Floristic composition and comparison of middle Eocene to late Eocene and Oligocene floras in North America

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In comparison to the early and middle Eocene, the late Eocene and particularly the Oligocene floral record is sparse in North America. Changing tectonic, environmental and climatic conditions during these times resulted in the development of fewer depositional systems favorable for fossil preservation. Floras are known from the Southeast, the Pacific Northwest and the Rocky Mountains. Each area has a distinct geological history that shaped both the vegetation adjacent to sites of deposition as well as the depositional environments themselves. The floristic change from middle to late Eocene, and then to Oligocene reflects a changing paleoclimate from the thermal maximum to cooler and drier conditions in the late Paleogene. In the present paper, major middle, and then late Eocene and finally Oligocene floras of North America are summarized, with an emphasis on their regional geology, depositional setting, paleoclimate and significant floral elements. The North American occurrences of coryphoid palms (*Sabal*) and cycads are reviewed in relationship to their biogeographic history. Finally, we suggest several directions for future research that will further illuminate the floristic changes from middle, to late Eocene and Oligocene that occurred in North America. • Key words: Claiborne, Eocene/Oligocene transition, Florissant, Okanogan Highlands, Tertiary floras.

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Assemblages of plant-bearing fossiliferous sedimentary rocks of the late Eocene and especially Oligocene ages are rare in North America (Wing 1987). There are several reasons why this is so. First, the extensive Paleogene fluvial plain covering the region once occupied by the Cretaceous Intercontinental Seaway became diminished, limiting the areas with the appropriate conditions necessary for plant preservation. Secondly, climate became drier, leading to fewer environments of deposition available for preserving megafossils. Thirdly, the ash-producing volcanism responsible for blocking drainage systems in the western Rocky Mountains to create depositional basins decreased during the Oligocene (Graham 1999). Thus the combination of changing geomorphology, drying climate and less volcanic activity all contributed to the decreased number and extent of fossil plant beds of this age. As a result, the transition from the robust fossil records of the early and middle Eocene into the late Eocene and Oligocene is only broadly understood.

Despite the limited late Eocene and Oligocene plant bed exposures in North America, this is an important time period to study for several reasons. First, these floras mark a major shift in climate from the warmer and more humid middle Eocene toward the cooler and drier conditions that continue to the present day. Floral response to climate change has been studied by both the Nearest Living Relative method (NLR) and leaf physiognomy. The NLR uses the distribution of closely related living plants to infer climate in fossil floras (*e.g.*, Axelrod 1957, 1966a). This method is valuable, however fossil forms may not have occupied identical niches or had equal physiological tolerances as their current relatives. Leaf physiognomic methods such as Leaf Margin Analysis (LMA), Leaf Area (LA) and Climate-Leaf Analysis Multivariate Program (CLAMP) are based on assemblages of extant leaves characterized by characters of size and shape correlated to their occurrence in modern environments. These taxon-free approaches provide a means independent of systematic affinities for estimating climate (Wolfe 1987, Graham 1999). Easily quantifiable leaf physiognomy techniques have become a powerful tool for providing numerical data that can be compared readily with other proxies, such as carbon isotopes. These two types of methods often are used in combination to establish estimates of paleoclimate and paleoelevation parameters (*e.g.*, Greenwood *et al.* 2005).

A second major area of interest is the origin and diversification of major taxonomic groups. As taxon-free methods have become *de rigueur* for climate reconstruction, traditional systematic studies of fossil plants have shifted toward novel applications that relate to molecular phylogenetics and biogeography (Manchester 1999, Manos & Stanford 2001, Tiffney & Manchester 2001, Manos *et al.* 2007, Manchester *et al.* 2009). Fossil occurrences act as an independent proxies for dating nodes of divergence for molecular and/or combined data sets. They also provide a means for examining character evolution, and broad responses of lineages to environmental change, as well as demonstrating past distributions. The middle to late Eocene and then Oligocene floras mark important chapters in the evolutionary and biogeographic history of major plant groups as they adapt, diversify, and wax or wane in the fossil record.

In this contribution the major floras of middle to late Eocene and Oligocene ages in North America are reviewed, with a brief description of the geological setting, depositional environment, and paleoclimate of each, followed by a description of significant floral elements (Table 1). This study presents more detail about several floras that to date have not been comprehensively summarized. Fossil occurrences of cycads and coryphoid palms are reviewed for North America in relationship to their biogeographic history. Lastly, directions for future research are suggested that will further illuminate an understanding of the late Eocene and Oligocene floras of North America.

Overview of the floras

Middle Eocene to Early Oligocene in the Southeast Mississippi Embayment

One of the best glimpses of the late Eocene and Oligocene floras comes from southeastern North America in the region of the Mississippian Embayment. These floras were initially surveyed by Berry (1916, 1922, 1924, 1925, 1930, 1941) who, over the course of 25 years, described more than 340 species of Eocene and Oligocene fossil plants, many from this floristic region (Pigg & DeVore 2007). Many of Berry's identifications have been reinterpreted, so subsequent papers should be consulted. A sustained effort in studying Mississippian Embayment floras from the middle Eocene Claiborne Formation commenced with Dilcher's (1963b, 1965) work on fossil leaves with epiphyllous fungi. Detailed taxonomic studies followed, based on the excellent cuticular preservation of fossil leaves and fruits from the Claiborne, leading to the eventual description of over 30 megafossil genera in approximately 15 families (Table 2).

Determination of precise ages and depositional environments within the Claiborne Formation is limited because stratigraphic units are difficult to correlate. The most extensively studied plants of the Claiborne occur in localized clay pits (*e.g.*, Puryear, Warman, Lamkin). These outcrops are small, discontinuous units not found in conjunction with marine deposits or other biostratigraphically informative sediments. In contrast to localities in the West that are commonly associated with intense orogenic activity during the Cenozoic, the Mississippian Embayment is on the passive margin of the North American plate and typically lacks datable ashes and other igneous units. Since radiometric dating is not available, floras in the region are correlated primarily by pollen zonation (Elsik & Dilcher 1974, Potter & Dilcher 1980, Table 1).

The depositional environments of the Claiborne Formation have been interpreted in several ways. Originally, Berry (1916) considered the Claiborne to be the result of a series of fluvial and lacustrine deposits in back-beach areas of the Gulf of Mexico. Dilcher (1971) attributed the clay lenses of Henry and Weakley Counties of Tennessee to deposits in abandoned river channels of oxbow lakes occupying a low-lying floodplain. In one study Moore *et al.* (2001) suggested that the section exposed at the Wilbanks Clay Pit in western Tennessee may have been deposited in one to several seasons.

Multiple overlapping clay lenses with truncated margins, cut-and-fills, and cross-bedded sandstones containing clay rip-ups were found in northeastern outcrops of the Claiborne. Some of these plant-bearing clays are interpreted as being deposited within a braided stream system (Moore *et al.* 2003). Based on the three-dimensional structure of several clay lenses characterized by distinct lower contacts and fine laminated bedding, Moore *et al.* (2003) later proposed that rates of infilling probably occurred in these deposits over a 1,000–2,000 year period. Future studies, particularly within the context of basin analysis, may help to clarify the apparent contrasting modes of deposition within the Claiborne.

The Mean Annual Temperature (MAT) for Claiborne has been estimated variously as between 20–28 °C or 22–30 °C (Graham 1999). Dilcher (1973) suggested that the climate was similar to coastal Louisiana (21 °C) or to southern peninsular Florida (24 °C). These estimates, with MAT above 20 °C, indicate a megathermal flora (Wolfe 1987). The Claiborne is characterized as a dry tropical forest (Wolfe 1978) with the dominant plant groups being lauraceous leaves, castaneoid and transitional oaks and legumes representing all three major groups (Dilcher 1963a; Crepet & Dilcher 1977; Crepet & Daghlian 1980; Herendeen & Dilcher 1990a, b, c). Very large monocot leaves (up to 75 cm wide) with entire margins assigned to Araceae occur (Dilcher & Daghlian 1977), as do Juglandaceae of subfamily Engelhardiodeae,

today a completely Asian clade (Dilcher & Manchester 1986, Manos & Stanford 2001, Manos *et al.* 2007). Other families reported from the Claiborne Formation include Eucommiaceae, Euphorbiaceae, Oleaceae, Theaceae, Rhamnaceae and Ulmaceae (Table 2). Palms are common and almost all are coryphoid. Interestingly, the only aquatic plant found in the Claiborne Formation is the floating *Ceratophyllum* (Herendeen *et al.* 1990). Unlike many other middle Eocene floras, Betulaceae and taxoidaceous conifers are rare if at all present, and the only published conifer remains have been attributed to *Podocarpus* (Dilcher 1969).

To the southwest of the Claiborne, the Catahoula Formation of east Texas is a rare record of early Oligocene plant megafossils in the Mississippian Embayment. Along with the Claiborne, the Catahoula provides some invaluable insights regarding the biogeography of the Mississippian Embayment. Berry (1916) first reported fossil plant remains near Huntsville, Texas, but the leaf material was in a rather coarse sandstone bed. Additional fossils in a finer matrix that preserved excellent plant cuticle were recovered during the 1970s–80s, when the Riverside Crushed Stone Company was actively quarrying the region.

In the 1990's when the quarry was transformed into a lake and became used as a site for certifying scuba divers, most of the significant fossil plant beds became inaccessible.

Galloway (1977) believed that two depositional systems are represented in east Texas: the Gueydan bedload fluvial system of the Rio Grande Embayment and the Chita-Corrigan mixed load fluvial system of the Houston Embayment. Freile *et al*. (2003) reported the presence of glauconite in the Huntsville section and interpreted this occurence to indicate shelf (60–550 m) or shallow marine environments and/or a transgressive episode. The lithology of samples indicates a multiple provenance rock that includes volcanic grains, sub-rounded chert and quartz grains, while other quartz clearly is metamorphic in origin.

The Catahoula flora is rich in legumes, transitional oaks and other Fagaceae, palms, juglandaceous and possibly euphorboid fruits (Daghlian *et al.* 1980, Herendeen & Dilcher 1990a, Herendeen *et al.* 1992, Manchester & Dilcher 2007). The site is especially important in documenting the early evolution of Fagaceae with pollen-bearing flowers of intermediate and trigonobalanoid oaks occuring side-by-side with modern-appearing, apparently black oak leaves and white oak acorns (Daghlian & Crepet 1983; Crepet & Nixon 1989a, b). A spiny cupule (the "frilly fruit") with possible affinities to Fagaceae, also known from the Claiborne has been reported (Pigg *et al.* 2001a), and *Taxodium* seed cones and leaves have been identified (DeVore, personal observation).

