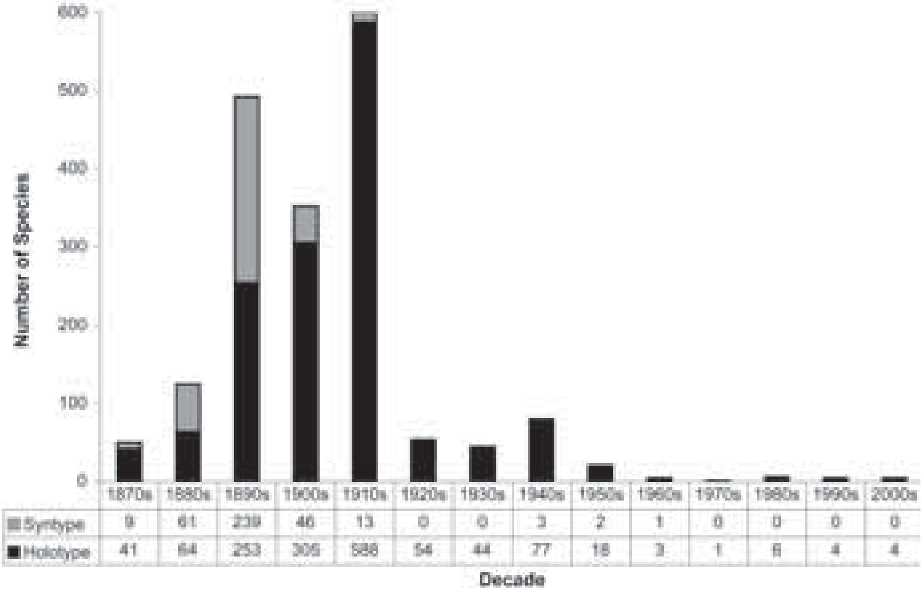

Figure 5. Number of originally described new species per decade, some of which were later subsumed by synonymy in later works. The majority of species descriptions were based on single holotype specimens, although some workers (e.g., Scudder, 1890) designated multiple syntype specimens to define new species. Results are based on the January 2006 version of the database.

TABLE 3. PUBLICATIONS CONTAINING THE LARGEST NUMBER OF REFERENCES TO FLORISSANT SPECIMENS

Author	Year of issue	Title	Specimens cited
Scudder, S.H.	1890	The Tertiary insects of North America	1008
MacGinitie, H.D.	1953	Fossil plants of the Florissant Beds, Colorado	935
Scudder, S.H.	1893	Tertiary rhynchophorous Coleoptera of the United States	435
Lesquereux, L.	1883	Contributions to the fossil flora of the western territories, Part III, The Cretaceous and Tertiary floras	346
Carpenter, F.M.	1930	The fossil ants of North America	342
Knowlton, F.H.	1916	A review of the fossil plants in the United States National Museum from the Florissant lake beds at Florissant, Colorado, with a description of new species and a list of type specimens	286
Scudder, S.H.	1894	Tertiary Tipulidae, with special reference to those of Florissant, Colorado	266
Cockerell, T.D.A.	1908	The fossil flora of Florissant, Colorado	208
Scudder, S.H.	1900	Adephagous and clavicorn Coleoptera from Tertiary deposits at Florissant, Colorado, with descriptions of a few other forms and a systematic list of the non-rhynchophorous Tertiary Coleoptera of North America	206
Brues, C.T.	1910	The parasitic Hymenoptera of the Tertiary of Florissant, Colorado	188
Melander, A.L.	1949	A report on some Miocene Diptera from Florissant, Colorado	152
Wickham, H.F.	1914	New Miocene Coleoptera from Florissant	142
Wingate, F.H., and D.J. Nichols	2001	Palynology of the uppermost Eocene lacustrine deposits at Florissant Fossil Beds National Monument, Colorado	142

Note: Publications with at least 100 references to specific Florissant specimens, ranked according to number of specimens referenced.

Applications to Education and Interpretation

A Virtual Museum for the Layperson

Although the database Web site provides the comprehensive documentation and search capability that is needed by scientific researchers and museum curators, its complexity may quickly seem overwhelming to a layperson. To provide information for less-specialized users, the database was used to derive a digital photographic gallery that includes condensed interpretive information (to be available as a link from www.nps.gov/flfo).

This "online museum" allows users to choose two optional portals: (1) a simple slide show of some of the most impressive fossils, and (2) a series of Web pages that discuss Florissant's geology and paleontology in more detail. Some of the most impressive specimens were selected, and these are accompanied by descriptions of the fossil organisms and an illustrated overview of the geologic history of the Florissant fossil beds. A succession of Web pages leads users through various levels of the major taxonomic groups, including common names, and culminating with generic examples.