The Middle Eocene in the Rocky Mountains – The Green River flora

In the West, the Eocene to Oligocene is well represented in the Rocky Mountains, particularly in Colorado, Utah and Wyoming. During the early and middle Eocene in this area significant floras were preserved in three basins occupied by extensive, shallow lakes: Uinta Basin (Lake Uinta), Green River Basin (Lake Gosiute) and Fossil Basin (Fossil Lake; Roehler 1993, Graham 1999). The flora of the Green River Formation, primarily exposed in the Green River Basin was treated by R. Brown (1934) and MacGinitie (1969).

The Green River Formation is one of the most diverse lacustrine systems in the world and contains several tuff beds that provide a means of dating and determining rate of sediment accumulation and timing of faunal and floristic changes (G. Smith *et al.* 1998). A broad range of facies are represented and these have been described and subdivided into facies associations as (1) evaporative, (2) fluctuating profundal, and (3) fluvio-lacustrine (Carrol & Bohacs 1999). A fluvial-lacustrine facies association is represented by the Luman Tongue. This horizon contains defining mudstone, sandstone, coal and coquina lithologies in conjunction with root casts, coarse lamination and fluvial channels. Typical parasequences grade from calcareous mudstones and silstones into shelly coquinas, deltaic sands and thin coals. All of these features are definitive of a hydrologically open lake (Horsfield *et al.* 1994, Carrol & Bohacs 1999). The Luman Tongue is fossiliferous, and contains more of a fauna and less of a flora than the slightly younger Parachute Member, which is widely known for its economically valuable oil shale deposits and rich fossil records of insects and plants (McGinitie 1969). Like the Luman Tongue, the Parachute Member represents a hydrologically open lake stage of Lake Uinta (MacGinitie 1969). Outcrops of the Parachute Member are best exposed in the Piceance Creek Basin, near Douglas Pass, Colorado and in the Uinta Basin near Bonanza, Utah. Radiometric ages from ^{40}Ar/^{39}Ar laser fusion of biotite and hornblende crystals date the fossiliferous horizon above the Mahogany marker bed at 48.13 ± 0.71 and 48.22 ± 0.71 (Malchus *et al.* 2002, Boucher *et al.* 2003).

The Green River flora is the Western assemblage that bears the closest resemblance to the Claiborne, and accordingly has been studied extensively by Dilcher and colleagues. Floristic similarities with the Claiborne include coryphoid palms, legumes, *Ceratophyllum Engelhardia*, and *Eucommia* (Herendeen *et al.* 1990; Call & Dilcher 1994, 1997). The most abundant Green River megafossil elements in addition to palm leaves are the climbing fern *Lygodium* (Manchester & Zavada 1987) and *Sapindus. Ptelea* (Call & Dilcher 1995), *Typha*, *Musophyllum*, and *Zingiberopsis* are also common, and

Table 1. Comparison of floras discussed in text. Abbreviations: e – early, m – middle, l – late, Fm – Formation, High – Highlands, Is – Island, Mem – Member, Mtn – Mountain, ss – sandstone; lo – lower, mid – middle, up – upper; BC – British Columbia, CO – Colorado, ID – Idaho, KY – Kentucky, MT – Montana, TN – Tennessee, UT – Utah, WA – Washington, WY – Wyoming; * – interconnected organs.

Flora Main references	Age (Ma) Data source	Locality Stratigraphy	Depositional environment	MAT (^{o}C)	Inferred vegetation type(s)	Significant taxa
Southeast						
Claiborne Dilcher (1973), Wolfe (1978), Wolfe & Poorle (1982)	m Eocene palynology	TN, KY Claiborne Fm	fluvial – oxbow lakes	20–28 22–30	tropical dry deciduous	Lauraceae, legumes, transition oaks, Araceae, palms
Catahoula Galloway (1977)	e Oligocene palynology	east TX Catahoula Fm	fluvial – deltaic	unknown	tropical dry deciduous	Legumes, transition & modern oaks, palms
Rocky Mountains						
Green River Graham (1999), Malchus *et al.* (2002)	e m Eocene 48.13 ± 0.71 48.22 ± 0.71 ^{40}Ar/^{39}Ar laser fusion	east UT, west CO Green River Fm, Parachute Creek Member	lacustrine	16	savanna woodland tropical dry forest at lower elevations; deciduous – middle; mixed hardwood coniferous – upper	Palms, legumes, *Lygodium, Sapindus*; *Cedrelospermum*, Populus*, Pseudosalix*, Sygioides*, Gilisenium**
Florissant Evanoff *et al.* (2001); Meyer (2003)	l Eocene 34.07 ± 0.01 single crystal ^{40}Ar/^{39}Ar sanidine from pumice in ss & debris flow	central CO Florissant Fm lower and middle shales	2 lacustrine episodes, 1 fluvial unit between	12.5	savanna – woodland, tropical – dry	*Cedrelospermum, Fagopsis, Florissantia,* Rosaceae
Creede Wolfe & Schorn (1989), Ratte & Steven (1967)	l Oligocene 27.2 K-Ar of ash-flow tuffs	southwest CO Creede Fm	deep lake lacustrine – deltaic	4.5	chaparral, woodland, western montane coniferous	Rosaceae, Pines, *Juniper, Mahonia, Ribes, Populus, Nuphar,* legumes, *Abies*
Pacific northwest						
Chuckanut S. Johnson (1982 1984a), Mustoe & Gannaway (1997), Mustoe *et al.* (2007)	m Eocene 49.9 ±1.2 Fission track of tuff bed above basal contact	Coastal & Interior northwest WA Chuckanut Fm Bellingham Bay & Slide Mem (lo) Padden Mem (up)	fluvial – flood basin	15 B Bay (66); 16 Slide (30); 12 Padden (64)	Bellingham Bay and Slide: tropical Padden: more temperate	Coryphoid palms, ferns: *Lygodium, Woodwardia, Cyathea, Glyptostrobus, Taxodium, Mseocyparis, Metasequoia, Alnus, Betula, Platanus*
Puget Group Wolfe (1968, 1978); Burnham (1990, 1994)	l Eocene Radiometric dates and biostratigraphy	Coastal west WA Puget Group	fluvial and overbank	15–18.6	tropical	Diverse ferns, *Zelkova, Metasequoia,* monocot leaves, *Acer, Populus*
Republic localities Wolfe & Wehr (1987), Wolfe *et al.* (2003), Greenwood *et al.* (2005)	e-m Eocene 49.42 ± 0.54 ^{40}Ar/^{39}Ar	Okanogan High north central WA Klondike Mtn Fm, Tom Thumb Tuff Mem	lacustrine	11.4, 10	mixed hardwood coniferous early western montane coniferous	Rosaceae, *Acer, Ulmus, Langeria, Tsukada, Macginitiea, Pinus, Abies Corylus, Trochodendron*
One Mile Creek Greenwood *et al.* (2005), Dillhoff *et al.* (2008)	e Eocene 52.08 ± 0.12 U-Pb zircons	Okanogan High south central BC Hardwick SS	lacustrine	9.3, 8.3	mixed hardwood coniferous early western montane coniferous	*Betula leopoldae*, Cercidiphyllum, Pinus, Abies, Acer, Neviusia, Prunus, Ulmus*
Thomas Ranch Greenwood *et al.* (2005), Dillhoff *et al.* (2008)	e Eocene 52.08 ± 0.12 U-Pb, zircons	Okanogan High south central BC Hardwick SS	lacustrine	9.3, 8.3	mixed hardwood coniferous early western montane coniferous	Conifers, *Azolla, Acer*

Table 1. continued

Flora Main references	Age (Ma) Data source	Locality Stratigraphy	Depositional environment	MAT (°C)	Inferred vegetation type(s)	Significant taxa
McAbee Dillhoff *et al.* (2005)	e-m Eocene 51 ± 2 to 52 ± 2	Okanogan High south central BC Kamloops Group, unnamed fm	lacustrine	9.5 (45)	mixed hardwood coniferous early western montane coniferous	Betulaceae, Fagaceae, Ulmaceae
Quilchena Mathewes & Greenwood (2007)	e Eocene 51.5 ± 0.4 ⁴⁰Ar/ ³⁹Ar sanidine tephra	Okanogan High south central BC	lake & swamp complex	Unknown	mixed hardwood coniferous early western montane coniferous	*Taxodium, Keteleeria Calocedrus, Nyssa, Glyptostrobus, Metasequoia, Decodon*
Falkland R. Smith *et al.* (2007)	50.61 ± 0.16 U-Pb zircons	Okanogan High south central BC	lacustrine	9.2 LMA	mixed hardwood coniferous early western montane coniferous	*Glyptostrobus, Ginkgo, Macginitiea, Prunus, Acer, Dipteronia, Ulmus*
Princeton Chert Stockey (2001), Little *et al.* (2009)	m Eocene 48.7 K-Ar of ash layer #22	Okanogan High south central BC Princeton Group, Allenby Fm	lake or mire	unknown	subtropical	Ferns, Monocots, Pines, *Eorhiza*, Nymphaeaceae, Lythraceae, Rosaceae, Lauraceae, Vitaceae, *Metasequoia**
Clarno Nut Beds Manchester (1994)	m Eocene vertebrate biostratigraphy	Pacific Northwest Interior central OR Clarno Fm	stream and lake delta	16, based on W Branch Creek	tropical to paratropical	Juglandaceae, Cornaceae, Icacinaceae, Platanaceae Menispermaceae,
Appian Way Little *et al.* (2001), Mindall *et al.* (2009)	Eocene palynology; decopod crustaceans, mollusks and shark teeth	Pacific Northwest Coastal, Vancouver Is, BC	forest litter in marine nodules	unknown	paratropical?	Ferns, Moss, Fagaceae, Cupressaceae, Icacinaceae, Platanaceae, Juglandaceae
Badger's Nose Myers (2006)	l Eocene 34–35 K/Ar; ⁴⁰Ar/³⁹Ar	Pacific Northwest Interior, northeast CA Steamboat Fm	lacustrine	13.8	intermediate warm subtropical/cool temperate, woodland	Betulaceae, Rhamnaceae, Tiliaceae, *Acer, Deviacer Metasequoia, Alnus, Decodon, Mahonia*
Bridge Creek Meyer & Manchester (1994)	e Oligocene 33.6 ³⁹Ar/⁴⁰Ar	Pacific Northwest Interior central OR John Day Fm	lacustrine	10–12	deciduous	*Metasequioa, Alnus, Cunninghamia, Asterocarpinus, Paracarpinus, Acer, Florissantia, Eucommia*

Acer, *Platanus*, *Pterocarya* and *Zelkova* also occur. A MAT of 16 °C has been calculated for the Green River flora (Graham 1999).

Among the most informative occurrences at Green River are of specimens that show organic attachments of flowers, fruits, and leaves to the same stem, thereby confirming the identity of these organs as belonging to the same plant. These studies often reveal mosaic combinations of characters not seen in extant taxa, and provide clues to the evolutionary history of families. Examples include *Cedrelospermum* (Manchester 1989); *Populus* (Manchester *et al.* 1986); *Pseudosalix* (Boucher *et al.* 2003); *Syzygioides* (Manchester *et al.* 1998), and the herbaceous *Gilisenium* (Lott *et al.* 1998). An atlas of the Parachute Creek flora is available as an online resource (K. Johnson *et al.* 2002; see http://www.paleocurrents.com).

Middle Eocene Pacific Northwest: Chuckanut, Swauk and Puget Group

The Pacific Northwest contains some of the most complex geological history in North America. During the Late Cretaceous, a stable platform formed by the accretion of terraines in western Washington State. The platform underwent extensive strikeslip faulting and deformation during the early to middle Eocene to form a series of sedimentary basins. These basins experienced rapid subsidence and provided a depositional environment capable of accommodating extensive amounts of nonmarine sediments. Thick sequences of strata were produced associated with intrabasinal volcanics and intrusional, crystalline bodies (S. Johnson 1985, Brownfield *et al.* 2005). One of the thickest of these nonmarine sequences is the Chuckanut Formation, which

Table 2. Flora of the Claiborne Formation.

Family	Taxon	Reference	Localities
Aracaceae (Coryphoideae)	*Amesoneuron* sp.	Daghlian (1978)	Lawrence
Aracaceae (Coryphoideae)	*Costapalma philipii*	Daghlian (1978)	Lamkin
Aracaceae (Coryphoideae)	*Palmicites eocenica*	Daghlian (1978)	Several sites
Aracaceae (Coryphoideae)	*Palustrapalma agathae*	Daghlian (1978)	Several sites
Aracaceae (Coryphoideae)	*Sabalites grayensis*	Daghlian (1978)	Many sites
Aracaceae (Coryphoideae)	*Sabal dortchii*	Daghlian (1978)	Lamkin
Araceae	*Philodendron limnestis*	Dilcher & Daghlian (1977)	Several sites
Araliaceae	*Dendropanax eocenensis*	Dilcher & Dolph (1970)	Lawrence, New Haven, Warman
Ceratophyllaceae	*Ceratophyllum incertum*	Herendeen *et al.* (1992)	Fayette Co. TN
Eucommiaceae	*Eucommia eocenica*	Call & Dilcher (1977)	Bovay, Idalia, LaGrange
Euphorbiaceae	*Hipppomaneoideae warmanensis*	Crepet & Daghlian (1982)	Warman
Euphorbiaceae	*Crepetocarpon perkinsii*	Dilcher & Manchester (1988)	
Fagaceae	*Berryophyllum*	Jones & Dilcher (1988)	
Juglandaceae	*Oreoroa claibornensis*	Dilcher & Manchester (1986)	Lamkin, Puryear, Somerville, Warman
Juglandaceae	*Eokachyra aeolius*	Crepet *et al.* (1975)	Several sites
Juglandaceae	*Eoengelhardtia puryearensi*	Dilcher *et al.* (1976)	Puryear
Juglandaceae	*Paraoremunnea puryearsnsis*	Dilcher *et al.* (1976)	Lamkin, Puryear
Juglandaceae	*Paraoremunnea stoneana*	Dilcher *et al.* (1976)	Lamkin, Warman
Lauraceae	*Ocotea obtusifolia*	Dilcher (1963a)	Puryear
Leguminosae Papilionoideae	*Eomimosoidea plumosa*	Herendeen & Dilcher (1990a)	Warman
Leguminosae Papilionoideae	*Diplotropis claibornensis*	Herendeen & Dilcher (1990b)	Bell City, Warman
Leguminsae Caesalpinioideae	*Crudia grahamiana*	Herendeen & Dilcher (1990c)	Lawrence, Warman
Leguminosae Caesalpinioideae	*Crudia brevifolia*	Herendeen & Dilcher (1990c)	Lawrence, Warman
Leguminosae Caesalpinioideae	*Caesalpinia claibornensis*	Herendeen & Dilcher (1991)	Puryear, Warman
Nyssaceae	*Nyssa eolignitica*	Dilcher & McQuade (1967)	Lawrence, Puryear
Oleoaceae	*Fraxinus wilcoxiana*	Call & Dilcher (1992)	Puryear, Warman
Podocarpaceae	*Podocarpus*	Dilcher (1969)	not listed
Proteaceae?	*Knightiophyllum wilcoxianum*	Dilcher & Mehrotra (1969)	Puryear
Rhamnaceae	*Rhamnus marginalis*	Jones & Dilcher (1980)	Puryear, Lawrence, Lamkin
Rubiaceae	*Paleorubioceophyllum eocenicum*	Roth & Dilcher (1979)	Puryear, Miller, Lawrence, New Lawrence, Rancho, Lamkin
Theaceae	*Gordonia lamkinensis*	Grote & Dilcher (1989, 1992)	Lamkin, Miller
Theaceae	*Gordonia warmanensis*	Grote & Dilcher (1989, 1992)	Warman
Theaceae	*Gordoniopsis polysperma*	Grote & Dilcher (1989, 1992)	Lawrence
Ulmaceae	*Eoceltis dilcheri*	Zavada & Crepet (1981)	Lawrence, Puryear

is exposed in the vicinity of Bellingham, Washington and extends northeastward to the Canadian border. A second sequence, the Swauk Formation, outcrops on the flanks of the Cascade Mountains to the southeast and has been interpreted as part of the Chuckanut Formation that was faulted (Mustoe 2001, Mustoe *et al.* 2007). This interpretation is supported by the floristic and lithologic similarities between the two formations.

The Chuckanut Formation consists of about 9000 m of conglomerate, arkosic sandstone, siltstone and coal and is best exposed in western Whatcom and Skagit counties, in northwestern Washington State, where it unconformably overlies accreted Paleozoic and Mesozoic terrains (Mustoe & Gannaway 1995, 1997; Mustoe *et al.* 2007). S. Johnson (1984a, 1984b) interpreted the sequence as representing a braided-meandering river system with point bar deposits being represented by crossbedded arkose beds associated with sandy units indicating crevasse splay deposits. Plant fossils are richest in siltstone beds interpreted as flood basin deposits, with lacustrine sediments rare in the sequence (Mustoe *et al.* 2007). While the Swauk Formation to the southeast has been consistently dated as Eocene since the time of Knowlton (1893), the age of the Chuckanut has been a matter of debate.

The Chuckanut was thought to be the nonmarine extension of the marine Nanaimo Group and therefore of late Cretaceous to Paleocene age (Mustoe *et al.* 2007). It is now clear that the Chuckanut is not related to these marine units. The Chuckanut Formation has been dated by several means. A fission track age of 49.9 ± 1.2 Ma is based on a tuff bed approximately 2,600 m above the basal contact (S. Johnson 1984a). Other radiometric dates determined for the formation fall outside the main outcrop belt in areas of uncertain stratigraphy (see Fig. 3 of Mustoe *et al.* 2007). Detrital zircons show that the oldest Chuckanut beds are no older than late Paleocene, while volcanic interbeds are late Eocene in age.

The Chuckanut can be divided into three units, the older Bellingham Bay and younger Slide Member and a third and uppermost unit, the Padden Member. The Bellingham Bay and Slide Members have similar megathermal assemblages, while the flora in the Padden Member is distinct from them. The Bellingham Bay and Slide Members include a diverse fern component that was described by Marie Pabst (1968). Pabst studied the flora as a whole but was unable to complete her work before her death in 1963. Taxa include both temperate ferns such as *Lygodium*, *Pteris*, *Woodwardia*, and *Dennsteadtia*, as well as the tree fern *Cyathea* which today is found primarily in tropical to subtropical areas. The flora also includes the taxodiaceous conifers *Glyptostrobus*, *Taxodium*, *Mesocyparis*, and *Metasequoia*. *Sabalites* palms are common, along with dicot elements such as *Alnus*, *Betula*, *Platanus* and *Quercus banksiaefolia* (Mustoe & Gannaway 1997, Mustoe *et al.* 2007). The Bellingham Bay flora is subtropical and estimated to have a MAT of 15 °C based on a CLAMP analysis of 66 leaf morphotypes, while that of the Slide Member was estimated at 16 °C based on 30 morphotypes (Mustoe & Gannaway 1997). In contrast, the younger Padden Member flora lacks palms, ferns and lowland conifers and instead contains small-leafed dicots and has an estimated MAT of 12 °C based on CLAMP of 64 morphotypes (Mustoe & Gannaway 1997, Mustoe *et al.* 2007).

The Swauk Formation and related plant-bearing units (including the late Eocene Roslyn and Chumstick Formations) follow the northwest-southeast trending Cascade Mountains. Tropical coastal floras west of the Cascades are very similar to that of the lower Chuckanut members. In contrast, those east of the Cascades, floras of the Roslyn and Chumstck Formations typically lack palms and some of the other tropical elements (Mustoe 2001). These floras are not well published, however, note Mustoe & Gannaway (1995, 1997), Mustoe (2001, 2002a), and Pigg & Wehr (2002).

Additional megathermal floras are known from the late Eocene Puget Group, an undivided unit in the Green River Area of southwest Washington that is associated with four other significant coal-producing units. All five of these sequences represent deposition in a variety of shallow-marine, brackish, deltaic and fluvial environments (Burnham 1986, 1990, 1994; Reineck & Singh 1980; Brownfield *et al.* 2005). The Puget Group has a large proportion of fluvial and/or distributary channel and overbank deposits. Regionally, nonmarine rocks increase in abundance upsection and prograding is recorded throughout the Eocene. The Puget Group overlies unexposed basement rock and underlies a sequence of volcanics at the very end of the late Eocene. Comparisons with the time-equivalent Skookumchuck Formation near Centralia, Washington place the age of the Puget Group as late Eocene (Brownfield *et al.* 2005).