Utilizing the Database to Develop an Undergraduate Curriculum

Another application currently under development will provide an educational curriculum for undergraduate students. Once completed, this can be located by link from www.nps.gov/flfo. This curriculum will serve as a stand-alone laboratory supplement for paleontology courses, and as an introductory exercise that could be used by the many field geology classes that visit Florissant during the summer. It will use a subset of selected leaf macrofossils from the database, and students will be able to obtain random samples that they can analyze to identify characteristic taxa and develop hypotheses about paleoecology and paleoclimate. This curriculum has several objectives: (1) to expose students to the functionality of the database, (2) to develop skills in understanding taxonomy and identifying fossil leaves, (3) to analyze physiognomic characters of fossil leaves as a basis for climate reconstruction, and (4) to create a virtual geologic map based upon outcrop and rock photographs.

Developing Other Media

The accessibility to information that resulted from the compilation of the database was critical in developing the first publication that listed the entire taxonomic diversity and bibliography for Florissant (Meyer, 2003). This made it possible to summarize concisely some of the most important aspects of Florissant's paleontology in the format of a book that was intended for a broad audience, ranging from amateurs to professional paleontologists. The database was invaluable for accomplishing this and for locating some of Florissant's most impressive, well-preserved specimens for illustration. Key components of the database were synthesized for use as appendices, including a

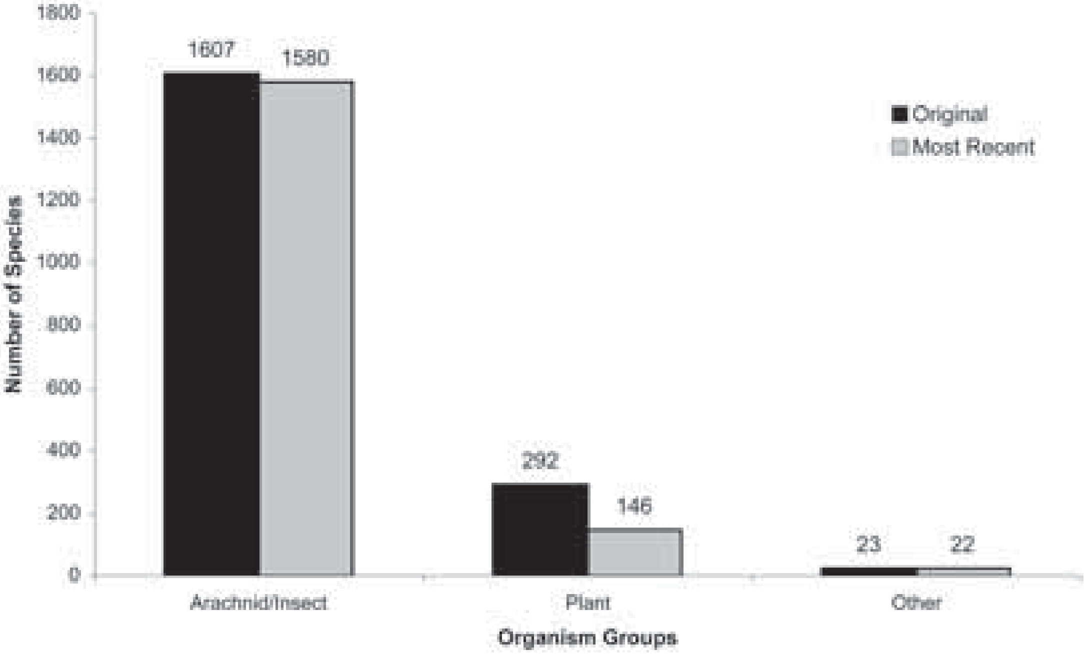

Figure 6. Number of megafossil species originally described compared with the number still valid in the most recent published treatment. "Other" includes bivalves, gastropods, diplopods, crustaceans, fish, and birds. Definitions of "original" and "most recent" are given in the Appendix under Reference Table, definition for "status." Palynomorph taxa that were included in the taxonomic counts for plant groups in Table 2 are not included in the plant counts for this figure, which illustrates only megafossil data. Results are based on the January 2006 version of the database.

listing of museums with Florissant collections, and a taxonomic compilation that lists the authors of all species, the year in which each species was described, and the location of the primary type specimen (holotype or syntypes). The database also provided the source for publishing a complete bibliography in the book.

New exhibit designs are currently under way for Florissant Fossil Beds National Monument and the database is providing a source for locating unique specimens that will be incorporated into exhibits as photographs to help illustrate some of the important interpretive themes. The database Web site, including the general user's "online museum," will provide an interactive kiosk exhibit to help visitors understand Florissant's paleontology.