Plants from the Puget Group were studied by Wolfe (1968) who described 31 genera including 25 new taxa. Burnham (1994) updated the taxonomic list to include around 45 genera and numerous morphotypes (see Burnham 1994, Appendix 4). Among the taxa included are *Equisetum*, ferns including *Asplenium*, *Dryopteris*, *Allantodiopsis,* *Cyathea*, *Dennstaedtia*, and *Salvinia*, taxodiaceous conifers *Metasequoia* and *Glyptostrobus*, several types of monocot leaves including *Zingiberopsis*, and among dicots *Acer*, *Betula*, *Castanopsis*, *Fraxinus*, *Populus*, *Salix*, *Vitis*, *Zelkova*, and leaves of affinities to the families Cercidiphyllaceae, Euphorbiaceae, Juglandaceae, Lauraceae, and possibly Menispermaceae.

The Okanogan Highlands

To the northeast of the Chuckanut and Swauk Formations is a region based on early-middle Eocene strata known as the Okanogan Highlands ("Okanagan" in Canada; Archibald & Greenwood 2005). These deposits formed after the geological processes described below: Extensive strikeslip faulting occurred in northeast Washington during the late early to early middle Eocene. During this time, the southern Cordillera of northernmost central Washington, and up into south-central British Columbia, experienced episodes of right-lateral faulting responsible for producing a set of northwest-trending grabens and half-grabens (Ewing 1981, Matthews 1991, Mustoe 2005). A volcanic arc in south-central British Columbia provided a source of large volumes of volcaniclastic sediments and basalt flows in these basins. In the quiescent periods between volcanic activity, a rich array of fossil fish, insects and plants were preserved. The preserving lacustrine and fluvial sediments typically are described as clastic, however Mustoe (2005) has suggested that geochemical alternation of diatomaceous deposits may be responsible in part for the production of these siliceous shales.

In contrast to the coastal Chuckanut Formation and Puget Group, the Okanogan localities today exist at elevations ranging from 500–1100 m and, are believed to have been at, or above, this present elevation during the Eocene (Archibald & Greenwood 2005). Major plant assemblages

of the Okanogan Highlands occur at Republic and at Princeton, Quilchena, Falkland, and MacAbee, British Columbia [BC]. Smaller and/or less collected sites are found at Horsefly and Driftwood Creek, BC, and a variety of other locations (Archibald & Greenwood 2005, Greenwood *et al.* 2005, Mustoe 2005, Pigg et al. 2007, R. Smith *et al.* 2007).

The best known and most diverse of the Okanogan Highlands floras is from a series of localities in and near Republic, Washington, in the Klondike Mountain Formation (Wing 1987, K. Johnson 1996). First considered a primarily conifer-dominated flora (Wolfe & Wehr 1987, Schorn & Wehr 1996), Wolfe & Wehr (1987) named 24 dicots (exclusive of Ulmaceae) from Republic. Since then, and largely through the collecting efforts of Stonerose Interpretive Center in Republic, massive numbers of leaf, fruit, seed and insect specimens have been collected. Republic is known now to have over 250 plant genera, the majority of them represented by dicot leaves and reproductive structures (Wehr 1995, Wehr & Manchester 1996, Pigg & Wehr 2002). The Republic flora is illustrated at the Burke Museum of Natural History & Culture website at: http://www.washington.edu/burkemuseum/collections/paleontology/stonerose/.

Two sites with significant leaf compression floras that occur near Princeton, BC, in the Allenby Formation are the One Mile Creek locality (also known as Allison Creek) and the Thomas Ranch site (also known as Tulameen Road; Dillhoff *et al.* 2008). One Mile Creek is dominated by leaves, fruits, and pollen catkins of *Betula leopoldae* (Crane & Stockey 1986). Other common elements are leaves of *Cercidiphyllum*, *Acer* fruits (Wolfe & Tanai 1987), *Abies*, *Prunus*, and well preserved cones and needle fascicles of *Pinus*. This flora is currently under study and is more diverse than previously thought, with 70 morphotypes representing 57 species (Dillhoff *et al.* 2008). The Thomas Ranch site is well known for the whole *Azolla* plants that occur in paper shale containing gypsum crystals (Arnold 1955). To date, a total of 66 morphotypes have been recognized at this site, representing aroud 56 species (Dillhoff *et al.* 2008).

The McAbee site near Cache Creek, BC has been collected and studied in detail recently by Richard and Thomas Dillhoff, and is represented online at the Evolving Earth Foundation website at: http://www.evolvingearth.org/paleocollaborator/index.php.

The McAbee site is dominated by numerous conifers, *Fagus* leaves and nuts (Manchester & Dillhoff 2004), fruits and leaves of *Ulmus* (Denk & Dillhoff 2005), *Betula*, and *Alnus* (Dillhoff *et al.* 2005). This site contrasts with Quilchena, which is considered the "warmest and wettest" of the Okanogan Highlands sites (Mathewes & Greenwood 2007). Quilchena has been dated at 51.5 Ma with a mesothermal MAT of 15 °C (Greenwood *et al.* 2005). This flora

differs from other Okanogan Highlands floras in having several thermophilic taxa that are absent at the other sites including *Keeteleria*, *Taxodium* and *Nyssa* (Mathewes & Greenwood 2007). Well preserved fruits and abundant seeds of *Decodon* are also present (Mathewes, pers. comm. 2005). The Falkland site is dated at 50.61 ± 0.16, or early Eocene with a MAT of 9.2 ± 2.2 °C (using LMA, based on 38 leaves, R. Smith *et al.* 2007). A paleocological study of this site is in progress (R. Smith *et al.* 2007). Recent summaries on the floristics, depositional environment, and biogeography of the Okanogan Highlands compression floras include: Archibald & Greenwood (2005), DeVore *et al.* (2005), Dillhoff *et al.* (2005), and Pigg & DeVore (2007). DeVore & Pigg (2007) have reviewed the western North American occurrences of Rosaceae, concentrating on the Okanogan Highlands.

Although many paleobotanists are interested in floral components that have diversified and radiated within the tropics there has been little attention paid to the origin and evolution of temperate families. The Okanogan Highlands floras are important in this regard because they contain the earliest known occurrences for many temperate genera (*e.g.*, *Corylus*, *Carpinus*, *Amelanchier*, *Neviusia*, and *Corylopsis*; Wehr & Hopkins 1994, K. Johnson 1996, Pigg *et al.* 2003, DeVore *et al.* 2004, Radtke *et al.* 2005). New taxonomic work has been completed from several of these floras: at Republic: Trochodendraceae (*Trochodendron, Nordenskioldia, Tetracentron*, Pigg *et al.* 2001b, 2007); Betulaceae (*Corylus, Carpinus*, and *Palaeocarpinus*, Pigg *et al.* 2003); at One Mile Creek: Rosaceae (*Nevuisia*, DeVore *et al.* 2004); Betulaceae (*Palaeocarpinus,* Pigg *et al.* 2003); Hamamelidaceae (*Corylopsis* and *Fothergilla*; Radtke *et al.* 2005), and Trochodendraceae (*Tetracentroni*, Pigg *et al.* 2007); and at McAbee: *Ginkgo* (Mustoe 2002b); Fagaceae (*Fagus,* Manchester & Dillhoff 2004), Ulmaceae (*Ulmus*, Denk & Dillhoff 2005), Trochodendraceae (*Trochodendron*, Pigg *et al.* 2007), and the "Eocene mystery plant" *Dillhoffia* (Manchester & Pigg 2008). Ongoing studies include the description of *Prunus* flowers (Benedict *et al.* 2008), and *Nuphar* flowers, stigmatic discs and seeds (Wehr & Manchester 1996, DeVore & Pigg 2008), both from Republic.

Late Eocene floras in the Pacific Northwest

Several additional late Eocene floras of interest in the Pacific Northwest include the megathermal coastal floras at La Porte and Susanville in northern California (Potbury 1935, Wolfe 1978), and the Goshen and Comstock floras of central Oregon (Chaney & Sanborn 1933, Sanborn 1935). These sites are typically referred to as tropical rainforests with MATs of 24–27 °C (or around 20 °C with CLAMP; see Graham 1999). In contrast, late Eocene floras to the

east of north/south trending mountains include the Thunder Mountain flora of central Idaho (Axelrod 1998) and the Copper Basin flora of northeastern Nevada (Axelrod 1966b, Wing 1987), both of which are described as mixed hardwood-coniferous floras with a MAT of around 11 °C (Graham 1999). The latest Eocene Badgers Nose flora in far northeastern California is an "in-between" flora with an intermediate combination of elements including megathermal "Goshen type" magnoliaceous and lauraceous leaves along with plants of the early Oligocene deciduous "Bridge Creek type" such as *Alnus*, *Parrotia*, *Cercidiphyllum* and *Metasequoia* (Myers 2006).

Eocene permineralized floras

Three floras that provide detail about the anatomical structure of Eocene plants are known in the Pacific Northwest. The first is the Princeton chert from near Princeton, south central British Columbia. This flora was initially studied by James Basinger and, since the early 1980s, by Ruth Stockey, students and colleagues. This locality consists of 49 interbedded chert and coal layers with occasional ash beds. Some of the cherts split and anastomose, resulting in around 70 layers altogether (Little *et al.* 2009). Stratigraphically, the chert is found within the Princeton Group, Allenby Formation, and was initially dated as middle Eocene by Hills & Baadsgaard (1967) using potassium argon dating. A recently resampled date obtained by Baadsgaard was 48.7 Ma from ash layer # 22 (see Little *et al.* 2009).

The Princeton chert has been interpreted variously as a swamp or mire with different layers containing several distinct assemblages. Many of the plants are aquatic and are thought to be essentially autochthonous (Cevallos-Ferriz *et al.* 1991, Klymiuk *et al.* 2009). This interpretation is based on the growth position of rhizomatous *Eorhiza* stems (Stockey & Pigg 1994), aerenchymatous plant tissues (*e.g.*, *Dennsteadtiopsis*), and affinities with extant aquatics including *Decodon*, Nymphaeaceae, and Araceae. Certain layers have assemblages of moncots and conifers. Other elements (*e.g.*, Rosaceae, Magoliaceae, Vitaceae) are much rarer and are thought to have been transported (Cevallos-Ferriz *et al.* 1991).