Problems and Limitations

Understanding the Complexity of the Data and the User Requirements

To obtain meaningful results from more complex database queries, users must have a thorough understanding about the nature of the data content as well as concepts of paleontology, museum cataloging practices, taxonomy, and nomenclatural procedures. Seemingly simple searches often can become much more complex than what was anticipated.

For example, a user might search the taxonomy table as a simple means for determining the diversity at Florissant (Table 2), yet the resulting hit list of 1994 total records would be misleading. In part, this is because two fundamentally different approaches to naming palynomorphs have been used at Florissant, resulting in duplicate names that cannot be correlated easily between these publications. Further, many of these palynomorph taxa are organ duplicates of leaf and fruit species known from the macrofossil record. Consideration of such anomalies results in a total taxonomic estimate of ~1700 species (Meyer, 2003). As another example, a query to determine how many species were originally described in a particular monograph requires combining multiple syntype specimens into a single species category during the search. Users must formulate their queries carefully, and presentations of data tabulations frequently require some degree of qualification and explanation.

In designing a database, user requirements ideally should be well defined before the actual design begins. Unfortunately, database design and data collection often occur without a clear vision about how the information ultimately will be used. As users refine their needs, the ability to answer complex questions may be inhibited or prohibited by the relationships among tables or the fields within the tables. Ultimately, this limitation can be addressed through the addition or modification of tables or fields, although this increases the risk of adding ad hoc patches to the database, which may add unnecessary confusion and require more overhead in maintenance.

CONCLUSIONS

The Florissant database is designed to serve as a long-lasting digital repository that provides public access to a broad spectrum of information about the most important fossils from Florissant and their treatment in various publications. Site-specific databases such as this synthesize collection-level documentation of paleontological diversity that has broad applications to the science. Collectively, such databases can provide valuable tools for assessing previously published literature in order to provide synthesized information about biodiversity trends through time, patterns of evolution, the biogeography of particular taxonomic groups, and the nature of regional and global community evolution through time, and for defining the specific needs for new field- and specimen-based research (Alroy, 2003). The Florissant database contributes to this by completely documenting our knowledge of this diversity at one of the world's most productive paleontological sites.

Development of this database helps to fulfill the objective of Florissant Fossil Beds National Monument to provide information that will stimulate ongoing, innovative paleontological research at Florissant. Such information contributes to understanding Florissant's significance as a unique locality in relation to the global paleoecosystem of the late Eocene and to providing a basis for comparison with other paleontological sites worldwide. It is hoped that the methods used for inventorying the Florissant collections and in developing this database and Web site can be modified for application to other significant paleontological sites that share with Florissant such characteristics as very high taxonomic diversity, a rich publication history, and widely dispersed collections between numerous repositories.

APPENDIX. DEFINITIONS OF DATABASE FIELDS

Specimen Table

Inventory_Number	Primary key. A unique inventory number is assigned to each specimen in the database. The same inventory number is assigned to corresponding halves of a specimen if they are at the same museum, even if that museum assigned separate catalog numbers to each of these. If the corresponding halves of the same specimen are at different museums, each half is assigned a separate inventory number.
TaxonomicID	Foreign key. A unique number that links each specimen to a single taxonomic record.
Catalog_Number	Institutional acronym and specimen catalog number.
Museum	Acronym of the institution to which the specimen belongs.
Dimensions	If measurements have been taken, they can be indicated here, although the scale in the photograph usually suffices for measurement.
Item_Count	Number of individual items that are documented by the inventory number (generally used to indicate whether a specimen consists of two corresponding halves).
Element_Organ	Element or organ represented by the specimen (e.g., wing, fruit, leaf, feather, body).
Description	A description of the specimen can be included under this field.
Collector	Original collector of the specimen.
Collecting_Date	Date of collection.
Locality	Locality number.
Locality_Description	Description of the locality.
Accession_Number	Accession number, if one was assigned by the museum where the specimen is currently housed.
Original_Catalog_No	Original catalog number(s) if such a number is different than the current catalog number. The number is preceded by the institutional acronym or the collector, and in some cases, this may differ from the institution where the specimen presently resides. More than one original catalog number may be indicated in this field.
Counterpart_Number	Catalog number for the corresponding counterpart of a specimen if that number differs from the catalog number above. The number is preceded by the institutional acronym, which may differ from the institution indicated for catalog number if the counterpart is housed at a different museum.
Other_Numbers	Any other numbers that appear on the actual specimen.
Object_Status	This indicates the object status as “specimen missing” or “on loan.”
Notes	Remarks about the nature or condition of the specimen, or a description of points of confusion.
Observer	Person who examined the specimen for inclusion in the database.
Date_Observed	Date the specimen was inventoried on-site.
Entered_By	Person who created the database entry.
Date_Entered	Date the database entry was created.