Over 30 plants have been described from the Princeton chert (Basinger & Rothwell 1977, Pigg & Stockey 1996, Stockey 2001). Included are five types of ferns (Stockey *et al.* 1999, Karafit *et al.* 2006, S. Smith *et al.* 2006). Conifers are represented by the taxodiaceous *Metasequoia milleri* (see below), *Pinus arnoldii* (Miller 1973), pine leaves of several types and pollen cones. Dicots include fruits and seeds of Cornaceae, Lauraceae, Lythraceae, Nymphaeaceae, Myrtaceae, Rosaceae and Vitaceae; wood is known of Magnoliaceae and *Prunus*. Six types of monocots are known, and numerous fungi (not discussed).

Of the most completely preserved plant remains in this flora, *Metasequoia milleri* (Cupressaceae) has been reconstructed as a whole plant (Basinger 1981, 1984; Rothwell & Basinger 1979). A complete series of floral buds, flowers and fruits are known for *Princetonia allenbyensis* (Stockey 1987, Stockey & Pigg 1991), a taxon of unknown affinities, and the vegetative plant body has been described for the rhizomatous semiaquatic *Eorhiza* (Robison & Person 1973, Stockey & Pigg 1994) which is hypothesized to be the parent plant of *Princetonia*. Other flowers that have been described include those of the extinct *Paleorosa* (Basinger 1976, Cevallos-Ferriz *et al.* 1993); *Wehrwolfea* (Erwin & Stockey 1990) and an extinct species of S*arurus* (S. Smith & Stockey 2007a, b). In addition to detailed floral structure, these flowers all have *in situ* pollen. Fruits, seeds, stems and roots are known of the aquatic *Decodon* (Lythraceae) (Cevallos-Ferriz & Stockey 1988; Little & Stockey 2003, 2005). Additional lythraceous leaves at Princeton are more similar to those of the mangrove plant *Duabanga*, suggesting either that a second genus is present or that the plant with *Decodon* reproductive and other vegetative features was a mosaic taxon with distinctive leaves (Little *et al.* 2004).

Clarno

A discussion of the Eocene of the Northwest would be incomplete without a mention of the important middle Eocene floras of the Clarno Formation. These floras are located in the John Day Basin of north central Oregon, in the same region as the early Oligocene Bridge Creek flora (see below). Best known among these sites are the Clarno Nut Beds, which have been described in detail by Manchester (1994). The Clarno Nut Beds contain anatomically preserved fruits and seeds *e.g.*, Juglandaceae, Platanaceae), many of which are of subtropical families such as Icacinaceae and Menispermaceae. This flora has numerous taxonomic similarities with the London Clay (Reid & Chandler 1933, Collinson 1983) and Messel floras (Manchester 1994, 1999; Collinson *et al.* 2010). Of the compression floras closely associated with the Clarno Formation, the West Branch Creek site is described as a tropical to paratropical locality with a calculated CLAMP of 16 °C (Graham 1999). Also significant is a recently completed study of the Clarno woods, summarizing wood occurrences of additional taxa and providing support to determinations made from the fruit and seed record (Wheeler & Manchester 2002). The Clarno woods provide one of the few known examples of a diverse assemblage of fossil wood types that can be directly linked with fruit and seed remains.

A third Eocene locality in the Pacific Northwest with anatomically preserved plants, fungi and marine faunal elements has been described from the Appian Way site south

of the Campbell River on the eastern coast of Vancouver Island, BC. The Appian Way plants, fungi and faunal remains occur in marine calcarous nodules in a sandy siltstone matrix and are interpreted as representing a shallow marine environment (Mindall *et al.* 2009). The age of the unit has not been clearly established. Based on palynology it is late Paleocene to early Eocene (Sweet 1997). More recent studies based on decopod crustaceans, mollusks and shark teeth suggest middle to late Eocene age (Schweitzer *et al.* 2003). Stratigraphic studies are still in progress (Cockburn & Haggart 2007, Mindell *et al.* 2009). Nodules containing the fossil wood, fruits and seeds have clearly been transported and abraded (Little *et al.* 2001). Based on the association of plant remains found together, the plant parts found within nodules are thought to be torn up fragments of forest vegetation that became buried rapidly in high energy coastal deposits (Steenbock *et al.* 2009).

The Appian Way flora is of value for its beautifully preserved anatomical structure. Among the taxa that have been described are a moss gametophyte (Steenbock *et al.* 2009), two filicalean ferns (*Gleichenia* and *Paralygodium*, Mindall *et al.* 2005, Trivett *et al.* 2006) and taxodiaceous conifers (Hernandez-Castillo *et al.* 2005, Ramírez-Peña *et al.* 2009). Dicots include members of the Platanaceae, Fagaceae, Junglandaceae, and Icacinaceae (Elliot *et al.* 2006; Mindall *et al.* 2006, 2007, 2009; Rankin *et al.* 2008). Additional families that are represented include Annonaceae, Magnoliaceae, and Cornaceae, as well as over a dozen additional unidentified forms (Little *et al.* 2001). Based on the taxa published to date and a broader preliminary overview, the Appian Way flora appears to have quite a few similarities with the Clarno Nut Beds and the London Clay (Little *et al.* 2001, Rankin *et al.* 2008, Mindall *et al.* 2009).

Late Eocene in the Rocky Mountains

Florissant flora. – The late Eocene basin formed by Lake Florissant of central Colorado provides one of the few occurrences for fossil floras in the Rocky Mountains after the middle Eocene (Leopold & MacGinitie 1972). MacGinitie (1953) produced a detailed treatment of the Florissant in which 114 species of fruits and leaves were described. In 1967, to protect this significant locality from land development, the Florissant Fossil Beds National Monument was established, ensuring that the rich record of vertebrates, insects, and fossil plants would be protected for future study. A volume providing status on the Florissant was prepared in 2001 (Evanoff *et al.* 2001), and subsequent years have seen numerous symposia dedicated to the site (*e.g.*, Meyer 2004).

The Florissant Formation represents a diverse assemblage of lithologies including coarse-grained units of arkosic and volcanoclastic sandstones and conglomerates and finer units of shale, tuffaceous mudstone and siltstone (Evanoff *et al.* 2001). These sediments were deposited in a paleovalley that was periodically blocked by lahars, producing lacustrine deposits. There are two lacustrine episodes: the lower shale unit represents the first while the caprock conglomerate marks the beginning of the second. A fluvial unit, containing fossil mammals and the famous fossil *Sequoia* stumps in the lower mudstones, marks the interval between the two lacustrine stages. Each lacustrine stage was terminated by first pumice gravel and later lahar breccias. Well-preserved fish and insects as well as leaves and plant reproductive organs are present in the lower shale unit, middle shale unit (just above the fluvial unit) and upper shale unit (Niesen 1969, Wobus & Epis 1978, Evanoff *et al.* 2001). Most of the well-known and best-preserved plant fossils come from the middle shale unit, which is the main quarry interval within the Florissant Fossil Beds National Monument (Evanoff *et al.* 2001).

The single crystal $^{40}Ar/^{39}Ar$ analysis of sanidine from pumice in sandstone and debris flow deposits of the upper Florissant Formation yielded an age of 34.07 ± 0.01 Ma (Evanoff *et al.* 2001), placing the Florissant Formation within the latest Eocene. The age is bounded by the underlying Wall Mountain Tuff dated at 36.7 Ma and overlying volcanics at 34.07 Ma. The presence of brontotheres from the upper section of the fluvial sequence between the two lacustrine episodes (lower mudstone unit) supports this age since brontotheres become extinct at, or near, the Eocene/Oligocene boundary (Obradovich *et al.* 1995). The presence of both brontotheres, as well as *Mesohippus* place the formation in the Chadronian NAMLA (Evanoff *et al.* 2001).

The flora of the Florissant has been summarized by MacGinitie (1953), updated by Manchester (2001), and beautifully illustrated by Meyer (2003), and we refer the reader to these references for details. The two most abundant angiosperm taxa are *Cedrelospermum* and *Fagopsis*. *Cedrelospermum* is based on *Zelkova*-like leaves found in attachment to stems bearing distinctive winged fruits, and is interpreted as an early successional species occupying the margin of Lake Florissant (Manchester 1989, Meyer 2003). *Fagopsis* is known only from the western North American Eocene and is the most abundant leaf type found at Florissant (Manchester & Crane 1983). These leaves, which superficially resemble *Fagus*, are found in attachment to stems with distinctive pistillate and staminate inflorescences that are unlike any known Fagaceae (Manchester & Crane 1983). The most unusual feature of *Fagopsis* is its pistillate inflorescence. About forty wedge-shaped units, homologous to fagaceous cupules and each containing three nuts, are spirally attached to an elongate receptacle. The wedge-shaped cupulate units are often found as strings and apparently were released as they unraveled from the inflorescence and may have been wind dispersed (Meyer 2003). *Quercus* is also well represented with nine species, and includes what

appears to be a mixture of both evergreen and deciduous type, many with affinities to oaks of the extant Southwest and northern Mexico (Meyer 2003).

The Rosaceae are also important components of the Florissant flora and have the greatest diversity of any family at the generic level (MacGinitie 1953, Wolfe 1987, Manchester 2001, Meyer 2003, DeVore & Pigg 2007). Florissant has some of the earliest occurrences of leaves and fruits of *cf. Cercocarpus* and *Crataegus*, leaves of *Holodiscus* (Schorn 1998), and *Rosa* leaves, fruits and stems with prickles (Meyer 2003). Examples of other rosaceous genera at Florissant that are also known from other earlier localities include *Rubus, Malus, Prunus,* and possibly *Vauquelinia.*

Although flowers are relatively rare in these fossil floras, the durable calyx of *Florissantia* was readily preserved and the fruits, still attached to the calyx and receptacle, serve as a dispersal unit (Manchester 1992). This distinctive malvalean flower has been found at Bridge Creek, and Republic, where specimens bearing petals have been recovered. *Florissantia* has yet to be recognized outside of North America and appears to be endemic to the Rocky Mountains and Okanagan Highlands floras.

Although angiosperms dominate the flora, it is the array of conifers at Florissant that is probably the most conspicuous, including the large stumps of *Sequoia* that made Florissant a popular tourist spot from the 1920s through early 1960s (Meyer 2003). In addition to *Sequoia,* Cupressaceae is represented by *Chamaecyparis*, and there are five species of *Pinus* in sections *Pinus* and *Strobus*. Taxaceae is represented by *Torreya*, which has a record based on its dispersed needles.

The most surprising aspect of Florissant is the relatively poor record of ferns and other pteridophytes. Two species of *Equisetum* have been reported, but the only filicalean fern described is *Dryopteris guyottii* (Meyer 2003). Unlike other fossil floras where many ferns occur in relatively dense stands (*e.g.*, *Onoclea*, Rothwell & Stockey 1989; *Woodwardia*, H. Smith 1938), it appears that pteridophytes inhabited dispersed microhabitats surrounding Lake Florissant. It is uncertain whether pteridophytes were lacking or were never captured by the depositional environment.

Leaf and pollen records were integrated to interpret the paleoenvironment represented at Florissant (Leopold & Clay-Poole 2001). Results suggested that the climate in the Lake Florissant region was warm-temperate to subtropical with moderate summer rainfall and mild, dry winters. The NLR method gave an estimate of MAT no lower than 17.5 °C, which is 4–6.8° warmer than CLAMP or multiple regression estimates (Leopold & Clay-Poole 2001). This estimate may reflect the fact that NLR data emphasize conditions immediately surrounding the lake. New records of taxa (Manchester 2001) were also added that indicate that some Florissant plants show connections with extant taxa

living in the warm-temperate zone of China, and in the eastern United States to the Ozark Plateau. These findings also support MacGinitie's belief that the montane elements of the Florissant flora (Pinaceae and Fagaceae) show affinities to taxa from the highlands in northeastern Mexico, and that scrub taxa were established in steep ecological gradients at Florissant.

Oligocene floras

Pacific Northwest: Bridge Creek. – In western North America, there are few Oligocene floras. The most significant are the early Oligocene Bridge Creek flora of the John Day Formation, central Oregon and the late Oligocene Creede flora (see below) of southwestern Colorado. The Bridge Creek flora is extraordinarily rich with 91 genera; 58 species known from fruits, seeds and cones and 110 species based on leaves (Meyer & Manchester 1997). Radiometric dates for ages of the assemblages at Bridge Creek range from 31.8 Ma (Painted Hills, K/Ar, Hay 1962) to 33.6 ± 0.19 Ma (Iron Mountain, ^{40}Ar/^{39}Ar, Swisher & Prothero 1990). The John Day Formation is lies uncomformably above the middle Eocene Clarno Formation.

The Bridge Creek flora occurs at seven different localities in the lower John Day Formation. These localities can be grouped into three "facies assemblages" as defined by Meyer & Manchester (1997). They include: (1) The Eastern Facies, at Painted Hills and Butler Basin; (2) the Southern Facies, at Crooked River and Lost Creek and (3) the Western Facies at Cove Creek, Fossil and Iron Mountain; Chaney 1924; Robinson *et al.* 1984, 1990; Meyer & Manchester 1997).

The John Day Formation is believed to represent depositional environments associated with a back-arc setting. Three sources of sediments contributed to the lithology of units present. Basaltic and trachyandesite flows near the back-arc setting are local, while rhyolitic ash-flow tuffs east of the present-day Cascades and pyroclastics from the western Cascade Range, represent distal sources of sediments (Robinson *et al.* 1984, 1990; Meyer & Manchester 1997). The fine-grained volcanic ash redeposited in lacustrine basins provided an ideal depositional environment for preserving an array of leaves and reproductive structures.

The Bridge Creek flora has an estimated MAT of 9–11 °C and is interpreted as a broadleaf deciduous assemblage (Graham 1999). Siginificant plants in this flora include *Metasequoia* (Chaney 1924), *Cunninghamia, Acer, Amelanchier, Alnus, Betula, Cercidiphyllum, Cercis,* cf. *Crataegus, Eucommia, Fagus, Florissantia, Ostrya, Pteleocarpum,* cf. *Pyracantha, Rosa* (leaves, fruits and prickles), *Rubus*, and the families Platanaceae, Tiliaceae, and Ulmaceae. The extinct betulaceous genus *Asterocarpinus* and its associated leaf type *Paracarpinus* have also been described from Bridge Creek (Manchester & Crane 1987).

Additional Oligocene floras of the Pacific Northwest. – Several other Oligocene floras in the Pacific Northwest include the Rujada and Gumboot Mountain floras (Meyer & Manchester 1997, Pigg & Wehr 2002). The Rujada Flora from west central Oregon has a MAT of 12–13 °C and a mix of broadleaf deciduous, broadleaf evergreen and coniferous taxa (Lakhanpal 1958). The Gumboot Mountain flora, which outcrops south of Mount St. Helena is known from the Oligocene of Washington State. In their monograph on the Bridge Creek flora, Meyer & Manchester (1997) list the following taxa as present at Gumboot Mountain: *Abies, Cunninghamia, Metasequoia, Sequoia, Pinus, Florissantia, Platanus, Pterocarya, Tilia, Ribes* and *Acer*, as well as taxa within Fagaceae and Rosaceae. One interesting occurrence exclusively at Gumboot Mountain is that of *Exbucklandia* (Hamamelidaceae; Manchester 1999, Pigg & Wehr 2002). In addition to the compression floras, several permineralized conifer cones have been described from the Twin River Group, a marine unit, of the northern Olympic Peninsula (C. Miller 1989, 1990).

Late Eocene–early Oligocene in the Rocky Mountains

Montana. – Mention should be made of the southwestern Montana late Eocene to Oligocene floras described, in large part, by Herman Becker. These include the Beaverhead Basins, York Ranch, Metzel Ranch, and Ruby River Basin (Becker 1961, 1969, 1972, 1973). Becker originally interpreted these floras as being of Oligo-Miocene age, but more recent studies have demonstrated their late Eocene to Oligocene age (Graham 1999). Precise ages are not known for these floras. The Beaverhead Basins flora is interpreted as a latest Eocene lacustrine deposit of comparable age to Florissant. Dominant dicots include *Quercus*, *Mahonia*, *Acer*, *Salix*, *Betula*, *Cassia* and *Zelkova* and the main conifers are *Abies* and *Picea*. Metzel Ranch and York Ranch are considered early Oligocene in age and represent low energy floodplain, pond and lake environments. In contrast to older Beaverhead Basins and the younger Ruby River Basin, the Metzel and York Ranch localities lack oaks and have few conifers, lacking *Picea* and *Abies*. These two floras are dominated by Rosaceae, Rhamanaceae, legumes and also have junipers, grasses and *Mahonia*, suggesting lower elevation, drier habitats. The slightly younger Ruby River Basin flora, which Becker (1961) refers to as being from intermontane lacustrine deposits, bears some similarities to Florissant, but lacks many of the more mesic elements such *Florissantia*, *Cedrelospermum*, *Acer*, and *Fagopsis*. As in the Pacific Northwest, isolated anatomically preserved conifer cones have been described from western Montana (*e.g.*, C. Miller 1969, 1970).

Creede. – The Creede Formation consists of an assemblage of predominantly lacustrine beds deposited in a deep lake occupying the Creede caldera in southwestern Colorado. Lithologies present include sequences of conglomerates, sandstones, siltstones, limestones, travertine and both airborne and reworked tuffs (Finkelstein *et al.* 1999, Larsen & Smith 1999). Localities yielding significant fossil plant material have been interpreted as being preserved in beds deposited close to the delta front, or within depositional environments close to a steep shore. Other areas, such as the Wason Cliffs section, likely represent deposition from small streams that had downcut into a landslide in the northeastern section of the caldera. Plant-bearing tuffs present in the 5-bridge section occur interbedded with sandstones that could represent an extension of the high-energy environment into the lake (Wolfe & Schorn 1989). The Creede localities have recently been interpreted as a set of environments where coarse-grained deposition is associated with lacustrine basins with sublacustrine-fan deposits. Clearly, Lake Creede was influenced by a complex interplay among the tectonic and volcanic history of the region and local climatic, geochemical and hydrological conditions (Finkelstein *et al.* 1999, Larsen & Smith 1999). Wolfe & Schorn (1989) accepted a radiometric date of 27.2 (Ratte & Steven 1967; correction made for recent decay constants), placing the formation in the late Oligocene.

The Creede represents the only well documented late Oligocene flora of the southern Rocky Mountains and has been systematically treated by Axelrod (1987) and Wolfe & Schorn (1990). Conifers include five species of *Pinus,* and one each of *Abies, Picea*, and *Juniperus* (Wolfe & Schorn 1990). The most diverse dicot family is the Rosaceae which includes leaves of genera assigned to Spiraeaoideae, *Stockeya*, a genus with affinities to C*hamaebatiaria, Sorbus*, *Crataegus*, *Potentilla*, *Cercocarpus* (with possible achenes), "?*Osmaronia*" (= *Oemleria*), and, rarely, *Prunus* (Axelrod 1987; Wolfe & Schorn 1989, 1990; DeVore & Pigg 2007). Other angiosperm families include Berberidaceae (*Berberis*, *Mahonia*), Salicaceae and Bignoniaceae, legumes and Grossulariaceae (3 species of *Ribes*).

The paleoecological distribution of taxa in the Creede flora was analysed using multivariate statistical techniques (Wolfe & Schorn 1989), and four major plant associations were recognized. The first association is a fir-spruce (*Abies-Picea*) forest estimated to have occupied regions 170 m above Lake Creede. Associates include the shrubs *Berberis* and *Ribes*. The second community is defined by the co-occurrence of *Abies* and *Pinus* in association with *Mahonia* and *Ribes*, with *Cercocarpus* also appearing. (3) The third association is the pine-juniper forest, representing an open-canopy or woodland. Here the dominant shrub is *Cercocarpus*, although *Mahonia* is also present. (4) The final association is a mountain mahogany chaparral that is interpreted as nearly treeless zone occupying a floodplain

dominated by *Cercocarpus*. Wolfe & Schorn (1989) concluded that all the taxa comprising these four communities had histories connected with Paleogene montane vegetation in the Rocky Mountains and have lineages recognized in the fossil record from Florissant, Ruby and Salmon as well as in the Okanagan Highland floras.

Spatial and temporal distribution of paleogene cycads and palms in North America

Analyses of leaf physiognomy (CLAMP, LMA, LA) are based exclusively on dicot leaf assemblages. Two important groups of plants with a Paleogene presence that are not included in these analyses are palms and cycads. Nevertheless, they play a significant role in Eocene and Oligocene floras of North America and provide additional opportunity for paleoclimatic inference.