Image Table

ImageID	Primary key. A unique number that identifies each record in the table.
Inventory_Number	Foreign key. Inventory number of the specimen, same definition as above; used in this table to link each image to a specimen.
File_Name	Name of the digital image file.
File_Path	Location of the digital file on the server.
Image_Format	Indicates the format of the image (e.g., jpg, tif).
Image_Caption	Caption of image, if one exists.
Image_Credit	Photographer of the specimen image in the database.
Image_Date	Date the image was created.
Description	General description of the image.
Notes	Internal notes regarding the image.
Entered_By	Person who created the database entry.
Date_Entered	Date the database entry was created.

(*continued*)

APPENDIX. DEFINITIONS OF DATABASE FIELDS (*CONTINUED*)

Reference Table

ReferenceID	Primary key. A unique number that identifies each record.
Inventory_Number	Foreign key. Inventory number of the specimen, same definition as above; used in this table to link each reference to a specimen.
BiblioID	Foreign key. Bibliographic identification of the citation.
Record_Number	A derivative of the inventory number, numerically sequenced by a decimal designation to indicate the chronological sequence of publication status.
Higher_Taxon	Informal breakdown into the major taxonomic groups.
Status	Each published reference to each specimen is documented as a separate record in the table. If a specimen has been referenced in multiple publications (often under different taxonomic assignments), the database includes a record for each of these and designates them as O*riginal* (first publication in which the specimen was cited), *Most Recent* (most recent published treatment for the specimen), or *Intermediate* (published treatments of the specimen between its original and most recent publications). Each specimen *must* contain *both* an original and most recent record, and hence a record is indicated as *Original and Most Recent* if the original published citation of the specimen also remains the most recent one.
Order Family Genus Species	Each of these fields indicates the designated taxonomic rank. This rank can include any past classification scheme or naming system that was used in a published reference to the specimen.
Author	Name of the author(s) for the species.
Reference	Publication in which the specimen was cited.
Page	Initial page number on which the species is described in the reference.
Figure	Figure, or plate and figure, where the specimen is illustrated in the reference, or notation that the specimen is unfigured.
Type	Type status for the specimen as designated by the above reference. Terms used include *holotype*, *syntype*, *paratype*, *lectotype*, *paralectotype*, *allotype*, *figured*, *mentioned*, and *unpublished*. *Figured* and *mentioned* refer to specimens that are specifically cited in publication, but are not types.
Remarks	Remarks pertaining to the treatment of the specimen in the above publication
Common_Name	A generally accepted common name for the taxon can be indicated here.
Entered_By	Person who created the database entry.
Date_Entered	Date the database entry was created.

Bibliography Table

BiblioID	Primary key (autonumber) that uniquely identifies each bibliographic citation.
Resource_Name	Every publication within this portion of the database is assigned a unique name based on the author's last name, the year it was published, and a letter indicating the order in which it was published if the author published more than one publication in that year.
Author	The name of the author(s) on the publication.
Title	Title of the article or document.
Periodical_Name	Title of the journal, periodical, bulletin, or monograph in which the article or document was published.
Periodical_Issue	Volume, number, series, article, etc.
Book_Citation	Bibliographic citation to a book if the article or document was published as a contribution to an edited volume.
Page	Page numbers within the book, periodical, or monograph on which the article appears.
Plates	Plate numbers within the book, periodical, or monograph, if these were not included within the page sequence.
Year_of_Issue	Year of publication.

(*continued*)

APPENDIX. DEFINITIONS OF DATABASE FIELDS (*CONTINUED*)

Date_of_Issue	Precise date of publication, when available.
Library_Status	Indicates whether the library at Florissant Fossil Beds National Monument has obtained an original or photocopy of the publication.
Keywords	List of topics that describe the content of the publication (e.g., fossil insects, fossil plants, new genus, new species, geology).
Notes	Information that does not fit another field in the data table.
File_Name	A link on the Web site if there is a scanned pdf copy of the document on file.
File_Path	Path to the file on the server.
Entered_By	Person who created the database entry.
Date_Entered	Date the database entry was created.
	Taxonomy Table
TaxonomicID	Primary key. A unique number that links each specimen to a single taxonomic record.
Kingdom Phylum_Division Subphylum Class Subclass Superorder Order Suborder Superfamily Family Subfamily Tribe_Supergenus Genus Species Subspecies_Variety	Each of these fields represents a taxonomic rank based on the modern classification scheme (see text for clarification).
Author	Name of the author(s) for the genus-species binomial.
Reference	Bibliographic source for the taxonomic name.
Extinct	This field indicates whether the genus is extant (“0”) or extinct (“-1”).
Notes	Any remarks that do not fit another field in the table.

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