Cycads

Cycad fossils in North America have been described from the Mississippi Embayment, the northern Rocky Mountains and Western Interior, and the Pacific Northwest including Alaska. Forms similar to *Zamia* were described for the Eocene of southeastern North America, Puerto Rico, and the Virgin Islands (Hollick 1932). *Zamia* is known from Paleocene fluvial deposits in the Western Interior and Rocky Mountains areas formerly occupied by the Cretaceous Intercontinental Seaway (R. Brown 1962). In the Rocky Mountains a "whole plant reconstruction" of a cycad has been documented from the highly diverse, tropical flora of the Early Paleocene Castlerock locality in central Colorado (I. Miller *et al.* 2007). Well-documented cycad leaves with cuticle, some attributed previously to the fern genus *Allantodiopsis,* were described from Paleocene floras of Wyoming and the Eocene Clarno Formation of Oregon (Kvaček & Manchester 1999). In the Pacific Northwest fossils resembling *Ceratozamia* and two species of *Dioon* were reported from the Eocene of Alaska (Hollick 1932). The most intriguing North American locality where cycad leaves have been reported is the Republic flora of northeastern Washington (Hopkins & Johnson 1997). This report is based on two isolated pinnules that resemble modern *Zamia* and *Ceratozamia*. Typically, cycads are assumed to be limited to tropical and subtropical regions, therefore it is curious that they occur at Republic, a locality estimated to have a MAT of 10–13 °C, a cold month mean of less than 1 °C, and a paleoelevation estimated to be between 727–909 m (Wolfe & Wehr 1987) and 900–1100 (Archibald & Greenwood 2005). Presumably, microhabitats occur at the Republic site that allowed for thermophilic taxa.

Cycads appeared in the fossil record at least by the Permian and are usually associated with warm, subtropical environments (Kvaček & Manchester 1999, Kvaček 2002). Because of their long history and rich fossil record during the Mesozoic, as well as the disjunct occurrences of many extant genera, there is a tendency to characterize the present distribution of cycads as relictual. However, when viewed in the context of phylogeny based on extant taxa, modern cycads appear to result from recent radiations among crown taxa. Since some groups appear post PETM, Cenozoic populations may have been impacted by later, less intense warm periods.

This hypothesis is yet to be fully tested. A critical examination of the Cenozoic record is needed since the relationships between Cenozoic and modern taxa are unclear. Some fossil forms have a mosaic of characters not present in modern taxa. Still others could be erroneously attributed to ferns (*e.g.*, *Allantodiopsis*). Despite these difficulties, there is no compelling evidence to indicate that modern cycads are relict taxa. A stronger hypothesis is that they represent the recent evolution of terminal lineages in a group deeply rooted in the fossil record.

Fossil record of coryphoid palms in North America

The palm genus *Sabal* (subtribe Coryphoideae) has a current North American distribution similar to that of the cycad *Zamia.* The two genera occupied the same regions during the Tertiary. The systematics of extant *Sabal* is well known and can be integrated with the fossil record to assess the biogeographical history in some detail.

Gulf Coast coryphoid fossil palms from the early and middle Eocene include five well-defined genera (Daghlian 1978). *Sabal, Sabalites, Costapalma, Palmacites,* and *Palustrapalma* were recognized on the basis of leaf morphology and detailed cuticular studies. *Sabal dortchii* is an Eocene plant with well-preserved cuticle that shows the stomatal complex morphology indicative of the genus. *Sabalites grayanus* and *Costapalma philipii* are coryphoid palms but they cannot be placed in the modern genus *Sabal*. While *Sabal*, *Sabalites* and *Costapalma* are all costapalmate forms, *Palustrapalma* and *Palmacites* are palmate forms that possess a mosaic of characters, including those found in genera from Clade 4 (Fig. 1, see below). A sixth genus, *Amesoneuron*, was established for palm leaves that lack definitive taxonomic characters (Daghlian 1978). Coryphoid palms remain in the coastal plains of the Mississippi Embayment into the Oligocene where they are found in the Catahoula Formation of east Texas (Daghlian *et al.* 1980).

In the Great Plains and northern Rocky Mountains, fossil sabaloid leaves have been documented from Paleogene

floras (R. Brown 1962, Hickey 1977) including well-preserved specimens from extensive lacustrine deposits of the Green River Basin. Presently, *Sabal* or *Sabalites* leaves of Oligocene age are unknown from the region.

In the Pacific Northwest, coryphoid palms assigned to *Sabalites* are known from Eocene localities, extending from the Gulf of Alaska (Wolfe 1977) to the Chalk Bluffs flora of coastal California (McGinitie 1941). Some of the most spectacular remains are the nearly entire fronds of *Sabalites campbelli* from the Chuckanut Formation of Washington (Mustoe & Gannaway 1997). Coryphoid palms are also known from the anatomically preserved Princeton chert. The genus *Uhlia* was established for permineralized stem fragments with attached petiole bases and roots that were found in association with isolated petioles, midribs, laminae and roots (Erwin & Stockey 1994). *Uhlia* is interpreted as having similarities to the extant genera *Rhadophyllum* and *Brahea*, but having a combination of characters not in concert with any extant genus within the subfamily.

Sabalites persisted into the Oligocene in the Northwest and has been described from the Rujada flora of Oregon (Lakhanpal 1958) and Eagle Creek flora of Washington (Chaney 1920). In southern California, fossil palm taxa persisted into the Miocene and Pliocene (Tuta 1967) where today the only native extant forms are three species of *Washingtonia* (Mustoe & Gannaway 1997). Natural populations of *Washingtonia filifera* also are known in the Kofa Mountians and southern Yavapai County of western Arizona, where they are thought to be relicts (D. Brown *et al.* 1976). Based on the distribution of fossil taxa of *Sabal* and *Sabalites*, this lineage of palms dispersed during the Tertiary along coastal plains associated with the Mississippian Embayment, the Intercontinental Seaway, and in coastal plains in the Pacific Northwest, including a broad embayment extending into central Oregon and Washington. All three of these regions are fluvial paleoenvironments, on broad flood plains, at relatively low elevations suggesting that coryphoid plans persisted in similar habitats throughout the Tertiary.

Phylogeny of extant *Sabal*

Based on the phylogenetic relationships and distributions of extant species, Zona (1990) hypothesized that *Sabal* had a North American origin. A later study (Santiago-Valentin & Olmstead 2004) incorporated data from both Zona's (1990) monographic work and molecular phylogenetic analysis (Asmussen *et al.* 2000) to generate an area cladogram. In this phylogenetic biogeographical analysis of Caribbean plants, a basal position was indicated for *Sabal minor*, a species distributed in the southeastern United States (indicated as Clade 1 in Fig.1). In this analysis, *S. minor* is sister to a second clade (Clade 2 in Fig. 1) consisting of four species found in the Bahamas, Bermuda, Cuba and southeastern United States. These two basal clades are distinct from a third clade of three western Mexican species (Clade 3 in Fig. 1) and the fourth, most derived clade in the genus (Clade 4 in Fig. 1). This fourth clade consists of six taxa distributed in Central America, Central Mexico, Cuba, Jamaica, Hispaniola, and Puerto Rico. The sister group to *Sabal* has been identified as a clade consisting of *Chelyocarpus*, *Coccothrinax*, *Crysophila*, *Thrinax*, and *Trithrinax*. This sister clade has an inferred ancestry in South America, based on extant members (Asmussen *et al.* 2000, Santiago-Valentin & Olmstead 2004).

Integrating the coryphoid palm fossil record and phylogeny with biogeography

Bjorholm *et al.* (2006) synthesized data from the worldwide fossil record of sabaloid palms (including Europe and Asia), the phylogeny of extant *Sabal* and the current geographic distribution of the genus. In this study, a regression analysis was performed to evaluate the importance of environmental and spatial variables on distributional pattern. The study suggested that the richness patterns for Coryphoideae reflect historical, rather than environmental factors. The paleoenvironments preserving *Sabal* and *Sabalites* all are low elevation fluvial or lacustrine environments. It seems unlikely that basal *Sabal* have shared an immediate common ancestor with those from western Mexico (Fig. 1).

We include an illustration of the distribution patterns of modern clades of *Sabal* superimposed onto a paleogeographic map of middle Eocene age; 50 Ma (Fig. 1). The cladogram to the right is from Zona (1990).

After examining the records from Paleodatabase (accessed 2007) for these taxa in North America, it became apparent that their distribution corresponds with the former position of the Intercontinental Seaway and both its eastern and western coastal regions. The implication of this for estimating dispersal from North America into the Caribbean and northern South America is significant. It seems unlikely that basal *Sabal* species distributed in the southeastern United States, Bahamas, Bermuda and Cuba could have shared an immediate common ancestor with those from western Mexico. If there were a single introduction, *Sabal* species would have had to disperse up through higher elevations to re-enter the Caribbean. Instead, it seems more plausible that the genus was introduced at least once via the Mississippian Embayment and at least once via the Pacific (Fig. 1). The widespread distribution of *Sabal* and *Sabalites* in Asia and Europe could potentially mean that the basal members of *Sabal* shared a lineage with European species while the more derived lineages in Mexico are aligned with a Pacific lineage.

Nypa and Mangrove Associations

A second palm, the Old World mangrove *Nypa* (sometimes spelled *Nipa*) today has an Indo-Australian distribution, but in the past, was clearly a significant member of mangrove communities with a worldwide distribution (Reid & Chandler 1933, Collinson 1983, Gee 2001). This plant was a dominant component of the early Eocene London Clay and also occurred throughout other European sites including in the Brussels area and the Paris Basin (Collinson 1993). In North America *Nypa* pollen assigned to *Spinizonocolpites* first appears in the Gulf Coast in Alabama and Georgia from the early Eocene Tallahatta Formation of the Wilcox Group (Frederiksen 1980, 1981, 1988). The first megafossil record of *Nypa* in North America comes from the Popes Creek Flora of Maryland (Tiffney 1999), also during the early Eocene. Subsequent records of *Nypa* and *Spinizonocolpites* show this palm subfamily reaching its maximum range in the Gulf regions (Casa Blanca Flora) by the middle Eocene before having its range contract back to Alabama, Georgia and Mississippi during the late Eocene. There are no known records of *Nypa* in North America during or after the Oligocene (Gee 2001).

In addition to documenting the fossil record of the genus *Nypa*, it is instructive to look at the fossil record at a community level for the mangrove assemblages within which *Nypa* typically occurs. Based on palynofloras, Graham (1995) documented the following floristic progression in mangrove communities of Gulf/Caribbean regions throughout the Ceonozoic. 1) First, an early Eocene community occurred defined by four principal genera (including *Acrostichum*, *Brevitricolpites variabilis*, and *Pelliceria*); 2) *Aviennia* first appears in the Miocene; 3) By the middle Pliocene mangrove communities diversify to six mangroves (*Acrostichum*, *Avicennia*, *Crenea*, *Laguncularia*, *Pelliceria*, and *Rhizophora*) with three associated genera (*Acacia*, *Hampea/Hibiscus*, and *Pachira*); members of the black (Avicenniaceae), red (Rhizophoraceae) and white mangroves (Combretaceae) became the prominent mangrove taxa in the region; and 4) Further diversification through the Quaternary includes the dominant mangrove genus *Concarpus* with further additions continuing into the present day community consisting of approximately 27 genera of mangroves and associates.

Mangrove taxa have evolved a highly specialized suite of characters to thrive in habitats inhospitable to most other angiosperms. Highly specialized features and modifications of both anatomical and morphological type, as well as altered physiology, are not easily reversed back to the initial states these features evolved from. In essence, like aquatic plants, mangroves most likely could not evolve out of the mangrove habitat. Because they occupy such coastal environments as tidal inlets and coastal lagoons, they are in a position to readily disperse their propagules. Their persistence and ranges today represent their ability to be distributed by cur-
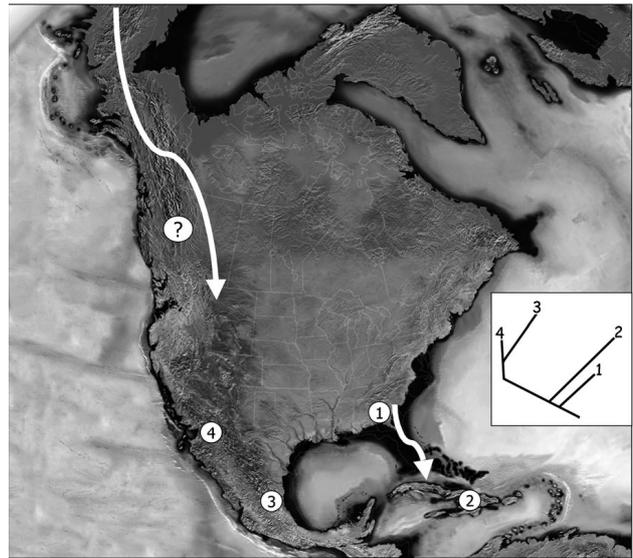

Figure 1. Middle Eocene reconstruction (50 Ma) of North America with the position of the four clades of extant *Sabal* (1–4) shown in relation to current distribution of the genus (from Zona 1990). • Clade 1 – *Sabal minor*. Arrow indicates dispersal of this basal clade into the Caribbean. • Clade 2 – four species found in the Bahamas, Bermuda, Cuba and southeastern United States. • Clade 3 – three western Mexican species. • Clade 4 – six taxa distributed in Central America, Central Mexico, Cuba, Jamaica, Hispaniola, and Puerto Rico. The arrow to the left with the question mark indicates potential dispersal of the more derived taxa in Clade 4 from the Pacific region. Phylogenetic information from Zona (1990). Paleomap redrawn from Blakey (2005).

rents into new, favorable habitats. Thus, current distributions of mangrove taxa not only reflect their evolutionary history, but also the chance arrival of new species in a region.

Conclusions

Late Eocene and Oligocene plant fossil localities in North America can be tracked in three major regions: the Southeast (Mississippian Embayment); the Pacific Northwest; and the central Rocky Mountains. In the Mississippian Embayment the differences between the middle Eocene Claiborne and the early Oligocene Catahoula floras are subtle. Selected elements from the diverse and well collected Claiborne are also found in the less known Catahoula. Both floras have palms, legumes and transitional oaks, although lauraceous leaves are less common in the Catahoula. Given the shear amount of collecting that has taken place for many years from numerous commercial clay pits in the Claiborne, the diversity might be expected to be considerably greater than what is known from the less studied Catahoula.

In the Pacific Northwest, floras are known from the middle Eocene coastal Chuckanut and Swauk formations and late Eocene Puget Group, and the early-middle Eocene upland floras of the Okanogan Highlands. Fewer Oligocene floras are known, most notably the Bridge Creek flora of

Oregon, and Gumboot Mountain in Washington State. The coastal floras of the Puget Group, and Chuckanut floras occurring west of the Cascades, have megathermal assemblages with palms, lauraceous leaves and ferns at their localities except for the youngest Padden Member which lacks palms and diverse ferns. Similar patterns of coastal megathermal and interior cooler temperature floras occur through the end of the Eocene. The diverse "upland" floras of the Okanogan Highlands are dominated by microthermal elements, although some warm temperate elements (*e.g.*, cycads, see above) have been reported (Archibald & Greenwood 2005, Hopkins & Johnson 2007).

Several floral elements, primarily from the Okanogan Highlands, persist into the late Eocene Florissant and early Oligocene Bridge Creek floras including *Abies*, *Pinus*, *Cercidiphyllum*, *Acer*, *Florissantia, Betula*, and *Tilia*. Among the Rosaceae, some genera that have their earliest appearance at Republic (*e.g.*, *Amelanchier*, cf. *Crataegus*, *Rubus*, cf. *Pyracantha*) are known in greater diversity in the Florissant and at Bridge Creek, while others, such as *Rosa* are first seen in western North America at Florissant. *Fagus*, once thought to be of Oligocene origin, is now known from the early Eocene McAbee site (Manchester & Dillhoff 2004). Taxa that first appear in Bridge Creek include *Ostrya, Paracarpinus*, *Asterocarpinus*, and *Cercis.* Uniquely, the Oligocene flora at Gumboot Mountain has infructescences of the genus *Exbucklandia* (Hamamelidaceae; Manchester 1999, Pigg & Wehr 2002).

In the Rocky Mountains, the middle Eocene is represented by the Green River flora, the late Eocene by Florissant, and the late Oligocene by the Creede flora. The Green River shares many megathermal elements with plants of the Claiborne Formation that are lost by late Eocene times when mesic elements dominate the diverse lacustrine Florissant assemblage. By the Late Oligocene, the Creede flora is dominated by cooler and drier taxa including Rosaceae, pines, legumes, *Abies*, *Picea* and *Juniperus* (Axelrod 1987, Wolfe & Schorn 1990). Vegetative assemblages of the Creede foretell the later dry conifer and chaparral floras that cover much of western North America today.

Questions for future work

Lastly, we offer a series of what we feel are important questions to be addressed with future work on the late Eocene and Oligocene floras of North America.

1. How do you integrate leaf physiognomy and Nearest Living Relative (NLR) method?

Some studies of late Eocene and Oligocene floras have focused on using fossil plants as a source of proxy data (MAP & MAT measurements) just as they have in studies tracking climate change across the Paleocene-Eocene boundary (see Pigg & DeVore 2010). One difference we see in floras of the late Eocene and Oligocene is the appearance of more fossil taxa that can be assigned to extant genera, such that the Nearest Living Relative method might be used with more confidence (Graham 1999). In particular, studies that incorporate the NLR method for taxa not scored for leaf physiognomic studies such as ferns, conifers and monocots provide an opportunity to assess estimates of paleoclimate parameters in a noncircular context.

In the present paper, we have seen examples where NLR methods estimate a temperature slightly higher than those generated by LM analyses (*e.g.*, Florissant). However, there continue to be more efforts to integrate both NLR and leaf physiognomic methods in a meaningful way and many studies incorporate a combination of approaches. One such effort recently proposed by Yang *et al.* (2007) is Overlapping Distribution Analysis (ODA). This method uses both NLR and the MAT (of NLRs) methodologies, but is based on local plant distributions of living relatives and data from meteorological stations located in a determined area representing the region of overlap of the NLRs. This method was devised for climatic reconstruction of the Miocene Shanwang Basin, but may also prove useful for reconstructing climate based on late Eocene and Oligocene floras. A useful avenue of research would be exploring additional ways to integrate NLR and leaf physiognomic data so that results from each method can be used for the purpose of cross-validation of estimates of paleoclimate and paleoelevation.

2. How do we integrate fossil data into phylogenetic studies of key taxa present in modern plant communities?

The use of fossils to date times of divergence of phylogenies based on modern taxa is too broad a topic to discuss here and it lies outside the focus of the present paper. However, there have been detailed studies that incorporate extant-based phylogenies and the fossil record to analyze the biogeography of modern genera. One of the best examples has been studies of the Fagaceae. Manos & Stanford (2001) integrated phylogenetic analyses based on several regions of chloroplast and nuclear ribosomal DNA of genera in the Fagaceae. They used the resulting phylogenies to generate ancestral area reconstructions based on dispersal-vicariance analysis (DIVA). They then compared these results with the fossil record of Fagaceae to estimate migration and divergence times for *Castanea, Fagus*, *Quercus* and *Trigonobalanus*. The use of fossils in historical biogeographical studies based on phylogenies of modern taxa is still being developed. However there are the follo-

wing important caveats: 1) The distributional history of a group may not always be closely estimated based on a cladistic analysis of its modern relatives and their present distributions; 2) The first appearances of taxa in the fossil record may not correspond with the basalmost clade in a phylogenetic tree; and 3) Sometimes taxa that had a widespread distribution in the past (*e.g. Nypa*), today have a restricted distribution that is interpreted as endemic. Using fossil distributions to cross-validate biogeographical histories based on extant plants is becoming more prevalent and has been used effectively with some groups (*e.g.* palms, Bjorholm *et al.* 2006). Potentially, as more data are integrated into Paleodatabase and other similar resources, researchers whose work is focused on extant groups can easily plot records of taxa found in the fossil record onto paleogeographical reconstructions to better assess the biogeographical history of the modern plant taxa.

3. Continued reconstruction of taxa found in Eocene-Oligocene floras.

Several taxa that appear within late Eocene and Oligocene floras represent mosaics and transitional forms. In the case of *Quercus*, transitional and modern forms are found together in the early Oligocene Catahoula Formation (Crepet & Nixon 1989b). In some cases, there are entire plant organs that are hard to interpret and relate to modern forms (*Fagopsis* inflorescenes). The only link between the past and the present is through morphology. Clearly, how the combinations of characters found within fossil taxa are interpreted within the context of evolutionary histories based on extant taxa will be a significant endeavor. It is after the Eocene-Oligocene boundary where we can begin to make the closest connections between some dominant angiosperm taxa today and their relatives in the fossil record.

Acknowledgements

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